

Importance of Copepoda in Freshwater Aquaculture

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Wojciech Piasecki, Andrew E. Goodwin, Jorge C. Eiras, Barbara F. Nowak (2004) Importance of copepoda in freshwater aquaculture. Zoological Studies 43(2): 193-205. In recent decades, aquaculture has become an increasingly important part of the world economy. Other than marketing concerns, the biggest challenge facing fish farmers is to control the many complex abiotic and biotic factors that influence the success of fish rearing. An example of the complexity involved in managing aquatic systems is the need to control copepod populations by manipulating the pond environment. Copepods play major roles in pond ecosystems, serving as 1) food for small fish, 2) micropredators of fish and other organisms, 3) fish parasites, 4) intermediate hosts of fish parasites, and 5) hosts and vectors of human diseases. Planktonic animals, especially rotifers, cladocerans, and copepods of the order Cyclopoida are the most important food items in freshwater aquaculture, and copepod nauplii are especially valuable for feeding fry. Copepods used as natural food are either cultured or collected from natural water bodies. Adult and advanced copepodid stages of cyclopoids are micropredators that target early life stages of cyprinids (Cyprinidae). Other copepods in aquaculture are fish parasites. The most common adult copepod parasites of freshwater fishes are Lernaea cyprinacea, Ergasilus sieboldi (and related species), Salmincola californiensis, S. edwardsii, Achtheres percarum, Tracheliastes maculatus, and Caligus lacustris. In addition, copepodids of Lernaea and chalimus larvae of Achtheres and Salmincola attach to gill filaments and cause epithelial hyperplasia and may be indirectly responsible for fish-kills. Copepods are also intermediate hosts for important fish parasites, including tapeworms and nematodes. Damage from these parasites may lead to fish mortalities or reduce the market value of the fish products. Finally, copepods serve as intermediate hosts for parasites that infect humans and can serve as vectors of serious human diseases like cholera. http://www.sinica.edu.tw/zool/zoolstud/43.2/193.pdf

Key words: Copepoda, Aquaculture, Parasite, Host, Micropredator.

Overexploitation of wild fish populations has greatly increased the importance of aquaculture as a source of fish protein. In both intensive and extensive fish culture systems, relationships between fishes and crustaceans representing the subphylum Copepoda must be controlled to maximize fish production. In aquaculture, copepods serve as 1) food for small fish, 2) micropredators

of fish and of other organisms, 3) fish parasites, 4) intermediate hosts of fish parasites, and 5) hosts and vectors of human diseases. In this review, we present an overview of these complex relationships, give examples of interesting cases, and where possible, suggest solutions to copepod challenges.

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Food for small fish

Freshwater finfish seed production often faces a problem of an adequate food supply. Artificial feeds are widely used, but planktonic animals are very important, especially rotifers, cladocerans, and copepods. Virtually all fish feed on plankton, especially in their early life phases. Planktivorous fish depend on small invertebrates throughout their entire lives. Copepods of the order Cyclopoida are the most important food items in freshwater aquaculture, and their nauplii are especially valuable for feeding fry (Szlauer and Szlauer 1980). Copepods as natural food are either cultured or collected from the wild.

Free-living copepods, and zooplankton in general, may be harvested from the wild. Zooplankton may be collected from specific depths in lakes using a custom-made mechanical device (Szlauer et al. 1978) that operates by propelling water through a huge plankton net using an outboard boat engine. Sendłak (1980) surveyed the possibilities of acquiring different planktonic animals, mainly cladocerans and copepods, from lńsko Lake, Poland. According to his studies, annual lake productivity in Poland ranged from 6.25 to 62 g m⁻³ of water (possibly even 90 g m⁻³ in eutrophic lakes). The second major method of acquiring copepods relies on harvesting plankton from small rivers flowing from lakes. Such outlet rivers contain large amounts of zooplankton. The diel and annual plankton flow from Płoń Lake, Poland by the River Płonia has been estimated to be 372 and 135 000 kg, respectively, while the same river removed 65.0 and 25 251 kg, respectively, from Miedwie Lake, Poland (Szlauer 1976, 1977, 1983/84). In Central Europe, several attempts have been made to actually use copepods and other components of zooplankton for feeding fish in aquaculture (Anwand 1978, Szlauer and Szlauer 1980 1982). The results were promising, but better infrastructure and funding are needed.

Copepods can also be cultured to supply food for fish. Culture methods for marine copepods are well advanced (Ogle 1979, Ohno and Okamura 1988, Payne and Rippingale 2001), but relatively few attempts have been made to culture freshwater species. One example may be a method of mass culture of *Paracyclops fimbriatus* developed recently by Szlauer (1995) using observations made from a mass occurrence (13 000 individuals L⁻¹) during experiments on municipal sewage sludge.

Taiwanese scientists have been successful at rearing brackish-water copepods. Prof. Shin-Hon Cheng has developed a method of culturing Apocyclops rovi on a semi-industrial scale (Cheng et al. 1999 2001). Some 20 metric tons of different brackish-water and marine copepods are exported each year from Taiwan to Japan (Dr. Masato Kubota, pers. comm.). There are very few cases of using copepods as fish feed on an industrial scale. One of the most recent examples is an American company (Argent) that is marketing a product that they claim is made of cyclopoid copepods. According to the supplier, these copepods are a "selectively bred, biologically engineered microorganism cultured in a pristine Arctic lake." These copepods are reported to contain the highest known concentration of the fundamental and critical biological pigment, astaxanthene, accounting for their striking orange coloration. Complimenting this pigmentation are previously unknown levels of highly unsaturated fatty acids (HUFAs), and especially those of the famed 'omega-3" family. The high levels of omega-3 HUFAs are essential for aquaculture applications involving fish larvae and typically exceed 40 times those obtained from hatching the highest quality Artemia eggs. A nutritional report on their commercial product, Cyclopeeze, is available on the web site: http://www.argent-labs.com/argentwebsite /cyclopeeze.htm. A number of companies offer dried copepods as food for aquarium fishes; for example, Sera Products from the UK sells FD-Cyclops.

Micropredators of fish and of other fish food items

Some cyclopoids are micropredators of fish larvae, and especially vulnerable are the early stages of cyprinids (e.g., carp) due to the small size of the young fish. Fish larvae are attacked by adult copepods (e.g., Acanthocyclops robustus) and by more-advanced copepodid stages. The results are serious lesions of the fins, blood vessels, volk sac, head, nares, and particularly the gills (Fabian 1960, Zuromska 1967a b, Lillelund 1967; Kabata 1970, Fritzsche and Taege 1979, Hartig et al. 1982, Schäperclaus 1992, Mamcarz 1990). Piasecki (2000) documented the process of predation and its results on fish larvae, noting that mortality rates depend on the cyclopoid density and on the availability of alternative food (e.g., rotifers) for copepods. If copepods have enough rotifers to feed on, they tend not to harm fish larvae. The most frequent fish attackers were mature males (33%), copepodids IV (29%), and copepodids V (22%). Females usually fed upon the already killed larvae (Piasecki 2000).

The State of Arkansas in the US produces a lot of cyprinids and hybrid striped bass. These species are stocked in ponds as small fry and are very vulnerable to attack by cyclopoids. Farmers use several strategies to avoid this problem. The first is to time the filling of the pond and fertilization so that the fry can be stocked prior to the development of large copepod populations. Another strategy is to use Dylox (trichlorfon) to kill predatory copepods just prior to fish stocking. However, some copepod micropredators may be beneficial to fishes in that they consume copepod fish parasites. Kasahara (1962) observed that some freeliving copepods such as Mesocyclops sp. prey on free-swimming larvae of Lernaea sp. Some freeliving copepods are also enemies of mosquito larvae and can reduce numbers of these insects in aquaculture waters (Marten et al. 1994).

Fish parasites

The cyclopoid family Lernaeidae is represented by freshwater parasites that are highly adapted to a parasitic way of life. The majority of lernaeids have undergone extensive morphological adaptations hiding their close affinity with their freshwater cousins of the genus Cyclops. Fish parasites within this family belong to 14 valid genera (Ho 1998) with 180 nominal species (The World of Copepods 2002) and about 110 valid species (Ho 1998). Representatives of the genus Lernaea have been studied more intensively than any other freshwater copepod group due to its economic importance. Lernaeids are probably the best known copepod parasites, and examples appear in most invertebrate zoology textbooks. There are 105 nominal Lernaea species (The World of Copepods 2002) of which only about 37 are valid (Kabata 1979). Poddubnaja (1973) complicated understanding of the species concept of lernaeids by producing different phenotypes, resembling different described species of Lernaea from a single maternal specimen. Lernaea species occur on all continents, with the majority in Africa. The only cosmopolitan species is Lernaea cyprinacea, which can infect a variety of freshwater fishes. Originally, L. cyprinacea was not present in South America and Australia, but it was accidentally introduced there with cyprinids.

Female Lernaea are highly metamorphosed

vermiform ectoparasites (not mesoparasites) without segmentation that reach lengths of 12-16 mm (plus an additional 6 mm of egg sacs). The head, equipped with "antlers" that anchor the parasite in the subdermal tissues of a host fish, earned the parasite its vernacular name of "anchor worm". The rest of the body and egg sacs protrude into the water. This particular way of attachment is very pathogenic by its nature (Dzidziul 1973, Khalifah and Post 1976, Kabata 1985, Shariff and Roberts 1989). Initially the skin and muscles adjacent to the head become hyperemic, swollen, and susceptible to secondary infections. The parasite's attachment evokes severe acute inflammation. The host's connective tissue reacts to the parasite, forming a thick fibrotic capsule around the anchor. Lernaea spp. can cause severe fin damage. Wounds caused by the parasite's implantation occasionally develop into fistulae, penetrating the visceral cavity, including the heart and sometimes resulting in peritonitis and death (Kabata 1985). Considering the invasive method of attachment and severity of the associated damage, it is surprising that Lernaea-induced fish kills are not common (Shariff and Roberts 1989).

Feeding and the gut structure of Lernaea were described by Sabatini et al. (1988). The life cycle comprises 3 nauplius stages, 5 copepodid stages, and adults (Grabda 1963a). Copepodids settle on fish, mature, and copulate; and then males die and females undergo transformation while attached permanently to the host. Lernaea spp. are warm-water parasites, and according to Schäperclaus (1979) in some areas of the United States, no fewer than 10 generations can appear in the course of a year. The history of fish mortalities caused by Lernaea spp. goes back to 1880, when in one of the lakes of the Masurian Lake District (presently in Poland), lernaeosis almost wiped out an entire population of the crucian carp (Benecke, cited by Kocyłowski and Miączyński 1960). According to Kocyłowski and Miączyński (1960) a mass mortality of crucian carp was also reported by Kozikowska in Karasiowe Lake, Poland and by Grabda in Wilczak Hatchery, Poland. The copepod intensities reached 40 parasites per fish. An interesting account of site selection by adult L. cyprinacea was published by Dorovskikh (1996). In recent years, the numbers of Lernaea have drastically declined in Central Europe. In Poland, there has been no published record of Lernaea within the last 30 years although more than 280 papers dealing with fish parasites were published during that period (Piasecki and Woliński, unpubl. data).

In North America, Lernaea spp. infect a number of cultured freshwater fishes. In summer. in waters with temperatures ranging from 25 to 28 °C, this parasite finds excellent conditions for reproduction utilizing a number of fish cultured for food and ornamental purposes. An interesting case of unusual fish mortality caused by L. cyprinacea was published by Goodwin (1999). During June and July of 1998, at least 3 Arkansas fish farms polyculturing bighead carp (Hypophthalmichthys nobilis) with channel catfish (Ictalurus punctatus) suffered major losses of channel catfish associated with massive infections by L. cyprinacea. The catfish had few adult Lernaea attached to their skin, but there were from 8-50 copepodids on the surface of each catfish gill filament (Figs. 1, 2). The copepodids were grazing on the gill tissue, and their feeding activity was associated with gill

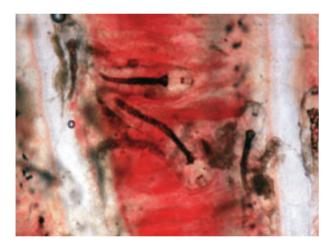


Fig. 1. Copepodids of *Lernaea* sp. on the gills of a catfish (Goodwin unpubl. photo).

damage including epithelial hyperplasia, telangiectasis, and hemorrhage. Catfish skin was also covered by copepodids (Fig. 3). Bighead carp in the same ponds were reported to have had numerous adult copepods on their skin but did not die during the epizootic. It is possible that the filter-feeding apparatus of the carp captured the copepodids thus preventing heavy infection of the gill filaments (Goodwin 1999). Lernaea copepodids have not been implicated previously in fish losses resulting from parasite damage to gills. The loss of catfish in these cases is likely to have been due to their being polycultured with the bighead carp, a species that is a common host for adult lernaeids. There is no treatment for Lernaea infections that is legal for use with food fish. Most farmers have guit polyculturing these 2 fish species.

Lernaeids also cause problems for small baitfish and ornamental fish species. Arkansas produces millions of dollars worth of minnows each year. These fish are marketed when they are only 5 cm long. Lernaeid infections are common, and a single parasite in a critical location is enough to kill a minnow. In goldfish and koi, lernaeids cause some mild infections, but disfigure the fish making them unsuitable for sale. The primary method for control of this species in non-food fish is the pesticide Dimilin (diflubenzuron).

Lernaea cyprinacea was introduced into South America in the beginning of the 20th century via the importation of the common carp, *Cyprinus carpio*. Since then, the copepod has spread very quickly, is now a common parasite infecting all farmed species in Brazil, and is also very common in wild fish in all main drainage basins throughout the country. Gabrielli and Orsi (2000) studied 8



Fig. 2. Copepodids of *Lernaea* sp. on the gills of a catfish (Goodwin unpubl. photo).



Fig. 3. Copepodids of *Lernaea* sp. on the skin of a catfish (Goodwin unpubl. photo).

fish species on 53 fish farms of the State of Parana for the presence of lernaeids. All fish species were infected, but 100% prevalence was found only in C. carpio, Leporinus macrocephalus, and Prochilodus lineatus. Wild fishes in rivers were infected at low intensities. In Brazil, lernaeids cause mortality in several species of farmed fish. Another issue is the presence of parasites in a growing number of "fish-and-pay" enterprises. At fish-and-pay facilities, anglers pay for the privilege of fishing in well-stocked ponds (usually earthen ponds). The demand for this kind of leisure activity has led to the construction of thousands of fishand-pay sites in Brazil. The presence of fish parasites, especially lernaeids in fish-and-pay ponds, and the uncontrolled movement of fish throughout the country pose serious health threats to the fish farm industry (Pavanelli et al. 2000). Lernaea cyprinacea has also been recorded on cultured fishes on Caribbean islands (Fajer et al. 1985).

Another area relatively recently conquered by lernaeids is Australia (Hall 1983, Rowland and Ingram 1991, Langdon 1992). Heavy infections with Lernaea sp. resulted in mortality of golden perch (Macquaria ambiqua), Murray cod (Maccullochella peeli), and silver perch (Bidyanus bidyanus) broodstock held in ponds (Callinan 1988). In Oct. 1978, there was a heavy infection of Lernaea sp. on Murray cod broodfish in 2 ponds at a research station following the use of common carp as a forage fish. Replacement of carp by goldfish (Carassius auratus) as a forage fish seemed to stop the problem (Rowland and Ingram 1991). This suggests that carp is an important host to Lernaea sp. and may be responsible for the spread and increased prevalence of infections in native fish (including those cultured in ponds) (Rowland and Ingram 1991). Carp were introduced to Australia more than a century ago and have since reached such a substantial biomass that they are considered a pest not unlike rabbits are on land. Carp are blamed for spreading, not only lernaeids, but also the pathogenic tapeworm, Bothriocephalus sp., and other disease agents. A recent survey in New South Wales showed that the incidence of externally visible abnormalities of fish was correlated with the density of carp (http://www.asl.org.au/asl poldoc carp.htm).

In Africa, rapid increases in *Lernaea* burdens have been observed in association with growing environmental stress in some areas. High prevalences of "anchor worm" were recorded by Oldewage (1993) in tilapia of Lake Victoria.

The 2nd major branch of freshwater cyclo-

poids parasitic on fishes is represented by the genus *Lamproglena* spp. These copepods typically are gill dwellers, and as such they have the potential to cause fish losses in aquaculture. *Lamproglena* comprises more than 40 nominal species (Piasecki 1993a). They occur in Africa (Marx and Avenant-Oldewage 1996, Ibraheem and Izawa 2000), Asia (Kuang and Qian 1985, Kumari et al. 1989), and Europe (Cakić et al. 1998, Galli et al. 2001). To date, no fish kills caused by *Lamproglena* spp. have been reported.

The family Ergasilidae (Poecilostomatoida) comprises 24 valid genera (Amado et al. 1995) with 249 nominal species (The World of Copepods 2002). The overwhelming majority of species occurs in freshwater environments. The morphology of ergasilids largely resembles that of free-living cyclopoids, but some may be extensively transformed, e.g., *Mugilicola*. The best known ergasilids are representatives of the genus Ergasilus, which contains 153 nominal species (The World of Copepods 2002) and more than 80 valid species (Kabata 1985). The best known species is Ergasilus sieboldi, which is 1.7 mm long and attaches to fish gills using its 2nd antennae. The antennae, transformed into powerful hooks, hold the gill filaments tightly and can cause tissue damage and obstruct blood flow. Parasites feeding on epithelial cells stimulate hypertrophy and consequently a coalescence of secondary gill lamellae. This in turn drastically reduces the surface available for gas exchange. Lesions on gills are often attacked by secondary pathogens such as bacteria and fungi. Feeding of E. sieboldi was described in detail by Einszporn (1965a b). This particular species attaches to the outside of the gill allowing some of its congeners to explore the space between the gill filaments. In cases of extremely heavy infections of whitefish, the parasite attaches not only to gill filaments but also to the fins (Kozikowska 1975). The life cycle comprises 6 nauplius stages, 5 copepodid stages, and adults. Males die after copulation, while females remained attached to the fish host (Abdelhalim et al. 1991).

In Central Europe, the 1st spring generation of *E. sieboldi* becomes sexually mature in mid-June. Their eggs hatch and the copepodids attack fish. They mature and produce a 2nd generation in September. Sometimes a 3rd generation follows by the end of the season. One female can produce 200 offsprings. Theoretically, the ensuing 2nd generation can comprise 40 000 descendants and in the 3rd, as many as 8 million (Schäperclaus 1992). *Ergasilus sieboldi* is not host-specific and can infect a majority of freshwater fishes; however the tench, *Tinca tinca*, appears to be the most susceptible. This fact is attributed to the sluggishness of this fish, which may make it more vulnerable to copepod attack. Other less-infected fishes include pike (*Esox lucius*), bream (*Abramis brama*), white-fish (*Coregonus lavaretus*), vendace (*Coregonus albula*), carp (*Cyprinus carpio*), and roach (*Rutilus rutilus*).

Schäperclaus (1954) described a case of a single, 36-cm-long tench that harbored some 3600 specimens of E. sieboldi on its gills. This heavily infected fish had a condition factor of only 0.88. Similarly, intensive infection of peled (Coregonus peled) was reported by Abrosov and Bauer (1959 1961) from Pskov Lake, Russia. Heinemann (1934) found 5431 specimens of E. sieboldi on a single tench that died of asphyxia. Severe infection with E. sieboldi can result in heavy losses in the yield of tench. In Lake Scharmuzel, Germany, the yield of tench dropped from 5000 kg before the appearance of E. sieboldi to 350 kg after its unwanted introduction. In 2 other small German lakes, the yield of tench dropped from 31-47 to 16.5 kg ha-1 after the invasion of this parasite and with copepod prevalences of only 50%. In Lake Grimiz, Germany, the yield of tench between 1926 and 1931 declined from 4583 to 111 kg (Schäperclaus 1992), again a reduction apparently related to Ergasilus infections.

The 2nd most common host of *E. sieboldi* is the pike. Pike deaths attributed to *E. sieboldi* infections were described from 2 Pomeranian lakes in Germany by Lehmann (1924) and Rumphorst (1924). Deaths of whitefish (*Coregonus wartmanni*) in Zugersee, Germany were described by Baumann (1913). A very extensive account on aspects of *E. sieboldi* occurrence in different hosts was published by Grabda (1963b). *Ergasilus sieboldi* causes mass fish-kills not only of tench but also of perch, *Perca fluviatilis* in Włodawa Lake, Poland (Kocyłowski 1954), whitefish in Cugersk Lake in the USSR, and bream in a number of lakes (Markevič 1956).

In Southeast Asia, *Ergasilus* sp. occurs on the gills of cultured fishes including *Osteophilus hasselti*, *O. gouramy* (in Indonesia), *Ctenopharyngodon idella* (in Malaysia), and on *Oxyelotris marmoratus* (in Thailand). The parasite has the potential to adversely affect aquaculture in this region, but so far, no major outbreak attributed to *Ergasilus* sp. has been reported. (Kabata 1985). Another ergasilid, *Sinergasilus major*, may have impor-

tance in Central Asian aquaculture, including the former Soviet republics and China regarding the host *Ctenopharyngodon idella* (cf. Bauer and Babaev 1964). *Sinergasilus lieni* is another important parasite, affecting *Hypophthalmichthys molitrix* (cf. Musselius 1973). In Japan, Nakajima and Egusa (1973) found *Pseudoergasilus zacconis* on gills of cultured ayu, *Plecoglossus altivelis*. In spite of this record, Egusa (1992) saw no serious threat by ergasilids to Japanese freshwater aquaculture.

Traditional treatment of ergasilosis included the use of organophosphate compounds, pesticides, or a mixture of copper sulfate and ferric sulfate. It has been observed that well-developed aquatic vegetation helps reduce infection levels. It apparently limits movements of small bream that otherwise spread this parasite all over the lake (Schäperclaus 1992).

Another important group of freshwater parasites is the family Lernaeopodidae (Siphonostomatoida). The freshwater branch of this family is represented by the 7 genera of Salmincola, Achtheres, Coregonicola, Basanistes, Tracheliastes, Pseudotracheliastes, and Cauloxenus (cf. Kabata 1979). This group is characterized by their relatively large size, comparable to that of Lernaea. Their lernaeopodid attachment mechanism is unique, however, and seems to inflict less damage than that associated with Lernaea or Ergasilus spp. The body of a lernaeopodid female can be divided into 3 major parts: the large genital trunk (responsible for reproduction), the elongate and movable cephalothorax surmounted with mouth appendages, and finally a pair of more or less powerful "arms", which are transformed 2nd maxillae. The maxillae are fused to a mushroomshaped anchoring structure known as a bulla. The bulla, a product of the frontal gland, is attached to the host. From an aquaculture perspective, the most important lernaeopodid genus is Salmincola with 16 valid species (Kabata 1969). The vernacular name for Salmincola spp. is the gill maggot, and the genus has a circumpolar distribution in the northern hemisphere. Gill maggots may occur in high intensities and create serious problems for fish kept at high densities in cages and other aquaculture facilities (Kabata 1970, Vaughan and Coble 1975, Kabata and Cousens 1977, Sutherland and Wittrock 1985). In natural fish populations, the prevalence and intensity of infection are usually low and have little impact on fish (Black 1982, Black et al. 1983, Bowen and Stedman 1990, Amundsen et al. 1997). The life cycle of the gill

maggot, *S. californiensis*, was described by Kabata and Cousens (1973). It consists of 6 stages: the copepodid (free-swimming infective stage), 4 chalimus stages (which attach to a host by the frontal filament), and adults (the adult female attaches to a host by a bulla, while the male remains mobile).

The best known species of gill maggot is S. californiensis. It was originally confined to salmonid fishes of the genus Oncorhynchus in streams emptying into the northern Pacific Ocean, but has recently moved eastwards in the US, e.g., to Missouri and Arkansas (Hoffman 1984) and subsequently to Iowa, New Jersey, and West Virginia (Sutherland and Wittrock 1985). Sutherland and Wittrock (1985) reported the parasite from an aquaculture site in lowa, stating a prevalence of 83% and a mean intensity of 4.6 female copepods. Infections were associated with hyperplasia of gill filaments caused by female copepods and atrophy or growth inhibition of affected gill filaments. The above authors also noticed a harmful effect of chalimus larvae, such as hyperplasia and sometimes fusion of the basal elements of adjacent gill filaments. Gall et al. (1972) found evidence of the influence of S. californiensis on the reproductive performance of a domesticated strain of rainbow trout. Johnson and Heindel (2001) reported problems with high numbers of S. californiensis in broodfish of chinook salmon, O. tshawytscha, and they described a method for their manual removal.

Another significant species from the same genus is *Salmincola edwardsii*, a parasite specific to Arctic charr, *Salvelinus alpinus*, and brook trout, *Salvelinus fontinalis*. This parasite inflicted health problems in fishes cultured in Quebec and New Brunswick, Canada (Parissa Irani-Bunin, pers. comm.). *Salmincola salmoneus* is specific for Atlantic salmon, *Salmo salar*. Heavy infestations with this parasite of salmon broodstock kept in hatcheries in the Maritime Provinces of Canada were reported by McGladdery and Johnston (1988).

Salmincola carpionis was reported from central Japan infecting cultured brook trout and whitespotted charr, Salvelinus leucomaenis (cf. Nagasawa et al. 1997 1998). Salmincola stellatus were recently reported in Hokkaido, Japan in the buccal cavity of cultured taimen, Hucho perryi, with intensities ranging from 10 to 50 individuals per fish (Nagasawa et al. 1994).

The closest relatives of *Salmincola* spp. are representatives of *Achtheres*. The latter genus dif-

fers from the former one in having a prominent genital process. According to Kabata (1969), there are 6 valid species of this genus. Achtheres percarum which occurs in Europe on perch (Perca fluviatilis) and zander (Sander lucioperca) can be pathogenic to fish. Because of its attachment to gill filaments, it can trigger epithelial hyperplasia, which fuses gill lamellae, and cause partial or total loss of gill filaments. Prevalences often reach 100%, and the number of Achtheres females can reach 40 per fish (Kozikowska et al. 1957). The highest observed number of all stages of the parasite in zander was 117 (Piasecki 1993b) and 81 individuals in perch (Piasecki and Wołoszyn 1991). The life cycle of A. percarum includes 7 stages: nauplius, copepodid, 4 chalimus stages, and adults (Piasecki and Kuźmińska 1996).

Basanistes huhonis is another "cousin" of Salmincola. It looks similar to Salmincola spp. but is covered with 12 prominent humps or outgrowths. It infects Danube salmon, *Hucho hucho*, and broodstock may host very high numbers of this parasite (Ivaska 1951, Witkowski and Błachuta 1980).

The least known freshwater lernaeopodid genus is *Tracheliastes* (Fig. 4), and the most-pathogenic species within this genus is *T. maculatus*. This copepod has a very slim appearance, it is slightly longer than *Lernaea*, and its bulla attaches permanently to the scales of common bream. Its presence is initially associated with focal inflammation about its feeding area, with pronounced congestion of the skin and extravasations of blood. With heavy infections, diffuse inflammation of the skin can be observed and even extensive perforation of the scales (Fig. 5) to which the parasite's

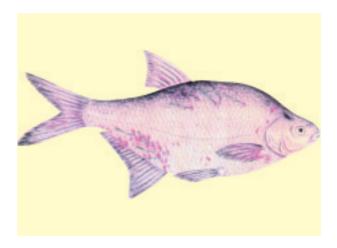


Fig. 4. Adult females of *Tracheliastes maculatus* on the skin of common bream (J. Wierzbicka unpubl. photo).

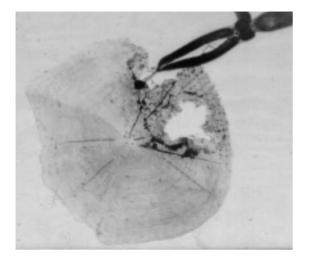


Fig. 5. Adult female of *Tracheliastes maculatus* attached to a scale. Note the scale perforation caused by the parasite (K. Wierzbicki unpubl. photo).

bullae are attached. There are 2 documented cases of extreme infection levels of this parasite on bream. The 1st was in Jamno Lake, Poland and was associated with fish mortalities. The intensity reached 56 individuals per fish (Grabda and Grabda 1958). The other mass infection occurred in Pierzchały Lake, Poland with an intensity of 61 individuals per fish (Piasecki 1991). The life cycle of *T. maculatus* consists of 7 stages: premolt nauplius, infective copepodid, 4 chalimus stages, and adults (Piasecki 1989).

Sea lice or fish lice of the family Caligidae (Siphonostomatoida), pathogenic to marine fishes cultured in cages, have only 1 freshwater representative, *Caligus lacustris*. This copepod has caused only 1 known outbreak in cultured salmonids (Rokicki 1987) but may have the potential to negatively affect freshwater aquaculture operations.

Intermediate hosts of fish parasites and vectors of fish diseases

Another unfavorable impact of copepods on aquaculture facilities is that they may serve as intermediate hosts of important fish parasites such as tapeworms or nematodes. The presence of parasites may lead to fish mortalities or adversely affect the market value of the fish or fish products when parasites are present in fish muscle. Some important human parasites utilize copepods and fishes as intermediate hosts. A number of parasitic diseases can affect humans, when an infected copepod is accidentally ingested with water.

One of the better known and the most spec-

tacular parasites are representatives of the genus Ligula. They commonly occur in Europe, Asia, and North America in temperate zones. The final hosts are piscivorous birds. The first intermediate hosts are planktonic copepods of the genera Cyclops, Eucyclops, Megacyclops, Acanthocyclops, and Eudiaptomus. The 2nd intermediate hosts for these parasites are fishes, mainly of the family Cyprinidae. This tapeworm occurs in the peritoneal cavity of fish in the form of larvae known as plerocercoids. Plerocercoids are usually between 10 cm and 1 m long (Dubinina 1966). Infection leads to cachexia, impairment of fish growth, arrested reproduction, and death (Bryliński 1972). Bream infect themselves in their 1st years of life when they feed on plankton. The infection is fatal. All large, market-size bream are those fortunate individuals which avoided infection in their early life. Once they grow up and change the planktonic copepods in their diet to benthic macrofauna, their chances of becoming infected with Ligula spp. decrease. Large plerocercoids can occur in the muscles of fishes (Jeżewski and Karbowiak 2002). In the US, liqulosis is a sporadic problem in fathead minnows, but given the small size of the host and the large size of the parasite, outbreaks can be quite severe.

Another interesting tapeworm transmitted by planktonic copepods is Triaenophorus nodulosus (or T. crassus). Its scolex is armed with 4 characteristic anchors. The final hosts are predacious fishes such as pike. The 1st intermediate hosts are copepods representing Cyclops, Eucyclops, Mesocyclops, Paracyclops, Acanthocyclops, Orthocyclops, Diaptomus, and Eudiaptomus. In the intestine of the final host, the adult tapeworms are no longer than 30 cm and are not pathogenic. However, plerocercoids occurring in fishes serving as the 2nd intermediate host can be pathogenic, settling in the liver where they become encapsulated. The presence of such plerocercoids in fish fry can lead to abdominal distension, other serious lesions, and death. Mortalities of fry associated with Triaenophorus spp. infections have been recorded at many European aquaculture facilities and lakes. In Königsee (Bauern, Germany), this parasite was a factor that strongly limited the size of the local population of Arctic charr (Shäperclaus 1992).

The Asian tapeworm, *Bothriocephalus* acheilognathi, occurs in grass carp (*Ctenoph*aryngodon idellus) and carp, not only in Asia but also in Europe and North America. This tapeworm has only 1 intermediate host, which are various species of free-living cyclopoids. Bothriocephalus acheilognathi is less than 20 cm long, and in Europe it can be pathogenic, occurring in 1-2-moold fish in high numbers (e.g., 20-40 parasites per fish). Intensities in 2-yr-old fish varied from 1 to 362 parasites per fish. Mortalities have been reported, even in older fish, especially after overwintering (Klenov and Vasil'kov 1972). The Asian tapeworm was introduced into the US more than 20 yr ago. It is a major problem in grass carp and golden shiners. Infections severe enough to cause loss of fish are rare, but there are many regulations regarding interstate transport that prohibit the movement of infected fish. The State of Utah requires that all grass carp coming into the state to be treated with the antihelmintic, praziguantel, before transport.

Other important cestodes include representatives of Proteocephalus. These species have 4 characteristic circular suckers on their scolices, and they only use cyclopoids as intermediate hosts. Proteocephalus exiguus infects coregonids, and densities of this species and its congeners may be high and can lead to local destruction of the intestinal mucosa. In the US, a closely related tapeworm, Corralobothrium sp., is commonly seen in cultured channel catfish but is of no commercial importance. The broad fish tapeworm, Diphyllobothrium sp., is potentially pathogenic to humans and can be very abundant in fishes in some areas in North America. In the area of along the border of Maine and the Province of New Brunswick, Canada (e.g., Spednic Lake) in the mid-1990s, the viscera and muscle of fishes were so heavily infected that the fish were useless for human consumption and were thus unmarketable (Piasecki unpubl. data).

The most interesting parasite in eel management in Europe has been the nematode Anguilicola crassus. This species was accidentally introduced to Western Europe in the 1970s along with imported Japanese eels, and by the end of 20th century, it managed to spread with eels to most of Europe. This nematode's only intermediate hosts are planktonic copepods. Small fish serve as paratenic hosts, and the adult nematode inhabits the swimbladder of eels. In the estuary of the Odra River (Szczecin Lagoon) in Poland, almost 70% of eels were infected (Garbacik-Wesołowska et al. 1994), and intensities can be very high. In recent years, the entire swimbladder is sometimes found to be filled with these uglylooking nematodes, and infections may affect the marketability of the eels.

Parasitic copepods are potentially capable of transmitting viruses and bacteria that cause important fish diseases. Nylund et al. (1991 1993) discussed the possibility of transmission by sea lice of the furunculosis bacterium, *Aeromonas salmonicida*, and the virus that causes infectious salmon anemia (ISA). Sea lice are considered marine copepods, but freshwater fish-lice (*Caligus lacustris*) can also become abundant in aquaculture cages (Rokicki 1987) and may be disease vectors. *Salmincola* is reported to transmit IHN virus between fishes (Mulcahy et al. 1990), but the actual transmission mechanism is unclear because *Salmincola* adult females are immobile.

Hosts and vectors of human diseases

The broad fish tapeworm, Diphyllobothrium latum, is probably one of the better-known fish parasites because humans are its final host. This parasite uses 2 intermediate hosts, the 1st a copepod, the 2nd a fish. Plerocercoids in fish muscles can be accidentally eaten by humans when the fish is consumed raw or undercooked. Many papers have described infections of people with adult broad fish tapeworms (e.g., Dick et al. 1991), but only a few represented cases where humans had become intermediate hosts for this parasite. A good example is so-called "sparganosis" recorded in some Far Eastern countries. It occurs when humans replace fish as the 2nd intermediate host of broad fish tapeworms by drinking water carrying Diphyllobothrium-laden copepods (e.g., Kim and Lee 2001).

The most important human disease linked to copepods is cholera. The association of Vibrio cholerae, the causative agent of cholera, and its copepod host has been under study for more than 25 yr. It is now well documented that V. cholerae is autochthonous to aquatic environments and closely associated with copepods. Seasonal cholera outbreaks are associated with algal blooms, which in turn provide enough food to cause rapid growth of planktonic copepods. The V. cholerae associated with copepods also rapidly reproduces. To cause disease, the number of V. cholerae 01 cells ingested must be high enough to constitute an infective dose, estimated to be 10⁴ to 10⁶ cells (Hug and Colwell 1996). The presence of copepods carrying V. cholerae at aquaculture sites in certain endemic areas can be dangerous. An open question becomes whether V. cholerae can be transferred to fishes. Other species of Vibrio such as V. anguillarum and V. ordali are specific to

fishes, and they are responsible for vibriosis, an important fish disease. A non-01 *V. cholerae* was isolated from a fish in Japan (Muroga et al. 1979), and in the early 1990s in the Ukraine, several people contracted cholera apparently from fish caught in a river polluted with municipal sewage.

Conclusions

Copepods play very important and diverse roles in freshwater aquaculture operations, including some that are beneficial and others that are extremely adverse and may result in complete production losses. Some copepod roles are obvious, for example, copepods that serve as food for small fish or copepods that are fish parasites. Others, however, are not often considered, such as copepods as micropredators of fish, their role as intermediate hosts of fish parasites, and their role as hosts and vectors of human diseases. While progress has been made in better understanding the biology of copepods in aquaculture, some areas still require further research, especially including studies of the taxonomy of different copepod species.

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REFERENCES

- Abdelhalim Al, JW Lewis, GA Boxshall. 1991. The life-cycle of *Ergasilus sieboldi* Nordmann (Copepoda: Poecilo-stomatoida), parasitic on British freshwater fish. J. Nat. Hist. **25:** 559-582.
- Abrosov VN, ON Bauer. 1959. Ergasilose des Peleds (*Coregonus peled*) in den Seen des Pskowsker Gebiets. Izv. gosud. naučno-issled. Inst. ozern. rečn. rybn. Hozâist. **49:** 213-216. (in Russian)
- Abrosov VN, ON Bauer. 1961. Die Peladmarane ein neues Object der Fischwirtschaft. Ztschr. F. Fisherei. **10:** 299-307. (in German)
- Amado MAPM, JS Ho, CEF Rocha. 1995. Phylogeny and biogeography of the Ergasilidae (Copepoda, Poecilostomatoida), with reconsideration of the taxonomic status of the Vaigamidae. Contr. Zool. **65**: 233-243.
- Amundsen PA, R Kristoffersen, R Knudsen, A Klemetsen. 1997. Infection of *Salmincola edwardsii* (Copepoda: Lernaeopodidae) in an age-structured population of Arctic

charr: a long-term study. J. Fish Biol. 51: 1033-1046.

- Anwand K. 1978. Zooplankton und seine Gewinnung als Futtergrundlage für die industriemässige Fishauzucht.
 Z. Binnenfischerei DDR 25: 216-222. (in German)
- Bauer ON, B Babaev. 1964. Sinergasilus major (Markewitsch, 1940), its biology and pathogenic significance. Izv. Akad. Nauk Turkmen. SSR, Biol. 3: 63-67. (in Russian)
- Baumann F. 1913: Parasitische Copepoden auf Coregonen. Rev. Suisse Zool. **21:** 147-178. (in German)
- Black GA. 1982. Gills as an attachment site for Salmincola edwardsii (Copepoda: Lernaeopodidae). J. Parasit. 68: 1172-1173.
- Black GA, WL Montgomery, FG Whoriskey. 1983. Abundance and distribution of *Salmincola edwardsii* (Copepoda) on anadromous brook trout, *Salvelinus fontinalis* (Mitchill) in the Moisie River system, Quebec. J. Fish Biol. **22**: 567-575.
- Bowen CA II, RM Stedman. 1990. Host-parasite relationship and geographic distribution of *Salmincola corpulentus* (Copepoda: Lernaeopodidae) on bloater (*Coregonus hoyi*) stocks in Lake Huron. Can. J. Zool. **68:** 1988-1994.
- Bryliński E. 1972. Effect of tapeworm *Ligula intestinalis* (L.) on fecundity and reproduction of bream, *Abramis brama* (Linnaeus, 1758). Roczn. Nauk Roln. Warszawa. Seria H, **94**: 7-16. (in Polish)
- Cakić P, Z Petrović, D Kataranovski, S Fišter. 1998. Detection of the parasitic copepods *Lamproglena pulchella* Nordmann, (1932) and *Larnaea* [sic] *cyprinacea* Linnaeus, 1758 on the gills of fish from Yugoslav waters. Acta Vet. Belgrade **48:** 131-138.
- Callinan RB. 1988. Diseases of Australian native fish. *In* Fish diseases. Post Graduate Committee in Veterinary Science University of Sydney, Proceedings 106, Sydney, Australia:Post Graduate Committee in Veterinary Science University of Sydney:pp. 459-474.
- Cheng SH, HC Chen, SL Chang, TI Chen, IC Liao. 2001. Study on the optimal density of mass culture in copepod *Apocyclops royi*. 6th Asian Fisheries Forum, 25-30 Nov 2001, Kaohsiung, Taiwan: Asian Fisheries Society., p. 58.
- Cheng SH, HC Chen, MS Su, JS Ho. 1999. Effects of temperature and salinity on the maturation in *Apocyclops royi* (Cyclopidae, Cyclopoida). The 7th International Conference on Copepoda, Curitiba, Brazil, 25-31 July 1999; Program and abstracts. Curitiba, Brazil: The World Association of Copepodologists., p. 80.
- Dick TA, B Dixon, A. Choudhury. 1991. *Diphyllobothrium*, *Anisakis* and other fish-borne parasitic zoonoses. SE Asian J. Trop. Med. Public Health **22:** 150-152.
- Dorovskikh GN. 1996. Location of *Lernaea cyprinacea* (Copepoda: Lernaeidae) on the body of crucian. Parazitologiâ **30:** 540-544. (in Russian)
- Dubinina NM. 1966. Cestoda: Ligulidae. Fauna SSSR. Izd. Nauka, Moskva-Leningrad. (in Russian)
- Dzidziul A. 1973. The pathogenicity of *Lernaea cyprinacea* L. in the cases of heavy infestation, in *Carassius carassius* (L.). Acta Parasit. Pol. **21**: 281-288.
- Egusa S. 1992. Infectious diseases of fish. Rotterdam-Brookfield: AA Balkema.
- Einszporn T. 1965a. Nutrition of *Ergasilus sieboldi* Nordmann. I. Histological structure of the alimentary canal. Acta Parasit. Pol. **13:** 151-160.
- Einszporn T. 1965b. Nutrition of *Ergasilus sieboldi* Nordmann. II. The uptake of food and the food material. Acta Parasit. Pol. **13:** 373-382.
- Fabian MW. 1960. Mortality of freshwater and tropical fish fry

by cyclopoid copepods. Ohio J. Sci. 60: 268-270.

- Fajer E, A Prieto, M Vinjoy. 1985. Lernaea cyprinacea (Copepoda: Lernaeidae) en peces en cultivo intensivo en Cuba. Revis. Salud Anim. 7: 411-414.(in Spanish)
- Fritzsche S, M Taege. 1979. Schädigungen bei der Aufzucht von Fischbrut (*Hypophtalmichthys molitrix*, *Cyprinus carpio* und *Coregonus albula*) industriemäßigen Produktionsanlagen durch starkes Vorkommen von Ruderfußkrebsen (Copepoda). Z. Binnenfischerei DDR **26:** 304-308. (in German)
- Gabrielli MA, ML Orsi. 2000. Dispersao de Lernaea cyprinacea (Linnaeus) (Crustacea, Copepoda) na regiao norte do estado do Parana, Brasil. Revis. Brasil. Zool. Curitiba. 17: 395-399. (in Portuguese)
- Gall GAE, EL McClendon, WE Schafer. 1972. Evidence on the influence of the copepod (*Salmincola californiensis*) on the reproductive performance of a domesticated strain of rainbow trout (*Salmo gairdneri*). Trans. Am. Fish. Soc. **101**: 345-346.
- Galli P, G Crosa, S Bertoglio, L Mariniello, M Ortis, S D'Amelio. 2001. Populations of *Lamproglena pulchella* von Nordmann, 1832 (Copepoda: Eudactylinidae) in cyprinid fish in rivers with different pollution levels. J. Appl. Ichthyol. **17**: 93-96.
- Garbacik-Wesołowska A, A Szkudlarek, E Sobecka. 1994: Nematode *Anguillicola crassus* in eels from the Szczecin Lagoon and Lake Łętowskie. Bull. Sea Fish. Inst. **2:** 34-37.
- Goodwin AE. 1999. Massive *Lernaea cyprinacea* infestations damaging the gills of channel catfish polycultured with bighead carp. J. Aquat. Animal Health **11**: 406-408.
- Grabda E, J Grabda. 1958. Tracheliastosis in the common bream, Abramis brama L. in Lake Jamno. Zool. Pol. 8: 325-334.
- Grabda J. 1963a. Life cycle and morphogenesis of *Lernaea cyprinacea* L. Acta Parasit. Pol. **11:** 169-198.
- Grabda J. 1963b. On the invasiology of *Ergasilus sieboldi* Nordm. in Poland. Acta Hydrobiol. **5:** 245-259. (in Polish)
- Hall DN. 1983. Occurrence of the copepod parasite *Lernaea* cyprinacea L., on the Australian grayling, *Prototroctes* maraena Günther. Proc. R. Soc. Victoria **95**: 273-274.
- Hartig JH, DJ Jude, MS Evans. 1982. Cyclopoid predation on Lake Michigan fish larvae. Can. J. Fish. Aquat. Sci. 39: 1563-1568.
- Heinemann E. 1934. Gross-Schadliche. Der Kiemenkrebs (*Ergasilus sieboldi* Nordm.). Biologia **3:** 284-287. (in German)
- Ho JS. 1998. Cladistics of the Lernaeidae (Cyclopoida), a major family of freshwater fish parasites. J. Marine Syst. 15: 177-183.
- Hoffman GL. 1984. Salmincola californiensis continues the march eastward. Am. Fish. Newslett. 12: 4.
- Huq A, RR Colwell. 1996. Environmental factors associated with emergence of disease with special reference to cholera. East. Mediter. Health J. 2: 37-45. Available at http://www.emro.who.int/Publications/EMHJ/0201/05.htm
- Ibraheem MH, K Izawa. 2000. On the morphology of Lamproglena monodi Capart, a parasitic Copepod on the gills of tilapia in Egypt. Zool. Middle East 21: 103-108.
- Ivaska S. 1951. Danube salmon and its proper culture. Bratislava: Vyd. Tatran. (in Slovakian)
- Jeżewski W, G Karbowiak 2002. *Ligula intestinalis* (L., 1758) in muscles of bream *Abramis brama* (L.) from the lake Gosławskie, the first record in Poland. 5. Slovenské a České Parazitologické Dni. 28-31.05.2002 r. Kongresové

Centrum Academia, Stará Lesná, Vysoké Tatry, Slovenská Republika. Kosice: Slovak Republic: Parazitologicky ustav SAV., p. 51.

- Johnson KA, JA Heindel. 2001. Efficacy of manual removal and ivermectin gavage for control of Salmincola californiensis (Wilson) infestation of chinook salmon, Oncorhynchus tshawytscha (Walbaum), captive broodstocks. J. Fish Dis. 24: 197-203.
- Kabata Z. 1969. Revision of the genus Salmincola Wilson, 1915 (Copepoda: Lernaeopodidae). J. Fish. Res. Bd. Can. 26: 2987-3041.
- Kabata Z. 1970. Crustacea as enemies of fishes. In SF Snieszko, HR Axelrod, eds. Diseases of fishes. Book 1. Jersey City, NJ: TFH Publications.
- Kabata Z. 1979. Parasitic Copepoda of British fishes. London: Ray Society.
- Kabata Z. 1985. Parasites and diseases of fish cultured in the tropics. London and Philadelphia, PA: Taylor & Francis.
- Kabata Z, B Cousens. 1973. Life cycle of Salmincola californiensis (Dana, 1852) (Copepoda: Lernaeopodidae). J. Fish. Res. Bd. Can. **30**: 881-903.
- Kabata Z, B Cousens. 1977. Host-parasite relationship between sockeye salmon, *Oncorhynchus nerka*, and *Salmincola californiensis* (Copepoda: Lernaeopodidae). J. Fish. Res. Bd. Can. **34**:191-202.
- Kasahara S. 1962. Studies on the biology of the parasitic copepod *Lernaea cyprinacea* Linnaeus and the method for controlling this parasite in fish-culture ponds. Contr. Fish. Lab. Fac. Agric. Univ. Tokyo **3:** 103-196.
- Khalifah KA, G Post. 1976. Histopathological effect of *Lernaea cyprinacea* (a copepod parasite) on fish. Prog. Fish-Cult. 38: 110-113.
- Kim JR, JM Lee. 2001. A case of intramuscular sparganosis in the sartorius muscle. J. Korean Med. Sci. 16: 378-380.
- Klenov AP, GV Vasil'kov. 1972. Seasonal and growth dynamics of bothriocephalosis in grass carp in the Mironovskij fish pond. Bjull. Vses. Inst. Gel'mintol. im. K.I. Skrjabina. Moskva 8: 25-27. (in Russian)
- Kocyłowski B. 1954. Ergasilosis. Gosp. Rybna **6:** 16-17. (in Polish)
- Kocyłowski B, T Miaczyński. 1960. Diseases of fish and crayfish. Warsaw: PWRiL. (in Polish)
- Kozikowska Z. 1975. Ergasilus sieboldi Nordm., adaptations of the parasite to the morphology and biology of hosts and additional data on the occurrence of other species of parasitic crustaceans in the area of Warmia and Masuria. Acta Univ. Wratislav. No. 301, Prace Zool. 7: 3-40. (in Polish)
- Kozikowska Z, Z Jara, E Grabda. 1957. Achtheres percarum Nordm. sur la perche et la sandre. Essai d'explication de la relation mutuelle des formes percarum et sandrae). Zool. Pol. 7: 219-267. (in Polish)
- Kuang PR, JH Qian. 1985. Three new species of the genus *Lamproglena* from China (Copepoda: Cyclopoida, Lernaeidae). Acta Zootax. Sin. **10:** 363-369. (in Chinese)
- Kumari P, S Khera, NK Gupta. 1989. On six new species of the genus Lamproglena Nordmann (Copepoda: Eudactylinidae), ectoparasitic on freshwater fishes of India. Res. Bull. Panjab Univ. Sci. 40: 9-23.
- Langdon JS. 1992. Major protozoan and metazoan parasitic diseases of Australian finfish. *In* DI Bryden, ed. Fin Fish Workshop, Post Graduate Committee in Veterinary Science, University of Sydney, Proceedings. Sydney, Australia: University of Sydney, **182**: 1-28.
- Lehmann C. 1924. Das Hechtsterben in Jamunder See bei

Köslin. Mitteilungen Fischerei Vereine Provinzen Brandenburg, Ostpreußen, Pommern Grenzmark. **16**: 261-263.(in German)

- Lillelund K. 1967. Experimentelle Untersuchungen uber den Einfluss carnivorer Cyclopiden auf die Sterblichkeit der Fischbrut. Z. Fisch. NF **15:** 29-43. (in German)
- Mamcarz A. 1990. Conditions for growth of peled larvae, *Coregonus peled* (Gmel.) during net-pen rearing. Acta Acad. Agric. Techn. Olst. Protectio Aquarum Piscatoria. Supplement. A, 17(379): 3-57. (in Polish)
- Markevič AP. 1956. Parasitic copepods of fishes of the USSR. Kiev: Izdatel'stvo Akademii Nauk Ukrainskoj SSR. (in Russian)
- Marten GG, ES Bordes, M Nguyen. 1994. Use of cyclopoid copepods for mosquito control. Hydrobiologia **292/293:** 491-496.
- Marx HM, A Avenant-Oldewage. 1996. Redescription of *Lamproglena clariae* Fryer, 1956 (Copepoda, Lernaeidae), with notes on its occurrence and distribution. Crustaceana **69**: 509-523.
- McGladdery SE, CE Johnston. 1988. Egg development and control of the gill parasite *Salmincola salmoneus*, on Atlantic salmon kelts (*Salmo salar*) exposed to four different regimes of temperature and photoperiod. Aquaculture **68:** 193-202.
- Mulcahy D, D Klaybor, WN Batts. 1990. Isolation of infectious hematopoietic necrosis virus from a leech (*Piscicola* salmositica) and a copepod (*Salmincola sp.*), ectoparasites of sockeye salmon Oncorhynchus nerka. Dis. Aquat. Organ. 8: 29-34.
- Muroga K, S Takahashi, H Yamanoi. 1979. Non-cholera Vibrio isolated from diseased ayu. Bull. Jpn. Soc. Sci. Fish. 45: 829-834.
- Musselius VA. 1973. Parasites and diseases of phytophagous fishes of the far-east complex in pond farms of the USSR. Trudy vses. naučno-issled. Inst. prud. ryb. Hoz. 22: 4-129. (in Russian)
- Nagasawa K, K Ikuta, S Kitamura. 1997. Distribution of Salmincola carpionis (Copepoda: Lernaeopodidae) in the buccal cavity of salmonids. Bull. Nat. Res Inst Aquacult. 26: 35-39.
- Nagasawa K, K Ikuta, H Nakamura, T Shikama, S Kitamura. 1998. Occurrence and effects of the parasitic copepod Salmincola carpionis on salmonids in the Nikko District, central Japan. In H-U Dahms, T Glatzel, HJ Hirche, S Schiel, HK Schminke eds. Proceedings of the 6th International Conference on Copepoda. J. Mar. Syst. 15: 269-272.
- Nagasawa K, JR Watanabe, S Kimura, A Hara. 1994. Infection of Salmincola stellatus (Copepoda: Lernaeopodidae) on Sakhalin taimen Hucho perryi reared in Hokkaido. Bull. Faculty Fish. Hokkaido Univ. 45: 109-112.
- Nakajima K, S Egusa. 1973. Parasitic copepod, *Pseudoergasilus zacconis* Yamaguti, found on the gills of cultured ayu, *Plecoglossus altivelis*. I. Morphology. Fish Pathol. (Gyobyu Kenkyo) 8: 106-110.
- Nylund A, B Bjørknes, C Walace. 1991. *Lepeophtheirus salmonis* - a possible vector in the spread of diseases on salmonids. Bull. Eur. Assoc. Fish Path. **11:** 213-216.
- Nylund A, C Walace, T Hovland. 1993. The possible role of Lepeophtheirus salmonis (Krøyer) in the transmission of infectious salmon anemia. In GA Boxshall, D Defaye, eds. Pathogens of wild and farmed fish: sea lice. Chichester, UK: Ellis Horwood, pp. 367-373.

Ogle J. 1979. Adaptation of a brown water culture technique to

the mass culture of the copepod *Acartia tonsa*. Gulf Res. Rep. **6**: 291-292.

- Ohno A, Y Okamura. 1988. Propagation of the calanoid copepod, *Acartia tsuensis* in outdoor tanks. Aquaculture **70**: 39-51.
- Oldewage WH. 1993. The past, present and future role of piscine parasitic copepods in Africa. Fifth International Conference on Copepoda. University of Maryland Baltimore County, 06-12 June 1993.Baltimore, USA: The World Association of Copepodologists, p. 73.
- Pavanelli GC, JC Eiras, RM Takemoto, MJ Ranzani-Paiva, ARM Magalhaes. 2000. Sanidade de peixes, rãs, crustáceos e moluscos *In* WC Valenti, CR Poli, JA Pereira, JR Borghetti, eds. Aquicultura no Brasil. Bases para um desenvolvimento sustentável. Brasília: Conselho Nacional de Desenvolvimento Científico e Tecnológico, pp. 197-245. (in Portuguese)
- Payne MF, RJ Rippingale. 2001. Intensive cultivation of the calanoid copepod *Gladioferens imparipes*. Aquaculture **201:** 329-342.
- Piasecki W. 1989. Life cycle of *Tracheliastes maculatus* Kollar, 1835 (Copepoda, Siphonostomatoida, Lernaeopodidae). Wiad. Parazyt **35:** 187-245.
- Piasecki W. 1991. Tracheliastosis of bream, Abramis brama (L.) in Pierzchalskie Lake near Braniewo. Materiały XVI Zjazdu Polskiego Towarzystwa Parazytologicznego; Poznań, 12-13 September 1991. Poznań, Poland: Polskie Towarzstwo Parazytologiczne. p. 28. (in Polish)
- Piasecki W. 1993a. Comparative morphology of the three species of *Lamproglena* (Copepoda, Cyclopoida, Lernaeidae) described by von Nordmann, based on reexamination of the types. Mitt. Zool. Mus. Berlin **69:** 307-315.
- Piasecki W. 1993b. Crustacean parasites from three fish species from the Odra River estuary, Poland. Acta Ichthyol. Piscat. 23: 77-87.
- Piasecki W, E Kuźmińska. 1996. Developmental stages of Achtheres percarum von Nordmann, 1832 (Lernaeopodidae) parasitic on perch - Perca fluviatilis L. Sixth International Conference on Copepoda. Oldenburg Bremerhaven, Germany, 29 July- 3 Aug. 1996. Oldenburg, Germany: The World Association of Copepodologists, p. 89.
- Piasecki W, A Wołoszyn. 1991. Mass infection of Achtheres percarum von Nordmann, 1832 (Copepoda, Siphonostomatoida, Lernaeopodidae) in perch Perca fluviatilis in the estuary waters of the Odra River. Materiały XVI Zjazdu Polskiego Towarzystwa Parazytologicznego. Poznań, 12-13 Sept. 1991. Poznań, Poland: Polskie Towarzystwo Parazytologiczne, p. 27. (in Polish)
- Piasecki WG. 2000. Attacks of cyclopoid *Acanthocyclops robustus* (Sars) on newly hatched cyprinids. Electr. J. Polish Agric. Univ. Fish.**3**(1). Available at http://www.ejpau.media.pl/series/volume3/issue1/fisheries/art-02.html
- Poddubnaja AV. 1973. Variability and specificity of *Lernaea* from pond fishes. Trudy vses. naučno-issled. Inst. prud. ryb. Hoz. **22:** 159-173. (in Russian)
- Rokicki J. 1987. Copepods of the Salmonidae in the Bay of Puck. Wiad. Parazyt. **32:** 509-510. (in Polish)
- Rowland SJ, BA Ingram. 1991. Diseases of Australian native freshwater fishes. Sydney: NSW Fisheries, pp. 33.
- Rumphorst H. 1924. Über Ergasiliden. (Schmarotzer-Krebschen). Mitteilungen Fischerei Vereine Provinzen Brandenburg, Ostpreußen, Pommern Grenzmark. **16**:

305-308. (in German)

- Sabatini MA, M Marini, B Fratello, C Gelosini, L Mola, I Benedetti. 1988. The digestive apparatus of the parasitic copepod *Lernaea cyprinacea* L. during development and in the adults. Acta Embryol. Morph. Exp. 8: 389-409.
- Schäperclaus W. 1954. Fischkrankheiten. 3 Auflage. Berlin: Akademie-Verlag. (in German)
- Schäperclaus W. 1992. Fish diseases (English translation of "Fischkrankheiten", 5th corrected and substantially enlarged edition 1986). Rotterdam: AA Balkema.
- Send∤ak H. 1980. Mechanical catch of zooplankton in a lake. PhD thesis, Agricultural University of Szczecin, Poland. (in Polish)
- Shariff M, RJ Roberts. 1989. The experimental histopathology of *Lernaea polymorpha* Yu, 1938 infection in naive *Aristichthys nobilis* (Richardson) a comparison with the lesion in naturally infected clinically resistant fish. J. Fish Dis. **12**: 405-414.
- Sutherland DR, DD Wittrock. 1985. The effects of Salmincola californiensis (Copepoda: Lernaeopodidae) on the gills of farm-raised rainbow trout, Salmo gairdneri. Can. J. Zool. 63: 2893-2901.
- Szlauer B. 1976. Possibilities of using zooplankton removed by the River Płonia from lakes to feed young fish. Acta Ichthyol. Piscat. **6 (2):** 39-53.
- Szlauer B. 1977. The zooplankton removal from lakes the River Płonia. Acta Ichthyol. Piscat. **7 (1):** 59-79.

Szlauer B. 1983/1984. Possibilities of obtaining zooplankton

from the River Płonia to feed young fish. Acta Hydrobiol. **25/26:** 165-171.

- Szlauer B, L Szlauer. 1980. The use of lake zooplankton as feed for carp (*Cyprinus carpio* L.) fry in pond culture. Acta Ichthyol. Piscat. **10** (1): 79-102.
- Szlauer L. 1995. On the culture of *Paracyclops fimbriatus* (Cyclopoida) and the potential of the species as live food for juvenile fish. Acta Ichthyol. Piscat. **25 (2):** 15-27.
- Szlauer L, Z Kwidziński, P Nowakowski, H Sendłak. 1978. Mechanical methods of plankton capture for fish larvae feeding. Zesz. Nauk. Akad. Roln. Szczecinie Ser. Ryb. Morskie No. **70:** 73-83. (in Polish)
- Szlauer L, B Szlauer. 1982. Utilization of autumn zooplankton in carp fry rearing. Acta Ichthyol. Piscat. 12 (2): 71-81.
- The world of copepods. 2002. Available at http://www.nmnh.si.edu/iz/copepod/
- Vaughan GE, DW Coble. 1975. Sublethal effects of three ectoparasites on fish. J. Fish Biol. **7**: 283-294.
- Witkowski A, J Błachuta. 1980. Occurrence of Basanistes huchonis (Schrank, 1786) (Copepoda parasitica, Lernaeopodidae) on the Danube salmon, Hucho hucho (L.). Przegl. Zool., Wrocław 24: 463-467. (in Polish)
- Zuromska H. 1967a. Assessment of mortality of eggs and larvae of roach (*Rutilus rutilus* L.) in lacustrine spawning. Roczn. Nauk Roln. No. **90:** 539-556. (in Polish)
- Żuromska H. 1967b. Some causes of mortality of eggs and larvae of roach (*Rutilus rutilus* L.) in lacustrine spawning grounds. Roczn. Nauk Roln. **No. 90:** 557-579. (in Polish)