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SYMPOSIUM

Hatching Strategies in Monogenean (Platyhelminth) Parasites that Facilitate Host Infection

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Synopsis In parasites, environmental cues may influence hatching of eggs and enhance the success of infections. The two major endoparasitic groups of parasitic platyhelminths, cestodes (tapeworms) and digeneans (flukes), typically have high fecundity, infect more than one host species, and transmit trophically. Monogeneans are parasitic flatworms that are among the most host specific of all parasites. Most are ectoparasites with relatively low fecundity and direct life cycles tied to water. They infect a single host species, usually a fish, although some are endoparasites of amphibians and aquatic chelonian reptiles. Monogenean eggs have strong shells and mostly release ciliated larvae, which, against all odds, must find, identify, and infect a suitable specific host. Some monogeneans increase their chances of finding a host by greatly extending the hatching period (possible bet-hedging). Others respond to cues for hatching such as shadows, chemicals, mechanical disturbance, and osmotic changes, most of which may be generated by the host. Hatching may be rhythmical, larvae emerging at times when the host is more vulnerable to invasion, and this may be combined with responses to other environmental cues. Different monogenean species that infect the same host species may adopt different strategies of hatching, indicating that tactics may be more complex than first thought. Control of egg assembly and egg-laying, possibly by host hormones, has permitted colonization of frogs and toads by polystomatid monogeneans. Some monogeneans further improve the chances of infection by attaching eggs to the host or by retaining eggs on, or in, the body of the parasite. The latter adaptation has led ultimately to viviparity in gyrodactylid monogeneans.

Introduction

There are three major groups of parasitic flatworms (platyhelminths) that comprise the Neodermata (see Perkins et al. 2010). Two groups, the cestodes or tapeworms and the digeneans or flukes, are endoparasites. Species cycle between at least two host species, mostly by trophic transmission, and their fecundity is high (e.g., 20,000 eggs/parasite/24 h up to 2×10^6 eggs/parasite/24 h in some tapeworms) (Whittington 1997). They differ fundamentally from the third group, the monogeneans, most of which are strictly host-specific ectoparasites of the skin and gills of fishes, but a few are endoparasitic in amphibians and aquatic chelonian reptiles. Monogeneans have direct, single-host, water-based life cycles and relatively low fecundity. Tinsley (1983) stated that most monogeneans deposit fewer than 100 eggs/parasite/24 h and many deposit fewer than 25. However Mooney et al. (2008) collected *in vivo* 400 to 1,400 eggs/parasite/24 h from *Heteraxine heterocerca*. With some exceptions (see below) monogeneans shed eggs freely into water. Their eggshells are physically strong and chemically resistant, but a detachable lid or operculum permits escape of the infective larva (oncomiracidium). Most larvae are ciliated and swim freely, but their energy reserves and therefore their lifespan are limited, so their task, against all odds, is to find, identify, and infect a suitable specific host before reserves are

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expended. The diet of the host therefore plays no role in parasitism by monogeneans.

Given the strict host specificity and comparatively low fecundity of monogeneans and the enormous diversity of their fish hosts in terms of species, habits, and habitats, one may anticipate that selection will favor any trait of the parasite that is likely to improve the chances of contacting their specific fish host. Among these adaptations, timing of hatching is likely to be critical. Not until 1960 was evidence for a host-generated hatching stimulus by a monogenean discovered when Euzet and Raibaut (1960) reported enhanced hatching in *Squalonchocotyle torpedinis* in the presence of its host, the electric ray, *Torpedo marmorata*.

Chemical substances leaking from or secreted by fishes are not the only host-generated cues that might influence hatching. In the past 50 years, significantly more has been determined about environmentally cued hatching in monogenean parasites.

Rhythmic hatching

There were early indications (Bychowsky 1957, p. 92, Zeller in Bovet 1967) that monogenean hatching may not be continuous throughout a 24-h period. Kearn (1973) confirmed this experimentally when embryonated eggs of the sole skin parasite *Entobdella soleae* were exposed to an artificial day/night cycle. When fully embryonated, hatching was spontaneous but larvae emerged in pulses, not continuously, corresponding to the first 2 or 3 h after "dawn" on each day. Further evidence indicated that this hatching rhythm had a strong endogenous (circadian) component. This periodicity is significant because the host, the common sole (*Solea solea*), is nocturnally active, feeding mainly on bottom-dwelling polychaetes, and spending most daylight hours partly buried in sediment. The implication is that parasite larvae hatching at dawn from eggs on the sea bed have an inactive target host and the daylight period to locate their specific host. The free-swimming life of the larva is limited to about 24 h.

The time period over which hatching occurs exceeds the period of oviposition. Eggs laid by *E. soleae* over 2–3 days mostly hatch over a similar period but small numbers continue to hatch in the absence of the host over at least a 2-week period (Kearn 1973). By extending hatching, the parasite "hedges its bets", ensuring that on any day at least a small number of larvae retain the potential to infect a resting sole. *E. soleae* also has a second hatching option (see below).

Another teleost flatfish, the halibut (*Hippoglossus hippoglossus*) is infected by a congener, namely *E. hippoglossi*. Halibut behavior differs fundamentally from that of the sole because it is a large predator with a diet that includes other fishes, crustaceans, and some cephalopods. It is likely that the halibut hunts during the day and rests at night and, predictably, *E. hippoglossi* eggs hatch soon after dusk at a time when its specific host is most likely to rest (Kearn 1974a).

Hatching rhythms are reported in representatives of several monogenean families (Table 1). In many but not all cases (see below), there is experimental evidence of an endogenous (circadian) component. Hatching rhythms are known among parasites of skin and gills and also occur in parasites inhabiting more obscure and specialized habitats such as the cloaca and nasal fossae of elasmobranchs and the bladders of frogs.

Daily periods of hatching may be long or short. In *Benedenia rohdei* and *B. lutjani*, emergence is spread throughout the illumination period (Ernst and Whittington 1996), while in *Discocotyle sagittata* hatching is usually confined to the first 2 h of illumination (Gannicott and Tinsley 1997). In *Dictyocotyle coeliaca* inhabiting the body cavity of *Raja naevus*, there is no rhythm and hatching occurs arhythmically throughout the day and night (Kearn 1975a).

In most experimental work on monogenean hatching rhythms, eggs were exposed to artificial cycles of illumination with abrupt changes in illumination at "dawn" and "dusk". However, rhythms persist when devices were employed to create a gradual change of illumination intensity at "dawn" and "dusk" (Kearn 1973, Whittington and Kearn 1986) or when eggs were exposed to natural cycles of illumination (Ernst and Whittington 1996).

Macdonald (1975) found that hatching patterns of eggs of *Diclidophora merlangi* collected at Arbroath in Scotland differed from the pattern in those collected at Plymouth in southern England. Eggs from parasites from Arbroath hatched soon after "dawn", while those from Plymouth hatched before "dawn". Macdonald suggested that this difference may reflect adaptations to small differences in behavior between widely separated host populations (Plymouth is 750 km from Arbroath). There was also an intriguing hint that there may be seasonal differences in hatching patterns in the Arbroath population. Hence, hatching rhythms seem particularly flexible in an evolutionary sense, adapting to the behavioral diversity among their specific hosts and capable of adjustment, perhaps rapidly, as selection pressures change.

Table 1 Some monogeneans with eggs reported to hatch rhythmically[a]

Family	Species	Host	Habitat	References
Capsalidae	*Entobdella soleae*	*Solea solea* (T)	Skin	Kearn 1973
	Entobdella hippoglossi	*Hippoglossus hippoglossus* (T)	Skin	Kearn 1974a
	Benedenia seriolae	*Seriola quinqueradiata* (T)	Skin	Kearn et al. 1992
	Benedenia rohdei	*Lutjanus carponotatus* (T)	Gills	Ernst and Whittington 1996
	Benedenia lutjani	*Lutjanus carponotatus* (T)	Skin	Ernst and Whittington 1996
Diclidophoridae	*Diclidophora merlangi*	*Merlangius merlangus* (T)	Gills	Macdonald 1975
	Diclidophora luscae	*Trisopterus luscus* (T)	Gills	Macdonald 1975
	Diclidophora denticulata	*Pollachius virens* (T)	Gills	Macdonald 1975
Diplozoidae	*Diplozoon homoion gracile*[b]	*Barbus meridionalis* (T)	Gills	Macdonald and Jones 1978
Discocotylidae	*Discocotyle sagittata*[b]	*Oncorhynchus mykiss* (T)	Gills	Gannicott and Tinsley 1997
Heteraxinidae	*Heteraxine heterocerca*	*Seriola quinqueradiata* (T)	Gills	Kearn et al. 1992
Hexabothriidae	*Rajonchocotyle emarginata*	*Raja* spp. (E)	Gills	Whittington and Kearn 1986
Microbothriidae	*Pseudoleptobothrium aptychotremae*	*Trygonorrhina fasciata* (=*dumerilii*) (E)	Skin	Glennon et al. 2006
Monocotylidae	*Merizocotyle icopae*	*Rhinobatos* (=*Glaucostegus*) *typus* (E)	Nasal fossae	Chisholm and Whittington 2000
	Neoheterocotyle rhinobatidis	*Rhinobatos* (=*Glaucostegus*) *typus* (E)	Gills	Chisholm and Whittington 2000
	Troglocephalus rhinobatidis	*Rhinobatos* (=*Glaucostegus*) *typus* (E)	Gills	Chisholm and Whittington 2000
	Calicotyle australis	*Trygonorrhina fasciata* (=*dumerilii*) (E)	Cloaca	Glennon et al. 2006
Polystomatidae	*Polystoma integerrimum*[b]	*Rana temporaria* (A)	Bladder	Macdonald and Combes 1978

A = Amphibia; E = Elasmobranch; T = Teleost.

[a] From Whittington et al. (2000) with updated information.

[b] Unless indicated by "b", all parasites are marine.

It is generally assumed that hatching rhythms of monogeneans have adaptive value related to host behavior, but Whittington and Kearn (1986) and Ernst and Whittington (1996) pointed out that predation on monogenean larvae, especially by filter-feeding invertebrates, may also influence the time of hatching.

Responses to shadows

There is experimental evidence that many of the rhythms in Table 1 have an endogenous basis, but this is not always so. In *Discocotyle sagittata*, Gannicott and Tinsley (1997) reversed the light/dark periods and noted immediate reversal of the nocturnal hatching rhythm, which was interpreted as evidence of a direct response to exogenous cues. An abrupt decrease in intensity of illumination, independent of the natural cycle of illumination, may occur in well lit, shallow waters when a host fish, cruising close to, or resting on, the bottom where most monogenean eggs reside, casts a shadow. To exploit such a cue, hatching must be rapid to ensure that contact is made with the host before it swims away. This has evolved independently in *Neoentobdella diadema* (Capsalidae) and *Plectanocotyle gurnardi* (Plectanocotylidae) (see Kearn 1982 and Whittington and Kearn 1989, respectively). Hosts of both species are bottom dwellers, *N. diadema* occurring on the skin of the stingray *Dasyatis pastinaca* and *P. gurnardi* infecting the gills of gurnards (*Aspitrigla gurnardi* and *Eutrigla gurnardus*). When shaded, eggs of each parasite species hatch with great rapidity (in seconds). An adaptation of the eggs of both species that permits this rapid hatching is the "pre-weakening" of the cement holding the operculum in place, so the force exerted by the rapidly extending larva is all that is required to dislodge the operculum. It is noteworthy that in *Entobdella soleae*, a relative of *N. diadema*, the larva typically takes 4 or 5 min to dissolve the opercular cement and escape from the egg (Kearn 1975b).

Responses to chemical cues

Kearn (1974b) discovered that location of hosts by *E. soleae* has another dimension that supplements rhythmic hatching. If a sole should settle on, or near, fully embryonated eggs on the sea bed, skin mucus from the sole activates unhatched larvae and hatching occurs within minutes. Mucus from the host's skin stimulates hatching at any time during the light/dark cycle. Other monogenean species known to respond to host-derived chemical cues are shown in Table 2.

Entobdella soleae retains the ability to hatch spontaneously in the absence of chemical cues from a host but other monogeneans rely on chemical stimulation only and use a "sit-and-wait" strategy. Eggs of *Acanthocotyle lobianchi*, a skin parasite of

Table 2 Some monogeneans with eggs reported to hatch in response to chemical stimuli[a]

Family	Species	Host	Habitat	Larval cilia present (+) or absent (−)	References
Acanthocotylidae	*Acanthocotyle lobianchi*	*Raja* spp. (E)	Skin	−	Macdonald 1974
	Acanthocotyle greeni	*Raja clavata* (E)	Skin	−	Macdonald and Llewellyn 1980
Capsalidae	*Entobdella soleae*	*Solea solea* (T)	Skin	+	Kearn 1974b
Dactylogyridae	*Pseudodactylogyrus bini*[b]	*Anguilla japonica* (T)	Gills	+	Chan and Wu 1984
Discocotylidae	*Discocotyle sagittata*[b]	*Oncorhynchus mykiss* (T)	Gills	+	Gannicott and Tinsley 1997
Enoplocotylidae	*Enoplocotyle kidakoi*	*Gymnothorax kidako* (T)	Skin	−	Kearn 1993
Hexabothriidae	*Squalonchocotyle torpedinis*	*Torpedo marmorata* (E)	Gills	−	Euzet and Raibaut 1960
	Hexabothrium appendiculatum	*Scyliorhinus canicula* (E)	Gills	+	Whittington 1987
Microbothriidae	*Leptocotyle minor*	*Scyliorhinus canicula* (E)	Skin	+	Whittington 1987
Microcotylidae	*Microcotyle salpae*	Box salpa (=*Sarpa salpa*) (T)	Gills	−	Ktari 1969

E = Elasmobranch; T = Teleost.

[a] From Whittington et al. (2000) with updated information.

[b] Unless indicated by "b", all parasites are marine.

Raja spp., fail to hatch spontaneously in the absence of a host, but when treated with skin mucus or washings from a host ray's body, hatching occurs within 2–4 s (Macdonald 1974). The fully embryonated larva contains lipid droplets, which diminish as the larva ages and probably provide resources that keep unhatched inactive larvae alive for up to 83 days. As in monogeneans that respond to shadows from a host, the operculum is pre-weakened and rapid extension of the folded larva within removes it. Given the rapidity of hatching and the proximity of egg and host, there is no requirement for the larva to swim and oncomiracidia of *A. lobianchi* are unciliated. Other parasites of flat elasmobranchs that, like *A. lobianchi*, have unciliated larvae and respond to mucus from the host are the congener *A. greeni* from the skin of *R. clavata* (see Macdonald and Llewellyn 1980) and the unrelated *Squalonchocotyle torpedinis* from gills of *T. marmorata* (see Euzet and Raibaut 1960). Larvae of the skin parasite *Leptocotyle minor* (Microbothriidae) and the gill parasite *Hexabothrium appendiculatum* (Hexabothriidae) also require chemical stimulation from the host but their larvae are ciliated. This may reflect the fact that the host, *Scyliorhinus canicula*, is an active, round-bodied dogfish.

The identity or identities of the chemical hatching-factors in skin mucus of teleost fishes such as *Solea solea* and *Onchorhynchus mykiss* (Table 2) remain elusive, but the active stimulant produced by rays and dogfishes has been identified as urea. Urease treatment destroys the effectiveness of mucus and washings from rays and dogfish as hatching stimulants for *A. lobianchi*, *L. minor*, and *H. appendiculatum* (see Kearn and Macdonald 1976; Whittington 1987, respectively), but effectiveness is readily restored by adding urea crystals. Whittington and Kearn (1990) demonstrated specificity for urea when compared with several structural urea analogs (e.g., methyl urea, dimethyl urea). Retention of urea in elasmobranch blood provides an osmotic advantage not available to teleosts. Consequently, the urea content in skin secretions of elasmobranchs is high and monogeneans like *Acanthocotyle* spp. have taken advantage of this quirk of fish physiology.

Enoplocotyle kidakoi has unciliated larvae and eggs that fail to hatch spontaneously. For hatching to occur, Kearn (1993) found that physical contact is required between eggs and skin of the moray eel host. This suggests that the unknown chemical stimulant has limited ability to diffuse far from the host's skin or that it rapidly loses potency with dilution. Physical contact is assured because the eggs of the parasite are attached to the walls of rock crevices inhabited by the host.

Responses to other cues

As fishes swim they generate turbulence. Mechanical disturbance of this kind stimulates hatching in some monogeneans (Table 3). Eggs of *Branchotenthes octohamatus* from the gills of the elasmobranch *Trygonorrhina fasciata* (=*dumerilii*) fail to hatch spontaneously or when treated with skin secretions of the host, but unciliated larvae hatch instantly when subjected to even relatively mild disturbances

Table 3 Marine monogeneans reported to hatch in response to mechanical disturbance[a]

Family	Species	Host	Habitat	Larval cilia present (+) or absent (–)	Reference
Diclidophoridae	*Diclidophora luscae*	*Trisopterus luscus* (T)	Gills	+	Whittington and Kearn 1988
Diplozoidae	*Diplozoon paradoxum*	Cyprinids (T)	Gills	+	Bovet 1967
Hexabothriidae	*Neonchocotyle pastinacae*	*Dasyatis pastinaca* (E)	Gills	–	Ktari and Maillard 1972
	Branchotenthes octohamatus	*Trygonorrhina fasciata* (=*dumerilii*) (E)	Gills	–	Glennon et al. 2006
Microcotylidae	*Microcotyle salpae*	*Box salpa* (=*Sarpa salpa*) (T)	Gills	–	Ktari 1969
Monocotylidae	*Dendromonocotyle kuhlii*	*Amphotistius* (=*Neotrygon*) *kuhlii* (E)	Skin	+	Kearn 1986

E = Elasmobranch; T = Teleost.

[a]From Whittington et al. (2000) with updated information.

(Glennon et al. 2006). The gill parasite *Microcotyle salpae* also has an unciliated larva. Ktari (1969) found evidence that a chemical factor from its teleost host (*Box salpa* = *Sarpa salpa*) stimulates hatching (Table 2), but he also discovered that hatching followed agitation. When disturbance is minimized, ciliated larvae of *Diclidophora luscae* hatch rhythmically (Macdonald 1975) but mass hatching follows more vigorous disturbance (Whittington and Kearn 1988).

Tinsley and Owen (1975) and Kearn (1986) observed rapid hatching during transfer of eggs of *Protopolystoma xenopodis* and *Dendromonocotyle kuhlii*, respectively, to a microscope stage. Tinsley and Owen suggested that *P. xenopodis* eggs may respond to a combination of "shock" stimuli, including heat, light, and mechanical disturbance during transfer. This range of stimuli might be experienced in the natural environment because the hosts (aquatic toads) are likely to stir up pond sediment and propel eggs into warmer, better illuminated waters.

All stimuli discussed so far are host-generated. An osmotic stimulus is implicated in hatching of the thin-walled eggs of *Eupolystoma anterorchis* from the bladder of the toad *Bufo pardalis* because eggs hatch as soon as they enter freshwater (Tinsley 1978).

Convergence between monogenean species parasitizing a single host species

Some specific fish may be infected by more than one, often distantly related, monogenean species. These parasites might be expected to evolve similar hatching patterns since they are subjected to the same selection pressures. This seems to be true in some relationships but not in others. For example, Chisholm and Whittington (2000) found that three species of monocotylid monogeneans, two of which were gill parasites (*Neoheterocotyle rhinobatidis* and *Troglocephalus rhinobatidis*) and the third species (*Merizocotyle icopae*) from the nasal fossae, parasitizing the same host, *Rhinobatos* (=*Glaucostegus*) *typus*, shared similar hatching rhythms. In contrast, two remotely related monogeneans, *Benedenia seriolae* (Capsalidae) and *Heteraxine heterocerca* (Heteraxinidae), from the skin and gills, respectively of the same host, *Seriola quinqueradiata*, had markedly different hatching rhythms (Kearn et al. 1992). A possible explanation for this difference offered by Kearn et al. is that the two parasite species may have different sites of invasion and that the optimal time for access to one of these sites may not be the best time for access to the other.

The most striking example of convergent evolution concerns the unrelated monogeneans *L. minor* (Microbothriidae) and *Hexabothrium appendiculatum* (Hexabothriidae). These species not only share the same hatching strategy, releasing ciliated larvae in response to urea in body washings from their shared host, the dogfish *Scyliorhinus canicula*, but their eggs are similar in shape, bear a filamentous appendage, and are readily carried into suspension by turbulence from foraging hosts (Whittington 1987).

Rhythms of egg-laying and egg retention

When and where eggs are deposited are likely to have an important influence on the success of hatching and of host infection. There are reports of rhythms of egg-laying in the freshwater gill-parasite *Diplozoon homoion gracile* by Macdonald and Jones (1978) and in the marine gill-parasites *Zeuxapta seriolae* and *Heteraxine heterocerca* by Mooney et al. (2006, 2008 respectively). In *D. homoion gracile*, this rhythm appears to be brought about by daily changes in the rate of egg production, which decreases during daylight, but *Z. seriolae* and *H. heterocerca* store eggs *in* *utero*, probably releasing stored eggs soon after dusk once every 24 h. Other monogeneans that store eggs temporarily *in utero*, such as *Diclidophora luscae* (see Whittington and Kearn 1988), may release them at a specific time during the 24-h period. This may ensure that eggs are deposited in an environment likely to be visited repeatedly at a particular time of day by potential hosts. The egg bundles of *D. luscae* have appendages like grappling hooks that may secure the eggs to reefs or wrecks known to be haunts of foraging hosts (the pouting, *Trisopterus luscus*).

A remarkable synchronization between egg assembly in a monogenean and spawning behavior of its host occurs in *Polystoma nearcticum* from the bladders of tree frogs, *Hyla versicolor* (see Tinsley 1991; Armstrong et al. 1997). Hosts congregate at freshwater spawning sites at night and remain there for <4 h. Egg production by the parasites begins as the visiting hosts become sexually active and quickly reaches >120 eggs/parasite/h, faster than any other monogenean. Egg production by the parasite is switched off equally abruptly when sexual excitement wanes. It has been hypothesized that hormonal changes in the hosts, monitored by the parasites during their blood meals, may control this precise on/off switch. However, this has not been confirmed experimentally.

Retention of monogenean eggs on the body of the host has been reported occasionally, but more commonly eggs are retained by the parasite, either internally or externally (Kearn 1986). If eggs are retained long enough, larvae may complete embryonation, hatch, and establish themselves on the host of the parent parasite (autoinfection). This strategy avoids some of the hazards facing a free-swimming, host-seeking larva and may generate a reservoir population with a high capacity for multiplication. This will promote mating between siblings, which, according to Llewellyn (1981), may have survival value by conserving specialized characters. *Acanthocotyle greeni* retains up to 80 eggs tethered externally to the parasite by their appendages (Macdonald and Llewellyn 1980). These egg bundles appear to be retained long enough for the oldest eggs to contain fully embryonated larvae, creating potential for autoinfection. Release of the egg bunch would permit younger eggs to embryonate on the sea bed, allowing new hosts to be infected when a host ray settles nearby (Table 2).

Retention of eggs by parasites is the single most important feature that has enabled polystomatid monogeneans to cope with the amphibious habits of their hosts (Tinsley 1983). For example, *E. anterorchis* assembles and stores up to 300 eggs *in utero* when the toad host (*Bufo pardalis*) is on land. When toads enter temporary rain pools, the parasites release their fully embryonated eggs *en masse*. Eggs hatch immediately, probably in response to an osmotic change (see above) and swimming larvae infect new toad hosts.

This trend toward ovoviviparity has culminated in viviparity in gyrodactylid monogeneans (Kearn 1998; Bakke et al. 2007). Oviposition has been suppressed and embryos develop into adults inside the parent. When born, the offspring are as large as their parents and establish themselves on the parental host, leading to a rapid increase in parasite burden. Most gyrodactylids spread to new hosts by contagion, i.e. by transfer when hosts make physical contact with each other (Fig. 9 in Kearn 1998; Bakke et al. 2007; Fig. 13.5 in Whittington and Chisholm 2008).

Conclusions

Hatching in most monogeneans is not haphazard. Timing of hatching is controlled endogenously and/or may be influenced by one or more of a range of cues generated by the host. Such adaptations maximize opportunities for monogeneans to infect specific hosts. High fecundity is supplemented by asexual multiplication in the first intermediate host by digeneans and in some tapeworm species (e.g., Table 1 in Whittington 1997). In comparison, the relatively low fecundity of most monogeneans, with no asexual reproduction to increase the number of infective stages, has likely been a significant evolutionary stimulus for some to exploit their hosts' predictability in terms of physiology and behavior (Whittington 1997). What is largely "a numbers game" for the trophic transmission of digeneans and cestodes is more subtle in monogeneans for their life cycle to succeed.

We noted earlier that the usually ciliated monogenean larvae must, against all odds, find, identify, and infect a suitable specific host. It is, therefore, especially interesting that hatching cues to which monogeneans respond are nonspecific. Shadows and mechanical disturbance can be created by any fish or other aquatic animal (Kearn 1986). Likewise, eggs of *Entobdella soleae* respond to skin washings from various fishes that are not hosts for *E. soleae* (see Kearn 1974b). Similarly, eggs of *A. lobianchi* hatch in response to urea, a chemical present naturally in secretions from the skin of most elasmobranchs (Whittington et al. 2000). However, the amplitude and duration of shadows cast and the frequency and intensity of vibrations from mechanical disturbance created by specific hosts may reveal a hitherto unexpected specificity to stimuli that are currently considered nonspecific.

Adaptations that may enhance the emergence of monogenean larvae and promote the finding of specific hosts may also relate to egg morphology and the timing of release of eggs, factors that could play a role in the dispersal, and fate of the eggs. Eggs of *A. lobianchi* and *E. soleae* are laid with cement that attaches them to sediment on the sea floor where their hosts live and egg bundles of *D. luscae* have hooked appendages that may entangle and maintain them in sites inhabited by their hosts (Kearn 1986). Synchronous rhythmical release of eggs *en masse* as reported for *Z. seriolae* and *Heteraxine heterocerca* by Mooney et al. (2006, 2008, respectively), complemented by rhythmical hatching, may focus larval emergence in time and space to regions commonly inhabited by the host species. Kearn (1986) suggested that a lack of specificity may not be disadvantageous if soles, the hosts of *E. soleae*, are locally abundant where the eggs of the parasites occur, so that a hatching stimulus is more likely to be provided by a sole than by a nonhost fish. Moreover, larvae of *E. soleae* emerging as a result of nonhost stimuli may survive, remain swimming, and exercise their preference for attachment to sole skin (Kearn 1967) rather than to skin of "alien" hosts. The same arguments may apply to larvae of *A. lobianchi* and *D. luscae* emerging from eggs tethered in areas where host rays and pouting live. Recent studies suggest that glycoproteins from the host may provide a specific stimulus inducing monogenean larvae to attach themselves to their hosts (Ohashi et al. 2007), but there is no information about whether swimming larvae, having contacted an unsuitable host, retain the ability to continue swimming and searching for an appropriate one.

For monogenean/fish systems, it is frustrating that in most cases, information about the specific biology and responses of eggs and larvae of the parasites exceeds that about the behavior of their specific hosts. This emphasizes how tractable some monogenean/fish "models" in aquaria are (e.g., *E. soleae* on *Solea solea*), but relating the results of laboratory experiments to the behavioral diversity of fish hosts in the natural environment provides challenges. Often more is known about frog and toad biology and has revealed a fascinating adaptive compliance between polystomatid parasites and their amphibious hosts (Tinsley 1983; Kearn 1986). The remarkable synchronization between the release of eggs by polystomatids and spawning by their anuran hosts, possibly controlled by the host's hormones ingested by the blood-feeding parasites, has permitted this colonization (Tinsley 1983, 1991; Armstrong et al. 1997).

We still know little about how recognized hatching cues are received by unhatched larvae. Pigment-shielded eyes present in larvae of some monogeneans, (e.g., *E. soleae*, see Kearn and Baker 1973) probably control direction of swimming with respect to illumination after hatching. Eyes without pigment-shields in some larvae, including *E. soleae* (see Lyons 1972), may be capable of monitoring day length and/or responding to shadows. The role of urea in stimulating eggs of parasites of elasmobranchs to hatch is established, but the identities of chemical cues generated by teleosts are unknown, as are the chemosensory organs that detect them. Eggshells must be translucent and permeable to chemical factors, but how mechanical disturbance is communicated to a larva inside an eggshell is unknown. These are promising areas of research for the future.

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