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# A review of *Argulus* spp. occurring in UK freshwaters

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British Trout Association
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Professor Mike Depledge    Head of Science

# EXECUTIVE SUMMARY

The genus *Argulus* causes problems in many types of aquatic systems throughout the world. Although there is a considerable literature available on this group of parasites, most is concerned with the taxonomy, morphology and development of the parasite, which aspects are fairly well understood. There is a much less reliable information available on other aspects of the biology of *Argulus*; in particular there is a need for quantitative and experimentally based studies.

The pathology caused by *Argulus* to its hosts is also well documented, but there is still an urgent need for more precise studies on the effect of the parasite, in particular on physiological impacts. It is also necessary to determine whether *Argulus* is indeed responsible for the pathology and behavioural changes observed in affected farms and fisheries. *Argulus* is an easily observed parasite and may be blamed for effects that are wholly or partially due to other factors.

At present there is a serious lack of control measures and management strategies against outbreaks of *Argulus,* particularly in still water fisheries. Improved chemotherapies, which are acceptable environmentally and in terms of human health, may be developed, but prevention through improved management practices is a more favourable option and may well be the most practical option when dealing with a large open water system. However, in order to successfully identify suitable practices a much better understanding of the parasite is necessary. The current study into the population ecology and epidemiology of *Argulus* in the UK may lead to the identification of risk factors associated with epizootics of *Argulus*. Although it is probably not practical to totally eradicate or eliminate populations of *Argulus* in many stillwater fisheries, it may be possible by the removal of risk factors to keep population numbers at a level that will not cause the major problems associated with an outbreak.

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# 1. INTRODUCTION

Species of the fish louse *Argulus* (Crustacea: Branchiura) are found distributed throughout the world (Fryer 1968, Kabata 1970, Post 1987 & Rushton-Mellor 1992) and 143 species in the genus have been described (Anon, 2001), although it is likely that many of these are synonymous. There are both freshwater and marine species.

*Argulus* spp have been reported to cause problems in fisheries and fish farms worldwide, including the UK. Many of the early records of *Argulus* in Europe refer to it as a problem in carp farming, and it is commonly named as the carp louse in much of the older German literature. In the UK, more recently *Argulus* has caused problems in stillwater trout fisheries (Knight 1996, Northcott, Lyndon & Campbell 1997, Gault, Kilpatrick & Stewart 2002, personal communications with representatives of the trout industry). Interestingly, the first known record of *Argulus* by Baldner 1666 (cited by Wilson 1902) describes it as predominantly affecting trout.

Three freshwater species have been found in the UK; *A. foliaceus, A. coregoni* and *A. japonicus.* These are also found throughout much of Europe and many other parts of the world (Post, 1987). One marine species of *Argulus, A. arcassonensis,* has also been recorded in UK coastal waters (Rushton-Mellor 1992), although this will not be considered further here. *Argulus* spp. Are louse-like in appearance, are semi-transparent, with a pale green or brown cryptic colouration. They are broadly ovoid in shape, dorso-ventrally flattened and convex dorsally. *A. foliaceus* and *A. japonicus* are of similar size, adults being around 6-8mm in length (Shafir & Van As 1986, Rushton-Mellor & Boxshall 1994). They are smaller than *A. coregoni* the adult of which can reach 12mm in length (Gurney 1948).

As a result of the problems experienced in the UK in recent years a project to study the factors influencing the abundance of *Argulus* in fisheries has been funded at the Institute of Aquaculture by the Environmental Agency and the still water trout fishing industry. A cross-sectional study of UK stillwater trout fisheries, selected at random from each region in the ‘Trout Masters 2for1’ fishing guide and the ‘Association of Stillwater Game Fisheries Managers’ (ASGFM) members list, was carried out by the authors. This showed that *Argulus* can cause epizootics leading to massive mortalities, but more commonly, the main problem caused by *Argulus* is the loss of appetite and subsequent condition of heavily infected fish. This in turn is deterring anglers, either because they are unable to catch fish or because the appearance of the fish is unappealing.

Although the fishing rights to trout fisheries in England and Wales (including running water) are estimated to be worth around £500million (Environment Agency 2001), sport fisheries often have very narrow profit margins which means that the effect of *Argulus* can be devastating to a business or syndicate water. In addition to the direct effects on a fishery, there could be significant secondary economic effects. Angling makes a substantial contribution to the economy of rural Britain, supporting between 5000-6000 full time equivalent jobs through the supply, retail and independent sectors (Countryside

Alliance 2001). There are currently approximately 430,000 trout anglers in England and Wales alone, spending around £300 million on game fishing and contributing £6 million to the Environment Agency through rod licence fees (Environment Agency 2001 & 2002). The vast majority of trout waters rely on supply by the trout farming industry and hauliers to obtain their stock. In the year 2000, 121 farms in England and Wales produced 3427 tonnes of trout for the purpose of restocking and growing, with an additional 843 tonnes being produced in Scotland (CEFAS 2001). These figures indicate that the failure of a fishery could have considerable effects along the economic chain.

Over the last century much literature has been published on *Argulus*, but it is of variable quality and there is no recent review of the subject. In view of the emergence of *Argulus* as a problem in UK stillwater fisheries, a review of the pertinent species seems timely. This review aims to summarise the literature available on *Argulus*, with particular reference to species indigenous to the UK, and their impact on the UK trout fishing industry. The systematics and morphology of *Argulus* spp. has been dealt with in detail elsewhere and will not be considered here.

# 2. DEVELOPMENT AND LIFE CYCLE

*Argulus* spp. lay their eggs off the host on a suitable surface (Kimura 1970, Shimura & Egusa 1980), in rows that are attached by a gelatinous material that appears to harden on contact with water (Martin 1932, Bower-Shore 1940, Shafir & Van As 1986, Rahman 1995). Eggs of *A. foliaceus* and *A. japonicus* are laid in batches comprising 2-4 rows, with each batch containing up to 400 eggs (Bower-Shore 1940, Kimura 1970, Shafir & Van As 1986), *A. coregoni* lays its eggs in mats. According to Kimura (1970) *Argulus japonicus* can lay between 1 & 10 batches of eggs over their life-span but the number of eggs laid on each occasion is variable. Eggs are mainly laid at night in the bottom to middle layers of ponds (Kimura, 1970, Shimura & Egusa, 1980, Mikheev, Pasternak, Valtonen & Lankinen 2001). This may be due to reduced levels of UV light, as a defence against drying if the water level were to drop, or to a lack of filamentous algae growing at these depths, which could smother the eggs. Mikheev *et al*. (2001) found that not only were more eggs laid at depth, but those batches in deeper water contained a higher percentage of viable eggs.

Eggs of *A. foliaceus* are laid on firm surfaces such as rocks, mainly on a vertical face and, in the case of rivers' on a face downstream of the flow (Mikheev *et al*. 2001). Shimura & Egusa (1980) also suggest that *Argulus coregoni* show a preference for a moderately roughened surface, over a smooth or very rough surface, upon which to lay their eggs. This suggests *Argulus* spp. are relatively selective about the surface upon which they lay their eggs and Mikheev *et al*. (2001) found that eggs strings were often laid on top of one another several layers deep on rocks. These authors hypothesised that this was due to the limited availability of substrates suitable for egg laying. In a stillwater reservoir, Gault *et al.* (2002) found eggs of *A. foliaceus* to be laid on the concrete reservoir walls and water tower, plastic containers, submerged rocks and tree stems. Studies by the authors on several stillwater fisheries in the UK have found eggs on similar substrates, but also on the undersides of boats and even on signal crayfish and swan mussels living in the same habitat.

When laid eggs are ovoid and measure approximately 0.2mm x 0.3mm. They are a white to pale yellow colour, but within 24 hours their colour changes to a deeper yellow/light brown as described for *A. foliaceus* and *A. japonicus* (Bower-Shore 1940, Shafir & Van As 1986, Rahman 1995). After egg-laying Shafir & Van As (1986) describe three subsequent developmental stages in *A. japonicus*; the first is the development of eye spots, the second the development of the thoracic appendages, whilst the third stage includes the movement of the embryo at approximately 24-48 hours before hatching. The rate at which these stages occur is dependent on temperature. Rahman (1995) carried out more detailed observations of the developmental stages in the eggs of *A. foliaceus* and describes nine stages in total. At 23°C Rahman (1995) noted that the initial colour change occurred after just 3 hours.

Stages 2 –7 took approximately 12 days, during which time Rahman (1995) describes cell multiplication, the development of vacuoles followed by their disappearance, and details the subsequent development of the embryo. Eye pigmentation and the appearance of appendages was not noted until stage 8 (15-16 days after laying). Stage 9 is the hatching stage and occurred at around day 17 at 23°C, when the juvenile exits the egg through a longitudinal split on the dorsal surface.

Hatching times of the eggs of *Argulus* appear to vary between species and with temperature. Bower-Shore (1940) states that the eggs of *A. foliaceus* take 30-35 days to hatch at an undisclosed temperature. Shafir and Van As (1986) studied the effects of temperature on the hatching times of *A. japonicus.* They found eggs to hatch in an unsynchronised fashion both within the egg string and between batches. Pasternak, Mikheev & Valtonen (2000) agreed with this statement but found eggs of *A. foliaceus* that had overwintered to be more synchronised in their hatching. They hypothesised that synchronicity may increase with host density, suggesting that in waters where hosts are scarce, extended periods of recruitment would be beneficial as the availability of a host will be unpredictable. Below 8-10°C, eggs do not appear to develop, and they may overwinter until more favourable conditions in spring and summer (Macheen 1940, Hindle 1948, Stammer 1959, Shimura 1981, Shafir & Van As,1986). Pasternak *et. al.* (2000) found this to be the case with eggs of *A. foliaceus*, but eggs which had overwintered suffered a much-reduced hatching success, although Mikheev *et al*. (2001), working in northern latitudes, found that eggs of *A. coregoni* are able to remain viable under conditions of low temperature for up to 2 years. Shafir & Van As (1986) found that, at 15°C, eggs of *A. japonicus* took 61 days to hatch, which is in agreement with Tokioka (1936), who found them to take 60 days at the same temperature. Shafir & Van As (1986) and Shafir & Oldewage (1992) showed that the hatching rate of *A. japonicus* increased proportionally with an increase in temperature. The greatest degree of hatching success was at 25°C. Kimura (1970) recorded a hatching success of between 66.7-96.5% in *A. japonicus* at temperatures between 14.4 to 30$^0$C, but suggested that low hatching rates might be because the eggs used had been scraped from their attachment surface, which could reduce hatching success by 30%. In a subsequent experiment where eggs were left attached to a surface, a 95.2-100% hatch success was observed.

Shafir & Van As's (1986) study on egg laying, development and hatching in *A. japonicus* produced an interesting finding that may warrant further investigation. They found there was a greater hatching success and that eggs developed faster in their 'control tanks' than in their trial tanks. They hypothesised that the greater degree of temperature fluctuation observed in the control tanks (2$^0$C in control tanks compared to 0.5$^0$C in trial tanks), was responsible for the increase in hatch success and rate of egg development. If this were true it could have consequences for small stillwaters, which are prone to large diurnal temperature fluctuations. Bai (1981) showed that in the case of *A. siamensis* both photoperiod and light intensity were important in determining the rate of hatching and this study suggested that long photoperiods of high light intensity reduced development time of eggs. However, it is not clear in this case whether it was light intensity or photoperiod that was causing the effect as both variables were adjusted at the same time. Mikheev *et al*. (2001) found that eggs of *A. coregoni* buried in sediment had a reduced hatch success and took longer to hatch. This was attributed to light intensity as an increase in the latter improved rate of hatching and hatch success.

Temperature is not only important in the development of the egg, but also plays an important role in the post-hatching development of *Argulus*. Schluter (1979) showed that growth rate increased with temperatures between 16 & 28 °C but that this relationship was not linear. It has also been suggested that high temperatures increase moult frequency, and that the shorter the frequency the greater the growth between moults. Kimura (1970) demonstrated that the time from hatching until the first egg laying (maturity) of *A. japonicus* decreases as temperature increases between 16 & 29°C. At temperatures lower than 16°C, the time until maturity was considerably increased. Kimura concluded that longevity increases in a linear fashion with decrease in temperature in both larvae and adult *Argulus*.

There appears to be some confusion over the number of developmental stages between hatching to adulthood in the three species of *Argulus* found in the UK. In the case of *A. coregoni*, both Stammer (1959) and Shimura (1981) describe 9 stages. Stammer (1959) also suggests that there are 9 stages in *A. japonicus,* whereas Tokioka (1936) describes only 7 stages. Rushton-Mellor & Boxshall (1994) cast doubt on Stammer's observations, suggesting his observations were inadequately detailed. The most debate, however, appears to occur in the case of *A.foliaceus*, with Rushton-Mellor & Boxshall (1994) describing 11 stages until adulthood, Stammer (1959) describing 9, Clark (1902; as cited by Rushton-Mellor & Boxshall 1994) 6 and Claus (1875) only 5. Of all of these descriptions, those by Rushton-Mellor & Boxshall (1994) for *A. foliaceus*, Tokioka (1936) for *A. japonicus* and Shimura (1981) for *A. coregoni* appear to be the most detailed.

It is well established that in *A. foliaceus, A. japonicus* and *A. coregoni* the parasite hatches out at a relatively advanced stage, known as a "metanauplius", which is recorded by some authors as a copepodid (Tokioka 1936, Shafir & van As 1986, Rahman 1995). Not all species of *Argulus* hatch as a metanauplius, some, for example *A. africanus,* hatch at a more developed juvenile form that resembles the adult (Fryer 1968).

Rushton-Mellor & Boxshall (1994) describe the metanauplius as sub-oval in shape, transparent, and with two highly visible black compound eyes. The metanauplius is approximately 0.7mm in size in all three UK species (Tokioka 1936, Shimura 1981, Rushton-Mellor & Boxshall 1994, Lutsch & Avenant-Oldewage 1995). The metanauplius of all three UK species are extremely similar, and it is not until the parasite reaches the mid-developmental stages that they can be accurately speciated by their gross morphology (Shimura 1981, Rushton-Mellor & Boxshall 1994).

Both the pre-oral spine and mouth tube are present in the metanauplius, demonstrating that even though this stage is morphologically very different from the adult, it is a feeding stage (Tokioka 1936, Shimura 1981, Rushton-Mellor and Boxshall 1994, Lutsch

& Avenant-Oldewage 1995). The first antenna is hooked as in the adult and probably aids in host attachment along with the 1st maxilla. The main characteristic features of the metanauplius are the antennal exopod and mandibular palp, which are the main locomotory organs. The thoracic appendages, which are the main locomotory organs in the adult, are all relatively underdeveloped at this stage (Tokioka 1936, Shimura 1981, Rushton-Mellor & Boxshall 1994, Lutsch & Avenant-Oldewage 1995).

As the juveniles develop they begin to acquire adult characteristics thus, after the first moult, the antennal exopod and mandibular palp have degenerated and the thoracic appendages begin to develop. In developmental stages 1-5, in the case of *A. foliaceus* and *A. coregoni*, and stages 1-4 in the case of *A. japonicus*, the first maxilla is not a developed sucker as in the adult, but is a strong hook for attachment. It is not until the subsequent moult (i.e.stage 6 in *A. foliaceus* and stage 5 in *A. japonicus*) that the hook is completely modified and the sucker is fully formed. Also at this point, the genital sockets and pegs become clearly visible in males on the coxa of the 3rd limb and the basis of the 4th limb, respectively. After this point, *Argulus* continue to develop, through 5 stages in the case of *A. foliaceus,* until they reach sexual maturity each stage showing subtle morphological differences and increases in size. Once adulthood is reached *Argulus* continue moulting and growing (Gurney 1948). This is in contrast to sea lice and other copepods, which do not undergo further moults once adulthood is reached.

Adult male and female *Argulus* mate on or off the host. During copulation, Martin (1932) suggested that the genital pegs and sockets lock together, trapping the 4th thoracic appendages of the females between the 3rd and 4th of the males, thus preventing escape. Gurney's (1948) description of copulation showed it to occur in a similar fashion. Unlike Claus (1875), Martin (1932) did not believe the pegs and sockets to be involved in sperm transfer, but instead considered that this is done through a single median opening on the ventral side of the last thoracic segment. This was shown to be the case in *A japonicus* by Avenant-Oldewage & Swanepoel (1993). The adult female has a single median ovary, separated from the haemocoel, which runs the entire length of the thorax. The abdomen of the female holds a spermatheca, into which the male transfers sperm during copulation. Although several matings may be observed, it is thought that one is sufficient to fertilise all the eggs that a female will ever produce (Kollatsch 1959). These sperm are then used to fertilise eggs individually upon laying (Martin 1932, Avanent-Oldewage & Swanepoel 1993). Melanophores are found covering the testes in males and the ovary in female (Poly 1998). This is possibly to protect them from UV light which has the potential to damage genetic material, or to cover what are likely to be otherwise quite reflective areas of the parasite to make them less conspicuous to predators.

# 3. POPULATION DYNAMICS

At the level of the individual waterbody, the population biology and ecology of *Argulus* throughout a year appears to be at least partially correlated to temperature. In temperate lake systems, numbers of *Argulus* tend to be low in winter (Kimura 1970, Shimura & Egusa 1983b, Shafir & Oldewage 1992, Pasternak *et al*. 2000, Gault *et al*. 2002), with laboratory experiments suggesting that most lice die off in cold winter conditions (Kimura, 1970) and after periods of reproduction (Pasternak *et al*. 2000). As already noted, eggs appear to lie dormant at temperatures of less than 10°C, allowing them to survive the colder months unhatched until spring. At this time a rise in temperature causes the majority of eggs to hatch over a short period. This spring hatch of metanaupli makes up the bulk of the lice population at this time (Shimura 1983b, Shafir & Oldewage 1992, Pasternak *et al.* 2000, Gault *et al*. 2002), some eggs, however, take longer to hatch leading to an extended recruitment (Mikeev *et al*. 2001). According to the work of Shimura (1983b) on *A.coregoni,*approximately one month after hatching, the first juvenile stage is the most prevalent stage, with metanaupli making up only 10% of the population. Development at this point is slow, probably related to the low spring temperatures. Mature *Argulus* can be found from the start of summer and become very abundant by mid-summer, for example Gault *et al*. (2002) found intensity and prevalence of *A. foliaceus* to be highest in July. Newly laid egg batches are found at the start of summer. Shafir & Oldewage (1992) found that in their study water, peaks in the population of *A. japonicus* corresponded with reduced water levels as well as high temperatures. This may suggest the peak was due in part to the fact that fish would have been effectively crowded at such times allowing increased contact rates between host and parasite. Lice were present throughout the year but juvenile recruitment only occurred in summer. In the case of *A. foliaceus* there is also no recruitment of juvenile parasites during winter and the prevalence and intensity of infection begins to drop rapidly and significantly, although egg laying appears to continue (Bower-Shore 1940). The die off of lice in winter is possibly due in part to the high energetic cost of year round gravidity and the harsh climate (Shafir & Oldewage 1992). Pasternak *et al.* (2000) support this hypothesis finding numbers of female lice to drop significantly at the end of summer, suggesting a high mortality after egg laying. Poulin & Fitzgerald (1989b), however, found no evidence for this in *A. canadensis*.

Kimura (1970) also found that *A. japonicus* tended to die in autumn. In *A.* coregoni it appears that eggs laid from the end of summer to the beginning of autumn by the second generation of lice and the remnants of the first, overwinter and do not hatch until the following spring (Shimura & Egusa 1980). Similar patterns of development have been noted for both *A. foliaceus* and *A. japonicus* although there is some debate over the number of generations and periods of egg laying in a year. For *A. foliaceus*, Claus (1875) suggested 3 reproductive seasons, whereas Gault *et al.* (2002) suggest there are 2 full generations in a year with continuous egg laying from May to October, ceasing when the water temperature drops below 10ºC. Pasternak *et al.,* (2000) found there to be 2 generations in a fish farm in Finland, but only one in a Finnish lake.

Information on the sex ratio of *Argulus* is conflicting. Poulin & Fitzgerald (1989b) and Shafir & Oldewage (1992) suggest a male biased sex ratio for *A. canadensis* and *A.japonicus*, respectively. Shimura (1983b) found a 1:1 sex ratio in *A. coregoni* populations. Kollatsch (1959) noted a 1:1 ratio in *A. foliaceus* populations as did Pasternak *et al*. (2000), except in August when they noted females to outnumber males. Gault *et al*. (2002) found a female biased sex ratio throughout the year in a population of *A. foliaceus* in Northern Ireland.

# 4. BEHAVIOUR AND HOST SPECIFICITY

*Argulus* are obligate parasites and must therefore be able to locate and attach to a host in order to survive. To locate a host, *Argulus* must have good host finding mechanisms, but the chance of finding a host can be further increased by having a wide range of host species. Fryer (1968) suggests that some African species of *Argulus* are more selective than others, but this may be due to a lack of other suitable hosts in their habitat. In general *Argulus* appear to have a wide host tolerance and have been recorded on most species of fish found in the UK (Bower-Shore 1940, Fryer 1968, Kabata 1970), indeed some species of *Argulus* have even been recorded on frogs and tadpoles (Wilson 1902).

Despite this wide host range, some fish species appear to be more susceptible to *Argulus* than others. Gurney (1948) found no evidence of host selection but Bower-Shore (1940) states that highly coloured fish are less susceptible than duller fish, using the example that brown trout are often infected more readily than the brighter rainbow trout. Mishra (1991) observed that hybrid fish were more susceptible to infection by *Argulus* than catla, rohu, mrigal and silver carp, although no satisfactory explanation for this was given. Kimura (1970) found common carp and wild goldfish were more prone to infection than silver carp and also found the number of *Argulus* on a variety of ornamental species increased with an increase in caudal fin length. This could be because fish with elaborate finnage are sluggish in their behaviour, possibly making them more susceptible to infection. A study by Buckley & Morrice (1976) compared the intensity of *A. foliaceus* lice infections on grass carp, mirror carp, roach and rudd. Grass and mirror carp had the highest numbers of lice and did not differ significantly from one another in this respect. Roach had significantly fewer lice and rudd had significantly fewer still. The reasons for these differences were unclear, but factors may include differences in fish size, colouration, scale pattern, behaviour or immunological response. Shafir & Oldewage (1992) found *A. japonicus* to be most prevalent on *Labea capensis* in their study on a South African reservoir, even though this species was not the most common and suggested that this fish was actively selected over other species. LaMarre & Cochran (1992) attempted to determine whether host preference could be due to evolutionary factors by comparing selection by *A. japonicus* on goldfish (which they suggest is their natural evolutionary host) and fathead minnows. The study showed no significant differences in attachment/detachment on the two hosts, suggesting evolutionary routes do not play a role in host selection. Mikheev, Valtonen & Rintamati-Kinnunen (1998) studied host finding in *Argulus* and found perch to be selected over roach in a darkened aquarium, Pasternak *et al.* (2000) also found this to be the case in the wild. A subsequent study by Mikheev, Mikheev, Pasternak & Valtonen (2000) showed this selection to be due to both fish behaviour and colouration. The high infection levels observed in perch in darkened conditions corresponded with their relatively sedentary behaviour in comparison with roach. In light conditions perch were more active and were infected less frequently than in the dark. Roach were more active but were infected more often in the light than the dark, suggesting their bright, reflective coloration was an important factor. This conflicts with the views of Bower-Shore (1940). More evidence that fish behaviour plays an important role in the selection of hosts is provided by Poulin & Fitzgerald (1988). They noted that fish living lower in the water column were more likely to become infected than those located higher in the water column.

Before *Argulus* can infect a host it must be detected either by a random chance encounter or by active selection. Poulin & Fitzgerald (1987) demonstrated a positive correlation between fish density and the percentage of a parasite population attached to fish. This finding is not surprising, as, by increasing the number of hosts, there would be an increase in the rate of contact that occurs between a host and a parasite and therefore the chance of a random encounter. However, there is also substantial evidence that *Argulus* actively seek their host. *Argulus* are able to detect chemical cues in the mucus of fish and become active in its presence (Galarowicz & Cochran 1991, Mikheev *et al.* 1998, Mikheev *et al.* 2000), attaching to a surface coated in mucus more readily than one without (Kaestner 1980, as cited by Galarowicz & Cochran 1991). *Argulus* also appears to be stimulated by light. In a highly reflective environment *Argulus* swim 4.4 times faster than in darkness and are attracted towards bright objects such as knives (Mikheev *et al.,* 1998). Bai's (1981) and Rahman's (1995) observations concur with these findings as they note metanauplii to be photopositive, congregating in well-illuminated sites within an aquarium. Low rates of infection were noted in a highly reflective environment, suggesting the parasites became disorientated and were unable to home in on a fish and, in aquaria which were illuminated but had no reflection, infection success was much greater (Wilson 1902, Mikheev *et al.*1998). In low light conditions cues other than light may be important. The rheosensitive bristles at the anterior edge of the cephalon may be the most important sense organ in such conditions (Madsen 1964, as cited by Mikheev *et al.*1998). Mikheev *et al.* (1998, 2000) found hydromechanical disturbance (turbulence) to be an important factor in the stimulation of *Argulus*, and showed that a fish must be within 6cm of the parasite for an infection to be attempted. They also found that male *A. foliaceus* can attach to a host significantly faster (1.6 times) than females, however Poulin & Fitzgerald (1989b) showed infection success of males and female *A. canadensis* to be similar.

Mikheev *et al.* (2000) studied the behaviour of *Argulus* under light and dark conditions and compared it with that of the host. Their results suggest that *Argulus* adopts two different strategies that have evolved to coincide with their hosts' behaviour. During the day when most fish are active, *Argulus* acts as an ambush predator remaining still in the water column until a fish swims past. This sit and wait strategy could also fulfil another purpose as, by remaining relatively motionless in the water column thus saving energy, the parasite maybe less conspicuous to any potential predators. At night however, when fish tend to be more sedentary, *Argulus* adopts an active searching behaviour in order to find a host. *Argulus* were shown to swim 4.7 times faster during the night than the day and to use up 25% more energy.

Fish that are already infected have an increased chance of further infection compared with uninfected fish (Poulin & Fitzgerald, 1989a), possibly because of chemical cues given off by either the host fish as a distress response, or by attached parasites. The findings of Mikheev *et al.* (1998) suggest a behavioural explanation in that infected fish are likely to swim in an erratic fashion, causing reflected flashes of light that may attract the parasite. However, Buckley & Morrice (1976) found no evidence to suggest that infected fish were more prone to infection than uninfected fish.

Once a host is located and an infection has been successful, *A. foliaceus* appear to show preference for certain sites on the fish. *Argulus* tended to infect fish from the side or beneath, with the lateral regions being the most popular sites for initial attachment (Mikheev *et al*. 1998). Once attached, lice move to a site of preference (Thomas 1961). In the cases of *A. foliaceus* and *A. japonicus* this appears to be the head and the base of the caudal fin, followed by the dorsal and lower flanks (Bower-Shore 1940, Basal, lucky & Dyk 1969, Buckly & Morrice 1976 & Schluter 1978). Schluter (1978) found that mature parasites tended to congregate at the anterior end of the fish, whereas more juvenile parasites tended to be found at the tail end of the fish. A study on salmonid fish by Shimura (1983b) suggests that *A.coregoni* have different sites of preference on the fish to *A. foliaceus* and *A. japonicus*. The head, opercula, flanks and caudal regions appeared to remain reasonably free from *A. coregoni* and no significant difference was shown in the number found on either side of the fish. Lice of under 1.5mm were, however, found all over the fish. 96% of juvenile *A. coregoni* were found on the body of the fish, whereas 4% were found in the oral and gill cavities. As these parasites developed they would also move to the body of the fish. *A. coregoni* was generally found congregated on and around the pectoral and pelvic fins and behind the adipose fin. Juvenile parasites tend to be found on the fins with larger parasites found on the body around the fins. Differences in site preference by *A. coregoni* compared to *A. foliaceus* and *A. japonicus,* may be due to the species of fish that they tend to live on or the fast flowing habitat that they inhabit. It could be that the locations on and around the host's fins provide some shelter from the strong hydrodynamic forces that are likely to be encountered by *A. coregoni* in riverine habitats.

# 5. ATTACHMENT AND FEEDING

Adult *Argulus* attaches to the host by means of the suckers formed from the maxilla and by the hooked antenna. These provide a secure attachment to the surface of the fish but allow the parasite to readily detach and move over the fish or leave the host altogether. Some authors suggest that the attachment organs cause abrasions of the body surface of the fish leaving the attachment site haemorrhagic and erythmic (Prabhavathy & Sreenivasen 1976, Post 1987, Rahman 1996). The most serious pathology, however, is probably caused by the feeding behaviour of *Argulus*.

On the mid-ventral line of the cephalon is the pre-oral spine, the proposed role of which has been much debated. This is separate from the mouth tube or proboscis (Martin 1932, Gurney 1948, Shimura 1983a, Shafir & Van As 1986). The pre-oral spine has often regarded as a “poison” spine and is a delicate organ made up of two sections (Claus 1875, Shimura 1983a, Shafir & Van As 1986). The proximal end is connected to a ‘poison’ sac, whilst the distal end is able to retract into the basal segment, before being thrust out to penetrate the host epidermis. Shimura (1983) suggests that the spine may have two roles; the first being a chemosensory role, indicated by the presence of a pore at the distal end of the spine. The pore has no known function, but the fact that the spine has been observed repeatedly puncturing the host in rapid succession, provides some evidence for this hypothesis. The second function of the spine seems to be to inject some form of active product from the “poison” sac . This product has been described as a toxin and although its role is not fully defined, Shimura & Inoue (1984) showed the toxin to cause severe haemorrhaging, but no haemolytic or cytotoxic effects. This would suggest that the purpose of the toxin is to allow continued blood flow to the feeding site. This is in contrast to Bower-Shore’s (1940) hypothesis that the toxin causes cellular lysis, the products of which can then ingested via the spine as the spine was considered too narrow to suck up whole blood cells. Wilson (1902) and Stammer (1959) made similar suggestions. However, the results of Martin (1932), Gurney (1948) and Shimura (1983a) strongly suggest that the pre-oral spine plays no role in uptake of food, and that a separate mouth tube is used for this purpose.

The mouth tube lies posterior to the pre-oral spine. During feeding it is held at 90° to the plane of the ventral surface of the parasite. When not in use, the tube is held flat to the body in a groove between the parasite’s suckers (Martin 1932, Shimura 1983a). Both Martin (1932) and Shimura (1983a) describe the mouth tube as being formed from an upper lip and a larger crescent shaped lower lip. The mandibles themselves are completely enclosed within the mouth tube. On the distal end of the tube are two conical projections with a glandular pore. Both authors concur that these projections are the first part of the mouth tube to come into contact with the host and probably apply the same toxin that is injected by the pre-oral spine. The mandibles held within the mouth tube may act as cutting structures during feeding (Fryer 1968), whilst the pre-oral spine repeatedly punctures the skin to induce blood flow to the feeding site (Bower-Shore 1940, Kabata 1970).

# 6. PATHOLOGY

*Argulus* do not normally cause a problem in natural environments as a single or a few parasites are unlikely to cause significant damage or lead to mortalities except when infecting very small or weakened fish (Fryer 1968). In artificial or manipulated systems, however, populations of *Argulus* can grow to the point of causing mass mortalities (Wilson 1902, Fryer 1968, Menezes, Ramos, Pereira & Moreira da Silva 1990, Northcott *et al.* 1997).

Rahman (1996) found over 80% of 1.5-2cm carp to be killed within 24 hours when experimentally infected with 20-30 metanaupli while Stammer (1959) found that 175-200 lice would kill carp of 15 inches held at 21°C within 2 weeks of infection. Menezes *et al.* (1990) and Northcott *et al.* (1997) describe cases of massive mortalities in still waters where lice numbered up to 1500 lice per fish and Jafri & Ahmed (1994) report mortalities of 30-40 fish/day caused by infections of 70-100 lice on 15-25cm carp, in an Indian fish farm. Mortality may also have a significant effect on wild fish populations. After studying *A. canadensis* in a community of three different species of stickleback, Poulin & Fitzgerald (1987) hypothesised that *Argulus* could actually play a role in structuring a fish community as mortalities in certain species were highly significant. This appeared to be dependent on the behaviour of the particular species of fish.

Heavily infected fish may show obvious clinical signs. For example, Menezes *et al.* (1990) found large numbers of lice on the skin, gills and in the oral cavity of fish which, as a result, had pale gills and oral mucosa, skin abrasions, severe haemorrhaging and ulcerative lesions. Rahman (1996) found that such lesions could extend into the muscle of fish. Infected fish may also show increased mucus production (Post 1967).

*Argulus* infected fish may show noticeable behavioural changes that develop as the severity of the outbreak increases. Early in an outbreak, fish in lakes are reported to jump, flash and swim erratically, possibly in an attempt to rid themselves of the lice. Following this, feeding is reduced and the fish become uncatchable to anglers. As infection levels rise, fish have been observed to swim in tight shoals, possibly a parasite avoidance mechanism (Poulin & Fitzgerald 1998d). This is followed by a period of sluggish, aimless swimming before a loss of equilibrium, which is normally shortly followed by death (Prabhavathy 1976, Hoffman 1977, Post 1987, Knight 1996, Jafri & Ahmed 1994, Rahman 1996, Northcott *et al.* 1997).

Argulus-infected fish may show a significantly reduced growth rate, and loss of physical condition makes them susceptible to stress and secondary infection (Chen 1933, Prabhavathy 1976, Shimura, Inoue, Kudo & Egusa 1983, Poulin & Fitzgerald 1987, Singal *et al.* 1990, Jafri & Ahmed 1994, Rahman 1996). Singal *et al.* (1990) found that over an eight week period the mean increase in weight of carp infected with *Argulus* was 0.24% compared to 2.6% in uninfected fish; there was also a highly significant reduction in the condition factor of infected fish. These effects will obviously affect production in farm ponds (Jafri & Ahmed 1994), but they also reduce the aesthetic appeal of fish in a sports fishery to anglers (personal communications with fishery owners and anglers).

There are very few histopathological studies on the effect of *Argulus* on fish. Kabata (1970) & Rahman (1996) describe hyperplasia of the epithelium and congestion of blood vessels in infected carp. Ultimately, haemorrhagic, ulcerative lesions may develop. However, in a study on the effects of *A. foliaceus* on trout, Nolan *et al.* (2000) found there to be no significant effect on the total number of mucous cells nor was there significant on cellular proliferation. Their study did, however, show that there could be an increased turnover of mucous cells. Van der Salm *et al*. (2000) also found no change in the number of mucous cells. These authors did not find cell death in the upper epidermis to be characteristic of *Argulus* infection, although they acknowledge this was shown in other SEM studies. They did, however, show that there was increased apoptosis in certain cell types in the lower epidermis of what?

*A. coregoni* infection of trout was shown by Shimura, Inoue, Kasai & Saito (1983) to increase plasma glucose concentration after 24 hours but, after 10 days, no significant difference could be seen between treated and control fish. After 10 days, infected fish had lower erythrocyte, leucocyte and haemoglobin concentrations and haemocrit values had also decreased, although in some fish immature erythrocyte counts appeared to increase. A study on the effects of *Argulus* infections on haematological parameters by Tavares-Dias, Martins & do Nascimento Kronka (1999) found an increase in monocytes and special granulocytic cells, and an increase in the numbers of thrombocytes in *Piaractus mesopotamocus* Holmberg 1887. Raune *et al*. (1999) found *A. joliaceus* infection to increase plasma cortisol levels, as did Nolan *et al*. (2000), although this increase was not significantly different from uninfected control groups. Ruane, McCarthy & Reilly (1995) showed that although there was no mucosal antibody response to antigens from *A. foliaceus*, there was a significant humoral response in rainbow trout. There was also evidence that the observed antibody response was cross-reactive with sealice antigens. There is no evidence that this host response had any protective effect against the *Argulus* infection.

*Argulus* spp. have often been associated with secondary infections or as a vector for other disease causing agents. Shimura, Inoue, Kudo & Egusa (1983) showed that levels of the bacterial infection, furunculosis, increased in fish infected with *A. coregoni,* although lesions caused by furunculosis could not be directly correlated with the attachment sites of *Argulus*. Bower-Shore (1940), Singhal, Jeet & Davies (1990) and Rahman (1996) showed a similar association between *Argulus* infections and infections by the fungus *Saprolegnia*. Rahman (1996) showed the onset of infections with *Saprolegnia* to be rapid and extensive in the presence of *Argulus*. The fungus was found to impede the healing process following infection by *Argulus*.

Pfeil-Putzien & Baath (1978) isolated the spring-viraemia virus, *Rhabdovirus carpio,* from both carp and *A. foliaceus*. A subsequent study by Pfeil-Putzien (1978) showed that *Argulus* could indeed transfer the virus to carp. Ahne (1985) proved *A. foliaceus* to act as a mechanical, but not a biological vector for the virus. *A. foliaceus*has also been shown to be an intermediate host for skrjabillanid nematodes, which infect the sub-cutaneous tissues of the fins, swimbladder and abdominal cavities of different fish species in Hungary (Molnar & Szekely 1998). Moravec, Vidal-Martinez & Aguirre-Macedo (1999) also found *Argulus* to act as an intermediate host for the nematode, *Mexiconema cichlasomae auth*.

# 7. DISTRIBUTION

Two of the species of *Argulus* found in Britain can be regarded as native; these are *A. foliaceus* and *A. coregoni*. *A. foliaceus* is a widely recorded species found largely in mesotrophic and eutrophic lakes. *A. foliaceus* can also tolerate waters with salinities of up to 8-12% at a range of temperatures (Moller 1977). Pasternak *et al*. (2000) also notes that *A. foliaceus* can reach epiozootic proportions in brackish waters. *A. coregoni* is mostly recorded from rivers, streams and cool oligotrophic lakes with a large flow (Gurney 1948, Rushton-Mellor 1992, Campbell 1971, Okland 1985), although mixed populations of *A. foliaceus* and *A. coregoni* have been noted in Finland (Mikeev *et al.* 2001). The third species of louse recorded in Britain, *A. japonicus,* is regarded as a non-native species probably introduced from the Far East through the ornamental trade (Rushton-Mellor 1992, Northcott; Lyndon & Campbell 1997). *A. japonicus* is widespread throughout Europe, Africa, North America and the Far East. At present there are limited records of *A. japonicus* in the UK, but it is possible that it has been mis-recorded as *A. foliaceus,* due to difficulty in differentiating the two species, especially in the case of females. Little is known about the rate of spread, tolerance to the British climate or the virulence of *A. japonicus* in comparison with *A. foliaceus,* but Rushton-Mellor (1992) suggested *A. japonicus* was confined mainly to the South of England.

*Argulus foliaceus* and *A. coregoni* are both widely distributed and frequently recorded in England and Wales. Both species are recorded from Scotland but less commonly than in England and Wales, possibly due to the harsher climate or fewer studies. Rushton-Mellor (1992) described *A. japonicus* as being restricted to south of the central Highlands and Campbell (1971) reviewed waterbodies in Scotland where *Argulus* has been found. More recent work by Northcott *et al.* (1997) described the occurrence of several epizootics of lice in Scotland. The most northerly record appears to be in Perthshire (SOFEAD Annual Report). At present there appear to be no published records of *A. japonicus* in Scottish lochs or rivers.

The prevalence of *Argulus* in UK stillwater trout fisheries was determined as part of a random cross-sectional study carried out by the authors in 2001. The most comprehensive lists of fisheries available were divided into regions and sites were selected using a random number generator. Of the 70 randomly selected fisheries providing data suitable for analysis, 42% had a known history of *Argulus*, and 29% stated they had suffered from ‘problem’ *Argulus* in at least one lake in the year 2000. ‘Problem *Argulus*’ is defined as a population sufficient to cause fish to go off their feed and lose condition. This randomised survey detected *Argulus* only in central and southern England (South of Liverpool) and Wales with 39% of waters in these areas suffering from problem *Argulus* in 2000. This would suggest that *Argulus* is less prevalent in the North of England and Scotland. However, a number of reports of *Argulus* in waters in Scotland and the North of England were confirmed during the survey, all of which were south of the Highlands.

# 8. PREVENTION AND CONTROL

At present there are no chemicals or chemotheraputants licensed for use in the UK that are effective against *Argulus* . Much of the older literature describes the use of various organophosphate treatments and other pesticides. Chemicals such as Benzene Hexachloride, DDT, DFDT, Diptrex, Diflubenzuron, Dylox, Gammexane, Lysol, Potassium Permanganate, Pyrethrine and their appropriate doses have been described by Hindle (1948), Stammer (1959), Hoffman (1977), Hoffman (1980), Singhal, Jeet & Davies (1986), Post (1987), Knight (1996) Tonguthai (1997) and Williams (1997), many of which are banned, unavailable or ineffective. Of these treatments diptrex appears to be referenced most commonly for the treatment of *Argulus* and treatment is usually applied by spraying the surface of ponds. Thus, Tonguthai (1997), referring to its use in South East Asia, suggests sprinkling diptrex over the entire water surface so that the concentration is uniform at a dose of 0.3ppm. However, he states that this has no effect on the eggs; therefore 2-3 treatments must be applied over a period to kill recently hatched juveniles. Although many of these chemotheraputants appear to achieve some degree of success, diptrex and many of the other compounds listed above are potentially very damaging to the environment and human health and thus no licences for their use have been granted in the UK.

Raune *et al.* (1995) suggest the development of a vaccine may be possible in the future, but at present there appears to be little progress toward such a measure. Nolan *et al*. (2000) found that administration of cortisol reduced parasite establishment, finding this to be correlated to vesicle synthesis in the epidermis, but it is unlikely that this could be the basis of a successful control method.

Various measures have been proposed to prevent the introduction of *Argulus* into waters. The most obvious is to avoid the import of fish, weed, boats or equipment from potentially infected sources. Other measures include stopping the use of live bait and attempting to ensure that anglers dry or disinfect tackle, footware and equipment (Northcott & Walker 1996, Northcott & Walker 1997, Northcott 1997, Northcott 1998, Anon 1998. These measures might be most useful in closed waters, i.e. with no inflow. In open waters preventing the entry of *Argulus* will be much more difficult. Hoffman (1977) suggests that covering pond inlets with 3.2mm mesh could prevent the introduction of adult lice, although this may not be practical since filters may become blocked and will certainly require high maintenance.

In *Argulus*-infected waters, Hoffman (1977) suggests that increasing flow through the lake, fertilising to darken the water, refraining from stocking until after the ‘spring hatch’ and removing potential spawning substrates such as rocks, weed and wood may help control numbers. Although useful management tools in small farm ponds, in many fisheries such measures are not very practical. In small lakes it may be possible to add an artificial spawning substrate that could be removed and dried to reduce egg numbers (Bauer 1970, Hoffman 1977). Gault *et al*. (2002) appear to have had some success in controlling a population of *A. foliaceus* in a stillwater trout fishery using floating egg laying boards. Fifty, 1$m^2$ opaque corrugated plastic boards, suspended horizontally 6mm beneath the waters surface were placed around the edge of a 12.9 hectare reservoir. Boards were removed and replaced every 2 weeks. The year after this intervention was introduced there was a 146-fold reduction in egg laying, and the prevalence and intensity of the *Argulus* infection was reduced 9-fold and 6-fold, respectively. Longer-term studies are needed to provide evidence that this is a sustainable effect.

Wilson (1902) suggested that introduction of sticklebacks, small dace and roach could be an effective form of biological control. Although there is evidence that these species and several others will predate upon *Argulus* (Wilson 1902, Bower-Shore 1940, Thomas 1961, Bauer 1970, Kimura 1970, and observations by the authors), there is little evidence to suggest that this would be an effective control method in a fishery, and it could in fact exacerbate the problem by providing a wider reservoir of hosts.

If it is physically possible the best control method for *Argulus*-infected waters is to empty them of fish and allow a fallow period before re-stocking. This would have to be long enough to allow for the hatching of eggs and the death of resulting parasites. Alternatively lakes could be drained and left empty for sufficient time for eggs to be killed by desiccation or frost (Chen 1933,Stammer 1959, Jafri & Ahmed 1994, Tonguthai 1997). Liming of the dried lake bed is an extra measure. Dosage should be at least 40kg/acre. Limed lakes should be left for several days before being refilled and the pH be allowed to return to normal before restocking (Chen 1933, Stammer 1959, Jafri & Ahmed 1994, Tonguthai 1997). As far as possible great care should be taken not to reintroduce the parasite when the lake is refilled and restocked.

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