CarvajalCaligus elongatus and other sea lice of the genus *Caligus* as parasites of farmed salmonids: a review

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ABSTRACT

This review was prompted by reports of unusually large numbers of sea lice tentatively identified as *Caligus elongatus* infesting farmed salmon in northern Norway. Following a brief introduction to the sea lice problem in salmonid aquaculture, the review is divided into a further eight sections. The first is a review of existing information on the life cycle and behaviour of *Caligus* spp. The second is a description of the morphology of different stages in the life cycle of *C. elongatus*. The third describes the effects of caligid infestations on salmonid hosts. The fourth reviews information on the geographical distributions and host preferences of the six species of *Caligus* reported from farmed salmonids in different parts of the world: *C. elongatus, C. curtus, C. clemensi, C. rogercresseyi, C. teres* and *C. orientalis.* The fifth section describes interactions between farmed and wild fish and the sixth presents information on the genetics of *C. elongatus.* A section reviewing the different methods used to control sea lice infestations follows. The eighth section discusses the predicted effects of climate change and invasive host species on the distribution and occurrence of caligid copepods, and the ninth gives conclusions and recommendations on how to further investigate the infestation that prompted this review. These include the confirmation of the identity of the caligid causing the problem, confirmation of the genotype involved and a study of the vertical distribution in the water column of the infective stages.

KEY WORDS: *Caligus elongatus*; farmed salmon; life cycle; effects; control

1. Introduction

The parasitic copepod family Caligidae comprises 30 genera and 509 valid species (Dojiri & Ho 2013; Walter & Boxshall, 2020). Members of two of these genera – *Lepeophtheirus* and *Caligus* - have achieved notoriety by having the greatest economic impact of any group of parasites in salmonid fish mariculture (Costello 2006) and have become collectively known as "sea lice". Although this notoriety is mainly due to the particularly serious impact of the species *Lepeophtheirus salmonis* (Krøyer, 1837), members of the genus *Caligus* are also implicated. Johnson et al. (2004) estimated that in marine and brackish water fish cultures, 61% of copepod infestations are caused by members of the family Caligidae, 40% of which are caused by species of *Caligus* and 14% by species of *Lepeophtheirus.* Costello (2009) estimated that in 2006 the worldwide salmonid farming industry had a total loss of U.S. $480 million due to salmon lice infestations. Controlling salmon lice is one of the biggest challenges in Norwegian salmon farming and cost the aquaculture industry more than NOK 5 billion in 2014 (Iversen et al. 2016), corresponding to about 9% of the farms' income (Abolofia et al. 2017).

A major difference between *L. salmonis* and *Caligus* spp. lies in their host specificities: *L. salmonis* is essentially a parasite of salmonid fish (Kabata (1979) considered reports from non-salmonid hosts to be unusual and would probably offer no chance for further development and survival of the parasite), whereas many *Caligus* spp. tend to be much less host specific (Kabata 1979; Pike & Wadsworth 1999). Two hundred and sixty-seven valid species of *Caligus* are currently recognized (Walter & Boxshall, 2020). The most common species infecting farmed salmonids are *Caligus elongatus* von Nordmann, 1832 in the North Atlantic, *C. orientalis* Gussev, 1951 and *C. clemensi* Parker & Margolis, 1964 in the North Pacific, and *C. rogercresseyi* (Boxshall & Bravo, 2000) and *C. teres* Wilson, 1905 in Chile (Johnson et al. 2004). Those aspects of the biology and ecology of sea lice of relevance to mariculture were reviewed by Wootten et al. (1982), Pike & Wadsworth (1999), Tully & Nolan (2002), Johnson et al. (2004), Boxaspen (2006), Costello (2006) and Jones & Johnson (2014).

The present review was prompted by reports of unusually large numbers of caligid copepods tentatively identified as *C. elongatus* on farmed Atlantic salmon in North Norway (Imsland et al. 2019a, b). These copepods were readily distinguished from *L. salmonis* by their much smaller size, but specific identification has not been confirmed. This problem has affected salmon farms in north Nordland and Troms counties, but has been particularly severe in Finnmark. The present review has been undertaken prior to a detailed study of the specific identity of these copepods and possible reasons for their recent occurrence in such abundance in North Norway. This situation is unusual because epizootics of *C. elongatus* were previously rare in Norway (Boxaspen 2006), although Øines & Heuch (2007) confirmed that *C. elongatus* was present on salmon in North Norwegian farms. The review aims to collate the existing literature on those aspects of the biology and ecology of *C. elongatus* in particular and other members of the genus *Caligus* in general that we consider to be relevant to this problem.

2. Life cycle and behaviour of *Caligus* spp.

Most caligid species were earlier considered to have 10 developmental stages in their life cycle: two free-living planktonic nauplius stages, one free-swimming infective copepodid stage, 4 attached chalimus stages, one or two pre-adult stages and one adult stage (Wootten et al. 1982). It was then discovered that preadult stages were absent in three species of *Caligus* - *C. punctatus* Shiino, 1955, *C. elongatus* and *C. rogercresseyi* (see Kim 1993; Piasecki & MacKinnon 1995; Piasecki 1996; González & Carvajal 2003) and in one species of *Pseudocaligus* (see Ohtsuka et al, 2009). More recent studies have confirmed that the caligid life cycle has only 8 stages: members of the genus *Lepeophtheirus* have only two chalimus and two pre-adult stages, whereas those of the genus *Caligus* have a different life cycle, with four chalimus stages and no pre-adult stage (Hamre et al. 2013; Venmathi Maran et al. 2013) (Fig. 1). The following descriptions of the different developmental stages of *Caligus* spp. are based on those of Hogans & Trudeau (1989a) and Piasecki (1996) for *C. elongatus*.

The newly hatched nauplius I stage reflects the short cylindrical shape of the egg, shortly after which it attains the elongated oval shape characteristic of the nauplius stages I and II. Both nauplius stages are slightly less than 0.5 mm in length. They are free-swimming in the plankton and have three pairs of locomotory structures or limbs: antennules, antennae and mandibles. The duration of each naupliar stage lasts for 30-35 h at around 10˚C, but is considerably prolonged at lower water temperatures. The next stage is the infective copepodid, which has a more elongated hydrodynamic shape and is slightly longer than the nauplii but still less than 1 mm long. The copepodid has 10 limbs, with poorly developed postantennary processes, maxillules and maxillae, maxillipeds and three pairs of legs added to the antennules, antennae and mandibles of the nauplius. The life span of the copepodid is about 50 h at 13˚C. Nauplii and copepodid stages are both positively phototactic, with this ability being much more highly developed in the copepodid. Host location and contact by copepodids of *L. salmonis* were studied by Heuch & Karlsen (1997), who described a burst-swimming response to movements of water currents, such as that caused by movement of a fish within centimetres of the copepodid. Norði et al. (2015) found differences in the spatial distribution of copepods of *L. salmonis* and *C. elongatus* in a strait between two of the Faroe Islands where six salmon farms were located. They considered the differences to be possibly related to different vertical migration patterns between the two species. Copepodids of *L. salmonis* are most abundant in the top four metres of the water column (Hevroy et al. 2003; Costello 2006). There have been no studies designed to map the vertical distribution of *C. elongatus* copepodids, but the near surface distribution of *L. salmonis* copepodids may not be beneficial for *C. elongatus* because of its wider host range, which includes pelagic and demersal species.

On contact with a suitable fish host, the copepodid temporarily attaches to the host skin using the antennae and maxillae. It then extrudes a frontal filament which penetrates the epidermis and anchors into the basement membrane around the scale, after which it moults to the chalimus stage I. The first chalimus stage is slightly longer and wider than the copepodid, but still less than 1 mm long on average. The chalimus II is slightly larger again at 1-2 mm long and has added a fourth leg. The copepod continues to grow with the following two moults into chalimus stages III and IV. By stage III the sexes are distinguishable based on the number of abdominal segments and features of some of the appendages, and a fifth leg has been added. The fourth stage shows pronounced dorsoventral flattening, the cephalothorax has become wider, sexual dimorphism is more obvious and another ventral structure - the sternal furca - makes its first appearance.

After the final moult, young adults remain attached by the frontal filament for a short time before breaking free and becoming fully motile. Sexual dimorphism in *C. elongatus* adults is very obvious: males are smaller than females, with a slimmer posterior body region, and there are differences between the sexes in the structure of some of the accessory structures and appendages.

The entire generation time of *C. elongatus* is approximately 5 weeks at 10˚C. Hogans & Trudeau (1989a) found the optimum temperature for *C. elongatus* to be around 14˚C and that there are probably 4 to 8 generations completed annually in the Bay of Fundy. Studies of the epidemiology of *C. elongatus* infections on farmed salmonids show a consistent seasonal pattern which is quite different to that observed for *L. salmonis* (Revie et al. 2002; McKenzie et al. 2004). Wootten et al. (1982) found large numbers of chalimus stages on farmed salmon without any corresponding increase in adult stages thereafter, suggesting that either they failed to develop to maturity or had left the salmon after maturing, possibly to move to wild fish hosts.

Most caligids have direct life cycles as described above, without intermediate hosts. However, a study by Hayward et al. (2011) provided evidence of a possible two-host life cycle in some species, with different fish species serving as intermediate and final hosts. The *Caligus* sp. in this scenario - *C. chiastos* –- has become a serious pest of ranched tuna *Thunnus maccoyii* in South Australia, but it has never been reported from wild tuna. Adult stages only of *C. chiastos* were found on the ranched tuna, but larval stages were found in abundance on one out of a number of wild fish species examined from the immediate vicinity of the tuna cages. The host of the larval stages – Degen's leatherjacket *Thamnaconus degeni* – remains heavily infected at a time of year when there are fewer adult forms on tuna, suggesting the close presence of the natural final host. This indicates possible opportunistic behaviour resulting from the parasite coming into close contact with a naïve species – bluefin tuna - which it would not normally encounter. A similar situation occurs with cultured red seabream *Pagrus major* in Japan and Korea, where only adult forms of *Caligus sclerotinosus* are found on the bream, but in this case no possible intermediate host has been identified (Ho et al. 2004; Venmathi Maran et al. 2012). Such opportunistic behaviour is of considerable relevance to pest control management in mariculture, although no ontogenetic host switching of this kind has been reported for any of the *Caligus* species reported from farmed salmonids.

Adult caligids are frequently found in marine plankton samples, with 10 named species reported only from the plankton with no known fish hosts. The various hypotheses proposed to explain the presence of caligids in the water column were reviewed by Venmathi Maran et al. (2016). These are: 1) accidental occurrence, 2) behavioural detachment from the host during mate location, 3) host switching, and 4) an ontogenetic strategy as described above.

3. Morphology of *Caligus* spp.

The first detailed description of the morphology of an adult caligid copepod was that of *Caligus curtus* Müller, 1785, a common parasite mainly of gadid fish and the type species of its genus (Parker et al. 1968). This study formed the basis for the descriptions of the morphological features common to all adult caligids by Kabata (1979). Here we focus on the features that make the chalimus and adult stages of *Caligus* spp. such successful parasites and serious pathogens; we also highlight the features that serve as the most reliable for specific identification.

Schram (2004) compared the distinguishing features of the naupliar and copepodid stages of *C. elongatus* and *L. salmonis.* Basic measurements of the length and width of these stages are of little practical value because they overlap, but Schram described differences in shape, but more importantly in colour, which are of practical use in distinguishing between the two species: larvae of *L. salmonis* are black and brown, whereas those of *C. elongatus* are red.

Initial attachment of the infective copepodid to the host is achieved with the help of the antennae and maxillae. By the copepodid stage these have assumed the form of grasping appendages armed with strong claws that provide temporary attachment until the frontal filament is extruded and anchors the parasite securely, after which the copepodid moults into the chalimus I, followed by a further three moults into chalimus stages II, III and IV before reaching the final adult stage (Piasecki & MacKinnon 1995). There are very clear differences between *C. elongatus* and *L. salmonis* in the structure of the frontal filaments: that of *C. elongatus* is long and slender, whereas in *L. salmonis* it is short and stout (Pike et al. 1993).

The body of an adult caligid consists of four sections or tagmata: the cephalothorax, the fourth leg-bearing somite, genital complex and abdomen. The cephalothorax is formed from the fusion of the cephalon, the maxilliped-bearing somite, and the first, second and third leg-bearing somites (Kabata 1979; Dojiri & Ho 2013). The paired accessory structures on the ventral part of the chalimus IV and adult caligid cephalothorax consist of anntenules and antennae, postantennary processes, maxillules, maxillae, maxillipeds and three pairs of swimming legs (Fig. 2). The tenacious grip that adult caligids exert on the body surface of their host fish is due mainly to the convex shape of the dorsal shield or carapace that covers the cephalothorax. This low profile is ideal for attachment to a slippery surface that is often swept by strong water currents. The edge of the shield is sealed by a peripheral flap that acts as a marginal valve when suction is generated, preventing entry of water between the edge of the shield and the host's skin. Almost half of the genera in the family Caligidae, including *Caligus,* additionally possess two antero-lateral subcircular cups called lunules which act as accessory suckers. These are absent in some other caligid genera, including *Lepeophtheirus,* and are thought to have originated as a modification of the marginal membranes of the ancestral frontal plates (Kaji et al. 2012). A ventrally located cuticular structure called the sternal furca (Fig. 2) may also play a role by acting as a brake when the copepod is in danger of slipping backwards, and/or by raising the cephalothorax and so reducing pressure under it, thereby helping to increase the suction force (Kabata & Hewitt 1971; Kabata 1979). Further adhesion is supplied by the antennae and maxillipeds. The terminal hooks of the antennae pierce the epidermis of the host and anchor the parasite to its temporary site of attachment (Kabata 1979). The maxillipeds have a similar role, but were considered by Kabata (1981) to be of minor importance. These features all contribute towards the secure adhesion of an adult caligid to the skin of its host while also permitting it to move across the surface with ease.

The mouth in caligid copepods takes the form of a tube or siphon (the oral cone) formed by the overlapping labrum and labium, with associated features including a pair of mandibles (Fig. 3). When not in use it is folded against the ventral surface of the body; for feeding it moves in the anteroposterior plane to a position perpendicular to the copepod body (Kabata 1979). Pressing the distal end of the mouth into the skin spreads the marginal membrane to seal the opening, pushes away the labial fold and exposes a divided bar called a strigil which is armed with many fine sharp teeth (Fig. 4). The sawing action of the strigil releases pieces of epidermal tissue which are picked up by the mandibles and transferred into the buccal cavity (Kabata 1974). The musculature associated with the mouth tube in siphonostomatoid copepods was elucidated by Boxshall (1990), who referred to Kabata (1974) but redescribed some of the musculature associated with the oral cone.

Figures 5 and 6 show dorsal views of the females and males of the four most common species of *Caligus* infecting farmed salmonids. The first thing that strikes one on looking at these figures is the marked difference in size between *C. curtus* and the three other species. *Caligus curtus* is closer in size to *L. salmonis,* but much larger than the three other species of *Caligus* featured. The other major interspecific difference is the shape of the cephalothorax. It should be noted that the size and shape of the genital complex in female caligids may vary depending on the state of maturity and stage in egg-laying (Parker et al. 1968). In addition, the body size of a parasitic copepod may vary depending on the host species on which it is found (Cressey 1967; Lewis et al. 1969; Cressey & Collette 1970). The shape of the cephalothorax is a more constant feature, but for a confirmatory specific identification it may be necessary to check some finer details such as the structure of certain accessory structures and appendages.

4. Effects on the host

Kabata & Hewitt (1971) concluded that the attachment of caligids and their movements over the host surface contribute little or nothing to the damage resulting from their activities, but that feeding was mainly, or even solely, responsible for the damage caused. The lesions caused may be localised or more extensive, depending on the size of the fish and the number of parasites. Infestations can result in a broad range of clinical signs, ranging from skin irritation to ulcerations, reduced feeding activity, weight loss and mortality (Tørud & Håstein, 2008). According to a survey collecting information from fish health personnel in Northern Norway, Iceland and the Faroe Islands, *C. elongatus* represents a welfare challenge for farmed salmon even at light infestation levels when fish are small (Imsland et al. 2019a). Typically, infestations are manifested by the observation of increased jumping activity with subsequent stroke injuries, skin irritation, loss of appetite and secondary infections. The extent of the clinical findings is related to the number of lice on fish and fish size. These findings are also supported by Wootten et al. 1982. The damage caused by heavy infestations of caligids, in particular *L. salmonis,* on farmed salmonids has been well-documented (Johnson et al. 2004; Costello 2006), and includes descriptions of extensive areas of skin erosion and haemorrhaging. Hogans & Trudeau (1989a) and Brandal et al. (1976) demonstrated that blood was part of the diet of *C.* e*longatus* and *L. salmonis,* but according to Costello (2006) it is not an important component. Most studies of the pathological effects of caligid infections on farmed salmonids have been carried out on *L. salmonis.* This is due in large part to the fact that the infection intensities of *L.* s*almonis* tend to be higher and the effects on the host more severe than is the case with *Caligus* spp. *Lepeophtheirus salmonis* is a specialist parasite of salmonid fishes and is more likely to remain within the confines of a fish farm, whereas many *Caligus* spp., particularly *C. elongatus,* are much less host specific and therefore more likely to move between farmed salmonids and wild hosts of other species.

MacKinnon (1993) described the damage caused by the feeding of chalimus stages of *C. elongatus*: a hole lined with necrotic cells was excavated in the epidermis down to the basement membrane and in some cases there was evidence of slight hyperplasia around the excavated area. Hogans & Trudeau (1989a) found that adults of *C. elongatus* tended to congregate on the dorsal and lateral surfaces of the head and on the anterior portion of the abdomen between the opercula. The copepods stripped the mucous covering, then fed directly on the skin, musculature and blood. In severe cases they continued to feed through the skin into the subcutaneous musculature, eventually destroying somatic musculature and cartilage. The final cause of death is usually reported as osmoregulatory failure.

The distribution of attached and mobile stages of caligids on their hosts is an important factor in relation to the extent of damage caused to the host. Treasurer & Bravo (2011) studied the spatial distribution of chalimus and adult stages of *C. rogercresseyi* and *C. elongatus* on Atlantic salmon and compared their results with those for *L. salmonis.* Adults of both *Caligus* species had a predeliction for the abdominal surface of the body, while chalimus stages were more commonly found attached to the fins. These distributions were significantly different to those of *L. salmonis,* adults of which are significantly more common on the back and on the head of young salmon. No chalimi of either *Caligus* species was found on the gills, whereas chalimi of *L. salmonis* do occur on the gills. Treasurer & Bravo (2011) concluded that *L. salmonis* represents a more significant threat to salmon than either *Caligus* species due, along with other factors, to their propensity for sensitive areas where the epidermis is thin, such as the head.

An additional effect of infection of fish with ectoparasites such as caligids is to allow secondary bacterial or viral infections to infect areas stripped of mucous, or in epidermal tissue lesions. At some Scottish salmonid sea-cage sites in 1980, heavy infestations of *C. elongatus* were associated with outbreaks of vibriosis, although it was not clear whether the copepods were attacking fish already debilitated by the disease, or whether the infection was facilitated by the damage done by the copepods (Wootten et al., 1982). However, Nylund et al. (1991) found bacteria in the middle intestinal part of salmon lice. The microsporidian *Desmozoon lepeoptherii*, associated with chronic gill disease in Atlantic salmon, has also been identified in *C. elongatus* (Nylund et al. 2010). The possible role of *L. salmonis* in the transmission of the virus responsible for infectious salmon anaemia (ISA) was confirmed by Nylund et al. (1993). The results of their experiments were inconclusive, but Oelckers et al. (2014) confirmed that *C. rogercresseyi* is capable of transmitting the ISA virus to naïve salmon. The virus did not appear to be capable of replicating in the copepods, but remained viable after 48 hours away from the host from which they acquired the virus, thereby indicating that salmon lice species may also be vectors for other viral and bacterial diseases (Nylund et al. 1994). The probability of *Caligus* spp. being responsible for transmission of microorganisms is greater than for *L. salmonis* because the former parasitize a wider range of fish hosts.

5. Geographical distributions and host preferences of selected *Caligus* spp.

In this section we focus on those species of the genus *Caligus* that have been found on cultured salmonids.

5.1. C. elongatus

This species was earlier thought to have a cosmopolitan distribution, having been reported from most regions of the world, often under its incorrect name of *Caligus rapax* (see Kabata, 1979). Parker (1969) cited reports from the South Atlantic and South Australia, but Hayward et al. (2008) considered that earlier records from Australia and New Zealand were probably of *Caligus chiastos* Lin & Ho, 2003. *Caligus elongatus* appears to be most abundant in the North Atlantic and may be restricted to this region. It has a very low host specificity and has been reported from >80 fish species and one cetacean (Kabata, 1979; Øines et al. 2006; Ólafsdóttir & Shinn, 2013; Agusti-Ridaura et al. 2019). The only region where *C. elongatus* has been reported as being more abundant than *L. salmonis* on farmed Atlantic salmon is the Bay of Fundy in the Northwest Atlantic (Hogans & Trudeau, 1989a, b). One can only speculate on the reasons for this, but it may be that the copepods on different sides of the North Atlantic are different genotypes of *C. elongatus*. Prior to this the only report of *C. elongatus* on farmed salmonids in eastern Canada had been that of Sutterlin et al. (1976) on cultured brook trout *Salvelinus fontinalis* and rainbow trout *Oncorhynchus mykiss.*

Several publications identify lumpfish *Cyclopterus lumpus* as a favoured host for *C. elongatus.* Boxshall (1974) found chalimus larvae occurring commonly on the skin and fins of all 11 of the lumpfish he examined from the North Sea. Lumpfish were the preferred host for two genotypes of *C. elongatus* in experimental studies carried out by Øines et al. (2006), with one genotype also favouring cod *Gadus morhua* in one experiment. Heuch et al. (2007) found lumpfish to be the most heavily infected of 52 wild fish species examined for *C. elongatus* off the south-east coast of Norway, followed by tub gurnard *Chelidonichthys lucerna,* pollack *Pollachius pollachius* and sea trout *Salmo trutta.* Herring *Clupea harengus* and saithe *Pollachius virens* were other favoured hosts. Heavy infestations of North Sea herring with *C. elongatus* were reported by MacKenzie & Morrison (1989). A survey of the occurrence of *C. elongatus* on 6,334 individuals of 35 species of wild fishes caught in inshore waters off Maine in the northwest Atlantic found 10 species to be infected. Only one lumpfish was examined, but it had by far the highest median intensity of 22. Of the other infected species, three-spined stickleback *Gasterosteus aculeatus* was the most heavily infected at 12.3% prevalence (Jensen et al., 2016). *Caligus elongatus* also occurs commonly on wild Atlantic salmon *Salmo salar*, although levels of infection on returning wild salmon caught in the Northeast Atlantic were found to be much lower than those of *L. salmonis* (see Berland 1993; Jacobsen & Gaard 1997; Copley et al. 2005). Amongst farmed salmonids, arctic charr *Salvelinus alpinus* are more susceptible than Atlantic salmon to *C. elongatus* (Mustafa et al. 2005).

5.2. C. curtus

This is the type species of the genus *Caligus.* Its natural range is the Arctic-Boreal Atlantic and contiguous waters. It is predominantly a parasite of gadid fishes, but has also been reported from a variety of other fish, including elasmobranchs (Parker et al. 1968). It is one of only two species of *Caligus* reported from off the north coast of Norway, the other being *C. elongatus* (see Karasev 2003). It is not considered to be a serious pathogen of farmed salmonids: Hogans & Trudeau (1989a) found that it accounted for only 0.7% of all the sea lice collected from farmed salmon in the Bay of Fundy, despite the common occurrence of its gadid hosts around the salmon cages.

5.3. C. clemensi

This species is native to the Northeast Pacific where it infests a wide range of mainly pelagic fishes (Parker & Margolis, 1964). Jones & Johnson (2014) listed 13 fish species as reported hosts for *C. clemensi*, including Atlantic salmon and 6 species of the genus *Oncorhynchus*. Apart from *Oncorhynchus* spp., its main natural hosts appear to be Pacific herring *Clupea pallasi,* three-spined stickleback*,* and Alaska pollock *Theragra chalcogrammus* (see Parker & Margolis 1964; Arai 1969; Margolis et al. 1975; Arthur & Arai 1980; Margolis & Kabata 1988).

5.4. C. rogercresseyi

This species is native to the southeast Pacific where it occurs along the coast of Chile and southern Argentina (Bravo et al. 2006), and possibly the coast of Peru (Conroy 2001; Bravo et al 2011). It parasitizes a wide range of wild fish, but its most favoured host appears to be the rock cod or robalo *Eleginus maclovinus,* which occurs commonly around salmonid cages, along with the Chilean silverside *Odontesthes regia,* which has also been reported as a host (Carvajal et al. 1998). Salmonid farming began in Chile in the early 1980s, but *C. rogercresseyi* was not reported from these fish until 1992, when heavy caligid infestations were recorded on coho salmon *Oncorhynchus kisutch*, rainbow trout and Atlantic salmon by Gonzalez & Carvajal (1994) and Carvajal et al. (1998). These authors identified the copepod responsible as *Caligus flexispina* Lewis, 1964, but Boxshall & Bravo (2000) confirmed that it was a hitherto undescribed species which they named *C. rogercresseyi.* It is now the dominant species of *Caligus* affecting farmed salmonids in Chile, the most susceptible species being rainbow trout and Atlantic salmon (Mancilla-Schulz et al. 2018).

5.5. C. teres

Like *C. rogercresseyi,* this species is native to the southeast Pacific, where it has been reported from fish of a variety of taxonomic groups. It was first described by Wilson (1905) from the chimaera *Callorhynchus callorhynchus* and an unidentified ray off the coast of Chile, and has since been reported from the Peruvian hake *Merluccius gayi peruanus* and the silverside *Odontethes* sp. (see Fernandéz et al. 1986). It was the first native caligid to transfer to farmed salmonids in Chile in the early 1980s, when it was found infesting coho salmon (Reyes & Bravo 1983). When the culture of rainbow trout in Chile began in 1987, they were found to be highly susceptible to *C. teres* (see Bravo 2003). It is not considered to be as great a threat as *C. rogercresseyi* to Chilean salmonid farming.

5.6. *C. orientalis*

This species is distributed in the northwest Pacific Ocean off Russia, Japan and China. It is unusual amongst caligids in that it has been reported from a wide range of both marine and freshwater fishes. Heavy infections of cultured rainbow trout in brackish water in Japan were reported by Urawa & Kato (1991), but no further similar cases have been reported since and this copepod was not considered to be important for marine rainbow trout culture in Japan by Nagasawa (2015).

6. Interactions between wild and farmed fish

Large aggregations of wild fish are attracted to fish farms, one of the main reasons being the attraction of waste fish feed (Uglem et al. 2014). The extent and scale of both the attraction and repulsion of fish farms for wild organisms, and the reasons for it, were reviewed by Callier et al. (2018). Some of the wild fish species attracted to fish farms are natural hosts for *C. elongatus* and could be an important source of infection for the farmed fish. Saithe are the most abundant wild fish species reported as congregating around salmonid cages in Norway (Uglem et al. 2009). Because they are predominantly pelagic feeders, saithe are consistently found in higher concentrations immediately beside and beneath farm cages (Dempster et al. 2010). Dempster et al. (2009) found that saithe, cod and haddock *Melanogrammus aeglefinus* dominated the farm-associated wild fish assemblages around salmon farms in coastal Norway. These three species, plus mackerel *Scomber scombrus,* were significantly more abundant at farm than at control locations. Somdal & Schram (1992) found *C. elongatus* on only two out of 454 mackerel caught in the Northeast Atlantic, which suggests it is probably not a favoured host. Because lumpfish are commonly used as cleaner fish in salmon aquaculture, Mitamura et al. (2012) examined their movements in a north Norwegian fjord during their spawning season to assess their potential to act as vectors for transmission of parasites to farmed salmon. They found that wild lumpfish are not attracted to salmon farms in the same way as some other species. Other species commonly found around salmon farms included two-spotted goby *Gobiusculus flavescens* and poor cod *Trisopterus minutus* (see Carss 1990; Dempster et al. 2010). The latter species was listed among the hosts for *C. elongatus* by Kabata (1979).

7. Genetics

Genetic analyses of mitochondrial COI from samples of *C. elongatus* indicated two distinct clades, possibly revealing two closely related species (Øines & Heuch 2005). The different genotypes did not appear to be associated with sample site or host species. A later study (Øines et al. 2006) revealed that the two genotypes varied slightly in their host preferences, lice from wild lumpfish being all of genotype 1, while those from wild saithe were mainly of genotype 2. Adult *C. elongatus* from both original host species presented experimentally to lumpfish, sea trout, cod, Atlantic salmon and plaice *Pleuronectes platessa* showed a distinct preference for lumpfish and cod. In addition, the genotype 1 of *C. elongatus* was over-represented in wild fish samples collected during spring and genotype 2 gradually increased in samples collected in autumn (Øines & Heuch 2007). However, the study also showed that farmed salmon from Northern Norway (Finnmark), the Faroe Islands, Canada and Scotland had 100% of genotype 1, although samples were collected throughout the year (Øines & Heuch 2007). The differences between the two genotypes were investigated in more detail by Øines & Schram (2008), using two mitochondrial and one nuclear genetic markers, backed up by a morphological analysis of a selected group of characters. The mitochondrial genes indicated genetic distances between the two genotypes within the lower range previously reported for other crustacean species, but the nuclear 18S sequences showed no detectable difference. Two of the three selected morphological characters supported the division based on the molecular results. The authors were unable to draw any firm conclusion regarding the species status of the two genotypes, although their results did suggest the possibility of two sibling species. The *Caligus* species closest to *C. elongatus* in the molecular analysis were *C. gurnardi* and *C. belones,* which are also similar morphologically.

8. Control of sea lice

Since salmonid culture began in the 1960s, a great deal of time and effort has been expended in finding ways to control caligid infestations. In his review of the different methods used, Costello (1993) divided them into three categories: chemical, physical and biological. We discuss them below under the same headings.

8.1. Chemical methods

The first efforts to control *L. salmonis* on farmed salmonids in Norway used formalin and acetic acid baths with limited success (Hastein & Bergsjo 1976). Since these early days many chemicals, mostly insecticides, have been used against sea lice. At present, the most commonly used substances belong to five groups of compounds: orally administrated avermectins (emamectin benzoate) and benzoyl ureas (diflubenzuron and teflubenzuron), or bath treatments, using organophosophates (azamtiphos), pyrethroids (deltametrin and cypermetrin) and disinfectants (hydrogen peroxide; reviewed by Aaen et al. 2015). Some have been used in combination for greater effect.

Wootten et al. (1982) found that the effects of chemotherapy using Dichlorvos were similar on *C. elongatus* and *L. salmonis* on Scottish salmonid farms*,* but Landsberg et al. (1991) found a freshwater dip to be more effective than copper, formalin and trichlorfon treatments against *C. elongatus* on red drum *Sciaenops ocellatus* held in seawater ponds. Freshwater dips are not considered to be entirely effective, however, especially against older stages of sea lice (Stone et al. 2002; Wright et al. 2016). Bron et al. (1993a) found treatment with dichlorvos to be more effective against *C. elongatus* than against *L. salmonis.*

According to a survey performed in Northern Norway, Iceland and the Faroe Islands, oral administration of emamectin benzoate is currently the preferred and most effective chemical treatment against *C. elongatus* (Imsland et al. 2019a). Infestation is inhibited for up to 55 days after treatment (Stone et al. 2000), and there are no signs of *C. elongatus* developing drug resistance at this point (Agusti-Ridaura et al. 2019). Oral administration of benzoyl urea compounds against *C. elongatus* was only reported at the Faroe Islands and with mixed reports of its efficiency (Imsland et al. 2019a). These compounds inhibit moulting through inhibition of chitin synthesis, and will therefore only be effective in removal of chalimus stages (Campbell et al. 2006). For protection of non-target species, the use of benzoyl ureas has been banned or restricted in several salmon-producing countries (e.g. Canada, Iceland, Norway).

The bath treatments commonly used against *L. salmonis* or *C. rogercresseyi* also appear to be effective against *C. elongatus* (Agusti-Ridaura et al. 2019). However, pyrethroids are aimed at chalimus stages (Treasurer & Wadsworth 2004) and hydrogen peroxide against adult stages (MacKinnon 1997). This may be challenging in periods of high infestation rates, during which all stages of *C. elongatus* appear on the fish. Furthermore, the effect may be short-term, due to rapid re-infestation after treatment (Imsland et al. 2019a and references therein).

Although effective, these chemicals all carry environmental risks, can affect fish health and can impact negatively on the public image of aquaculture. They also carry the risk of reduced sensitivity and resistance to chemical treatments on the part of the parasites. Efforts have therefore been made to replace them with more environmentally friendly methods (Jackson et al. 2017; Bui et al. 2019), such as those described below.

8.2. Physical methods

These include methods involving modifications to the design and structure of farm cages or additions of filtration and sieving devices. The use of plankton nets or tarpaulin skirts around salmon cages has proved effective in reducing sea lice infestations on the farmed fish (Stien et al. 2018; Grøntvedt et al. 2018), although they may not completely prevent entry of copepodid stages. Increasing the depth of the nets also increases their efficiency. A recent development is the use of "snorkel" sea cages. These are cages with a net roof that hold the salmon deep in the water column but allow them access to the surface via an enclosed tarpaulin tube called a snorkel. This gives the salmon the opportunity to refill their open swim bladders by gulping air at the surface so that they can maintain their buoyancy in deeper water. This system was tested by Stien et al. (2016), Oppedal et al. (2017) and Geitung et al. (2019) and was found to significantly reduce loads of *L. salmonis* on farmed salmon. Oppedal et al. (2017) tested five different systems with net roofs set at 0, 4, 8, 12 and 16 metres and found that *L. salmonis* infestation decreased exponentially with depth: infestation levels in shallow snorkels (0 and 4m) were consistently 4 to 10 times higher than those in deep snorkels (12 and 16m). Geitung et al. (2019) found that barrier cages reduced newly settled lice on salmon by 75% compared to standard cages.

These plankton nets/tarpaulin skirts and snorkels are designed to keep farmed fish away from the near-surface layers favoured by infective stages of *L. salmonis*. While the use of plankton nets of the mesh size used in these situations may be effective in controlling *L. salmonis* infestations (Grøntvedt et al., 2018)*,* they may be not be as effective a barrier against the copepodids of smaller caligids such as *C. elongatus,* although this remains to be investigated. There is also evidence that copepodids of *C. elongatus* may occur at greater depths than those of *L. salmonis* (see Norðì et al. (2015).

In an effort to reduce the numbers of sea lice re-entering the marine environment via harvest water outflow, O'Donohoe & McDermott (2014) used a system consisting of two sieves of different sizes. They reported a reduction in sea lice numbers of 89.5%, thus considerably reducing the risk of re-infestation.

8.3. Biological methods

These methods include the use of cleaner fish (Imsland et al., 2014, 2018), fallowing (Overton et al., 2019), vaccination (Carpio et al., 2011), selective breeding (Robledo et al., 2019) and fish behaviour (Frenzl et al., 2014).

The cleaner fish selected for lice control on salmon farms in the northern hemisphere are wrasse (Labridae) and lumpfish. Wrasse are efficient cleaners but have the major disadvantage that they tend to become inactive in winter (Powell et al. 2017). Lumpfish, on the other hand, continue to feed at low temperatures and are thus the obvious candidate for use in salmon farms in colder regions such as northern Norway (Imsland et al., 2014, 2018). Lumpfish are generally effective in reducing numbers of *L. salmonis* on farmed salmon (Bolton-Warberg, 2017; Imsland et al., 2018), and have also been found to reduce the numbers of *C. elongatus* (Imsland et al. unpublished data). However, their use may come with a considerable risk attached, as lumpfish have been shown to be a favoured host of *C. elongatus* (see section 4 above). Another disadvantage of lumpfish as cleaners is that they are opportunistic feeders and may be less effective when other food sources such as zooplankton or salmon pellets are readily available (Imsland et al. 2015; Eliasen et al. 2018).

Fallowing is a method of controlling disease, including sea lice infestations, in aquaculture (Overton et al., 2019). In this method, sites are emptied of fish and not restocked for a period of time. Its effectiveness is linked to the persistence of the pathogen in the water with a reduced biomass of suitable hosts and the length of the fallowing period (Werkman et al. 2011). While fallowing is an effective method of controlling *L. salmonis* infestations, it has been found to have no observable effect on *C. elongatus* (see Bron et al. 1993b; Treasurer 1998; Revie et al. 2002), because the latter will persist around the fallowed site on its numerous natural wild hosts. The Norwegian lice surveillance programme requires each farm to develop a general plan for prevention and treatment of salmon lice (Torrissen et al. 2013, Overton et al., 2019). All farms are required to annually re-evaluate and update their lice management plans, and also provide details to the Norwegian Food Safety Authority (Torrissen et al. 2013)

Raynard et al. (2002) reviewed efforts to develop a vaccine against sea lice, but it remains elusive (Bui et al. 2019). To date the only reported successive trial is from Chile with *Caligus rogercresseyi* (see Carpio et al., 2011), where up to 75% reduction in infestation of adult female lice was achieved in the vaccinated groups.

Selective breeding for disease resistance is a long-established practice in terrestrial farming, but is still in the exploration phase in aquaculture, although studies of genomics and selective breeding of parasite-resistant salmon is increasing (Bui et al. 2019). Gharbi et al. (2015)

combined experimental trials and diagnostics to provide a practical protocol for quantifying resistance to *L. salmonis* in Atlantic salmon. Their model predicted that substantially fewer chemical treatments would be needed to control infestations in selected populations and that chemical treatment could be unnecessary after 10 generations of selection. Experimental exposures of different wild populations and families of farmed Atlantic salmon have demonstrated the considerable potential of selective breeding for increasing resistance to infestation with *L. salmonis* (see Gjerde et al. 2011; Lush et al. 2019) and *C. rogercresseyi* (see Llorente et al. 2012). The only similar experiments carried out with *C. elongatus* are those of Mustafa & MacKinnon (1999) and Glover et al. (2005). Mustafa & MacKinnon (1999) exposed lice-free farmed Atlantic salmon of 73 full-sibling families to salmon already infested with *C. elongatus.* The amount of variation in infestation levels they found between families indicated moderate genetic-based variability and suggested that resistance to infestation with *C. elongatus* may be heritable. Glover et al. (2005) measured the variations in abundance of both *L. salmonis* and *C. elongatus* between 30 full-sibling families of farmed Atlantic salmon. The differences in abundance between families were statistically significant for *L. salmonis*, but not for *C. elongatus*. The authors considered that this difference may have been a consequence of the low prevalence of *C. elongatus* on the fish when they were sampled.

Bui et al. (2019) proposed that natural host behaviour patterns could be harnessed to control parasitic infections, with particular reference to Atlantic salmon and sea lice. The reasoning behind this approach is that because wild salmon have co-evolved with *L. salmonis,* so certain behaviour patterns they use to avoid infestation in the wild should be retained in farmed salmon. To use these behavioural patterns to reduce sea lice infestations, fish farmers must draw on existing knowledge of wild salmon behaviour and also observe the behaviour of farmed salmon. Recognising the farmed salmon as a species with an evolutionary history and taking advantage of their naturally developed responses to parasites by modifying aquaculture systems accordingly will facilitate management of the health and welfare of farmed fish. This approach combined with selective breeding could signal the future direction of salmonid farming.

9. Predicted effects of climate change and invasions

Trying to predict the effects of climate change on any organism is a difficult task. Predictions are made on the assumption that current changes will continue into the future, which is by no means certain. What is certain is that climate change affects parasites in two ways: through direct effects on the parasite itself, and through indirect effects on other hosts in its life cycle. The probable effects of climate change on aquatic parasites were reviewed by Marcogliese (2001, 2008) and Lõhmus & Björklund (2015). Here we discuss the effects that are most likely to affect parasitic copepods, and caligids in particular.

The two effects of climate change most likely to affect caligid copepods are increasing acidification and temperatures in the sea. As atmospheric carbon dioxide continues to increase, more of it is being absorbed by both oceanic and freshwater systems, leading to changes in water chemistry and a continuous reduction in pH, with potentially serious consequences for many aquatic organisms. If current trends continue, it is predicted that many marine organisms, particularly pteropods and crustaceans, will have difficulty maintaining their external calcium carbonate exoskeletons (Orr et al. 2005). However, studies on the probable effects of increasing water temperature on free-living marine copepods indicate an antagonistic effect of increased warming and acidification. The impacts of future climate change on community structure, diversity, distribution and phenology of 14 different species of free-living marine copepods in the North Atlantic were evaluated by Villarino et al. (2015). Their projections indicated poleward shifts, earlier seasonal peaks and changes in biodiversity spatial patterns, but with important range variations between species. Other studies indicated that higher temperatures reduced energy status and decreased copepodid and nauplii abundance, but also that acidification partially counteracted some observed effects of increased temperature, while adding to others (Garzke et al. 2016; Pedersen & Hanssen 2017). Similar changes may be expected for parasitic copepods such as caligids. The optimum temperature for *C. elongatus* was found to be around 14˚C (Hogans & Trudeau 1989a) so, as temperatures increase, earlier seasonal peaks and more annual generations may be expected for northern parts of its distribution such as northern Norway. Other effects are more difficult to predict because of the above-mentioned antagonistic effects of temperature and acidification. A recent study (Thompson et al. 2019) of the effects of increased acidification on growth and metabolic rates on the early planktonic stages of *L. salmonis* indicated that these stages have mechanisms to compensate for increased concentration of $p\mathrm{CO}_2$ and that populations will be tolerant of projected future ocean acidification scenarios.

One of the results of current climate warming is expansion of host geographical ranges, with the result that species that have evolved in isolation may be brought into close contact. These host species carry their established parasites with them and expose them to new potential hosts, providing them with opportunities to expand their host range. Many invasive species have been introduced accidentally, while others have been introduced deliberately. The opening of the sea passage along the north coast of Siberia will inevitably lead to more introductions of North Pacific species into the northeast Atlantic and possibly beyond (Chan et al. 2018). One invasive species of relevance to this review is the pink salmon *O. gorbuscha,* which was introduced to rivers in the Kola Peninsula in northwest Russia in the period 1956-1959 and began to appear in Norwegian rivers from 1960 (Berg 1977; Mo et al. 2018). This salmonid is a known host of *C. clemensi* (see Parker & Margolis 1964). The only report of parasites in invasive pink salmon is that of Grozdilova (1974) from the White Sea, and *C. clemensi* was not found in this study. Another common host of *C. clemensi* is the Pacific herring, which also occurs in the White Sea along with Atlantic herring (Froese & Pauly 2019). Although there appears to be no report of *C. clemensi* parasitizing this particular population of Pacific herring, its close proximity to the Barents Sea and other parts of the northeast Atlantic, combined with the current trend of climate change, may provide an opportunity for *C. clemensi* to colonise this region in the future, with possibly serious consequences for salmonid culture.

10. Conclusions and recommendations

This review was prompted by reports of large numbers of sea lice identified as *C. elongatus* infesting farmed salmon in northern Norway. The salmon louse *L. salmonis* is usually the most numerous species of sea louse on salmon farms in the North Atlantic, including southern and western Norway, so the occurrence of such large numbers of *C. elongatus* is very unusual. Northern Norway has lower sea temperatures than regions further south, but the optimum temperature for *C. elongatus* is reported as being 14˚C (Hogans & Trudeau 1989a), and there are fewer generations produced per year at temperatures lower than this. The occurrence of such large numbers of *C. elongatus* in northern Norway thus contradicts the published information.

Assuming that the identification of the culprit as *C. elongatus* is correct, one possible explanation is that this infestation is caused by a different genotype of *C. elongatus* with a greater tolerance of cold temperatures. This hypothesis is given some credibility by the study of Øines & Schram (2008), who identified two genotypes of *C. elongatus* which were different enough to suggest the possibility of them being considered as sibling species. The dominance of *C. elongatus* over *L. salmonis* reported by Hogans & Trudeau (1989a, b) on farmed salmon in the northwest Atlantic may also be explained by the presence there of another genotype of *C. elongatus*. More research is needed into the genetics of *C. elongatus* in different parts of its wide geographical distribution.

Another possibility is that the copepods infesting the fish in these northern farms are not all *C. elongatus*, but a mix of this and another species. If we consider those species that are known to cause problems in salmonid farming, the most obvious candidates for the other species are *C. curtus* and *C. clemensi.* The former is not regarded as a serious pathogen of farmed salmonids and is easily recognized by its much greater size than other species of *Caligus* reported from farmed salmonids, although it is comparable in size to *L. salmonis. Caligus clemensi* has not been reported from the North Atlantic but, as discussed earlier in this review, one of its natural hosts is the invasive Pacific pink salmon, which is now caught on a regular basis in Norwegian rivers (Mo et al. 2018). Another of its natural hosts is the Pacific herring, which has a long-established resident population in the White Sea (Froese & Pauly 2019). An extension of the range of *C. clemensi* into north Norway is thus a distinct possibility. A less likely possibility, but still one to consider, is an infestation by another species of *Caligus* hitherto unreported from farmed salmonids.

The design of plankton nets/tarpaulin skirts and snorkels is aimed at keeping farmed fish away from the near-surface layers favoured by infective stages of *L. salmonis*. They may not be as effective against those of *C. elongatus,* which are found over a greater depth range. Fallowing is not effective against *C. elongatus.*

Our recommendations are therefore as follows.

- Confirm the identity (or identities) of the caligids causing this problem by having a large number of parasites examined by expert parasitologists.
- If *C. elongatus* is confirmed as the culprit, have a sample sequenced and compared with existing sequences for the two genotypes reported previously.
- If another species of caligid is present, further action will depend on its specific identity, distribution and host preferences.
- Determine which wild, including introduced, fish species present in the vicinity of the affected farms may be serving as reservoir hosts.
- Carry out a study of the distribution in the water column of copepodids of *C. elongatus* or whatever species is identified as causing the problem. This information will be necessary for the development of appropriate control measures.

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Figure legends

Figure 1. Life cycle stages of *Caligus elongatus*: 1 = nauplius I, 2 = nauplius II, 3 = copepodid, 4 = anterior of copepodid with frontal filament extended, 5 = chalimus I, 6 = chalimus II, 7 = chalimus III, 8 = chalimus IV, 9 = young adult male. Scale bars: 1-5 = 100 µm; 6-7 = 200 µm; 8-9 = 500 µm. (Modified from Hogans & Trudeau 1989a).

Figure 2. Ventral surface of caligid cephalothorax showing appendages: ant1 = antennule, ant2 = antenna, apr = apron of third leg, fp = frontal plate, lun = lunule, mmb = marginal membrane, mt = mouth tube, mx1 = maxillule, mx2 = maxilla, mxp = maxilliped, pan = postantennal process, sf = sternal furca, th1 = th3 = first to third legs, vel = velum (after Margolis & Kabata 1988,with terminology updated).

Figure 3. Mouth cone of *Caligus curtus* (after Kabata 1974).

Figure 4. Diagrammatic face-on view of caligid mouth (after Kabata 1974).

Figure 5. Comparison of dorsal views of females of the four most common *Caligus* spp. infecting farmed salmonids. Scale bars = 1 mm. (after Parker & Margolis 1964, Kabata 1979, Hogans & Trudeau 1989, Boxshall & Bravo, 2000).

Figure 6. Comparison of dorsal views of males of the four most common *Caligus* spp. infecting farmed salmonids. Scale bars = 1 mm. (after Parker & Margolis 1964, Kabata 1979, Hogans & Trudeau 1989, Boxshall & Bravo, 2000).