Zoological Studies

A Review of the Impact of Parasitic Copepods on Marine Aquaculture

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Stewart C. Johnson, Jim W. Treasurer, Sandra Bravo, Kazuya Nagasawa, and Zbigniew Kabata (2004) A review of the impact of parasitic copepods on marine aquaculture. *Zoological Studies* **43**(2): 229-243. Parasitic copepods are common on cultured and wild marine finfish, and there is a substantive literature describing their taxonomy, life cycles, and host ranges. Although many species have long been recognized to have the potential to affect the growth, fecundity, and survival of their hosts, it has only been with the development of semi-intensive and intensive aquaculture that their importance as disease-causing agents has become evident. Members of the family Caligidae are the most commonly reported species on fish reared in brackish and marine waters. These species, often referred to as sea lice, are responsible for most disease outbreaks. The impacts of sea lice on marine salmonid aquaculture are well documented, with catastrophic losses reported for disease outbreaks that have resulted in high levels of mortality. With the development of a variety of treatments and management strategies to reduce infection levels, mortality caused by sea lice has been greatly reduced. At present, economic losses due to sea lice are primarily from the costs of treatments, the costs of the management strategies, the costs associated with reduced growth rates that are a direct result of infection and/or treatment, and the costs of carcass downgrading at harvest. Indirect and direct losses due to sea lice in salmonid aquaculture globally are estimated to be greater than US$100 million annually. In other areas of marine aquaculture, the impact of parasitic copepods is not well documented. This is especially true for species such as Atlantic halibut, Atlantic cod, turbot, and haddock that have only recently entered commercial-scale production. This review discusses the global importance of parasitic copepods as disease-causing agents in marine aquaculture. We also provide a brief review of the environmental and husbandry factors that may affect parasitic copepod abundance and the potential roles that parasitic copepods play as vectors for other disease agents. http://www.sinica.edu.tw/zool/zoolstud/43.2/229.pdf

Key words: Sea lice, Disease, Caligidae.

Parasitic copepods are common on cultured and wild marine finfish, and there is a vast literature describing their taxonomy and host ranges. Many of these species have long been recognized to have the potential to affect the growth, fecundity and survival of wild hosts (White 1940, Kabata 1958, Hewitt 1971, Neilson et al. 1987, Johnson et al. 1996). With the development of semi-intensive and intensive brackish water and marine aquaculture, the importance of parasitic copepods as disease causing agents has become more evident. Members of the family Caligidae, also often referred to as sea lice, are the most commonly reported species on marine and brackish water

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cultured fish throughout the world, accounting for approximately 61% of all reports (Tables 1, 2). Members of this family have been responsible for most of the documented disease outbreaks.

Parasitic copepods feed on host mucous, tissues, and blood, and their attachment and feeding activities are responsible for any primary disease that develops. The relationship of the number of parasitic copepods to severity of the disease is dependent on 1) the size and age of the fish, 2) the general state of health of the fish, and 3) the species of copepod and the developmental stages present (Pike and Wadsworth 1999 and references therein). Losses associated with disease are the result of direct mortality, mortality due to secondary infections, reduced growth, loss of carcass value, and costs associated with treatment (Lin et al. 1994, Pike and Wadsworth 1999, Ho 2000).

Caligid copepods generally have direct life cycles consisting of 2 free-living planktonic nauplius stages, 1 free-swimming infectious copepodid stage, 4 to 6 attached chalimus stages, 1 or 2 preadult stages, and 1 adult stage (Johnson and Albright 1991a, Ogawa 1992, Lin et al. 1996, Lin et al. 1997, Pike and Wadsworth 1999). Notable exceptions include *Caligus punctatus* and *C. elongatus* in which the preadult stage is reported not to occur (Kim 1993, Piasecki and MacKinnon 1995, Piasecki 1996). Through their attachment and feeding activities, copepodid and chalimus stages cause variable amounts of localized damage that elicit only minor host tissue responses in most host species (Bron et al. 1991, Johnson and Albright 1992, Roubal 1994, Pike and Wadsworth 1999). However when present in high numbers especially on gills, chalimus stages can cause significant pathology that can result in mortality (Lin et al. 1994, Wu et al. 1997). In most cases, the preadult and adult stages are not very invasive, generally not penetrating deeply into host tissues and only causing minor tissue damage (Ono 1984, Ogawa 1992, Roubal 1994, Johnson et al. 1996). However, in situations of severe disease such as is seen in Atlantic salmon (*Salmo salar*) when infected by high numbers of *Lepeophtheirus salmonis*, extensive areas of skin erosion and hemorrhaging on the head and back, and a distinct area of erosion and sub-epidermal hemorrhage in the perianal region can be seen (Brandal and Egidius 1979, Pike and Wadsworth 1999). The formation of similar skin and head lesions on Atlantic salmon, Atlantic halibut (*Hippoglossus hippoglossus*), and the rabbit fish (*Siganus fuscescens*) has also been reported as the result of infection with

Caligus spp. (Wootten et al. 1982, Lin et al. 1996, Bergh et al. 2001). Infection of the gills and gill cavity of black sea bream (*Acanthopagrus schlegeli*) by juvenile and adult *Caligus multispinosus* was reported to cause gill congestion, other damage, and mucous proliferation (Lin et al. 1994). In disease situations, death may be caused by the development of secondary infections exacerbated by stress and the formation of open wounds, osmoregulatory failure, and in the case of the gills, respiratory impairment (Brandal and Egidius 1979, Wootten et al. 1982, Johnson et al. 1996, Bjorn and Finstad 1997, Pike and Wadsworth 1999, Bowers et al. 2000, Finstad et al. 2000).

Parasitic copepods from other families have also been reported from cultured fish and in some instances have been responsible for disease (Table 1). However, there are few reports of pathology associated with their attachment and feeding. The attachment and feeding activities of *Alella macrotrachelus* on black sea bream resulted in hyperplasia of the gill lamellae (Muroga et al. 1981). Hogans (1989) reported serious disease in Atlantic salmon infected with *Ergasilus labracis* that was characterized by severe gill hyperplasia and high levels of mortality. Infection of the gills of Borneo mullet (*Liza macrolepis*) with extremely high numbers of the ergasilid copepod, *Diergasilus kasaharai*, resulted in gill inflammation, necrosis, high levels of mucous production, and death of the hosts (Lin and Ho 1998). The formation of vacuoles within the gill tissues was reported for Malabar reef-cod (*Epinephelus malabaricus*) infected with *Ergasilus lobus* (Lin and Ho 1998).

IMPACT OF PARASITIC COPEPODS ON MARINE SALMONID CULTURE

In marine salmon aquaculture, sea lice belonging to the genera *Caligus* and *Lepeophtheirus* are commonly present, but their presence does not always result in the development of disease (Table 1, Ho and Nagasawa 2001). Unfortunately, under some circumstances, epizootics do occur and result in serious disease and high mortalities if untreated (Brandal and Egidius 1979, Wootten et al. 1982, Pike 1989, Pike and Wadsworth 1999). Although infection with sea lice is one of the major problems faced in marine salmon farming, economic losses due to sea lice are poorly documented. In addition to affecting the profitability of salmonid aquaculture, the presence

of sea lice on farmed salmonids and the necessity for treatments also affects the regulation and public perception of salmonid aquaculture in some regions of the world, especially in areas where they may affect wild salmonids.

NORTHERN HEMISPHERE

Major regions of marine salmon farming within the northern hemisphere include Japan, the east and west coasts of Canada, the northeastern US, Ireland, Scotland, and Norway. The major sea lice species reported from farmed salmonids in these regions are *Caligus clemensi* (Pacific Ocean), *C. elongatus* (Atlantic Ocean), and *L. salmonis* (Table 2, Johnson et al. 1997, Pike and Wadsworth, 1999). *Lepeophtheirus salmonis* has a circumpolar distribution and is limited in its host range to salmonids, except in very rare cases (Kabata, 1979). In comparison, *C. clemensi* and *C. elongatus* have broad host ranges that include both non-salmonid teleost and elasmobranch hosts (Margolis et al. 1975, Kabata 1979). Many of these non-salmonid hosts are common in the vicinity of seawater farms and serve as a source of parasites for infection of salmonids.

Of these species, *L. salmonis* is the most important with respect to disease. There is a vast literature on the biology and control of *L. salmonis* that is well summarized in a recent review by Pike and Wadsworth (1999). With the exception of Japan and the west coast of Canada, outbreaks of disease caused by sea lice have been frequently reported for all of these regions. In most of these regions, the initial outbreaks of sea lice disease resulted in high economic losses that were sustained until adequate treatment and management

Table 1. Major groups of parasitic copepods reported from fish cultured in brackish and marine waters. Proportions are based on publications cited in Table 2

Family/Genus	Proportion of all species reported
Caligidae	61%
Caligus	40%
Lepeophtheirus	14%
Ergasilidae	15%
Other families	24%
Lernaepodidae	8%
Lernanothropidae	5%

strategies were instituted. At present, outbreaks of disease caused by sea lice are rarely reported, although rates of sea lice infection remain high as evidenced by the frequent requirement for treatments. The lack of disease is due to the use of management strategies that rely on medicines and husbandry practices to maintain sea lice at low levels of abundance. In some countries such as Ireland, Scotland, and Norway, treatment thresholds for sea lice have been regulated (Eithun 2000, McMahon 2000). These regulations have been put into effect as a response to concern that sea lice emanating from farmed salmonids might be responsible for sea lice problems seen on wild sea trout and Atlantic salmon. Treatment thresholds in Ireland are set at 0.3 to 0.5 egg-bearing females per fish in the spring and 2 egg-bearing females per fish at other times of the year (McMahon 2000). The treatment threshold for Norway is set at 1 to 5 adult females per fish depending on the season, water temperature, and site location (Eithun 2000). In Scotland, a voluntary code sets the treatment threshold at 1 ovigerous female per 10 fish in the spring (Rae 2002). In New Brunswick, Canada, treatments are often initiated when there are > 5 preadults per fish and/or 1 egg-bearing female per fish depending on the water temperature and season.

With the reduction in the occurrence of severe sea lice disease, economic losses due to fish mortality and carcass downgrading have been substantially reduced. However, sea lice still have a significant economic impact due to reduced growth performance resulting from the presence of the sea lice and/or chemical treatments, as well as from the costs of the treatments themselves (Sinnott 1999, Rae 2002). As mentioned previously, there are few accurate estimates of the economic costs of sea lice to salmonid aquaculture. Rae (2002) estimated the cost of sea lice to the Scottish salmon farming industry at between $US31 and 46 million per annum based on a harvest of 130 000 tons (t). This cost includes an approximately $US20 million loss due to stress and loss of growth, and $US6.2 to 7.2 million loss due to the cost of therapeutics. Another estimate of the cost of sea lice infections in Scotland ranges between US$0.18 and 0.45 kg^{-1} of salmon (Sinnott 1999). Norway's annual losses due to sea lice infection have been estimated to be approximately $US67 million. Mustafa et al. (2001) estimated an additional cost of US$0.08 to 0.11 kg^{-1} of fish due to sea lice infection for sites in New Brunswick, Canada that regularly treat for sea lice. Without

treatment, they estimated that farmers would lose approximately US$0.35 kg^{-1} salmon through downgrading of damaged fish and losses due to mortality.

In Japan, the salmonid aquaculture industry farms both coho salmon (*Oncorhynchus kisutch*) and to a lesser extent rainbow trout (*Oncorhynchus mykiss*). *Lepeophtheirus salmonis* is commonly found on both of these species (Nagasawa and Sakamoto 1993, Urawa et al. 1998, Ho and Nagasawa 2001, Nagasawa 2003). Infection with *L. salmonis* occurs immediately after salmonid juveniles are introduced into sea net-pens in late fall. The source of this infection is larvae released from adult female parasites on migrating wild chum salmon, *Oncorhynchus keta*. Sea lice abundance is reported to increase through the on-growth period; however, unlike in Scotland, Norway, and Eastern Canada, *L. salmonis* is not a serious problem in Japan, and treatments for sea lice on salmonids are not carried out. The absence of disease caused by sea lice has been attributed to the rearing of coho salmon, a species which is resistant to infection, and to the practice of rearing fish for only 1 year prior to harvest (Ho and Nagasawa 2001). It is known that salmonids heavily infected with *L. salmonis* are disliked at fish markets, and they thus have lower commercial value (Nagasawa and Sakamoto 1993).

With respect to other groups of parasitic copepods, a single outbreak of disease caused by the ergasilid species, *E. labracis*, was reported in Atlantic salmon parr being held in brackish (14 ppt) waters in New Brunswick, Canada (Table 2, Hogans 1989, O'Halloran et al. 1992). In that instance, large numbers of all infectious developmental stages of *E. labracis* were present on the gills, resulting in severe gill hyperplasia and high levels of mortality until treatment was administered (Hogans 1989).

SOUTHERN HEMISPHERE

In the southern hemisphere, Atlantic salmon, coho salmon, and rainbow trout are farmed commercially in Chile, New Zealand, and Tasmania. Sea lice have not been reported to cause disease in New Zealand or Tasmania. In Chile, marine salmonid aquaculture began in the 1980s with the introduction of commercial-scale coho salmon production. This was quickly followed with the development of marine rearing of rainbow trout and Atlantic salmon. At present, Chile is the 2nd-largest producer of farmed salmonids with an estimated production of 230 000 t in 1999 (Anonymous in press). As in the northern hemisphere, sea lice were quickly recognized as economically important disease causing agents (Reyes 1983, Reyes and Bravo 1983a b).

Since 1840 when *Caligus ornatus* was first described by Milne-Edwards, there have been a wide variety of caligid copepods reported from wild marine fishes in Chilean waters. Many of these species have cosmopolitan distributions (Fagetti and Stuardo 1961). To date, 2 species of sea lice, *Caligus teres* and *C. rogercressyi* (originally identified as *C. flexispina*), have been documented as economically important parasites of coho and Atlantic salmon and rainbow trout (Table 2, Reyes 1983, Reyes and Bravo 1983 a b, Carvajal et al. 1998, Boxshall and Bravo 2000, González et al. 2000). Both of these species have also been identified from a variety of wild marine fishes that are common within the vicinity of farm sites (Carvajal et al. 1998).

Under both laboratory and field conditions, coho salmon are generally less susceptible to infection with these sea lice species than are either rainbow trout or Atlantic salmon (González et al. 2000, Bravo 2001). Outbreaks of sea lice disease in Chile are most common in stocks of Atlantic salmon and rainbow trout (González et al. 2000). Due to establishment of a treatment threshold of > 10 sea lice per fish and the availability of effective treatments, there are now few instances where infection with sea lice results in mortality. However, infection with sea lice has a significant economic impact in Chile. The costs of treatments and reduced growth performance, as well as costs associated with delousing of the carcasses during processing are estimated to be approximately US$0.30 kg^{-1} (Carvajal et al. 1998). Based on a field study of a farm that required 3 treatments per year of emamectin benzoate (SLICE®, Schering Plough) to control sea lice on Atlantic salmon and rainbow trout, the estimated cost of treatments alone was approximately US$0.022 kg^{-1} for the production period (Sandra Bravo, pers. comm.).

In Chile, it is recognized that infection with sea lice can predispose fish to the development of other diseases such as infectious pancreatic necrosis, bacterial kidney disease, and salmonid rickettsial septicemia. These diseases are difficult to treat and can result in high levels of mortality (Sandra Bravo, pers. comm.).

IMPACT OF PARASITIC COPEPODS ON MARINE NON-SALMONID CULTURE

The presence of parasitic copepods has been reported on a large number of species of non-salmonid fish cultured in brackish and marine waters (Table 2). However there are few well-documented cases of disease and no estimates of the economic costs of these infections.

Ergasilid copepods have been reported from a variety of non-salmonid finfish reared in brackish and marine waters (Table 2). Outbreaks of disease caused by ergasilids are a major source of copepod-induced mortality in brackish water finfish culture. Heavy infections of *Ergasilus lizae* have been reported to cause mortalities in grey mullet (*Mugil cephalus*) cultured in brackish water ponds in Israel (reviewed in Paperna 1975). Lin and Ho (1998) reported 4 outbreaks of disease caused by ergasilid copepods on 4 different host species in Taiwan. Ergasilid copepods have also been reported to cause mortalities in the southern flounder (*Paralichthys lethostigma*) in the US and red sea bream (*Pagrus major*) in Japan (Yamashita 1980, Benetti et al. 2001). In all of these instances, heavy infections on the gills resulted in gill damage, morbidity, and in most instances, substantial mortalities.

Caligid copepods have also been reported from a large number of cultured non-salmonid finfish (Tables 1, 2, Ho 2000). As in salmonid culture, sea lice are responsible for most disease outbreaks that occur on non-salmonids when they are cultured in full salinity seawater. Infection of hatchery reared postlarval stages of Atlantic cod (*Gadus morhua*) with *C. elongatus*, *Holobomolochus confusus*, and *Clavella adunca* has been associated with the feeding of natural zooplankton assemblages (Karlsbakk et al. 2001). *Caligus* spp. are also known to be important parasites of wild juvenile Atlantic cod and haddock (*Melanogrammus aeglefinus*), and *C. elongatus* has been found on wild caught haddock and Atlantic cod broodstock (Neilson et al. 1987, Armstrong et al. 1999 cited in Bergh et al. 2001, Stewart Johnson, unpubl. data for Canada). *Lepeophtheirus hippoglossi* and *C. elongatus* have been reported from wild Atlantic halibut and have been collected from captive broodstock (Kabata 1988, Stewart Johnson, unpubl. data for Canada). Laboratory infections of Atlantic halibut with *L. hippoglossi* have resulted in the development of large hemorrhagic lesions that demonstrate the potential of this species to cause disease (Armstrong et al. 1999 cited in Bergh et al.

2001). Heavy infections of pen reared Atlantic halibut with *C. elongatus* have been reported in Norway (Bergh et al. 2001). Infections of greater than 100 copepods per 500 g fish resulted in the development of severe head lesions. These infections were successfully treated with organophosphates.

To date, there have been no published reports of sea lice causing disease in cultured Atlantic cod or haddock in Scotland, Norway, or Canada. However there have been verbal reports from cod farmers in Norway of sea lice problems (Frank Nilsen, pers. comm.). In one of these cases, examination of infected fish revealed infection by *C. elongatus* although there were also a few *C. curtus* present (Frank Nilsen, pers. comm.). The broad host range of *C. elongatus* and the presence of many of wild hosts in the vicinity of many marine farm sites suggest that disease problems caused by this species may become more common as production levels of Atlantic cod and haddock increase.

Pseudocaligus apodus and *Caligus pageti* have been reported to cause disease in mullet culture in the Eastern Mediterranean (Paperna 1975). Papoutsoglou et al. (1996) reported infrequent infection of European sea bass (*Dicentrarchus labrax*) with low numbers of *Caligus minimus* at sites in Greece, but no disease outbreaks. *Caligus minimus* has also been reported from European sea bass raised on the French Atlantic coast without mention of disease (Paperna and Baudin Laurencin 1979). Pavoletti et al. (1999) reported on a disease outbreak in European sea bass in Italy caused by *C. minimus*. In that instance, fish from 30 g to 2 kg in size were infected with an average of 40 copepods per fish. Infected fish were anorexic and lethargic, and there was approximately 9% mortality of the stock.

In Japan, there are 5 major species of non-salmonid marine finfish cultured: Japanese amberjack (yellowtail) (*Seriola quinqueradiata*), greater amberjack (*Seriola dumerili*), red sea bream, Japanese flounder (*Paralichthys olivaceus*), and tiger puffer (*Takifugu rubripes*). Other species, such as the black sea bream (*Acanthopagurs schlegeli*), striped jack (*Pseudocaranx dentex*), and spotted halibut (*Verasper variegatus*) are also cultured but at relatively low levels of production. Numerous species of parasitic copepods have been reported from these species in culture including: *Caligus spinosus*, *C. lalandei*, and *Eobranchiella elegans seriolae* from Japanese amberjack; *C. fugu*, *Psuedocaligus fugu*, and

Neobrachiella fugu from the tiger puffer; *A. macrotrachelus* from the black sea bream; *C. lalandei* from yellowtail amberjack; *C. longipedis* from striped jack; *Lepeophtheirus paralichthydis* from Japanese flounder; *L. longiventris* from spotted halibut; and unidentified caligid copepods from red sea bream (Muroga et al. 1981, Ogawa 1992, Ogawa and Inoue 1997, Ogawa and Yokoyama 1998, Ho 2000, Ho et al. 2001) (Table 2). *Caligus spinosus* infections on farmed Japanese amberjack occur mainly on the gill arches and rakers, and high levels of infection have resulted in mortalities (Fujita et al. 1968). Infected fish are emaciated, dark-colored, and inactive, often swimming near the water surface. Recently, Ho et al. (2001) reported *C. lalandei* on the body surface of farmed yellowtail amberjack from western Japan. The authors reported that the wild yellowtail juveniles used as seeds for culture are sometimes infected with *C. spinosus* or *C. lalandei*. *Caligus lalandei* is a cosmopolitan species found also in South Africa, Mexico, Chile, New Zealand, and Korea (Ho et al. 2001). *Eobrachiella elegans seriolae* is found near the base of pectoral fins and on the walls of the oral cavity of cultured Japanese amberjack. To date, there is no report of this species causing disease in Japan (Ono 1984). *Caligus lalandei* (reported as *Caligus* sp. in Ogawa and Yokoyama 1998) is also known to infect farmed yellowtail amberjack (Ho et al. 2001). Ho et al. (2001) noted that although this species has not yet caused serious problems in Japanese aquaculture, its larger size when compared to *C. spinosus* gives it the potential to be a serious disease causing agent.

As a parasite of black sea bream, the biology and impacts of *A. macrotrachelus* have been well studied (Kawatow et al. 1980, Muroga et al. 1981). This copepod attaches to and feeds on gill tissue resulting in hyperplasia of the gill lamellae (Muroga et al. 1981). Copepod numbers are generally seen to increase in fall and late spring or early summer and decline in winter and summer due a lack of recruitment and parasite death (Muroga et al. 1981).

Farmed striped jack can be infected with *C. longipedis*, with the body of infected fish showing bruising (Kubota and Takakuwa 1963 [as *C. amplifurcus*], Ogawa 1992). Ho (2000) compiled information on parasitic copepod infections by the 2 caligid genera *Caligus* and *Lepeophtheirus* on cage-cultured fishes in marine and brackish waters of Asia including Japan. Although information is very limited, Ho (2000) reported that *L. paralichthydis* and *L. longiventris* caused mortality of pen cul-

tured Japanese flounder and spotted halibut, respectively.

An unidentified species of Caligidae or Pennellidae (originally reported as *Ergasilus* sp.) was reported from the body surface of larval red sea bream in Japan (Yamashita 1980). On tiger puffer, *P. fugu* occurs on the body surfaces, and *C. fugu* and *N. fugu* on the walls of the buccal cavity. Of these species, *N. fugu* is the most commonly reported species, being present throughout the year with a peak population size during the warm water months (Ogawa and Inoue 1997). Diseases caused by these copepods have not been reported from Japanese waters.

In China, South Korea, and Taiwan, disease outbreaks caused by *Caligus* species have been reported from cultured milk fish (*Chanos chanos*), Mozambique tilapia (*Oreochromis mossambicus*), banded grouper (yellow grouper) (*Epinephelus awoara*), rabbit fish, black sea bream, common spade fish (*Scatophagus argus*), Malabar reef-cod, large scale mullet (*Liza macrolepis*), grey mullet (*Mugil cephalus*), blue tilapia (*Oreochromis aureus*), three-striped tigerfish (*Terapon jarbua*), snubnose pompano (*Trachinotus blochii*), and sea bass (barramundi) (*Lates calcarifer*) (Table 2, Lavinia 1977, Jones 1980, Lin and Ho 1993 1998, Lin et al. 1994 1996 1997, Choi et al. 1995, Wu and Pan 1997, Ho 2000). The species responsible for these disease outbreaks include *Caligus acanthopagri*, *C. epidemicus*, *C. orientalis*, *C. patulus*, and *C. rotundigenitalis* (cf. Ho 2000). In some of these cases, high levels of mortality were reported, but the economic impacts of these outbreaks were not quantified.

The economic impacts of parasitic copepods on non-salmonid marine aquaculture are unknown. Large scale mortality of adult yellowtail farmed in the Goto Islands, southern Japan, was reported in the spring of 1967 as being due to a heavy infection with *C. spinosus* (cf. Fujita et al. 1968). Other large scale mortalities have not been reported. The economic impacts of parasitic copepods on fish growth, susceptibility to other diseases, cost of production, and loss of product value have not been quantified.

FACTORS THAT INFLUENCE PARASITIC COPEPOD ABUNDANCE

A variety of environmental and biological factors and husbandry and management practices that may influence the abundance and impact of

Table 2. Parasitic copepods reported from finfish cultured in brackish and marine waters

Species	Hosts	Geographical location	References
Family Caligidae			
Caligus acanthopagri	black sea bream (Acanthopagrus schlegeli), common spade fish (Scataphagus argus), Malabar rock cod (Epinephelus malabaricus), Mozambique tilapia (Oreochromis mossambicus)	Taiwan	Lin et al. 1994; Lin 1996 cited in Ho 2000
	common spade fish, giant perch (Lates calcarifer), grey mullet (Mugil cephalus), large scale mullet (Liza macrolepis), Malabar rock cod, milk fish (Chanos chanos), Mozambique tilapia, snubnose pompano (Trachinotus blochii), three-striped tiger fish (Terapon jarbua), yellowfin bream (Acanthopagrus australis)		Regidor and Aurthur 1986; Roubal 1994 1995
Caligus antennatus	Sobaity sea bream (Sparidentex hasta) (listed as Acanthopagrus cuvieri)	Kuwait	Tareen 1986
Caligus brevicaudatus	olive flounder (Paralichthys olivaceus)	South Korea	Choi et al. 1995
Caligus clemensi	Atlantic salmon (Salmo salar), coho salmon (Oncorhynchus kisutch), rainbow trout (Oncorhynchus mykiss)	Pacific coast, Canada	Stewart Johnson unpubl. data
Caligus curtus	Atlantic cod (Gadus morhua), Atlantic salmon	Atlantic coast, Canada; Canada; Norway	Hogans and Trudeau 1989; Frank Nilsen, pers. comm.
Caligus elongatus	Arctic charr (Salvelinus alpinus), Atlantic cod, Atlantic halibut (Hippoglossus hippoglossus), Atlantic salmon, rainbow trout, striped bass (Morone saxatilis)	Atlantic coast, Canada; Northeast Atlantic coast, US; Ireland; Scotland; Norway	Bergh et al. 2001; Hogans and Trudeau 1989a b; Hogans 1994; Karlsbakk et al. 2001; Mustafa and MacKinnon 1993; Shaw and Opitz 1993; Tully 1989; Wootten et al. 1982
Caligus epidemicus	black porgy (Acanthopagrus schlegeli), blue tilapia (Oreochromis aurea)	Australia; Taiwan; Philippines	Lin and Ho 1992 1993; Lin 1996 cited in Ho 2000
Caligus fugu	tiger puffer (Takifugu rubripes)	Japan	Ogawa and Inouye 1997
Caligus lalandei	yellowtail amberjack (Seriola lalandi)	Japan	Ogawa and Yokoyama 1998; Ho et al. 2001
Caligus latigenitalis	black sea bream	Japan	Izawa and Choi 2000
Caligus longipedis	striped jack (Pseudocaranx dentex)	Japan	Kubota and Takakuwa 1963 (as Caligus amplifurcus)
Caligus minimus	European sea bass (Dicentrarchus labrax)	Atlantic coast, France; Italy; Greece	Ogawa 1992; Paperna and Boudin Laurencin 1979; Papoutsoglou et al. 1996; Pavoletti et al. 1999
Caligus multispinosus	black sea bream	Taiwan	Lin et al. 1994 1997
Caligus nanhaiensis	banded grouper (Epinephelus awoara)	China	Wu and Pan 1997; Wu et al. 1997
Caligus orientalis	black porgy, giant perch, grey mullet, large scale mullet	Japan; China; Taiwan	Hwa 1965; Lin 1996 cited in Ho 2000; Urawa and Kato

Table 2. (Cont.)

Species	Hosts	Geographical location	References
	Malabar rock cod, milk fish, Mozambique tilapia, snubnose pompano, rainbow trout		1991
Caligus oviceps	rabbit fish (*Siganus fuscescens*)	Taiwan	Lin et al. 1996
Caligus pageti	grey mullet, thinlip mullet (*Liza ramada*) (listed as *Mugil capito*), white sea bream (*Diplodus sargus sargus*)	France, Israel, Egypt	Papema 1975, Raibaut et al. 1980
Caligus patulus	milk fish	Philippines, Indonesia	Lavinia 1977, Jones 1980
Caligus pelamydis	Japanese sea perch (*Lateolabrax japonicus*)	South Korea	Choi et al. 1995
Caligus punctatus	black porgy, black sea bream, blue tilapia, giant perch, grey mullet, Japanese sea bass (*Lateolabrax japonicus*), large scale mullet, Malabar rock cod, milk fish, Mozambique tilapia, snubnose pompano, three-striped tiger fish	Taiwan	Lin 1996 cited in Ho 2000
Caligus rogercresseyi (identified by Carvajal et al. as *Caligus flexispina*)	Atlantic salmon, coho salmon, sea trout (*Oncorhynchus mykiss*)	Chile	Carvajal et al. 1998, Boxshall and Bravo 2000
Caligus rotundigenitalis	black porgy, black sea bream, common spade fish, Malabar rock cod	Taiwan	Lin et al.1994, Lin 1996 cited in Ho et al. 2000
Caligus spinosus	Japanese amberjack	Japan	Fujita et al. 1968
	(*Seriola quinqueradiata*)		Izawa 1969, Ogawa and Yokoyama 1998, Pironet and Jones 2000
Caligus sp.	dhufish (*Glaucosoma hebraicum*)	Australia	Leong and Wong 1986
Caligus sp.	black sea bass (*Lates calcarifer*)	Malaysia	Leong and Wong 1988
Caligus sp.	brown-marbled grouper (*Epinephelus fuscoguttatus*)	Indonesia	
	humpback grouper (*Cromileptes altivelis*), leopard coral grouper (*Plectropomus leopardus*), Malibar grouper (*Epinephelus malabaricus*), orange-spotted grouper (*Epinephelus coioides*)	Malaysia	Koesharyani et al. 1999
Caligus sp.	haddock (*Melanogrammus aeglefinus*)	Atlantic Coast, Canada	Stewart Johnson, unpubl. data
Caligus sp.	greater amberjack (*Seriola dumerili*)	Japan	Ogawa and Yokoyama 1998
Caligus teres	sea trout, coho salmon	Chile	Reyes and Bravo 1983, Carvajal et al. 1998, Boxshall and Bravo 2000
Lepeophtheirus atypicus	rabbit fish (*Siganus fuscescens*)	Taiwan	Lin et al. 1996
Lepeophtheirus cuneifer	rainbow trout, Atlantic salmon	Pacific coast of Canada	Johnson and Albright 1991c
Lepeophtheirus hippoglossi	Atlantic halibut (*Hippoglossus hippoglossus*)	Atlantic coast, Canada	Stewart Johnson, unpubl. data
Lepeophtheirus longiventris	spotted halibut (*Verasper variegatus*)	Japan	Ho 2000
Lepeophtheirus paralichthydis	olive flounder (*Paralichthys olivaceus*)	Japan	Ho 2000
Lepeophtheirus salmonis	Atlantic salmon, chinook salmon (*Oncorhynchus*)	Pacific and Atlantic coasts, Canada	Brandal and Egidius 1979, Wootten et al. 1982

Table 2. (Cont.)

Species	Hosts	Geographical location	References
	tshawytscha) coho salmon rainbow trout	Northwest and northeast coasts of the US Faroes Japan Norway Scotland Ireland	Hogans and Trudeau 1989a Tully 1989 Nagasawa and Sakamoto 1993 Shaw and Opitz 1993 Urawa et al. 1998 Pike and Wadsworth 1999 (and references within) Ho et al. 2001
Lepeophtheirus sp.	brown-marbled grouper humpback grouper leopard coral grouper Malibar grouper Orange-spotted grouper	Indonesia	Koesharyani et al 1999
Lepeophtheirus sp.	sea trout		Boxshall and Bravo 2000
Parapetalus occidentalis	cobia (*Rachycentron canadum*)	Taiwan	Ho and Lin 2001
Pseudocaligus apodus	grey mullet	Israel	Paperna 1975
Pseudocaligus fugu	tiger puffer (*Takifugu rubripes*)	Japan	Ogawa and Inouye 1997
Unidentified Caligoida	red sea bream	Japan	Ogawa and Yokoyama 1998
Unidentified Caligid or Pennellid	red sea bream	Japan	Ogawa and Yokoyama 1998 Yamashita 1980
Family Ergasilidae *Diergasilus kasaharai*	Borneo mullet (*Liza macrolepis*) milkfish tilapia (*Oreochromis* sp.)	Taiwan	Lin and Ho 1998
Ergasilus australiensis	yellowfin bream (*Acanthopagrus australis*)	Australia	Roubal 1995
Ergasilus	greasy grouper	Malaysia	Leong and Wong
borneoensis	(*Epinephelus malabaricus*)		1988
Ergasilus ceylonensis	Asian cichlid (*Etroplus suratensis*)	Sri Lanka	Wijeyaratne and Gunawardene 1988
Ergasilus labracis	Atlantic salmon	Atlantic Coast, Canada	Hogans 1989 O'Halloran et al. 1992
Ergasilus lizae	grey mullet carp (*Cyprinus* sp.)	Eastern Mediterranean	Paperna 1975
Ergasilus lobus	Malabar reef-cod	Taiwan	Lin and Ho 1998
Ergasilus sp.	southern flounder (*Paralichthys lethostigma*)	United States	Benetti et al. 2001
Psuedoergasilus zacconis	ayu (*Plecoglossus altivelis altivelis*)	Japan	Nakajima and Egusa 1973
Other Families *Alella macrotrachelus*	black sea bream yellowfin bream	Japan Australia	Muroga et al. 1981 Ueki and Sugiyama 1978 Roubal 1995
Alella sp.	Korean rockfish (*Sebastes schlegeli*)	South Korea	Choi et al. 1997
Bomolochus stocki	yellowfin bream	Australia	Roubal 1995
Clavella adunca	Atlantic cod	Norway	Karlsbakk et al. 2001
Lernanthropus atrox	yellowfin bream	Australia	Roubal 1995
Lernanthropus chrysophrys	yellowfin bream	Australia	Roubal 1995
Lernanthropus lappaceus	Sobiaty sea bream (listed as *Acanthopagras cuvieri*)	Kuwait	Tareen 1986
Colobomatus labrachis	European sea bass	Atlantic coast, France	Paperna and Baudin Laurencin 1979
Eobrachiella elegans seiolae	yellowtail amberjack	Japan	Ogawa and Yokoyama 1998
Hemobaphes disphaerocephalus	Atlantic salmon	Pacific coast, Canada	Kent et al. 1997
Holobomolochus confusus	Atlantic cod	Norway	Karlsbakk et al. 2001
Neobrachiella fugu	tiger puffer	Japan	Ogawa and Inouye 1997 Ogawa and Yokoyama 1998

sea lice on farmed salmonids have been identified (reviewed in Costello 1993, Pike and Wadsworth 1999, Rae 2002). These factors and husbandry practices have been used to develop management strategies for sea lice on farmed salmonids. Although empirically it would seem that these factors and husbandry practices should have an impact on sea lice abundance, this has not always been demonstrated experimentally or by analysis of sea lice abundance from the field. Revie et al. (2002) used sea lice counts from 35 Scottish farms collected from 1996 to 2000 to investigate factors affecting sea lice abundance. Analysis of the data revealed large differences between years in sea lice infestation parameters. Stock type, geographical region, level of coastal exposure, and water temperature did not appear to affect mean levels of abundance. However, treatments did have a pronounced effect on sea lice infection parameters. It is likely for any given farm site that a different suite of environmental and biological factors and husbandry practices will affect sea lice abundance, and that generalizations across sites are at present impossible to make. Regardless, knowledge of these factors and husbandry practices is important, as they are likely to also influence the abundance of other parasitic copepod species on non-salmonid finfish. A very brief overview of these factors and husbandry practices follows.

Environmental and Engineering Factors

Proper site selection and design of rearing structures can reduce the number of infectious stages that are transported to and/or retained within the rearing environment, as well as ensuring that fish stocks remain healthy and thereby more resistant to infection. Factors such as water depth, tidal range, patterns of water circulation, flow rate, temperature, and salinity have been suggested as important factors with respect to sea lice infection of salmonids (reviewed in Pike and Wadsworth 1999). As mentioned previously, Revie et al. (2002) were unable to demonstrate a relationship between *L. salmonis* abundance and stock type, geographical region, level of coastal exposure, or water temperature. However in Chile, salmonid culture sites that are located in closed bays and shallow waters are generally reported to have higher levels of *Caligus* spp. infection than those seen at sites in more open waters (Sandra Bravo, pers. comm.).

In Chile, sea lice are absent or present in only very low numbers on salmonids reared in brackish and estuarine waters. Under these conditions, sea lice are reported to have little effect on fish health and condition (Sandra Bravo, pers. comm.). Tucker et al. (2000) reported that *L. salmonis* had a higher growth rate and rate of settlement at a salinity of 34 ppt when compared to 24 ppt.

Temperature is the most important environmental factor controlling the development times of parasitic copepods and the rate at which their population size increases in the absence of treatments. With respect to *L. salmonis*, a great deal of effort has gone into determining the effects of temperature on growth, egg production, and larval settlement. Growth rates, egg production, survival, and recruitment are reported to be higher at higher water temperatures (Wootten et al. 1982, Hogans and Trudeau 1989a b, Tully 1989, Johnson and Albright 1991b, Tully and Whelan 1993, Boxaspen 1997, Wadsworth 1998, Pike and Wadsworth 1999 and additional references therein, Tucker et al. 2000). These data have been used in the development of management and treatment strategies for *L. salmonis*. For other species of parasitic copepods, the development of effective management and treatment strategies will require as a minimum, a good knowledge of development times over the range of temperatures experienced in the culture system. This is especially true for treatments that are not effective against all of the life history stages.

Husbandry Practices

Modification of husbandry practices can be a very effective method to reduce the magnitude of infection by parasitic copepods (Costello 1993, Pike and Wadsworth 1999). Using husbandry practices to control parasitic copepod abundance requires a good knowledge of parasite biology (e.g., growth rates, duration of survival of infectious stages off-host, etc.) and host range. As with other infectious diseases, any management activities (e.g., stocking density, water quality management, etc.) that reduce stress and maintain optimal fish health are likely to reduce the impact of parasitic copepods. It is well recognized that poorly smolted or otherwise unhealthy salmonids are more susceptible to infection by *L. salmonis* (cf. Grimnes and Jakobsen 1996, Finstad et al. 2000). In pond culture, overcrowding and poor water quality have been cited as factors responsible for the development of parasitic copepod diseases (Singhal et al. 1986, Tareen 1986).

Year-class separation is a very effective tech-

nique that can substantially reduce the infection rate of newly introduced juveniles. This technique has been successfully used in the salmon culture industry in Scotland, Norway, and Ireland (Grant and Treasurer 1993, Boxaspen 1997, Jackson et al. 1997, Rae 2002). Fallowing of sites prior to restocking can reduce subsequent infection rates, providing that the fallow period is long enough to ensure that all infectious stages have died due to a lack of hosts (Bron et al. 1993, Grant and Treasurer 1993, Rae 2002). The effectiveness of these husbandry techniques depends on the absence of wild hosts and/or other infected sites that are within transport distance for the infectious stages.

In situations where year-class separation and/or fallowing is not possible, treatment of fish on site prior to restocking will often reduce the rate of infection on newly introduced fish. When wild caught juveniles or broodstock are used in culture, administration of a treatment for parasitic copepods at the time of introduction to the rearing system will likely reduce the rate of parasite population increase. Ho et al. (2001) reported that wild yellowtail juveniles used as seeds for culture are sometimes infected with *C. spinosus* or *C. lalandei*. In Atlantic Canada, parasitic copepods present on wild Atlantic halibut and haddock broodstock at capture have caused problems in broodstock holding facilities (Stewart Johnson, unpubl. observ.). These problems were resolved by treatment and increasing the flushing rates of broodstock tanks.

Frequent cleaning of nets or other techniques that improve water flow through the rearing habitat may result in lower rates of infection, due to improved fish health and removal of infectious stages off-site. Net fouling has been demonstrated to result in the retention of high numbers of *L. salmonis* naupliar and copepodid stages within net pens (Costelloe et al. 1996). Increased flushing rates of a land based salmonid growout facility reduced the level of infection of rainbow trout by *Lepeophtheirus cuneifer* in British Columbia (Stewart Johnson, unpubl. observ.).

Biological Factors

It is well recognized that both wild and cultured fish have the potential to serve as reservoirs of infection for sea lice and other parasitic copepods (Paperna 1975, Carvajal et al. 1998, Ho and Nagasawa 2001). When selecting sites for aquaculture, the presence of wild hosts within the water source or within the local environment, as well as the distance and direction (with respect to water movements) of other aquaculture sites should be noted. Consideration of these factors will assist in the selection of sites with reduced rates of infection and/or sites that will have lower impacts with respect to parasitic copepod transfer from cultured to wild hosts. Parasitic copepods with relatively narrow host ranges, such as *L. salmonis*, can be easier to control, especially where there are few wild hosts present. Species with broad host ranges and/or abundant wild hosts in the vicinity of aquaculture sites are generally considerably more difficult to control. This has been well demonstrated in Chile where *Caligus* species that transfer from wild non salmonid hosts cause serious and chronic disease problems in salmonid aquaculture (Reyes and Bravo 1983a b, Carvajal et al. 1998, González et al. 2000).

SEA LICE AS VECTORS OF OTHER DISEASES

Due to their feeding activities on host mucous, tissue, and blood, it has been suggested that parasitic copepods may serve as vectors of viral and bacterial diseases of fish (Nylund et al. 1991 1993). The sea louse, *L. salmonis* has been demonstrated in the laboratory to be able to function as a vector for the viral agent responsible for infectious salmon anemia (ISA), especially during epidemic and endemic phases (Nylund et al. 1993 1994). Although not implicated in the transfer of the bacterium, *Aeromonas salmonicida*, the causative agent of furunculosis, it has been isolated from the surface of *L. salmonis* (Nesse 1992 cited in Nylund et al. 1993). More recently the virus responsible for infectious pancreatic necrosis has also been isolated from *L. salmonis* (Jim Treasurer, unpubl. data). Although there is no evidence from field studies that *L. salmonis* acts as vectors for diseases, as a precautionary measure, sea lice control has been adopted as an integral part of management strategies for the control of ISA in Atlantic Canada and Scotland.

CONCLUSIONS

In summary, parasitic copepods, especially sea lice, are economically important parasites in marine aquaculture. In salmonid culture, disease outbreaks and subsequent mortalities caused by sea lice are now rare due to the development of a

variety of effective treatments. However, large economic losses still occur as the result of reduced feed conversion and growth, indirect mortality, loss of product value, and treatment costs. Although it is well understood that parasitic copepods have a major impact on non salmonid aquaculture, there are relatively few published reports of disease and/or disease treatments. There are no reports of economic costs associated with these infections. Husbandry practices as well as a variety of engineering, environmental, and biological factors can have an impact on the level of infection by parasitic copepods. However, the relative importance of these factors in controlling copepod abundance varies between sites. There is no evidence from field studies to support the suggestion that parasitic copepods such as sea lice can act as vectors for fish diseases.

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