Host searching in *Argulus foliaceus* L. (Crustacea: Branchiura): the role of vision and selectivity

V. N. MIKHEEV[1], E. T. VALTONEN[2]* *and* P. RINTAMÄKI-KINNUNEN[3]

[1] *A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia*
[2] *Department of Environmental and Biological Science, University of Jyväskylä, PL 35, 40351 Jyväskylä, Finland*
[3] *Department of Biology, University of Oulu, Finland*

(*Received 26 August 1997; revised 8 December 1997; accepted 8 December 1997*)

SUMMARY

In laboratory experiments, the swimming behaviour of the ectoparasite *Argulus foliaceus* and its infection rates on juvenile perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) were examined. The highest infection rate and a preference for perch juveniles were obtained in darkness, the lowest infection rate and a lack of preference in the light, when aquaria with glass walls (high reflectivity) were used. In the light, when aquaria were lined with black plastic (low reflectivity) an intermediate level of infection for perch and the highest for roach was recorded. Under such conditions roach were significantly more heavily infected than perch; an attack rate 4 times greater was recorded for brighter (more reflective) roach juveniles than for perch. Within the aquaria with a low reflective interior parasites swam 4·4 times slower and were observed predominantly in the central area, while in the highly reflective aquaria fast swimming *A. foliaceus* were recorded mainly near the walls. The primary role of visual stimuli for the host search behaviour of *A. foliaceus* in the light is suggested. Parasites can effectively use such stimuli only in the low reflective surroundings. Highly reflective glass aquarium walls produce numerous secondary local light sources, which cause fast, erratic parasite movements and prevent the efficient location of potential hosts.

Key words: ectoparasite, searching behaviour, fish host, selectivity.

INTRODUCTION

Argulus foliaceus is a widespread ectoparasite of many freshwater fish species. It is an obligatory blood sucker and can survive for only a few days without the host fish. This period is even shorter (less than 48 h) for juveniles (Kollatsch, 1959). Juveniles hatch from eggs laid on the substrate. Consequently, they need to find a fish host at least once during their short life. It is possible for the host fish to die from the infection or for some other reason, or even get rid of the parasites. Thus, the need to search for another host can arise for *A. foliaceus* again and again, and, when host density is low, the *Argulus*–fish encounter rate can be a crucial factor influencing parasite survival and reproduction.

In order to describe and quantify host searching success of the free-swimming parasite we need to know its movement characteristics and perceptual abilities for the location of a potential host. These parameters of parasite behaviour, together with estimations of attack efficiency, provide the basis for the assessment of the host search rate. During the free-swimming period *A. foliaceus* face the same problems as any aquatic predator searching for food items or food patches (e.g. O'Brien, Evans & Browman, 1989; Getty & Pulliam, 1991; Mikheev, Pavlov & Pakulska, 1992). For example, a variety of foraging models developed for juvenile fish (e.g. Gerritsen & Strickler, 1977; Wright & O'Brien, 1984; Hart, 1989) which, under certain conditions, can predict food search success, at the very least contain information on predator visual ability (e.g. Confer *et al*. 1978; Wanzenböck & Schiemer, 1989) and swimming speed (e.g. Hunter, 1972; Fuiman & Webb, 1988). It had previously been well established that vision is of primary importance to juvenile fish in the search for food. In the case of *A. foliaceus* hunting for a host fish, the behavioural basis for a host search model is rather poor. Published data are rather fragmentary and, sometimes, controversial. Bohn (1910) observed that specimens of *A. foliaceus* were stimulated by the shadow of a fish passing above – this caused the parasite to move towards the fish. However, Herter (1927) found neither optical nor chemical stimuli which elicited any distant response of the parasite directed towards a swimming fish. According to the latter author, *A. foliaceus* encounter fish randomly. When close to the fish *Argulus* responds either to water movements produced by the fish or to tactile stimuli (Herter, 1927). Kollatsch (1959) observed rapid movements ('Schiessen') in *A. foliaceus* in response to sudden changes of illumination, but he considered these movements to be non-directional and unrelated to

---

* Corresponding author: Department of Environmental and Biological Science, University of Jyväskylä, PL 35, 40351 Jyväskylä, Finland. Tel: +358 14 602329. Fax: +358 14 602321. E-mail: etvalto@tukki.jyu.fi

the host search behaviour. However, random walk is a very inefficient way to find a host, and its seems to be rarely used by actively searching parasites. For instance, among trematodes, there is no actively host-invading species hitherto studied which finds its host purely by chance (Haas, 1994). The free-living infective stages of *Salmincola edwardsii*, ectoparasitic copepod of brook trout, greatly increased locomotor activity when stimulated by visual and mechanical cues (Poulin, Curtis & Rau, 1990). So far this paper is one of the very rare studies on host-finding behaviour of parasitic crustaceans.

The classical work by Herter (1927) is still the most detailed source of information on the behaviour of *A. foliaceus*. However, the data presented in this voluminous work are predominantly descriptive and provide no basis for quantitative assessment of the parasite search behaviour. Moreover, the role of vision in *A. foliaceus* seems considerably underestimated. According to Herter (1927), it serves only for the parasite to choose well-illuminated areas and avoid the surface zone with too much light. But, in the detailed anatomical description of *A. foliaceus* (see Madsen, 1964), it was emphasized that the lateral eyes are the most developed sense organs in this animal. The necessity for further experimental studies on the behaviour of the dispersal stages of parasitic crustaceans has been noted as of primary importance (Kabata, 1981; Poulin & FitzGerald, 1989*a*).

In addition to the influence of parasite behaviour on host–parasite encounter rate, a partial preference for a particular fish host might be suggested for *A. foliaceus*. Such a preference could be another important factor influencing host search success. Some authors (Kollatsch, 1959; Petrushevski, 1970; Shulman, 1970) emphasized a wide range of host species and a lack of specificity with regard to *A. foliaceus*. However, extensive field studies in a number of lakes in Finland have clearly demonstrated higher levels of infection in perch, *Perca fluviatilis* L., than for roach, *Rutilus rutilus* L., in terms of both prevalence and intensity (Valtonen, Holmes & Koskivaara, 1997). We believe that experiments under controlled conditions are needed to understand the factors leading to such a biased distribution on the hosts.

The objectives of this study were to describe and quantify the host search behaviour of *A. foliaceus* adults, and to compare the vulnerability of roach and perch 0+ juveniles to *Argulus* infection under various conditions of illumination.

MATERIALS AND METHODS

Parasite and host species

Parasites were collected from perch, *P. fluviatilis*, of various sizes which were caught every 2–3 days in Rutalahti Bay (Lake Päijänne in Central Finland) during August 1996. In the laboratory *A. foliaceus* were gently detached with forceps and held in 20 l glass aquaria filled with filtered lake water (20 ± 1 °C; 16:8 h light:dark) without fish. Parasites were used in experiments within 2–3 days after they had been collected from the host. Adult specimens with a body length 3·96 ± 0·37 mm (mean ± S.D.) were selected for tests.

Young (0+) perch, total length 32·2 ± 1·99 mm (mean ± S.D.), and roach, 30·6 ± 2·37 mm, were used as hosts in infection experiments. Perch juveniles were collected from Rutalahti Bay and roach from a small dammed stream, a tributary of the river Rutajoki. Fish were kept in separate tanks with flow-through lake water (18–20 °C; 16:8 h light:dark) and fed with zooplankton. When collected the stock of perch juveniles included fish infected with *A. foliaceus*. The infected fish usually had only 1 parasite/fish and the prevalence did not exceed 10 %. Only parasite-free perch were taken to keep in the holding tank. No *A. foliaceus* were found on roach juveniles, which were thoroughly inspected before release into the holding tank.

Experimental design and procedures

The study was carried out at the Tammen Mylly research station (University of Jyväskylä, Finland) during August 1996.

Swimming behaviour and response to surroundings were studied using a single *A. foliaceus* placed in a 4 l aquarium with a grid drawn on the bottom and enumerated in X–Y coordinates. The grid consisted of 8 × 10 squares of 23 × 23 mm. Two types of aquaria were used, a transparent glass aquarium and another covered with black plastic on the inside. The idea of using aquaria with a low or high reflectivity had arisen after pilot observations on the response of *A. foliaceus* to various materials inserted into the observation tank. In preliminary observations parasites were attracted by the objects with a highly reflective surface and avoided those with low reflectivity.

A standard trial with 1 specimen of *A. foliaceus* consisted of 3 × 5 min periods with a 10 min pause between consecutive periods of visual recording of parasite movements over the bottom grid. The *A. foliaceus* position was estimated in X–Y coordinates every 5 sec. First, these observations were carried out in the aquarium lined with black plastic. Then, a juvenile perch was released into the aquarium, and the observations were repeated. Following this, the parasite was moved into the aquarium with normal glass (highly reflective) walls, where the series of recordings was repeated. Seven individual *A. foliaceus* were tested in such trials. The average swimming velocity, as well as the frequency distributions of the parasite's occurrence as a function of

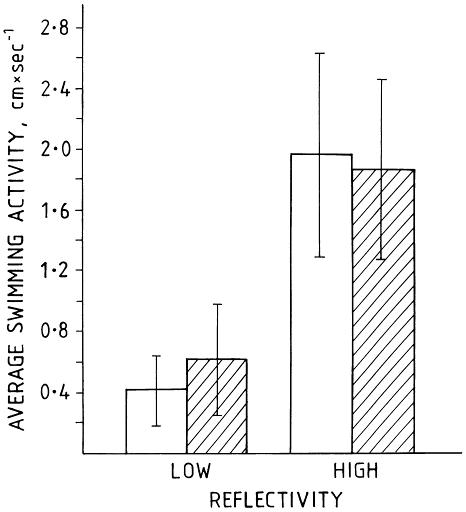

Fig. 1. Swimming activity of individual *Argulus foliaceus* under different optical conditions. (□) Without fish; (▨) with 1 juvenile perch. Means and S.D. bars are shown.

the distance from the nearest aquarium wall, were calculated using the resulting series of X–Y coordinates.

The experiments on infection rates were run in 4 l glass aquaria filled with filtered lake water (20 ± 1 °C) and illuminated with cool-white fluorescent tubes from above (250 lux at the water surface). Three fish, either perch or roach, were exposed to 3 parasites for 1 h under 1 of the 3 illumination regimes: (1) complete darkness (7 replicates with perch + *Argulus* and roach + *Argulus*); (2) 250 lux with the aquarium being lined with black plastic (condition of low reflectivity) (11 replicates); (3) 250 lux with the aquarium walls and bottom being transparent glass (condition of high reflectivity) (11 replicates). Fish were kept in the experimental aquarium for 15 min prior to release of the parasites. After the exposure, the number of parasites attached and their position on the fish body were assessed. The attack rate was calculated as the number of parasite jerks towards the swimming fish counted during 10 min periods (12 replicates). In the light *A. foliaceus* usually attack swimming fish while hovering or slowly gliding in the water column. Their jerks are easily recognizable as fast, directional movements towards the fish. Trials with perch and roach were run simultaneously between 10.00 and 18.00 h.

RESULTS

Swimming activity and response to surroundings

Differences in the reflectivity of the experimental tank interior changed the behaviour of *A. foliaceus* immediately and significantly. In the aquarium with a highly reflective interior its average swimming speed was 4·4 times faster (Wilcoxon matched-pairs test: $n = 7$, $P = 0{\cdot}018$) than that in the aquarium lined with black plastic (experiment without a fish) (Fig. 1). Frequencies of parasite visits to different zones of the aquarium were also very much different in 2 types of optical environment (Fig. 2). When in the aquarium with transparent glass walls, parasites strongly preferred to move close to the walls, attaching to them from time to time. The average frequency of occurrence in the nearest 2·3 cm zone from the wall was 5·6 times higher for *A. foliaceus* in the transparent aquarium than in the dull black one (Wilcoxon matched-pairs test: $n = 7$, $P = 0{\cdot}018$). The presence or absence of fish did not affect the results of this experiment.

The behaviour of free-swimming parasites in 2 optically different experimental environments was different not only in quantitative characteristics but also qualitatively. In the black aquarium, *A. foliaceus* was most frequently observed 'hovering' in the water column almost without any noticeable movement or slowly 'gliding'. Such a behaviour lasted from 10 sec to several min, then the parasite would change its position for the next 'hover station'. In the transparent aquarium such hovering was almost never observed. The parasites were swimming erratically with variations in velocity close to the walls and especially the corners, and occasionally striking the glass surface.

When 1 juvenile perch was placed into the aquarium with a free-swimming parasite, the behaviour of *A. foliaceus* was not changed in the case of the transparent aquarium (Figs 1 and 2) (Wilcoxon matched-pairs test: $n = 7$, $P = 0{\cdot}61$ for velocity; and $n = 7$, $P = 0{\cdot}61$ for occurrence near the walls). In the black aquarium, parasites were observed close to the walls rather less frequently, but the difference was not significant (Wilcoxon matched-pairs test: $n = 7$, $P = 0{\cdot}35$); the average swimming velocity of *A. foliaceus* increased noticeably when the fish was present, but the difference was not statistically significant (Wilcoxon matched-pairs test: $n = 7$, $P = 0{\cdot}09$).

The vulnerability of perch and roach juveniles to infection by A. foliaceus

The highest infection rate was obtained for perch juveniles in the dark (Fig. 3). Under the same conditions, roach were significantly less infected (Kruskal–Wallis ANOVA: $H(1,14) = 8{\cdot}95$, $P = 0{\cdot}003$). The lowest rates for both fish species were observed in the aquarium with a highly reflective interior (Fig. 3). In this case, the infection rates for perch and roach were not significantly different (Kruskal–Wallis ANOVA: $H(1,22) = 0,45$, $P = 0{\cdot}45$). The infection rate was the highest for roach and at the intermediate level for perch in the illuminated aquarium with a black interior (Fig. 3). Under such optical conditions, roach juveniles were more heavily infected than perch (Kruskal–Wallis ANOVA: $H(1,22) = 5{\cdot}64$, $P = 0{\cdot}018$).

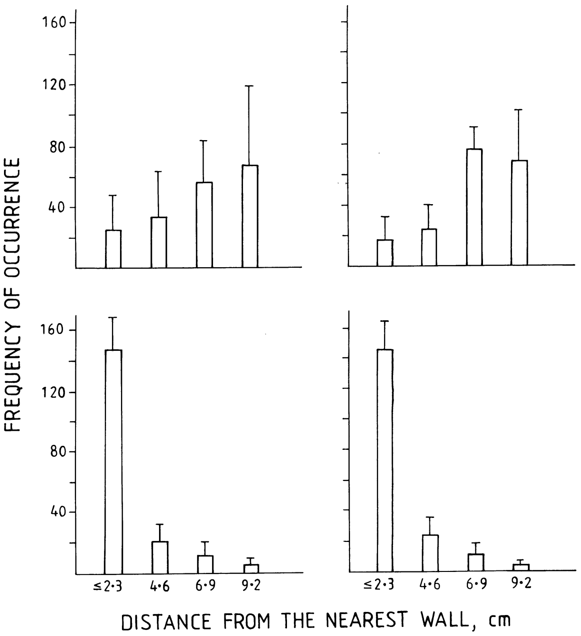

Fig. 2. Occurrence of individual *Argulus foliaceus* in different zones of the aquarium (relative to the walls) under the low (upper panel) and high (lower panel) reflective condition of the aquarium interior. Left histogram – *A. foliaceus* without fish; right histograms – with 1 juvenile perch. Means and S.D. bars are shown.

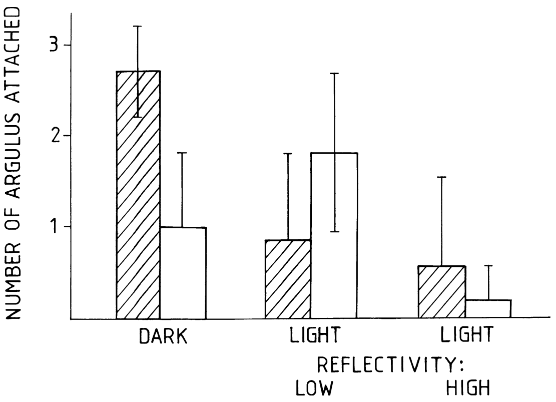

Fig. 3. Vulnerability of perch (▨) and roach (☐) to *Argulus foliaceus* under different optical conditions. Means and S.D. bars are shown.

Roach juveniles were noticeably more attractive to parasites than perch in the illuminated experiment with the low reflective environment. The average attack rate was significantly higher for roach (4·17 ± 2·37 attacks/parasite over 10 min; mean ± S.D.) than for perch (1·0 ± 0·85) (Kruskal–Wallis ANOVA: $H(1, 24) = 10·38$; $P = 0·001$). In the aquaria, swimming fish were most frequently attacked either from the side or from the bottom, but almost never from the top. The ratio of the attached parasite numbers counted on the dorsal:lateral:ventral regions of the fish was 1:10:1 for perch, and 1:15:4 for roach. In perch, parasites preferred the head area (anterior to the pectoral fins) than other parts of the body (posterior to the pectoral fins); the ratio being 2·7:1. Conversely, the silvery sides and belly were the most preferred sites in roach; the same ratio for roach was 1:2·2. The reactive distance for *A. foliaceus* attacking fish was usually between 2 and 6 cm. As a rule, *A. foliaceus* attacked fish from the 'hovering' position. In the highly reflective environment, the attack rate was much lower than 1 attack/parasite over a 10 min period, and did not appear to differ between roach and perch.

DISCUSSION

The present results reveal that optical conditions and reflectivity within an experimental tank strongly influence both the swimming characteristics of *A. foliaceus* and its rate of infection. Moreover, a clear preference for perch juveniles in the dark changed to a preference for roach juveniles in the light when fish and parasites were in an aquarium with a dark interior.

Juvenile perch as sympatric host for *Argulus* could potentially develop more efficient anti-parasite behaviour compared to roach that were caught from apparently *Argulus*-free water. However, in the present experiments, under constraints of limited time and space, fish seemed not to have adequate conditions to use all their anti-parasite repertoire. We observed no noticeable behavioural differences between juvenile roach and perch at the presence of *A. foliaceus*.

It is still unclear, whether olfactory or hydrodynamic cues, or both, or the lower motility of perch juveniles (Pavlov *et al.* 1981), cause perch to be more attractive than roach to *A. foliaceus* in the dark? Judging from the data on the anatomy *A. foliaceus* (Madsen, 1964), the rheosensitive bristles on the anterior margin of the cephalon and the dorsal surface of the carapace should be the most important sense organs of *Argulus* in the dark. The chemoreceptors on the antennules and antennae are very few and of questionable significance.

As to the behaviour of *A. foliaceus* in the light, the primary role of vision for free-swimming parasites in searching for the host is evident. Well-developed lateral eyes and the corresponding neuronal centres (Madsen, 1964) serve *A. foliaceus* not only in terms of its phototactic response which brings the parasite into areas with optimal illumination, as Herter (1927) concluded, but also plays the key role in the distant location of a host in the light. In the pilot experiments, we observed a strong positive response of *A. foliaceus* to highly reflective objects (like the blade of a stainless steel knife) plunged into the aquarium. In such a case, *A. foliaceus* made a very quick movement towards the bright object from distances of up to 10–15 cm. Kollatsch (1959) also observed very rapid movements of *A. foliaceus* in response to sudden changes of illumination in a part of an aquarium, but he stressed that they were not directed towards the light source and he did not consider such movements as a possible component of the host search behaviour. We observed similar movements to be rather directional. Perhaps, the differences between our observations and those of Kollatsch (1959) are related to the types of light sources used. Kollatsch (1959) used bulb flashes; rather than small, highly reflective objects, such as elongated polished pieces of stainless steel as were used in our case. Our data on the preference for more silvery (reflective) roach juveniles compared to perch (judging from the higher attack and infection rates in the aquarium with black walls) is more evidence for the importance of the parasite's optical-motor response in its host search behaviour. Moreover, we found newly attached parasites predominantly on the most reflective parts of the fish body (the sides and the belly in roach and the head in perch). Nevertheless, it should be stressed that these effects were observed only in aquaria with low reflective (black) lining. Regular glass aquaria, which are usually used in experiments with aquatic animals (but see Munk (1995) where black plastic tanks were used in experiments with larval fish), produce numerous secondary light sources, particularly in the corners and the wall–wall surface interface, which seem to be attractive to *A. foliaceus*. Ambient light could be also transmitted from surroundings. Such an abundance of spurious visual targets could cause a so-called confusion effect or sensory overload (Miller, 1922; Milinski, 1990) that makes a 'predator' less efficient at detecting prey (Dukas & Ellner, 1993).

The host search success of *A. foliaceus* would be positively correlated with its average swimming velocity if Herter's suggestion concerning the random swimming pattern during host searching was correct. However, in our experiments we have found just the opposite relationship. The higher the swimming velocity (in transparent aquaria), the lower the infection rate. Hunting *A. foliaceus* was most successful at locating and attacking fish while hovering, i.e. while almost motionless. We observed no advances towards fish from the actively moving parasite, even if a potential host was as close as 2–3 cm. There is published evidence consistent with the idea that many predators search prey only while paused and not while actively swimming (O'Brien *et al*. 1990).

Poulin & FitzGerald (1989*a*) discovered that juvenile three-spined sticklebacks, *Gasterosteus aculeatus*, infected with *Argulus canadensis* showed higher probabilities of acquiring additional parasites than uninfected individuals. The authors noticed that infected fish swam in an erratic way and suggested that the altered swimming behaviour of infected sticklebacks may make them easier to detect by other parasites, which may rely on hydrodynamic stimuli. Taking into account our results on the role of visual stimuli, we suggest that infected fish have an abnormal swimming behaviour that produces more flickering light reflections which are attractive to these parasites. In a natural situation, fish can use their anti-ectoparasite behaviour like enhanced shoaling (Poulin & FitzGerald, 1989*b*) or alter their microhabitat distribution in response to *Argulus* (Poulin & FitzGerald, 1988) that can modify an outcome of host–parasite interactions. Preference for silvery juvenile roach found in this study, can be related to a particular situation and could produce only a small effect on overall host preference. In fact, perch are much more infected than roach with *Argulus* in Finnish lakes (Valtonen, E. T. unpublished observations). Higher infection rate and preference for perch in darkness found in the present study, might be more significant for *Argulus* host preference in nature. Behavioural mechanisms of host location and selection by *A. foliaceus* still requires more detailed study. It is most likely that different sensory organs operate in the light and dark, making the results of the host search behaviour dependent not only on the parasite's abilities but also on the behaviour and spatial distribution of potential hosts. The twilight period appears to provide the most intriguing situation when considerable changes in the behaviour and distribution of both fish and *A. foliaceus* can significantly influence both the infection rate and selectivity.

As to the ecology of parasite transmission, it is obvious that an ability of *A. foliaceus* to infect various fishes both in the dark and light conditions enhances its overall host-finding success. An extended temporal overlap in the parasite and host activities together with the spatial one would result in more efficient functioning of a 'net of infectivity' (Rea & Irwin, 1995).

We thank the staff of the Tammen Mylly Research Station (University of Jyväskylä), especially Mr Markku Palmunen, for help in collecting both fish and parasites and for helping with the experiments. Drs R. Poulin, H. Ylönen and an unknown referee made valuable comments on the manuscript. Dr David I. Gibson kindly checked the English.

REFERENCES

BOHN, G. (1910). Sur les réactions comparées de deux parasites des poissons vis-à-vis de la lumière. *Comptes rendus de l'Association Française pour l'Avancement des Sciences* **38**, 726–729.

CONFER, J. L., HOWICK, G. L., CORZETTE, M. H., KRAMER, S. L., FITZGIBBON, S. & LANDESBERG, R. (1978). Visual predation by planktivores. *Oikos* **31**, 27–37.

DUKAS, R. & ELLNER, S. (1993). Information processing and prey detection. *Ecology* **74**, 1337–1346.

FUIMAN, L. A. & WEBB, P. W. (1988). Ontogeny of routine swimming activity and performance in zebra danios (Teleostei: Cyprinidae). *Animal Behaviour* **36**, 916–928.

GERRITSEN, J. & STRICKLER, J. R. (1977). Encounter probabilities and community structure in zooplankton: A mathematical model. *Journal of Fisheries Research Board of Canada* **34**, 73–82.

GETTY, T. & PULLIAM, H. R. (1991). Random prey detection with pause-travel search. *American Naturalist* **138**, 1459–1477.

HAAS, W. (1994). Physiological analyses of host-finding behaviour in trematode cercariae: adaptations for transmission success. *Parasitology* (Suppl.) **109**, S15–S29.

HART, P. J. B. (1989). Predicting resource utilization: the utility of optimal foraging models. *Journal of Fish Biology* **35** (Suppl. A), 271–277.

HERTER, K. (1927). Reizphysiologische Untersuchungen an der Karpfenlaus (*Argulus foliaceus* L.). *Zeitschrift für vergleichende Physiologie* **5**, 283–370.

HUNTER, J. R. (1972). Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. *Fisheries Bulletin* **70**, 821–834.

KABATA, Z. (1981). Copepoda (Crustacea) parasitic on fishes: problems and perspectives. *Advances in Parasitology* **19**, 1–71.

KOLLATSCH, D. (1959). Untersuchungen über die Biologie und Ökologie der Karpfenlaus (*Argulus foliaceus* L.). *Zoologische Beitrage* **5**, 1–36.

MADSEN, N. (1964). The anatomy of *Argulus foliaceus* Linne. *Lunds Universitets Arsskrift* **59**, 1–31.

MIKHEEV, V. N., PAVLOV, D. S. & PAKULSKA, D. (1992). Swimming response of the goldfish, *Carassius auratus*, and tetra, *Hemigrammus caudovittatus*, larvae to individual food items and patches. *Environmental Biology of Fishes* **35**, 351–360.

MILINSKI, M. (1990). Information overload and food selection. In *Behavioural Mechanisms of Food Selection* (ed. Hughes, R. N.), pp. 721–737. Berlin: Springer-Verlag.

MILLER, R. C. (1922). The significance of the gregarious habit. *Ecology* **3**, 122–126.

MUNK, P. (1995). Foraging behaviour of larval cod (*Gadus morhua*) influenced by prey density and hunger. *Marine Biology* **122**, 205–212.

O'BRIEN, W. J., EVANS, B. I. & BROWMAN, H. I. (1989). Flexible search tactics and efficient foraging in saltatory searching animals. *Oecologia* **80**, 100–110.

O'BRIEN, W. J., BROWMAN, H. I. & EVANS, B. I. (1990). Search strategies of foraging animals. *American Scientist* **78**, 152–160.

PAVLOV, D. S., NEZDOLII, V. K., KHODOREVSKAYA, R. P., OSTROVSKII, M. P. & POPOVA, I. K. (1981). *Down-stream Migrations of Young Fishes in the Rivers Volga and Ili*. Moscow: Nauka (in Russian).

PETRUSHEVSKI, G. K. (1970). Changes in the parasite fauna of acclimatised fishes. In *Parasitology of Fishes* (ed. Dogiel, V. A., Petrushevski, G. K. & Polyanski, Yu, I.), pp. 255–264. T.F.H. Publications, Hong Kong.

POULIN, R., CURTIS, M. A. & RAU, M. E. (1990). Responses of the fish ectoparasite *Salmincola edwardsii* (Copepoda) to stimulation, and their implication for host-finding. *Parasitology* **100**, 417–421.

POULIN, R. & FITZGERALD, G. J. (1988). Risk of parasitism and microhabitat selection in juvenile sticklebacks. *Canadian Journal of Zoology* **67**, 14–18.

POULIN, R. & FITZGERALD, G. J. (1989*a*). A possible explanation for the aggregated distribution of *Argulus canadensis* Wilson, 1916 (Crustacea: Branchiura) on juvenile sticklebacks (Gasterosteidae). *Journal of Parasitology* **75**, 58–60.

POULIN, R. & FITZGERALD, G. J. (1989*b*). Shoaling as an anti-ectoparasite mechanism in juvenile sticklebacks (*Gasterosteus* spp). *Behavioural Ecology and Sociobiology* **24**, 251–255.

REA, J. G. & IRWIN, S. W. B. (1995). The effects of age, temperature and shadow stimuli on activity patterns of the cercariae of *Cryptocotyle lingua* (Digenea: Heterophyidae). *Parasitology* **111**, 95–101.

SHULMAN, S. S. (1970). Specificity of fish parasites. In *Parasitology of Fishes* (ed. Dogiel, V. A., Petrushevski, G. K. & Polyanski, Yu, I.), pp. 104–116. T.F.H. Publications, Hong Kong.

VALTONEN, E. T., HOLMES, J. C. & KOSKIVAARA, M. (1997). Eutrophication, pollution and fragmentation: effects on parasite communities in roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) in four lakes in central Finland. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 572–585.

WANZENBÖCK, J. & SCHIEMER, F. (1989). Prey detection in cyprinids during early development. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 995–1001.

WRIGHT, D. I. & O'BRIEN, W. J. (1984). The development and field test of a tactical model of the planktivorous feeding of white crappie (*Pomoxis annularis*). *Ecological Monographs* **54**, 65–98.