Bull. Fr. Pêche Piscic. (1993) **328** : 105-114

STIMULI DE L'ENVIRONNEMENT, ORGANES DES SENS ET COMPORTEMENT DES MONOGÈNES JUVÉNILES ET ADULTES.

G.C. KEARN

School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, U.K.

RÉSUMÉ

Lorsque les larves de Monogènes (oncomiracidiums) établissent leur premier contact avec l'hôte, celà correspond à un changement fondamental dans leur mode de vie. La disparition de quelques structures sensorielles et l'acquisition de nouvelles en témoignent ; mais il existe certainement d'autres types de changements encore inconnus au niveau du système nerveux. Le développement larvaire lui-même, à ce moment là, est initié par des facteurs eux aussi inconnus. Nos connaissances du rôle des facteurs de l'environnement sur la vie des stades parasites juvéniles et adultes sont très limitées. Chez *Entobdella soleae*, parasite cutané de la Sole, il existe une réponse comportementale au changement de concentration d'oxygène ; chez l'adulte d'*Encotyllabe caballeroi*, chez qui des yeux se développent chez les post-larves, une réponse nette à la lumière existe. Les yeux persistants que l'on trouve chez d'autres Monogènes adultes, doivent avoir un rôle plus subtil dans le comportement. Le courant d'eau peut influencer le choix du site de fixation ou le développement dissymétrique du hapteur chez les Polyopisthocotylea, mais chez *Entobdella soleae*, parasite cutané, c'est le premier contact, et non une réponse au courant d'eau qui est déterminant dans l'orientation, la locomotion et éventuellement la migration. Ce contact est aussi certainement important dans la locomotion de certains parasites branchiaux comme *Tetraonchus monenteron*. L'attraction par des phéromones n'a pas été démontrée chez les Monogènes et l'environnement turbulent de la plupart d'entre eux rend ce mode de communication peu adapté. Cependant, les relations particulières entre *E. soleae* et son hôte poisson plat procurent une situation où ce phénomène serait possible et avantageux. Bien que les hormones des hôtes apparaissent jouer un rôle dans la biologie de la reproduction des hématophages comme les Polystomes, la démonstration expérimentale manque encore.

ENVIRONMENTAL STIMULI, SENSE ORGANS AND BEHAVIOUR IN JUVENILE/ADULT MONOGENEANS

SUMMARY

There is a fundamental change in the life style as monogenean larvae (oncomiracidia) establish themselves on the host. This is reflected in the loss of some sense organs and the acquisition of others and undoubtedly in deeper-seated changes in the nervous system about which nothing is known. At the same time, larval development is initiated by factors which are also unknown. Our knowledge of the role of environmental stimuli in the daily lives of the parasitic stages (juveniles and adults) is rudimentary. A behavioural response to changing ambient oxygen concentrations is well-documented in the flatfish skin parasite *Entobdella soleae* and a vigorous response to light occurs in adult *Encotyllabe caballeroi* in which eyes develop in post-oncomiracidia. Persistent larval eyes in other adult monogeneans may have more subtle roles in behaviour. Water currents may influence site selection or asymmetry development in polyopisthocotylean gill parasites but in the skin parasite *E. soleae* contact reception, not a response to water currents, is involved in orientation, locomotion and possibly migration. Contact reception is probably important also in locomotion in the gill parasite *Tetraonchus monenteron*. Pheromonal attraction in monogeneans has not been demonstrated and the turbulent environments of many of them may render this mode of communication unsuitable. However, the special circumstances of the relationship between *E. soleae* and its flatfish host, provide a situation in which this phenomenon would be feasible and advantageous. Although host hormones seem the most likely regulators of the reproductive biology of blood feeders such as polystomes, experimental support for their involvement is still lacking.

INTRODUCTION

The oncomiracidial (larval) stage in the life of a monogenean is brief and very different in life style from the parasitic stages. Until recent years, it was the behaviour of the oncomiracidium that attracted most attention from parasitologists. The responses of the free-swimming oncomiracidia to environmental stimuli and the role of these responses in host-finding have been intensively studied and this has been an attractive topic for reviewers (see, for example, LLEWELLYN, 1972; KEARN, 1981, 1986). The increasing recent interest in the behaviour of the parasitic stages (juveniles and adults) and their interaction with environmental stimuli, and the lack of any previous attempt to review this important area, have prompted the present communication.

CHANGES ASSOCIATED WITH HOST INVASION

Oncomiracidia respond to a variety of environmental cues which may stimulate hatching at an optimum time for host-finding and serve to enhance the chances of contact between the free-swimming oncomiracidia and their hosts (see, for example, KEARN, 1981). Important changes take place when the oncomiracidia establish themselves on their hosts. The newly attached parasite abandons ciliary propulsion and adopts leech-like locomotion and there is evidence of fundamental changes in sensory equipment. LAMBERT (1980) showed that some surface sensilla disappear and are replaced by new ones; in some post-oncomiracidia the eye lenses disappear (KEARN, 1971a), in others all traces of the eyes are lost and in *Encotyllabe* spp. eyes develop for the first time (WHITTINGTON and KEARN, 1992). Larval development begins at this time but how it is initiated is unknown. MACDONALD (1977) observed that clamps appeared in some, but not in all, oncomiracidia of *Diclidophora merlangi* that failed to hatch. One interpretation of these observations is that development begins spontaneously when the parasite reaches a certain age whether or not hatching occurs, but it is equally possible that some of the unhatched larvae received and responded to an unknown stimulus. In the polystome *Pseudodiplorchis americanus*, the involvement of an unknown stimulus is implicated in the resumption of development which is suspended while parasites remain in the lungs of their toad host (TINSLEY and JACKSON, 1986).

Soon after establishment on the host, juveniles of many monogeneans embark on migrations to sites where mating, egg assembly and egg laying take place.

ENVIRONMENTAL CUES AND THE RESPONSES OF JUVENILE/ADULT PARASITES

There are reasons to believe that the following environmental stimuli play a part in the behavioural events that contribute to the lives of juvenile/adult monogeneans.

1. Dissolved oxygen

Body undulations are a feature of the behaviour of many skin-parasitic monogeneans, for example *Entobdella soleae* and *Acanthocotyle lobianchi*. It was shown by KEARN (1962) that the rate of body undulation in *E. soleae* changes in relation to ambient oxygen concentration, increasing as oxygen levels fall and decreasing as oxygen levels rise. This is accompanied by changes in the surface area of the parasite, the body becoming thinner and flatter when the oxygen level falls. Fluctuations in ambient oxygen levels are likely to occur in the natural environment because most adult parasites live on the lower surface of a bottom dwelling flatfish, *Solea solea*, that spends time either buried in anoxic sediment or swimming close to the bottom, and the undulations will serve as breathing movements, enabling the parasite to adjust to these changes in oxygen availability. Presumably *E. soleae*, and probably other skin parasites in which this ability may have evolved independently, have sensors, as yet unrecognized, which are capable of monitoring environmental oxygen levels and adjusting the rate of body undulation and the surface area of the parasite to compensate for these changes.

2. Light

In most monogeneans, pigment-shielded eyes appear to be essentially larval organs, completing their development in the embryo and probably endowing the free-swimming larva with a directional response to light (see, for example, KEARN, 1980). An interesting exception to this was recorded recently by WHITTINGTON and KEARN (1992) who observed that the eyes of some *Encotyllabe* spp. develop in early post-oncomiracidia. A possible role for these late-developing eyes is suggested by the discovery of a remarkable response to light in adult encotyllabines (KEARN and WHITTINGTON, 1992a). Adult specimens of *E. caballeroi* attached to the pharyngeal tooth pads of their host respond to a sudden increase in light intensity by rapidly withdrawing their bodies into a pharyngeal crevice. They remain virtually hidden from view for 60-100s if the brighter lighting persists but re-extend if the light intensity is reduced. The function of this response, which is reminiscent of the giant-fibre mediated contractions of annelid worms, is obscure.

In *E. soleae*, the lenses disappear after invasion of the host but the pigment cups persist. In juveniles and adults there is no dramatic response to light like that of *Encotyllabe* and the persistent pigment cups could be regarded as non-functioning remnants. However, the rhabdomeres also persist inside the cups (KEARN, previously unpublished observation), suggesting that the eyes are still functional and we may have to look for a more subtle influence of light on behaviour. For example, juvenile and adult specimens of *E. soleae* migrate forwards on the upper surface of their flatfish host and then move onto the lower surface (KEARN, 1984, 1988a), but parasites on the lower surface show no tendency to migrate forwards and it is possible that the greater illumination experienced by parasites on the upper surface stimulates this migration.

There are indications that photoperiod may influence egg production in some monogeneans; for example, in *Diplozoon homoion gracile* MACDONALD and JONES (1978) collected more eggs during the night than during the day.

3. Water currents

Many monogeneans adopt striking orientations on the host which are often correlated with patterns of water flow generated by host swimming or by gill ventilation. Gill-parasitic polyopisthocotyleans in particular adopt positions in which the adhesive organs (clamps) are attached upstream with respect to the more or less continuous gill-ventilating current, and during larval development the bodies of many of them adopt permanent or facultative asymmetrical body shapes or poses which minimize the interaction between their bodies and the gill flow (LLEWELLYN, 1956, 1960). The arrangement of the gills is such that available attachment sites fall into one of two categories depending on whether gill-flow strikes one side of the primary gill lamella or the other, and some of these gill parasites are obliged to adopt correspondingly "left-footed" or "right-footed" asymmetry, depending on which site they occupy. As LLEWELLYN (1964) pointed out, it is not known whether the newly-settled bilateral oncomiracidia are predetermined genetically as either left- or right-footed individuals or whether they are potentially capable of development into one morph or another depending on the environmental influence. Therefore the direction of water flow is likely to have an influence either on choice of site or on the pattern of asymmetrical development.

The skin parasite *E. soleae* likewise adopts an orientation with the haptor upstream with respect to the flow of water over the skin of the host (effluent from the gills and currents due to host locomotion), but KEARN (1988b and see below) has shown experimentally that parasites adopt this orientation in the absence of any currents (on a freshly-killed host). However, water flow may play a part in the anterior migrations of parasites on soles (see p.5) and in the migrations of other parasites on their hosts. HARRIS and TINSLEY (1987) suspected that host olfactory water currents play a part in the detection of the nostrils of the clawed toad, *Xenopus laevis*, by the gyrodactylid *Gyrdicotylus gallieni* approaching over the host's skin and showed experimentally that a gentle water jet induces a temporary increase in "reaching activity" (flexing and stretching of the body).

4. Contact

a. General considerations

Intuitively we would expect tactile stimuli to play an important part in the biology of juvenile and adult monogeneans since contact is made with other parasites during mating and with host tissue during locomotion and feeding. Many monogeneans exchange spermatozoa, either by way of spermatophores or by intromission (see, for example, KEARN 1970, 1992 respectively), and this activity probably requires more accurate timing and positioning than any other behavioural event in their lives. However, virtually nothing is known about the sensory interplay between the partners. Tactile responses are likely to be important but chemical clues may also play a part. Many monogeneans are exposed to water turbulence and diffusible chemical signals (pheromones) seem unlikely to be effective except possibly over the shortest distances between the partners (but see below). Contact chemoperception, in which contact must be made with a chemical substance on the surface of the partner, may turn out to be more important in communication between individuals. Some features of the adoption of a premating posture by the skin-parasite *Benedenia seriolae* are consistent with the production of a chemical stimulant and possibly with contact chemoperception (KEARN, 1992).

Some monogeneans have no vagina and indulge in hypodermic impregnation, for example, *Gyrodactylus turnbulli* (see HARRIS, 1989) and the polyopisthocotylean gill parasites *Diclidophora merlangi* and *Gastrocotyle trachuri* (see MACDONALD and CALEY, 1975 and LLEWELLYN, 1983, respectively). In detached specimens of *D. merlangi* , impregnation is never mutual and the site of penetration is variable. If the assumption is made that these parasites behave in the same way on the host, then there is less need for precision and timing is less critical and the sensory equipment employed during mating seems likely to be correspondingly less sophisticated. This could be interpreted as an adaptation to the problems of positioning and timing imposed on gill parasites by the strong gill-ventilating currents, but LLEWELLYN (1983) has suggested that hypodermic impregnation is the ancestral condition in polyopisthocotyleans, with vaginae appearing later.

Skin parasites like *Entobdella soleae* and *Benedenia seriolae* readily attach themselves to glass or hard plastic surfaces and they undergo locomotion across these surfaces and attach the everted pharynx to them (KEARN, 1971b, 1992). Thus, tactile signals related to the degree of hardness or the texture of the surface and chemical signals such as those from host skin, do not appear to be involved in any significant way in haptor attachment, locomotion and at least the first stages of feeding in these parasites. It is somewhat paradoxical that the skin surfaces of other fishes such as plaice (*Pleuronectes platessa)* and rays *(Raja* spp.), that do not act as hosts for *E. soleae,* are less suitable than the skin of its natural host (*Solea solea*) for prolonged attachment of the parasite. KEARN (1967) showed that *E. soleae* is able to remain attached to plaice skin for little more than 24 h and although the parasite adheres to rays for longer periods, detachment occurs over a period of 2-8 days. Perhaps this failure to survive on alien hosts is related to some physical or chemical properties of the substrate that interfere with the proper functioning of the haptor, anterior adhesive areas or feeding apparatus, rather than detachment in response to inappropriate tactile/chemical signals from the skin surfaces.

b. The tactile sense in orientation, locomotion and migration

Experimental work on *Entobdella soleae* has revealed the importance of the tactile sense in orientation and leech-like locomotion. KEARN (1988b) found that the posteriorly projecting scales of the host greatly influence the orientation of the haptor and hence of the parasite. Resting parasites are almost invariably orientated with the posterior edge of the haptor lodged beneath a projecting scale and the longitudinal axes of the body and the haptor parallel with the longitudinal axis of the fish, i.e. with the body directed towards the tail of the fish. Whichever way the parasite moves, the angle between the haptor and the body is maintained, so that at the end of the "step" the longitudinal axes of the haptor and the fish are still parallel. KEARN also found that experimentally disorientated parasites readopt this characteristic attitude with respect to the scales even on a freshly dead host, and that reorientation is impaired on skin from which all scales have been removed. Thus, there is no evidence that water currents provide orientation cues and the sensory "awareness" of the scales is most probably based on contact reception. EL-NAGGAR and KEARN (1983) and KEARN (1988b) observed that specimens of *E. soleae* spend some time swinging in an arc from side to side about the attached haptor and also probe in different directions, and these activities seem well-suited to provide information about the scale pattern by way of the tactile sense. It is probably significant that the body margins of *E. soleae* are well-endowed with sensilla (EL-NAGGAR and KEARN, 1983) and are especially sensitive when touched with a chemically clean glass rod (KEARN, previously unpublished observation).

In contrast with the body margins and adhesive pads of *E. soleae* which are supplied with sensilla, none have been found on the haptor. However, the ventral surface of this organ carries projecting papillae and LYONS (1973) showed that these have a unique structure, containing a folded nerve ending but no ciliary elements. She suggested that these papillae are contact receptors.

The gill parasite *Tetraonchus monenteron* moves in a leech-like manner like *E. soleae* and seems to have a similar "awareness", probably based on its tactile sense, of the pattern of host secondary gill lamellae. The parasite attaches its head region with surprising accuracy during locomotion and the position of the head seems to determine the site of relocation of the haptor (KEARN, 1987a). The parasite has eversible adhesive sacs on each side of the head and after elongation of the body the head is twisted so that each adhesive border becomes cemented to the free distal edge of a secondary gill lamella. In this way, the head forms a bridge between two adjacent secondary lamellae and the detached haptor is inserted beneath this bridge into the space between the lamellae. Unlike *E. soleae*, *T. monenteron* has sensilla on the haptor and KEARN and GOWING (1989) observed differences not only in the lengths of these sensilla but also in their activity; most are non-motile but those of one pair are vibratile. KEARN and GOWING pointed out that the motion of the vibratile sensilla would increase interaction with chemical substances in the water and that they might, therefore, be chemoreceptors. On the other hand, an interruption in their motion by touching host gill tissue might be an effective way of registering contact. In *T. monenteron*, the projecting haptor sensilla are in good positions to register contact with the secondary gill lamellae and hence to initiate activity of the hamulus apparatus and marginal hooklets to ensure secure anchorage.

Experimental infection of the upper surface of the flatfish host (*Solea solea*) with oncomiracidia of *E. soleae* has shown that post-larvae migrate forwards on the host and eventually transfer themselves to the lower surface where they reach sexual maturity (KEARN, 1984). Adult or juvenile parasites may also find themselves on the host's upper surface as a result of transfer from the lower surface of another sole and they also migrate forwards and usually move onto the lower surface (KEARN, 1988a). The backwardly-directed scales provide a reliable "signpost" for migrating parasites and since the scales greatly influence the orientation of the parasite during locomotion, it is likely that contacts with scales guide the anterior migration. However, water flow generated by host locomotion and gill ventilation follows an antero-posterior direction over the host's upper surface and may provide an important directional clue for migrating parasites.

Contact receptors are likely to be involved in the transfer of adults or juveniles of *E. soleae* from host to host but we know nothing about the factor or factors that predispose these parasites to abandon one host for another. At least one monogenean, an undescribed species of the genus *Entobdella*, seems likely to relinquish all contact with its host at some stage of its life, since experimentally detached sub-adults swim vigorously by body undulations (KEARN and WHITTINGTON, 1991), but the factors that induce it to embark on this dangerous pursuit and the function of this behaviour are unknown.

5. Chemical substances

a. Pheromones

There is considerable evidence that pheromones play a part in pairing or clustering in some digeneans (see review by FRIED, 1986) but pheromonal communication has not yet been demonstrated in monogeneans. However, features of the relationship between the skin parasite *Entobdella soleae* and its flatfish host *Solea solea*, analyzed by KEARN, JAMES and EVANS-GOWING (in press), suggest, at first sight, that pheromones may play a part in the location of a mating partner. First, experimentally isolated *E. soleae* do not self-impregnate and are unable to make fertile eggs. This contrasts with the related *Benedeniella* spp. which are capable of self-impregnation via the uterus (KEARN and WHITTINGTON, 1992b). Secondly, population densities of *E. soleae* are low (a mean of 3 (1-9) parasites per infected host, according to KEARN, 1971b), while the living space provided by the body surface of their host is extensive in area. The chances of parasites meeting to exchange spermatozoa are higher than might be supposed because the adult parasites do not roam over the whole surface of the fish but show a preference for the lower surface. However, their restriction to the lower surface may have even greater significance.

The sole is an inactive, bottom-dwelling host and, when resting, uses only the upper opercular opening as an exit for the gill-ventilating current (YAZDANI and ALEXANDER, 1967). Consequently there is a thin layer of stagnant sea water trapped between the host and the sea bottom. It has been proposed by KEARN, JAMES and EVANS-GOWING (in press) that this is an ideal environment for the horizontal outward diffusion of pheromones from the thin flat bodies of the parasites, and unicellular glands, opening along the body margins may be a source of such chemical messengers (see EL-NAGGAR and KEARN, 1983). Body undulations (breathing movements) of the parasite and its ability to rotate the body about the attached haptor might also play a part in the dispersal and detection of pheromones. However, although pheromonal involvement in mating is an attractive proposition in *E. soleae*, random locomotion might be sufficient to provide a reasonable chance of meetings between potential mates.

KEARN, JAMES and EVANS-GOWING (in press) have estimated the chances of meetings between parasites moving at random at a speed of 2.26 cm/day (from KEARN, 1988a) on the lower surface of a sole 25 cm in length. *E. soleae* begins to lay eggs at about 85 days and lives for a further 100 days (KEARN, 1990), but the parasite is protandrous and may be capable of receiving spermatophores when about 65 days old. If the width of the search path of the parasite is assumed to be 1.5 mm (breadth of a young adult 2.5 mm long) then with two randomly searching parasites, the probability of a meeting taking place after 30 days is low (about 14%) and for three parasites is only about 20%. After 100 days, the corresponding probabilities are 40% and 53%. However, *E. soleae* has the ability to swing its head from side to side and this behaviour would increase the width of the search path to about 7 mm and increase the chances of contact between two parasites at 30 days to about 50% and with three parasites to about 65%. The corresponding probabilities at 100 days are 90% and 97%. This exercise suggests that most randomly moving parasites are likely to meet within a time span which would enable them to produce viable eggs during their life times. There are, however, some other considerations. First, the model of KEARN, JAMES and EVANS-GOWING considers a relatively small sole 25 cm in length. According to WHEELER (1978), soles reach a length of 60 cm and chances of meetings between parasites would be proportionately lower on larger hosts. Secondly, it is advantageous for the parasite to mate as soon as it is mature, to maximize its reproductive output. Random movement cannot ensure insemination of newly mature individuals, even on small hosts, but reinforcement with a pheromonal system, even if effective only at short distances, will transform near misses into contacts. So, the likelihood that pheromonal attraction plays a part in the biology of *E. soleae* is still a real one and deserves further investigation.

The turbulent environment of most other skin parasites seems unsuitable for the proper function of a system of mate attraction based on long-distance release of pheromones. Gill parasites, too, will be exposed to a strong and continuous flow, although, because of the unidirectional nature of gill ventilating currents it is conceivable that downstream parasites could be stimulated to move upstream towards other individuals releasing pheromones. For those living in restricted habitats, such as, for example, *Calicotyle kroyeri* in the cloaca and rectal gland (KEARN, 1987b), random movements without pheromonal reinforcement may provide all necessary mating contacts.

b. Host hormones

Migratory habits of many fishes and, in amphibians, the exploitation of terrestrial environments between brief aquatic periods, have been potent forces in the evolution of monogeneans. Only those monogeneans able to maintain the continuity of their life cycles during the travels of their migrating hosts, will survive, and the adoption of the blood-feeding habit by ancestral polyopisthocotyleans may have been the most important contribution to this survival. Host behavioural changes associated with breeding or feeding migrations may be controlled by hormones and these chemicals will provide readily accessible and reliable cues for blood-feeding parasites. Again, experimental evidence supporting the exploitation of such cues by monogeneans is not yet available but circumstantial evidence points in that direction.

Host invasion by oncomiracidia of *Gastrocotyle trachuri* is temporarily suspended in the summer when the fishes abandon benthic feeding grounds and become pelagic (LLEWELLYN, 1962); a temporary suspension of egg production may explain this phenomenon and host hormonal changes could provide the cues. The seasonal reproductive cycle of *Polystoma integerrimum* from the common frog *Rana temporaria* is well-known and the hormonal control of this cycle proposed by GALLIEN (1935) is attractive in view of the close correlation between host spawning activities and maturation and oviposition of the parasite. Attempts have been made to test this hypothesis experimentally but the results were not conclusive (see review by TINSLEY, 1990). Egg production and host sexual activities are even more closely correlated in *Polystoma nearcticum* . In this parasite egg production begins abruptly at the time when host sexual activity begins and stops just as abruptly when sexual excitement is interrupted (TINSLEY, 1991).

In the desert toad *Pseudodiplorchis americanus*, egg laying rather than egg production is closely correlated with host sexual activity. The uterus of the adult parasite in the bladder of its host is already packed with fully-developed, thin-shelled eggs, when, at the advent of the annual rains, the toads emerge from dormancy in deep burrows in the sand (TINSLEY and EARLE, 1983). The toads have 1-3 days in which to mate and spawn in temporary rain pools. Ideally, the eggs should be released by the adult parasites not just when the toad enters water but during a spawning congregation when many other toads are available for infection. TINSLEY (1990) found that egg release is not triggered simply by immersing infected toads or parasites in water, that is, osmotic change does not provide the cue, but is associated with the mating activities of toads in a spawning congregation, events that are likely to be under the control of hormones. Surprisingly, parasite oviposition was found to be correlated with a different facet of mating behaviour in the two sexes. In males, parasite oviposition occurs during intense sexual arousal - vocalization to attract females, interactions with other males and clasping the females - while in females, this does not occur until the females themselves start to oviposit. According to TINSLEY (1990), this arrangement maximizes opportunities for parasite transmission, because, during the very brief mating assemblies, all females spawn but only a small proportion of males mate.

CONCLUSIONS

Much attention has been paid to the behaviour of the free-swimming infective larvae (oncomiracidia) of monogeneans but our knowledge of the behaviour of the parasitic stages and the environmental factors that influence it, is in its infancy. There is a dramatic change in life style as the oncomiracidium establishes itself on the host and, in terms of behaviour, this is likely to be the most fundamental upheaval in the life of the parasite. Reports of the loss of some sense organs and the appearance of new ones undoubtedly reflect deeper-seated changes in the nervous system about which nothing is known. Soon after establishment on the host, larval development begins but, again, the factors that initiate this process are unknown.

It is clear that there is much still to be learned about the environmental stimuli that influence the behaviour of juvenile and adult monogeneans. Nevertheless, we do know more about this topic in monogeneans than in other parasitic flatworms and this undoubtedy reflects the accessibility of monogeneans and especially skin parasites to observation and experimental manipulation. *Entobdella soleae* in particular has yielded evidence of a response to ambient oxygen concentration, has revealed the importance of contact "awareness" of the host's scales in orientation, locomotion and possibly in migration and appears to be a good candidate for investigations of pheromonal involvement in finding a mating partner. Further studies of such relatively unspecialised skin parasites probably offer the best prospect for increasing our understanding of the role of environmental stimuli in the basic behaviour of parasitic platyhelminths.

Selection pressures exerted on monogenean parasites by the adoption of feeding migrations in some fish hosts and by the exploitation of terrestrial environments in amphibians, have led to a corresponding increase in the complexity of parasite behaviour patterns. In the polystome *Pseudodiplorchis americanus* there is a link between increased activity of its desert toad host and the commencement of migration of juvenile parasites from the lungs of the toad to the bladder through the alimentary canal; the nature of the host-derived stimulus is unknown but it has far-reaching consequences for the parasite, not only triggering migration but also setting in motion the outward transport and secretion of protective tegumental vesicles and the resumption of development (TINSLEY and JACKSON, 1986; CABLE and TINSLEY, 1992). It is generally supposed that the synchrony between the reproductive cycles of some polyopisthocotyleans (especially polystomatids) and the migrations/reproductive cycles of their hosts is achieved by the ability of the blood feeding parasites to monitor host hormonal changes but we still await the experimental proof of this supposition.

Observing living parasites has rarely been a popular pursuit among parasitologists. This is regrettable for two reasons:- first, it is much more enjoyable to see them alive than dead and, secondly, there is so much to be learned about the way they function and behave. I strongly recommend this approach to all students of monogeneans.

REFERENCES

CABLE J., TINSLEY R.C., 1992. Unique ultrastructural adaptations of *Pseudodiplorchis americanus* (Polystomatidae: Monogenea) to a sequence of hostile conditions following host infection. *Parasitology, 105*, 229-241.

EL-NAGGAR M.M., KEARN G.C.,1983. Glands associated with the anterior adhesive areas and body margins in the skin-parasitic monogenean *Entobdella soleae. Int. J. Parasitol, 13,* 67 - 81.

FRIED B., 1986. Chemical communication in hermaphroditic digenetic trematodes. *J. chem. Ecol., 12*, 1659 - 1677.

GALLIEN L., 1935. Recherches expérimentales sur le dimorphisme évolutif et la biologie de *Polystomum integerrimum* Fröhl. *Trav. Stn zool. Wimereux 12 ,* 1-181.

HARRIS P.D., 1989. Interactions between population growth and sexual reproduction in the viviparous monogenean *Gyrodactylus turnbulli* Harris,1986 from the guppy *Poecilia reticulata* Peters. *Parasitology, 98,* 245 - 251.

HARRIS P.D., TINSLEY R.C., 1987. The biology of *Gyrdicotylus gallieni* (Gyrodactylidea), an unusual viviparous monogenean from the African clawed toad, *Xenopus laevis. J. Zool., 212,* 325-346.

KEARN G.C., 1962. Breathing movements in *Entobdella soleae* (Trematoda, Monogenea) from the skin of the common sole. *J. mar. biol. Ass. U.K., 42,* 93 - 104.

KEARN G.C., 1967. Experiments on host-finding and host-specificity in the monogenean skin parasite *Entobdella soleae. Parasitology, 57*, 585-605.

KEARN G.C., 1970. The production, transfer and assimilation of spermatophores by *Entobdella soleae*, a monogenean skin parasite of the common sole. *Parasitology, 60*, 301-311.

KEARN G.C., 1971a. The attachment site, invasion route and larval development of *Trochopus pini*, a monogenean from the gills of *Trigla hirundo . Parasitology, 63,* 513-525.

KEARN G.C., 1971b. The physiology and behaviour of the monogenean skin parasite *Entobdella soleae* in relation to its host (*Solea solea*) *in* FALLIS A.M., Ecology and Physiology of Parasites, a Symposium, 161-187, University of Toronto Press.

KEARN G.C., 1980. Light and gravity responses of the oncomiracidium of *Entobdella soleae* and their role in host location. *Parasitology, 81,* 71-89.

KEARN G.C., 1981. Behaviour of oncomiracidia. *Parasitology, 82,* 57-68.

KEARN G.C.,1984. The migration of the monogenean *Entobdella soleae* on the surface of its host, *Solea solea. Int. J. Parasitol.,14,* 63-69.

KEARN G.C.,1986. Role of chemical substances from fish hosts in hatching and host-finding in monogeneans. *J. chem. Ecol., 12,* 1651 - 1658.

KEARN G.C., 1987a. Locomotion in the gill-parasitic monogenean *Tetraonchus monenteron. J. Parasit., 73,* 224-225.

KEARN G.C., 1987b. The site of development of the monogenean *Calicotyle kroyeri*, a parasite of rays. *J. mar. biol. Ass. U.K., 67,* 77-87.

KEARN G.C., 1988a. The monogenean skin parasite *Entobdella soleae*: movement of adults and juveniles from host to host (*Solea solea*). *Int. J. Parasitol., 18,* 313-319.

KEARN G.C., 1988b. Orientation and locomotion in the monogenean parasite *Entobdella soleae* on the skin of its host (*Solea solea*). *Int. J. Parasitol., 18,* 753-759.

KEARN G.C., 1990. The rate of development and longevity of the monogenean skin parasite *Entobdella soleae* . *J. Helminth., 64,* 340 - 342.

KEARN G.C., 1992. Mating in the capsalid monogenean *Benedenia seriolae*, a skin parasite of the yellowtail, *Seriola quinqueradiata*, in Japan. *Publs Seto mar. biol. Lab., 35,* 273 - 280.

KEARN G.C., GOWING R.,1989. Glands and sensilla associated with the haptor of the gill-parasitic monogenean *Tetraonchus monenteron* . *Int. J. Parasitol. , 19,* 673-679.

KEARN G.C., JAMES R., EVANS-GOWING R., in press. Insemination and population density in *Entobdella soleae*, a monogenean skin parasite of the common sole, *Solea solea. Int. J. Parasitol.*

KEARN G.C., WHITTINGTON I.D.,1991. Swimming in a sub-adult monogenean of the genus *Entobdella. Int. J. Parasitol. 21,* 739-741.

KEARN G.C., WHITTINGTON I.D., 1992a. A response to light in an adult encotyllabine (capsalid) monogenean from the pharyngeal tooth pads of some marine teleost fishes. *Int. J. Parasitol. 22,* 119 - 121.

KEARN G.C., WHITTINGTON I.D., 1992b. Diversity of reproductive behaviour in platyhelminth parasites: insemination in some benedeniine (capsalid) monogeneans. *Parasitology , 104,* 489 -496.

LAMBERT A., 1980. Oncomiracidiums et phylogenèse des Monogenea (Plathelminthes). *Annls Parasit. hum. comp., 55,* 281-325.

LLEWELLYN J., 1956. The host-specificity, micro-ecology, adhesive attitudes, and comparative morphology of some trematode gill parasites. *J. mar. biol. Ass. U.K., 35,* 113-127.

LLEWELLYN J., 1960. The attachment of the monogenean *Discocotyle sagittata* Leukart to the gills of *Salmo trutta* L. *Parasitology, 50,* 51-59.

LLEWELLYN J., 1962. The life histories and population dynamics of monogenean gill parasites of *Trachurus trachurus* (L.). *J. mar. biol. Ass. U.K., 42,* 587-600.

LLEWELLYN J., 1964. The effects of the host and its habits on the morphology and life-cycle of a monogenean parasite *in* Parasitic Worms and Aquatic Conditions, 147-152, Czechoslovak Academy of Sciences, Prague.

LLEWELLYN J., 1972. Behaviour of monogeneans *in* CANNING E.U., WRIGHT C.A., Behavioural aspects of parasite transmission, 19 - 30, Supplement No. 1., *J. Linn. Soc.,51.*

LLEWELLYN J., 1983. Sperm transfer in the monogenean gill parasite *Gastrocotyle trachuri. Proc. R. Soc., B., 219,* 439-446.

LYONS K.M., 1973. Scanning and transmission electron microscope studies on the sensory sucker papillae of the fish parasite *Entobdella soleae* (Monogenea). *Z. Zellforsch. mikrosk. Anat. , 137,* 471-480.

MACDONALD S., 1977. A comparative study of the structure of the oncomiracidia of the monogenean gill parasites *Diclidophora merlangi, D. luscae* and *D. denticulata. Int. J. Parasitol., 7,* 113-118.

MACDONALD S., CALEY J., 1975. Sexual reproduction in the monogenean *Diclidophora merlangi* : tissue penetration by sperms. *Z. ParasitKde., 45,* 323-334.

MACDONALD S., JONES A., 1978. Egg-laying and hatching rhythms in the monogenean *Diplozoon homoion gracile* from the southern barbel (*Barbus meridionalis*). *J. Helminth. 52,* 23-28.

TINSLEY R.C., 1990. Host behaviour and opportunism in parasite life cycles *in* BARNARD C.J., BEHNKE J.M., Parasitism and Host Behaviour, 158-192, Taylor and Francis, London.

TINSLEY R.C., 1991. The control of egg production in the monogenean *Polystoma. Abstracts of the Spring Meeting of the British Society for Parasitology.* April 1991, p. 46.

TINSLEY R.C., EARLE C.M., 1983. Invasion of vertebrate lungs by the polystomatid monogeneans *Pseudodiplorchis americanus* and *Neodiplorchis scaphiopodis. Parasitology, 86,* 501-517.

TINSLEY R.C., JACKSON H.C., 1986. Intestinal migration in the life-cycle of *Pseudodiplorchis americanus* (Monogenea). *Parasitology, 93,* 451-469.

WHEELER A., 1978. Key to the fishes of northern Europe. Warne. London, 380 p.

WHITTINGTON I.D., KEARN G.C., 1992. The eggs and oncomiracidia of *Encotyllabe* spp. and the relationship between encotyllabines and other capsalid monogeneans. *Parasitology, 104,* 253 - 261.

YAZDANI G.M., ALEXANDER R.M., 1967. Respiratory currents of flatfish. *Nature, Lond., 213,* 96-97.