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ORIGINAL PAPER

Co-invasion of a Red Sea fish and its ectoparasitic monogenean, *Polylabris* cf. *mamaevi* into the Mediterranean: observations on oncomiracidium behavior and infection levels in both seas

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Abstract This study investigated aspects of the biology of the monogenean gill ectoparasite *Polylabris* cf. *mamaevi* (Polyopisthocotylea: Microcotyleae) infecting rabbitfish, *Siganus rivulatus* (Forskal) (Teleostei: Siganidae). Both host and parasite are Lessepsian immigrants that have co-invaded the Mediterranean Sea via the Suez Canal. The infection prevalence and mean intensity of the polyopisthocotylean was examined in both native and immigrant host populations and found to be three times greater in the new biogeographical region. In vitro observations on parasite eggs from both areas indicated that hatching occurred almost exclusively in the dark. The reaction of the larval oncomiracidia to water flow and secreted host chemicals indicated that neither Red Sea nor Mediterranean oncomiracidia exposed to waterborne host metabolites displayed any significant response or change in behavior; however, upon encountering flow, they ceased to swim and drifted passively downstream. Host specificity of *P.* cf. *mamaevi* may have co-evolved with temporal synchronization of the parasite with the host's diurnal activity. Hatching of *P.* cf. *mamaevi* eggs was rhythmical and the timing coincided with the known nocturnal resting behavior of the hosts, when their schools lie immobile on the sea bottom. After hatching, abrupt cessation of active swimming by the oncomiracidia upon sensing host inhalant gill-ventilating currents is likely to facilitate rapid, passive entry into the gill chamber of a suitable host. The greater abundance of *P.* cf. *mamaevi* in the invading (Mediterranean) populations is probably due to the changed, new environment, possibly impacting host resistance to the parasite and encouraging heavier infections.

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Introduction

Polylabris is a genus of hermaphroditic, ectoparasitic blood-feeding flatworms (Monogenea: Polyopisthocotylea: Microcotylidae) with direct life cycles that inhabit the gills of a variety of perciform fish species (Hayward 1996). The adult worm produces spindle-shaped eggs with rigid shells that adorn two coiled long filaments, one at each pole, probably for entangling and attaching to the host gills. Upon hatching, the short-lived oncomiracidium (ciliated, swimming larva) takes to the waters, searches for a host and attaches to it using a disklike haptor, a unique monogenean attachment organ, equipped with several pairs of marginal hooklets (Hayward 2005). The subfamily Protomicrocotylinae, to which *Polylabris* belongs, is almost entirely restricted to warmer waters of the Indo-west Pacific Ocean. To date, the only reported exception is *Polylabris tubicirrus* (Paperna and Kohn 1964), which infests several species of *Diplodus* on both sides of the Atlantic Ocean and in the Mediterranean Sea (Hayward 1996). The specimens that were investigated in the present study, from both the Mediterranean and Red Sea, were established as belonging to the same species, tentatively identified as *P. mamaevi* (Hayward, personal communication). Unfortunately, definite identification could not be made since the type

specimens of this species are not available for loan. Nevertheless, *P. mamaevi* is readily distinguishable from the only other Mediterranean species, *P. tubicirrus*; thus, we refer to the worms in this work as *P.* cf. *mamaevi*.

At present, 20 species of the genus *Polylabris* were identified from the gills of various fishes. Of these, eighteen are oioxenic (strictly host-specific), infesting only one or few host species (Hayward 1996). Indeed, monogeneans are among the most host-specific of parasites (Rohde 1993). It has been shown that 74 to 78% of all studied monogenean species are confined to a single host species (Bychowsky 1957; Rohde 1979). Nonetheless, the mechanisms underlying this extreme host-specificity are still poorly understood (Whittington et al. 2000). The extent of host recognition through active oncomiracidium selection is unknown, but the relatively low number of infective stages produced by most monogenean species in comparison with other parasitic platyhelminths suggests that they are highly successful at locating their hosts (Whittington 1997). Chemical recognition is considered to play a significant role in this success (Whittington et al. 2000), and experiments performed on oncomiracidia of *Entobdella soleae* (van Beneden and Hesse) (Kearn 1967), *Neobenedenia girellae* (Hargis) (Yoshinaga et al. 2000), and *Benedenia seriolae* (Yamaguti) (Yoshinaga et al. 2002) strongly suggest that upon physical contact with the host, specific chemical(s) in the skin epidermis and/or skin mucus induce attachment. The results of recent studies, however, have also suggested that distance chemoreception plays a significant role in host location by the larvae of many symbiotic marine invertebrates. Notably, larval stages of some crustaceans and molluscs (e.g., Zimmer and Butman 2000) and trematodes and nematodes (Haas 2003) are attracted by specific waterborne chemicals emanating from their hosts. In spite of this, very few attempts have been made thus far to determine whether larval attraction could occur before physical contact in monogenean oncomiracidia. When tested, it was generally found that these larvae did not show a significant at-a-distance behavioral response to host tissue and only rarely swam toward it (Whittington et al. 2000). However, these "non-attraction" results were all obtained in still water, while studies involving larvae of other marine invertebrates (e.g., Tamburri et al. 1996; Pasternak et al. 2004a) have shown the importance of the combined effect of chemical attractants and flow on the host-finding ability of invertebrate larvae, who may not respond to the attractants unless they are coupled with a flow direction cue (Pasternak et al. 2004b).

P. cf. *mamaevi* and its host fish, the rabbitfish *Siganus rivulatus* (Forsskal), are both Lessepsian immigrants, i.e., have co-invaded the Mediterranean from the Red Sea via the Suez Canal (Paperna 1972; Diamant 1989b; Diamant 1998). *S. rivulatus* has been very successful and since its discovery in the Mediterranean more than seven decades ago (Steinitz 1927), has colonized most of the eastern Mediterranean basin (Golani et al. 2002). A comparison of the *P.* cf. *mamaevi* infection levels of the original and invading populations, as well as investigation of the infection mechanisms, might elucidate factors that govern monogenean proliferation. Since host location by the larvae is one of the most important processes regulating parasite population dynamics (e.g., Pawlik 1992), its study is of fundamental importance in understanding parasite prevalence. Consequently, the goal of the present work was twofold: (a) to examine the parasite abundance in the original and invading populations and (b) to determine whether at-a-distance chemical recognition may play a role in the host location process. In the study, we attempted to approximate the chemical stimulation facing the larvae in the natural environment. It is important to emphasize that the experiments were designed to establish whether distance chemoreception exists in this parasite and not to fully elucidate the infection process or the site of larval penetration. Therefore, we studied the reactions of oncomiracidia to a complex "cocktail" of odors emitted from whole live hosts and not a specific host tissue.

Materials and methods

Host fish, *S. rivulatus,* were caught at three sites along the northern Red Sea coast [total length (TL)=132–282 mm] and at three sites along the Israeli Mediterranean coast (TL=154–242 mm). Fish were caught by baited traps (Red Sea) or hook and line (Mediterranean). In the Red Sea, Fish were caught in January, March, July, and November 1999, while those in the Mediterranean in May, June, July, and August 1999. All fish were transported live to the laboratory in seawater at ambient temperature (AT=22–25°C) and were examined within several hours. The fish were then killed by spinal incision and gill arches were carefully removed and placed in a Petri dish containing 0.45 μ filtered seawater (FSW) and inspected under a stereomicroscope. Specimens of *P.* cf. *mamaevi* were separated and transferred into tissue culture plates containing FSW at AT, while recording the total number of parasites on each fish. Within several hours, egg-release occurred and eggs were transferred to clean tissue culture plates with FSW and kept at AT for monitoring of hatching rhythmicity (see below). After 4–8 days the eggs hatched, and larvae were removed once daily with pipette and taken for behavior experiments, which took place between 10:00–14:00. To assure settlement competency, each behavioral experiment included a mix of different-aged larvae, from young (4-h-old) to old (20-h-old). Host metabolite solution (HMS)

was prepared taking 1 l of water from a 10-l aquarium containing *S. rivulatus* that swam in FSW for 6 h.

For hatching rhythmicity analysis, worms were placed in individual well plates and produced eggs. A total of 120 Red Sea and 120 Mediterranean eggs were maintained in the laboratory at 24°C. FSW in the well plates was changed daily. The eggs were exposed to ambient natural light during daytime (06:00–18:00) and then covered and kept in the dark at night (18:00–06:00). The eggs were monitored throughout the 4–8-day embryonation period and examined with stereoscope four times each day, at 06:00, 12:00, 18:00, and 00:00, at which times hatched larvae were removed and recorded. Examination during the dark period was brief and with weak illumination.

The experimental setup of Pasternak et al. (2004a) was followed, using the same plexiglas flume. In brief, larval behavior was tested in the flow tank under four treatments of flow and waterborne host metabolites: (a) still water without HMS, (b) still water with HMS, (c) flow without HMS, and (d) flow with HMS. Larval motion was videotaped in the dark (using infrared illumination) for 10 min, and each experimental combination was repeated four times, recording ten individual larvae each time for a total of 40 larvae per combination. Contrary to most larval habitat selection experiments in flow, larvae were not allowed passes over the HMS source but rather were filmed downstream of it, sensing only those host metabolites that have drifted with the flow. Flow velocity was 5 mm s^{-1}, slower than the maximal swimming speed of the larvae (6.6±1.1 mm s^{-1}), which was measured for 20 larvae over 10 cm in still water. The resultant water velocity profile was almost totally straight downstream, with "quasi-laminar" properties (see Pasternak et al. 2004a,b). It should be stressed that this study did not attempt to either fully describe the flow, nor to simulate natural flow patterns over the seabed, but merely to study the potential behavioral and physical capabilities of the larvae in still and flowing water.

For behavioral analysis, larval paths were observed from above for as long as they remained within the camera viewing field. Trajectories were manually drawn on acetate sheets at a sampling rate of one point per frame (25 points per second) and were subsequently digitized at a 1 point $pixel^{-1}$ resolution using ImageJ (http://rsb.info.nih.gov/ij). Digitized trajectories were analyzed using MATLAB 6.5 (The MathWorks) to discover their direction of motion at each point in time. The following parameters were calculated: (1) host location ability (HLA), the percentage of larvae in the camera's field of vision to reach the permeable mesh; (2) behavior Pattern time distribution (BPTD), the percentage of time the larvae spent performing each different behavioral pattern. BPTD proportions were arcsine-transformed and statistical analyses were performed using two-way ANOVA tests followed by post hoc Scheffe's test.

Results

Parasite abundance

Parasite prevalence and mean intensity data are presented in Table 1. Prevalence levels in the Mediterranean are significantly higher than in the Red Sea samples (Kruskal–Wallis test, $p<0.05$), as is the mean intensity of infection ($p<0.05$). Both parameters in Mediterranean rabbitfish samples were approximately three times higher than in the Red Sea.

Egg hatching In the egg-hatching experiment, 101/120 (84%) of the Red Sea eggs hatched during the night, 33 (27%) between 18:00 and 00:00, and 68 (57%) between 00:00–06:00; 19 (16%) hatched during the day, all of them between 06:00–12:00. In the Mediterranean eggs, 111/120 (93%) hatched during the night, 49 (41%) between 18:00–00:00 and 62 (52%) between 00:00–06:00. Only 9 (7%) hatched during the day, 2 (1%) between 06:00–12:00 and 7 (6%) between 12:00–18:00. The hatching of eggs in both the native Red Sea and invading Mediterranean populations at night was highly significant (χ^2 test, $P<0.001$).

Larval response patterns Two-way ANOVA testing found no significant differences ($P=0.757$) between the five treatments shown in Fig. 2; however, there was a significant difference between the four motion patterns ($P<0.001$), with Scheffe's test attributing this difference to the motion pattern of "no motion," which was significantly different from all other motion patterns. There was an interaction between the two variables tested, "treatment" and "motion pattern" ($P<0.001$), suggesting that BPTD

Table 1 Sampled data (mean±SD) of host rabbitfish *S. rivulatus* and *P.* cf. *mamaevi*

Site	*N*	Fish total length (mm)	Prevalence (%)	Mean intensity
Mediterranean				
Mikhmoret	24	154–242	93	13.7±16.8
Hertzliya	28	180–242	52	4.6±6.0
Tel Aviv	38	163–211	82	6.2±7.7
Mediterranean (total)	90		76±21	8.2±10.2
Red Sea (Eilat)				
North beach	61	152–220	49	3.9±3.6
Harbor	20	162–221	15	2.7±2.1
Nature Reserve	47	132–282	15	1.7±1.1
Red Sea (total)	128		26±20	2.8±2.3

N Number of rabbitfish examined, *prevalence* percent of infected fish in sample, *mean intensity* number of worms per infected fish

was significantly different between the five treatments. To determine which treatments caused this difference, we performed two-way ANOVA tests for the still water treatments (with and without HMS) and for the flow treatments (with and without HMS and passive particles in flow). The interaction in these tests was insignificant both for the still water treatments (P=0.132) and for the flow treatments (P=0.445), indicating that BPTD was similar for all still water treatments and for all flow treatments, but different between these two groups.

In still water without host metabolites, the larvae were observed to perform three fundamental motion patterns (Figs. 1a and 2). (1) The first pattern was the circular motion, at circle diameters no greater than 1 mm and at very slow swimming speeds (<0.2 cm s^{-1}); this pattern was performed at 14±4% of the larvae's swimming time. (2) The next motion pattern was the straight, fast swim (0.6–0.7 cm s^{-1}), never lasting more than 4 s; this pattern was performed at 37±14% of the larvae's swimming time. (3) The last pattern is the helical swimming; this pattern was performed at 29±13% of the larvae's swimming time. In still water with host metabolites (Figs. 1a and 2), the same basic pattern as without host metabolites was revealed, but comprising a higher portion of helical motion (54±24% of larval swimming time) and lower portion of straight swimming (9±2% of larval swimming time). However, larvae did not swim toward the source of the host metabolites—HLA was only 3±4%. In flow without host metabolites (Figs. 1b and 2), larvae were passively swept downstream. The same behavioral pattern was observed in flow with host metabolites (Figs. 1b and 2), resulting in an HLA of 0±0%. In both treatments, this pattern was seen at >90% of the larvae's swimming time, the same as if they were passive particles in the flow (Figs. 1b and 2).

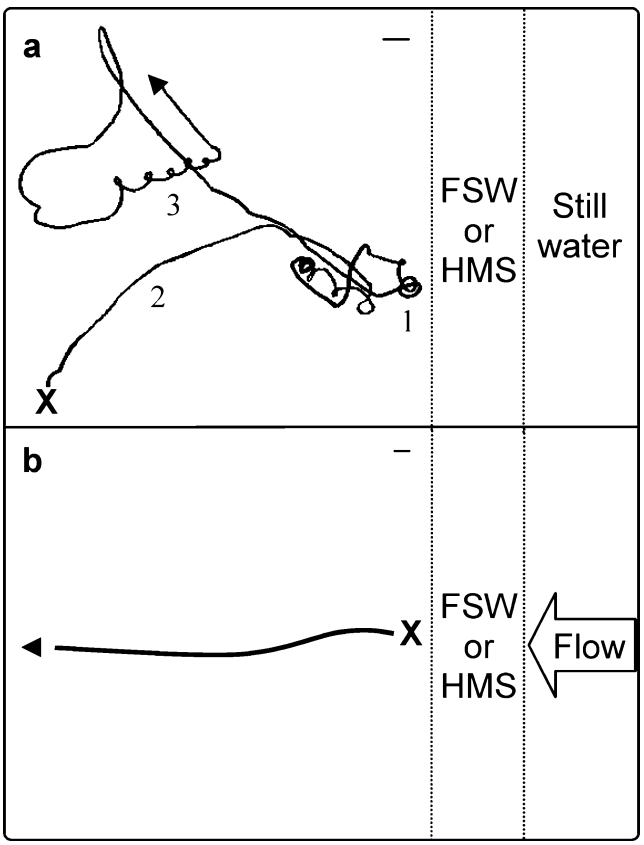

Fig. 1 Typical examples of *P.* cf. *mamaevi* larval motion patterns in still water and flow. Motion trajectories begin at the *X* sign and end with a *full arrow*. **a** Still water with and without host odor (numbers refer to behavior patterns described in the text). **b** Flow with and without host odor. Bar= 1 mm

Discussion

The prevalence levels of *P.* cf. *mamaevi* at the Israeli Mediterranean rabbitfish populations were very high, approximately three times greater than those found in the native populations of the northern Red Sea. This difference is further emphasized when considering that relatively low prevalence may be the rule rather than the exception in the genus *Polylabris*. Rohde et al. (1995) found that 28.6% of *Rhabdosargus sarba* (Forsskal) in NSW Australia were infected by *Polylabris rhabdosargi*, and 12.5 and 31.7% of the Eilat (Red Sea) fishes *Siganus argenteus* and *Siganus luridus* were infected with *P.* cf. *mamaevi*, respectively (A. Diamant, unpublished data). Since no behavioral differences between oncomiracidia originating in Mediterranean vs Red Sea worms were detected, it is unlikely that larval behavior is the cause of the observed difference in parasite population abundance between the original and invading host populations. In its newly adopted zoogeographical region, the invading *S. rivulatus* encountered quite different environmental conditions from its native Red Sea: absence of coral reefs, wider temperature range, different food sources, increased pollution loads, etc., all of which led to changes in school density, home range, and migratory behavior. The different diet and contact with a different bacterial flora, coupled with biotic and abiotic factors and environmental stressors, are known to influence parasite population size and alter susceptibility of the piscine host to infections (e.g., Overstreet 1993), including compromise of host immunity to parasitic invasion (van Muiswinkel 1995). Changes in the natural environment and impact of anthropogenic factors encountered by the rabbitfish in their new Mediterranean habitats may have acted to enhance the abundance of *P.* cf. *mamaevi* in the invading host populations. On the other hand, these same conditions do not seem to hamper its enormous success in forming large populations and constant westward extension of its range in the Mediterranean (D. Golani, personal communication). Clearly, more research is needed in this area.

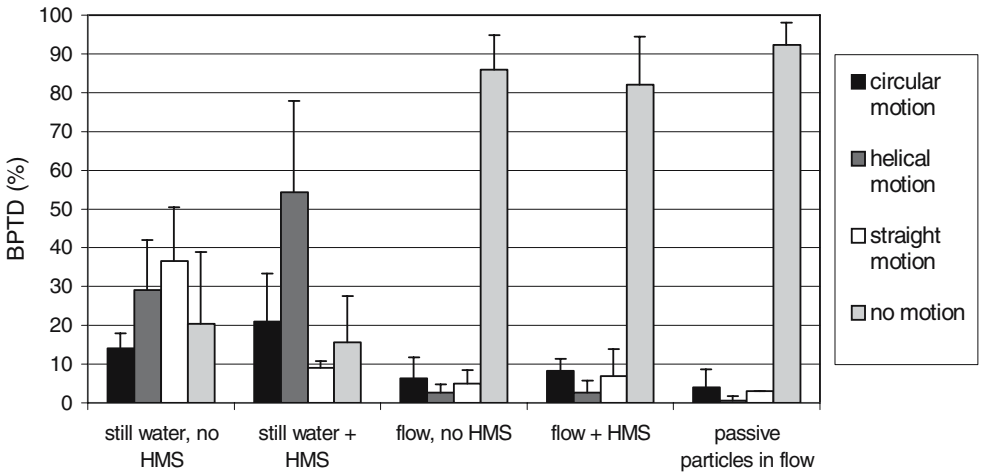

Fig. 2 Behavior Pattern Time Distribution of *P.* cf. *mamaevi* larvae and passive particles in different conditions of water speed and different attractants (see text for explanation)

Although there are additional reported cases of Monogenea invading new geographic areas, in all cases this was accidental through international translocation of finfish stocks (see Hayward 2005). The present case is the first documented of a monogenean invading a new biogeographical region by "natural" extension of its host range. Invading organisms tend to leave behind most of their natural parasites, retaining only a subset of the native suite of parasites to establish populations in the new biogeographic region (Torchin et al. 2003; Clay 2003). Accordingly, the known parasite species richness in Red Sea *S. rivulatus* populations is 24, as compared with only 9 species in the Mediterranean (Diamant 1989b; Diamant et al. 1999). Nevertheless, the successful Lessepsian immigrant parasite species of *S. rivulatus* include all monogeneans known from this host species in the Red Sea (Diamant 1989b, 1998). It is unknown, however, if and how the reduced parasite species richness in the new environment has somehow promoted heavier infections with this monogenean. It is noteworthy that Paperna et al. (1984) reported hyperinfections with this polyopisthocotylean in captive *S. luridus* in the Red Sea, in which a prevalence of 100% was recorded in flow-through seawater tanks, with heavy intensities of up to 1,133 worms on one fish, inducing severe anemia. Such occurrences are not uncommon in mariculture systems. For example, heavy infections with the polyopisthocotyleans *Heteraxine heterocerca* and *Zeuxapta japonica* have been reported in Asian aquaculture facilities in yellowtail and amberjack, respectively (see Ogawa 2005).

Host specificity of fish monogenean ectoparasites has been studied by various authors (e.g., Desdevises et al. 2002). It may have been developed from recurrent settlement of the larvae on a suitable host or from post-settlement factors such as larval rejection by an unsuitable one (Moulia 1999). In other groups of parasitic worms, mainly digenean trematodes and nematode hookworms, larvae (called miracidia and L3 larvae, respectively) often select their settlement sites actively, navigating according to waterborne chemical cues emitted from the target organism (Haas 2003). In the present study, however, when exposed to host odor, *P.* cf. *mamaevi* larvae did not display any change in behavior nor did they advance toward the host. Since each behavior experiment included a mix of different aged larvae (4- to 20-h old) and as the employed methodologies were previously tested (Haas 2003; Pasternak et al. 2004a,b), our results may imply that the competent oncomiracidia were either unable to sense the waterborne substances or did not respond to them. In contrast, the exposure of larvae to flow did produce a behavioral response, since the larvae ceased all swimming and were consequently carried away passively with the flow. A similar behavioral pattern was reported for *Diplozoon paradoxum* (Nordmann), a related monogenean gill parasite (Bovet 1967).

Parasite infections in wild populations of *S. rivulatus* were shown to be closely associated with host diet and behavioral patterns in the Red Sea (Diamant 1989a; Diamant et al. 1999). In light of the efficient infecting capacity of *P.* cf. *mamaevi*, we propose the following mechanism as a possible explanation of its high host specificity. The juveniles (length <25 mm) of *S. rivulatus* are benthic fishes that form closely packed aggregations of thousands of individuals that roam relatively shallow coastal marine habitats (Popper 1979). At night, the schools rest in tight formation on the ground at sites sheltered from flow (Popper 1979). Adult schools have similar nocturnal behavior, although sleeping individuals tend to be more spaciously distributed (A. Diamant, unpublished observations). Thus, if an oncomiracidium were to hatch at the appropriate time, it would encounter an environment consisting of weak ambient currents, shallow water, and static potential hosts in the immediate vicinity. Under such conditions, cessation of swimming upon sensing host-

inhalant gill-ventilating currents would be adaptive for a rapid, passive entry into the gill chamber of a suitable host. Endogenous circadian hatching rhythm correlating with the diurnal activity of the fish host was demonstrated in several monogenean species. For example, *E. soleae* oncomiracidia hatch during the first 4 h after dawn, when their host *Solea solea* (Linnaeus) is inactive and therefore easier to target (Kearn 1973). Chisholm and Whittington (2000) list three monocotylids from shovelnose ray *Rhinobatos typus* with distinct hatching patterns linked to light periodicity. (additional examples are given in the reviews of Whittington 1997, 2000, 2005). Our own observations on *P.* cf. *mamaevi* showed that eggs possess rhythmical hatching, almost exclusively at night. This synchronized process coincides with the cessation of oncomiracidia swimming upon sensing host metabolites and nocturnal rest of the host fishes when they tend to be relatively crowded and immobile, and therefore, would increase the probability of oncomiracidia to encounter a suitable nearby host.

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