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ORIGINAL ARTICLE

A PRELIMINARY REPORT ON THE ECOLOGICAL INTERACTION BETWEEN GYRODACTYLUS RYSAVYI AND MACROGYRODACTYLUS CONGOLENSIS, VIVIPAROUS GYRODACTYLID MONOGENEANS FROM THE SKIN AND FINS OF THE NILE CATFISH CLARIAS GARIEPINUS

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Abstract:

A preliminary report has been given of the ecological interaction between two cohabitant viviparous gyrodactylid monogeneans, namely Gyrodactylus rysavyi Ergens, 1973 and Macrogyrodactylus congolensis (Prudhoe, 1957) Yamaguti, 1963, skin dwellers of the Nile catfish Clarias gariepinus. These monogeneans are very highly host specific and occupy a definite niche on the catfish host. They showed considerable morphological, ecological and behavioural variations. The small-sized G. rysavyi is a fast-growing species and attains a high reproductive potential. In contrast, the cohabitant, large-sized M. congolensis is a slow-growing species and attains a comparatively lower reproductive potential. While the attachment of M. congolensis is highly destructive to the niche, the footprint of G. rysavyi is less destructive. On the feral catfish population, these monogeneans typically survive at low prevalence, mean intensity and abundance, and tend to aggregate in restricted niches, namely the dorsal surface of the head region. In all experimental bispecific monogenean infestation trials, G. rysavyi outnumbered its rival, M. congolensis. However, in all monospecific monogenean infestation trials, each species exhibited an exponential growth followed by a dramatic decline and eventual disappearance from the catfish host population. The proximate and ultimate causes as well as the consequences of the ecological interaction between G. rysavyi and M. congolensis are discussed in detail.

KEYWORDS:

Monogenea, Gyrodactylus rysavyi, Macrogyrodactylus congolensis, Clarias gariepinus, ecological interaction.

INTRODUCTION

Ecological interaction denotes the relationship between species that live together in a community. Ecological interaction between living organisms comprises competition, predation, parasitism, mutualism, commensalism and symbiosis. Gyrodactylid monogeneans are successful inhabitants of a broad spectrum of freshwater and marine fishes (Soleng and Bakke, 1997). This brand of the Monogenea had experienced permanent parasitism on the fish hosts. Many types of the ecological interaction have been previously recorded in the monogenean communities, for example, competitive exclusion (Paperna, 1964; Chung et al., 1984; Buchmann, 1988; Combes, 2001), competitive co-existence (El-Naggar and El-Tantawy, 2001), character displacement (Rohde, 1991), and co-occurrence (Bashirullah and Rado, 1987; Simkova et al., 2000, 2002; Johnson and Buller, 2011). According to Rohde (1991, 2005), monogenean species that possess similar copulatory organs are always spatially segregated on different microhabitats of their hosts,

whereas species with different copulatory organs co-exist peacefully together, implying that the spatial segregation is not induced by competition, but probably reflects a reinforcement of reproductive barriers.
Competition between individuals of the same species for identical resources such as food items, habitat place, light regimes and/or water supply is referred to as intraspecific competition (Sahney et al., 2010). This kind of competition seems likely to be intense because cohabitant individuals of the same species compete directly for the same resource items. On the other hand, competition between individuals of different cohabitant species for available and common resource items is termed interspecific competition (Sahney et al., 2010). Competition leads to the reduction of the fitness of one or both interacting species according to the competitive exclusion principle (Gause, 1935). Miller (2004) suggested two types of competition, namely exploitation competition and interference competition. Regarding the interference competition, one species may limit the access of a cohabitant species to a range of environmental resources, regardless of its abundance. Concerning the exploitation competition, competing species have roughly equal access to a specific resource but differ in how fast or efficiently they exploit it. Accordingly, the species that can use the resource more quickly would get more of the resource and hamper growth, reproduction and/or survival of the other species (Miller, 2004).

Witmer and deCalesta (1986) suggested that a rich habitat, with abundant and diverse environmental resources might allow ecologically similar species to share a common resource. Simkova et al. (2000) hypothesized that co-existence among competing species can be favoured by niche specialization and/or by reducing the overall intensity of competition via aggregated utilization of fragmented resources. According to Rohde (2011), two competing species may well co-exist on one limiting resource. A good example supporting this view is derived from the interaction (competitive exclusion) between the trematode Gorgodera euzeti and the monogenean Polystoma integerrimum, both infecting the urinary bladder of the frog Rana temporaria in the Pyrenees (Combes, 2001). The author found that the number of frogs examined was 1941; the number infected with the first species alone was 576, with the second species 280, with both species 39. Rohde (2011) calculated that the number should be at least 576×280/1941 = 83 if the double infections had occurred by chance alone. Similarly, Simková et al. (2000) investigated the co-existence of nine species of the genus Dactylogyrus in relation to the niche overlap, niche preference and intraspecific as well as interspecific aggregation. They reported that the niche overlap and niche preference do not seem to be affected strongly by competition.

A considerable body of data is available on the anatomical and biological features of gyrodactylid monogeneans of the Nile catfish Clarias gariepinus (Burchell, 1822) in Egypt (for example, El-Naggar and Serag, 1987; Arafa, 1999; Arafa et al., 2003; El-Abbassy, 2001, 2005). However, little is known about the behavioural aspects (El-Naggar et al., 2001, 2004) and ecological interaction between cohabitant gyrodactylid monogeneans of C. gariepinus. The present study aimed to throw light on the ecological interaction between two cohabitant viviparous gyrodactylid monogeneans, namely Gyrodactylus rysavyi Ergens, 1973 and Macrogyrodactylus congolensis (Prudhoe, 1957) Yamaguti, 1963 that graze over the skin surface and fins of C. gariepinus inhabiting Nile Delta, Northern Egypt. One of the objectives of the present study was to explore the ecological and behavioural similarities/differences between the studied gyrodactylid monogeneans and to test the null hypothesis that co-existing species, living in the same niche (fish host in the present study), should differ in their strategies of the host resources exploitation (for example, reproductive potential, nutritional requirements, transmission tactics and dispersal strategies, microhabitat deterioration/destruction, etc.) as well as in their intrinsic factors that promote their population growth.

MATERIAL AND METHODS

Macrogyrodactylus and Gyrodactylus worms used in the infestation experiments of the present study originated from naturally infested catfish caught from the Damietta Branch of the River Nile nearby Mansoura, Egypt. Sampled catfish individuals were divided into two main groups. Members of the first group were fixed via an immediate immersion in 10% formaldehyde solution to obtain mirror data of the field, in terms of the prevalence (percentage of infestation), mean intensity (mean number of worms/single infested catfish) and abundance (mean number of worms/examined host individuals). Naturally infested catfish individuals of the second group were kept in 100L aquarium containing dechlorinated tap water at 25±2 °C in a 12 h L: D regime and used for the infestation experiments.

To throw light on the monogenean activities on the catfish host, a group comprising 10 individuals of the naturally infested catfish was maintained in a 100L aquarium. Macrogyrodactylus worms (maximum total length = 3000 µm) were recognized on the skin and fins of the catfish by naked eyes, through the transparent wall of the glass aquarium. However, Gyrodactylus worms (maximum total length = 1400 µm) were hardly recognized by naked eyes. Therefore, a Waltex hand lens (2x and 4x) was employed to document a composite of the behavioural aspects of either Gyrodactylus or Macrogyrodactylus worms on the catfish host throughout the development of the monogenean infestation. These observations were enriched by stereomicroscope observations on freshly killed host fish. These behavioural aspects comprised intraspecific physical communication among Gyrodactylus or Macrogyrodactylus worms and interspecific physical interference between Gyrodactylus and Macrogyrodactylus worms over the skin surface of C. gariepinus.

A recipient system was designed as follows: specimens of the catfish were caught from the Damietta Branch of the River Nile nearby Mansoura and transferred, in aerated plastic bags, to 100L aquarium containing dechlorinated tap water at 25±2 °C in a 12 h L: D regime. To remove the monogenean worms as well as other ectoparasites from the recipient system, members of the catfish were immersed in an appropriate amount of the sea water collected from the Mediterranean Sea at Gamasa, near Mansoura, Egypt. Treated catfish individuals were returned to the recipient system and acclimated for 15 days prior to the infestation experiment.

An infested catfish was removed from the donor system and killed by a deep cut behind the head using a sharp scissor. Then, the skin sheets were dislodged off the donor catfish. Under stereomicroscope, Gyrodactylus and Macrogyrodactylus worms were sucked into a pipette and transferred gently into Petri dishes containing filtered riverine water. As long as detached worms remained attached to the bottom glass of the dish by their haptor and were capable of stepping and searching movements, they were considered to be viable and therefore employed in the infestation experiments. However, moribund worms may remain alive, but no longer capable of proper locomotion. Therefore, they were not involved in the infestation experiments. As gyrodactylids are sensitive to the host serum (Harris et al., 1998), they were carefully dislodged off from their attachment sites in order to avoid the contamination of parasites with the catfish body fluids.

To conduct an infestation trial, monogenean worms were individually sucked into a pipette and transferred gently into an aquarium containing non infested individual catfish suspended in a small amount of water. Few hours later, the catfish acquiring infection was transferred to the donor system. In monospecific monogenean infestation experiments, fishes of the recipient system were picked up individually and infested either by 5 Gyrodactylus worms or 5 Macrogyrodactylus worms. In bispecific monogenean infestation experiments, fishes of the recipient system were picked up individually and infested by a combination of 10 specimens of the two monogeneans (5 worms for each), 20 specimens (10 worms for each), 40 specimens (20 worms for each) or 100 specimens (50 worms for each). Accordingly, four host parasite systems, namely Gyrodactylus–Clarias system (monospecific Gyrodactylus infestation), Macrogyrodactylus–Clarias system (monospecific Macrogyrodactylus infestation) or Gyrodac - tylus–Macrogyrodactylus–Clarias system (bispecific or mixed Gyrodactylus–Macrogyrodactylus infestation) were developed. Each infestation experiment was repeated three times and the data was calculated as the mean value of these trials.

In order to assess the morphometrics of the epidermal cells on the skin surface of the catfish host, on which gyrodactylid monogeneans are resident, haematoxylin and eosin stained sections were prepared. Samples of the infested and non infested tissues were processed for paraffin wax sections (5 µm thickness), stained in haematoxylin and eosin dyes and mounted in Canada balsam. Under high power light microscope (Leitz–Labroux), the measurements of the epithelial cells of the catfish host were recorded using a micrometer. Thereafter, the measurements were calibrated on a standard scale.

RESULTS

Host specificity and Microhabitat specialization:

The present study as well as other parasitological surveys of the monogenean communities of the freshwater fish inhabiting the Nile Delta in Egypt over the last three decades indicates that the viviparous gyrodactylid monogeneans Gyrodactylus rysavyi and Macrogyrodactylus congolensis are very highly host specific and occupy a definite niche on the Nile catfish Clarias gariepinus. These monogenans are highly specialized in grazing over the skin surface and fins of the catfish host. They share an identical food resource, namely the outermost skin epidermal layers. Moreover, they are subjected to identical hydrodynamic forces, created by the actively swimming fish. These monogeneans have not been previously recorded from any of the cohabitant freshwater fishes of the River Nile, for example Bagrus bajad, Bagrus docmak, Oreochromis aureus, Oreochromis niloticus niloticus, Tilapia zilli, Sarotherodon galilaeus, Lates niloticus, Chrysichthys auratus, Cyprinus carpio carpio, Dicentrarchus labrax, Synodontis schall, Liza ramada, Malapterurus elctricus, Mormyrus kannume and Mugil cephalus.

Infestation levels on feral catfish host:

Out of 200 examined specimens of the Nile catfish C. gariepinus, the prevalence of infestation was 13% for G. rysavyi and 6% for M. congolensis. The mean intensity value was 7±3 for G. rysavyi and 3±1 for M. congolenesis. With the exception of accidental outbreaks of infestation, the maximum intensity values (maximum number of worms on a single infested fish) recorded for G. rysavyi and M. congolensis were 10 and 5 worms, respectively. The abundance of G. rysavyi and M. congolensis was less than one worm per examined fish.

Gyrodactylid monogenean activities:

Close observations, under high power stereomicroscope, on the skin surface and fins of the freshly killed catfish revealed a composite of behavioural aspects, including physical communication among Gyrodactylus or Macrogyrodactylus individuals, physical interference between Gyrodactylus and Macrogyrodactylus individuals and movement patterns exhibited by either parasite species. Either G. rysavyi or M. congolensis were observed to practice leech-like movement in a professional manner. Each movement trial lasts for approximately two seconds. Each worm was recognized to stretch its body while the haptor is firmly rooted on the substratum. Then, the anterior adhesive area is employed efficiently to glue to the host's epidermis. This was followed by an immediate withdrawal of the haptor, which was rapidly translocated and fixed just close to the anterior adhesion. Finally, the body proper of the parasite was observed to stand up at approximately right angles to the properly attached haptor.

A simple calculation, considering morphometrics of the parasites, reveals that G. rysavyi is capable of walking a distance measuring approximately 700 µm/s (42000 µm/min or 2520000 µm/hr). Accordingly, G. rysavyi can move about on the whole surface of the skin of a host individual measuring 50 cm in total length five times within an hour. A similar calculation indicates that M. congolensis is capable of moving a distance measuring approximately 1500 µm/s (90000 µm/min or 5400000 µm/hr). Accordingly, M. congolensis can dwell the whole surface of the skin of a host individual measuring 50 cm in total length eleven times within an hour. Moreover, the translocation of G. rysavyi was relatively continuous, however that of M. congolensis was intermittent, showing many pauses interspersed between bouts of movements. Hand lens observations on the freshly killed catfish revealed also that Gyrodactylus worms exercised rapid and frequent head-to-head and body-to-body displays, overlapping of the body proper of two adjacent worms, and marked prolongation of the body proper of one worm to communicate a conspecific over a neighbouring attachment site. Similar displays were recorded for Macrogyrodactylus worms; however these displays were less frequent and performed at a slow rate. Other types of movements were similar to those described by El-Naggar et al. (2001, 2004).

Morphometric measurements:

Macrogyrodactylus congolensis:

Morphological measurements (mean ± 1 standard deviation followed by the range in parentheses). Body elongate, 2700 (2400-3000) µm long, 480 (460-500) µm wide. Mouth opening, 70 (61-87) µm wide; Intestinal crura extending beyond the anterior edge of the testes, 1500 (1370-1850) µm long. Haptor roughly circular, 620 (590-640) µm long × 440 (400-470) µm wide. Total length of hamuli 370 (345-405) µm. Total length of marginal hooks 100 (95-115) µm; marginal hook blade 33 (29-37) µm long. The gaffing action of the marginal hooklets is a predominant feature in M. congolensis.

Gyrodactylus rysavyi:

Morphological measurements (mean ± 1 standard deviation followed by the range in parentheses). Body elongate, 1400 (1325-1415) µm long, 290 (260-310) µm wide. Mouth opening, 35 (31-39) µm wide; Intestinal crura extending beyond the anterior edge of the testes, 1000 (900-1200) µm long. Haptor roughly rectangular, 230 (210-250) µm long × 280 (260-290) µm wide. Total length of hamuli 170 (155-190) µm. Total length of marginal hooks 70 (65-80) µm; marginal hook blade 18 (16-19) µm long. Similar to M. congolensis, the gaffing action of the marginal hooklets is a predominant feature in G. rysavyi. The haptor of G. rysavyi seems to be formed of two functionally different compartments; the marginal hooklets are arranged in an amazing manner, creating a paddle-like system driving the parasite during migration into the water column, whereas the hamuli are packed into an independent tegumantal envelope.

Reproductive potential of parasites:

Starved Gyrodactylus and Macrogyrodactylus worms continued to give birth for a few days whilst isolated in Petri dishes. Thereafter, the parasites showed gradual decline in viability with time. On the one hand, Gyrodactylus worms multiplied three times; ten worms were encountered on the bottom of the dish by the end of the third day of incubation instead of only three worms registered at the first day. On the other hand, the number of Macrogyrodactylus worms multiplied two times; seven worms were recognized on the bottom of the dish by the end of the third day of incubation instead of only three worms registered at the first day.

Fed Gyrodactylus and Macrogyrodactylus worms attained an amazing reproductive potential. In some infestation experiments, only five Gyrodactylus worms registered at the initial phase multiplied rapidly and gave birth to approximately 25000 worms on the skin surface and fins of a medium-sized catfish (40±2 cm) within five weeks. In other infestation experiments, only five Macrogyrodactylus worms registered at the initial phase multiplied rapidly and gave birth to approximately 10000 worms on the skin surface and fins of a medium-sized catfish (40±2 cm) within four weeks. The infestation course was terminated in a dramatic infrapopulation decline and subsequent disappearance of either species from the aquarium.

Close observations of the pregnant Gyrodactylus and Macrogyrodactylus worms revealed that parent worms rarely give birth during the day light, indicating that the vast majority of births occurred during night. Only 10% of the pregnant worms were observed to give birth during the day light, however other births, encountered on the bottom of the dish in the morning of the next day, were delivered during night.

Monospecific and Bispecific infestation:

In all bispecific monogenean experimental infestation trials, G. rysavyi outnumbered its rival, M. congolensis. However, each species exhibited an exponential growth followed by a dramatic decline and eventual disappearance from the catfish host population in all monospecific monogenean infestation trials. The population time of G. rysavyi and M. congolensis was 35 days. The ceiling densities for M. congolensis and G. rysavyi were 0.8 worms/cm2 and 100 worms/cm2, respectively.

Monogenean nearest-neighbour distance:

Table (1) shows the mean nearest-neighbour distance of G. rysavyi and M. congolensis infrapopulation on the skin surface and fins of C. gariepinus. It could be noticed that the mean nearest-neighbour distance of either parasite species gradually decreases from a few centimeters during the first week to 0.03 cm for G. rysavyi and 0.51 cm for M. congolensis by the end of the infestation experiment on medium-sized catfish (40±2 cm).

Microhabitat deterioration:

Morphological measurements on paraffin wax sections of the normal skin surface of the Nile catfish indicated that the epidermis measures 100 µm in thickness. The number of epithelial cells was 20 cells/80 µm2. However, the number of mucous cells was 2 cells/80 µm2 and that of the club cells was 8 cells/80 µm2. The diameter of the mucous cells measured 15 µm, whereas that of the club cells reached 30 µm. Apparently, the skin epidermis was intact.

Morphological measurements on paraffin wax sections of Macrogyrodactylus-infested skin surface of the catfish revealed that the epidermal sector exposed to the suction force created by the haptor measures 75 µm in thickness. However, this thickness was reduced to 25 µm in the epidermal sector facing the pressing hamulus, and to only 10 µm opposite to the haptor tightly pressing on the host's epidermis. The epidermis appeared amorphous and rich in lymphocytic infiltration. There were no mucous cells in the vicinity of the haptoral attachment; however the diameter of the club cells was reduced to 15 µm. Morphological measurements on paraffin wax sections of Gyrodactylus-infested skin surface of the catfish revealed no changes in the epidermal components. Obviously, the epidermal components appeared intact and cell rich.

DISCUSSION

According to the present findings, the assumption of the null hypothesis is accepted. The viviparous gyrodactylid monogeneans G. rysavyi and M. congolensis exhibited considerable morphological, ecological and behavioural differences. On the one hand, the small-sized G. rysavyi is a fast-growing species, with high reproductive potential. This monogenean is highly active and an excellent swimmer. Comparatively, the cohabitant, large-sized M. congolensis is a slow-growing species, with low reproductive potential. This monogenean is moderately active and could not swim (see El-Naggar et al., 2004). The former species may be regarded as a superior competitor, while the latter species seems likely to be an inferior competitor. Moreover, the attachment of M. congolensis is highly destructive to the niche, where it compresses, tears and accelerates the weathering of the host's epidermis. In contrast, the attachment of G. rysavyi is less destructive to the niche, where it clings gently to the surface epithelium with the aid of the peripheral, tiny marginal hooklets, without employing the sharp massive hamuli. These differences seem likely to be key factors determining the occurrence and distribution of theses parasites within the host population.

Rohde (2002) hypothesized that the mating of the monogenean species that typically survive at low density and tend to aggregate is facilitated by their restricted niches, which probably reflect long-term behavioural and morphological adaptations. The author also hypothesized that the niche restriction exists even in the absence of competing species. Field and experimental work on gyrodactylid monogeneans of the Nile catfish over the last two decades indicated a marked temporal variability in the population build up of G. rysavyi and M. congolensis (for example, El-Naggar, 1994, 2007; El-Naggar et al., 2001, 2004; Hagras et al., 1999). On the one hand, the viviparous phenomenon G. rysavyi is a fast-growing species and attains a high reproductive potential. On the other hand, the cohabitant M. congolensis is a slow-growing species and exhibits a low reproductive potential.

Under natural conditions, either the small-sized G. rysavyi or the comparatively large-sized M. congolensis attains an optimal foraging, where the essential resources (food items and attachment sites) on the skin surface and fins of C. gariepinus are abundant and renewable. As a consequence, there is no opportunity for dietary or habitat overlapping between the two cohabitant gyrodactylid monogeneans. On the feral catfish population, mate-finding and cross-insemination between individuals of G. rysavyi or M. congolensis seem difficult, where the mating partners are widely-spaced on the skin surface of the host, and even being resident on dispersed and fast-moving catfish host individuals. The rarity of the cross-insemination could account for the low infestation levels of either parasite species on the wild catfish populations.

Miller (2004) suggested that as long as the essential environmental resources are plentiful, cohabitant species can utilize these resources, and hence each species come closer to occupy the fundamental niche (i.e. the full range of environmental conditions and resources an organism can utilize). However, as a result of limiting factors present in its habitat, the organism occupies only a part of the fundamental niche, namely the realized niche (Miller, 2004). The author hypothesized that the more the niches of two cohabitant species overlap, the more they compete with one another. Due to significant niche overlap, one of the competing species should migrate to another area, shift its feeding habits or behaviour, suffer a sharp population decline, or become extinct in that area.

Epidemiology of Gyrodactylus on the fish hosts is common (for example, Mo, 1984; Cable et al., 2000; Anttila et al., 2008; Johnson et al., 2011). Such phenomenon seems to be facilitated through the variable modes of reproduction (Cable and Harris, 2002; Cable et al., 2002 a, b) and amazing modes of transmission (Bakke et al., 1992; El-Naggar et al., 2001, 2004; Olstad et al., 2006) of this brand of the Monogenea. Exponential growth due to explosive infrapopulation proliferation of G. rysavyi is amazing. Only few worms registered at the initial phase multiplied rapidly to produce up to 25000 worms on medium-sized catfish (40±2 cm) at the terminal phase of the infestation course within only five weeks. A similar exponential growth was recorded for the cohabitant M. congolensis that reached up to 10000 worms at the terminal phase. Such exponential growth necessitates the possession of an adequate energy budget to support short-term embryonation and successive births of the overlapping generations. However, the mechanisms contributing to the explosive infrapopulation proliferation of G. rysavyi remain questionable. The overcrowding of Gyrodactylus worms during the oversaturation phase probably stimulates the cross-insemination, producing phenotypes with novel traits. Marked infrapopulation proliferation of G. rysavyi in captivity implies that this gyrodactylid seems likely to predict and assess its opportunity of future reproductive success and acts accordingly. In contrast, the comparatively limited infrapopulation proliferation of the cohabitant M. congolensis indicates that this monogenean may only be able to evaluate its past investments without any prediction for the risk of extinction following the destruction of the microhabitats.

Fish epidermis and constituting mucous cells act as the preliminary physical/chemical barrier, defending the fish against potential pathogens. Reports on the relationship between gyrodactylid infestations and mucous secretion and mucous cell density are controversial. On the one hand, some authors have recorded increased mucous secretion during Gyrodactylus infestation (for example, Lester, 1972; Heggberget and Johnsen, 1982, Mohamed et al., 2010). On the other hand, some authors noticed epidermal thinning and mucous cell reduction during Gyrodactylus infestation in the brook trout (for example, Cusack and Cone, 1986; Wells and Cone, 2006). In the present study, an epidermal thinning as well as mucous cell reduction was associated with Macrogyrodactylus infestation; however, no apparent changes were detected during Gyrodactylus attachment. Sterud et al. (1998) claimed that G. salaris can interfere with the differentiation of the host response in the epidermis by changing the dynamics of Malpighian and goblet cells turnover, to inhibit or reduce the development Gyrodactylus infestations generally lead to a decreasing number of mucous cells in the epidermis (for example, Cusack and Cone, 1986; Wells and Cone, 2006; Sterud et al., 1998).

Appleby et al. (1997) found no correlation between Gyrodactylus intensity and the number of mucous cells or epidermal thickness. Scanning electron and light microscope observations made by El-Naggar (2007) revealed that the local histopathological impacts induced by gyrodactylid monogeneans on the catfish host C. gariepinus comprised hundreds of thousands of microperforations against the blades of the marginal hooklets of attached gyrodactylids, numerous feeding pits, deterioration of the epidermal layers underneath the haptor, compression of the affected epidermal layers, and amorphous epithelium. In response to monogenean infestation, the host skin created numerous mucous (goblet) cells in the vicinity of established parasites.

The present study indicated that gyrodactylid monogeneans can influence epidermal cell structure in C. gariepinus. Macrogyrodactylus and Gyrodactylus worms injured the skin of the catfish not only through the intensive pinning attitudes, created primarily by the gaffing movements of the blades of 16 marginal hooklets, suction force created by the cup-shaped haptor, a specific aspect of M. congolensis, but also through the feeding pressure exerted by the growing infrapopulations of either parasite species. The affected host epidermis underwent marked compression, tearing and the normal arrangement of the epidermal layers was altered. The feeding pits comprised the outermost layers of the skin epidermis and interfered with the arrangement of the surface epithelial cells. According to Tinsley (2001), Gyrodactylus species feed on the epithelial cells and in very heavy infestations cause irritation and damage that has the potential to kill the host.

The viviparous gyrodactylid monogenean M. congolensis was found to create deep invagination underneath the haptor, while the cohabitant G. rysavyi exhibits superficial clinging to the outermost layer of the epidermis of the catfish host. This difference in the mode of attachment may account for a corresponding tendency for translocations between sites of attachment as well as between host individuals. On the one hand, the rapid detachment and translocation of M. congolensis seem difficult as a result of the deep implantation of the haptor of the parasite into the host epidermis. On the other hand, the superficial, gentle clinging of the haptor of G. rysavyi seems likely to facilitate its detachment and frequent translocation.

The body design of the Nile catfish implies that the surface is divided into two topographically different regions. The first region is located at the head area and characterized by a strong bony shield underneath the skin. The second region extends over the trunk and the tail regions and is characterized by powerful muscular bundles underneath the skin. Such topography probably necessitates the possession of different modes of attachment by an inhabitant monogenean, to cope with the nature of the substrate. The bony shield may obstacle the deep anchorage of the large hamuli of the haptor of M. congolensis, however it may permit the hamulus of the comparatively small cohabitant G. rysavyi to penetrate deeply into the host's body. At the trunk and tail regions, either parasite species could perform a complete anchorage of the hamulus into the host's skin.

Overcrowding of Gyrodactylus worms on limited host resources appears to stimulate an intense intraspecific competition between several thousands of Gyrodactylus individuals that are closely-spaced (haptor-to-haptor) on the skin surface. Under theses conditions, Gyrodactylus individuals would compete for two essential resources, namely the food items and vacant micro-settlement sites, which are dramatically declined. Moreover, the contamination of the niche is increased with the development of the infestation as a result of the enzymatic and waste discharges released by the parasites on the underlying host tissues (see Buchmann, 1998). This is in accordance with the hypothesis of interference competition between cohabitant species suggested by Miller (2004).

There is preliminary evidence that the birth time and the host-searching activity exhibited by gyrodactylid monogeneans are probably conducted during night. The Nile catfish is nocturnal (i.e. active by the night and inactive by the day) (DeMoor and Bruton, 1988; Bishai and Khalil, 1997). The nocturnal habit of the catfish necessitates the acquisition of highly efficient sense organs by the gyrodactylid monogeneans either to neutralize the darkness of the river bed or to encounter a fast moving catfish host. The swimming activity of G. rysavyi is advantageous and acts as an additional mode of transmission and makes it a pioneer species that colonizes previously uncolonized catfish individuals, leading to ecological succession.

Surprisingly, Brooker et al. (2011) found that G. salaris, a monogenean skin parasite of the Atlantic salmon, Salmo salar attains higher activity in the dark than in the light, indicating that this monogenean probably possesses photoreceptors. Similar to many platyhelminths, Watson and Rohde (1994) detected sense receptors in Gyrodactylus sp. Furthermore, Brooker et al. (2011) noticed that the movement parameters of G. salaris (velocity, distance traveled and turn rate) were higher and directional (sinuous) in the red light but lower and undirectional in the white light. According to Brooker et al. (2011), the long sinuous tracks traced by G. salalris probably reflect a host-searching behaviour; covering a large surface area of the water body may allow gyrodactylid monogeneans to identify a composite of environmental cues in the water body holding their fish host. Brooker et al. (2011) suggested that the ciliary structures, likely to be photoreceptors, may be profitable in a shadow response, allowing Gyrodactylus worms to monitor host individuals moving overhead in the water column or those traveling close to the river bed.

It may be hypothesized that the superior competitor G. rysavyi seems likely to be capable of immediately excluding its rival M. congolensis from any patch it would colonize. As the population density of the parasites increases, competition should decrease the availability and profitability of the optimal resources currently manipulated by all members of populations. The assessment of the precise degree of parasite-induced damage seems complicated by the extent to which the host nutritional intake can compensate for the continuous drain on resources and by the extent to which the catfish regeneration ability can compensate for extensive piercing attitudes created by the gaffing action of the marginal hooklets of the haptors of the proliferating gyrodactylid monogeneans.

REFERENCES

Anttila, P.; Romakkaniemi, A. Kuusela, J. and Koski, P. (2008). *Epidemiology of Gyrodactylus salaris (Monogenea) in the River Tornionjoki, a Baltic wild salmon river. Journal of Fish Diseases, 31 (5): 373–382.*

Appleby, C.; Mo, T. A. and Aase, I. L. (1997). *The effect of Gyrodactylus salaris (Monogenea) on the epidermis of Atlantic salmon Salmo salar in the river Batnfjordselva, Norway. Journal of Parasitolology, 83: 1173-1174.*

Arafa, S. Z. (1999). *Biological studies on some monogenean parasites of the teleost Clarias gariepinus in Dakahlia Province. Ph.D. Thesis, Faculty of Sciences, Mansoura University, Egypt.*

Arafa, S. Z.; El-Naggar, M. M. and Kearn, G. C. (2003). *Scanning electron microscope observations on the monogenean skin parasite Macrogyrodactylus congolensis (Prudhoe, 1957) Yamaguti, 1963. Acta Parasitology, 48 (3): 163-171.*

Bakke, T. A.; Harris, P. D.; Jansen, P. A. and Hansen, L. P. (1992). *Host specificity and dispersal strategy in gyrodactylid monogeneans, with particular reference to Gyrodactylus salaris Malmberg (Platyhelminthes, Monogenea). Diseases of Aquatic Organisms, 13: 63-74.*

Bashirullah, A. K. M. and Rado, N. E. (1987). *Co-occurrence of three species of Choricotyle (Monogenea: Diclidophoridae) in the grunt Orthopristis ruber and their host-specificity. Journal of Fish Biology, 30 (4): 419–422.*

Bishai, H. M. and Khalil, M. T. (1997). *Freshwater fishes of Egypt. Publication of the National Biodiversity Unit, No. 9, Department of Natural Protectorate, Egyptian Environmental Affairs Agency.*

Brooker, A. J.; Grano Maldonado, M. I.; Irving, S.; Bron, J. E.; Longshaw, M. and Shinn, A. P. (2011). *The effect of octopaminergic compounds on the behaviour and transmission of Gyrodactylus. Parasit Vectors, 4: 207.*

Buchmann, K. (1988). *Spatial distribution of Pseudodactylogyms anguillae and P. bini (Monogenea) on the gills of the European eel, Anguilla anguilla. Journal of Fish Biology, 32 (5): 801-802.*

Buchmann, K. (1998). *Histochemical characteristics of Gyrodactylus derjavini parasitizing the fins of rainbow trout (Oncorhynchus mykiss). Folia Parasitologica, 45(4): 312-8.*

Cable, J. and Harris, P. D. (2002). *Gyrodactylid developmental biology: historical review, current status and future trends. International Journal for Parasitology, 32: 255-280.*

Cable, J.; Harris, P. D. and Bakke, T. A. (2000). *Population growth of Gyrodactylus salaris (Monogenea) on Norwegian and Baltic Atlantic salmon (Salmo salar) stocks. Parasitology, 121: 621-629.*

Cable, J.; Scott, E. C. G.; Tinsley, R. C. and Harris, P. D. (2002a). *Behavior favoring transmission in the viviparous monogenean Gyrodactylus turnbulli. Journal of Parasitology, 88(1): 183-184.*

Cable, J.; Tinsley, R. C. and Harris, P. D. (2002b). *Survival, feeding and embryo development of Gyrodactylus gasterostei (Monogenea: Gyrodactylidae). Parasitology, 124(1): 53-68.*

Chung, H. Y., Lin, I. H. and Kou, G. H. (1984). *Study of the parasites on the gill of cultured eel in Taiwan. Fish Disease Research, 6: 24–33.*
Combes, C. (2001). *Parasitism. The ecology and evolution of intimate interactions. University of Chicago Press, Chicago and London.*
Cusack, R. and Cone, D. K. (1986). *A review of parasites as vectors of viral and bacterial diseases of fish. Journal of Fish Diseases, 9(2): 169-171*.
De Moor, I. J and Bruton, M. N. (1988). *Atlas of alien and translocated indigenous aquatic animals in southern Africa. South African National Scientific Programmes Report 114, South Africa.*
El-Abbassy, S. A. (2001). *Biological and histochemical studies on some monogenean parasites of the catfish Clarias gariepinus inhabiting Nile Delta Waters. M. Sc. Thesis, Faculty of Sciences, Mansoura University, Mansoura, Egypt.*
El-Abbassy, S. A. (2005). *Studies of the anatomical featues, histochemical components and pathological impacts of gyrodactylid monogenean parasites infesting the catfish Clarias gariepinus inhabiting Nile Delta Waters. PhD thesis, Faculty of Sciences, Mansoura University, Mansoura, Egypt.*
El-Naggar, A. M. (1994). *Ecological studies on the monogenean parasites of the teleost Clarias lazera inhabiting Nile Delta Waters. M. Sc. Thesis, Faculty of Sciences, Mansoura University, Mansoura, Egypt.*
El-Naggar, A. M. (2007). *Mode of attachment and local histopathological impacts of the vivparous monogeneans Gyrodactylus rysavyi and M. congolensis from the skin and fins of the Nile catfish Clarias gariepinus. Egyptian Journal of Zoology, 49: 293-308.*
El-Naggar, M. M.; El-Naggar, A. M. and El-Abbassy, S. A. (2001). *Microhabitat and movement of the vivparous monogeneans Gyrodactylus alberti, Macrogyrodactylus clarii and M. congolensis from the Nile catfish Clarias gariepinus. Journal of the Egyptian German Society for Zoology, 35 (D): 169-187.*
El-Naggar, M. M.; El-Naggar, A. A. and Kearn, G. C. (2004). *Swimming in Gyrodactylus rysavyi (Monogenea: Gyrodactylidae) from the Nile catfish Clarias gariepinus. Acta Parasitologica, 49(2): 102-107.*
El-Naggar, M. M. and Serag, H. M. (1987). *Redescription of Macrogyrodactylus clarii Gussev 1961, a monogenean gill parasite of Clarias lazera in Egypt. Arab Gulf Journal of Scientific Research and Agricultural Biological Sciences, 5: 257-271.*
El-Naggar, A. M. and El-Tantawy, S. A. (2001). *Competitive coexistence and microhabitat specialization of Pseudodactylogyrus anguillae, P. bini and G. anguillae, monogenean gill parasites of the immigrant European eel, Anguilla anguilla in Egypt. Journal of Union Arab Biologists, 16 (A) Zoology: 137-160.*
Ergens, R. (1973). *Two new species of Gyrodactylus from Clarias lazera (Vermes, Trematoda, Monogenoidea). Revue de Zoologie et de Botanique Africaine, 87: 77-80.*
Gause, G. F. (1935). *The Struggle for Existence (Williams and Wilkins, Baltimore).*
Hagras, A. E.; El-Naggar, M. M.; Kearn, G. C. and Arafa, S. Z. (1999). *Monthly occurrence, seasonal population dynamics and distribution of four monogeneans on the catfish Clarias gariepinus in Dakahlia Province, Lower Egypt. Journal of the Egyptian German Society for Zoology, 29(D): 49-66.*
Harris, P. D.; Soleng, A. and Bakke, T. A. (1998). *Killing of Gyrodactylus salaris (Platyhelminthes, Monogenea) mediated by host complement. Parasitology, 117(2): 137-143.*
Heggberget, T.G. and Johnsen, B.O. (1982). *Infestations by Gyrodactylus sp. of Atlantic salmon, Salmo salar L., in Norwegian rivers. Journal of Fish Biology, 21: 15-26.*
Johnson, P. T. J. and Buller, I. D. (2011). *Parasite competition hidden by correlated coinfection: using surveys and experiments to understand parasite interactions. Ecology, 92(3): 535-541.*
Johnson, M. B.; Lafferty, K. D.; van Oosterhout, C. and Cable, J. (2011). *Parasite Transmission in Social Interacting Hosts: Monogenean Epidemics in Guppies. PLoS One, 6(8): e22634.*
Lester, R. J. G. (1972). *Attachment of Gyrodactylus in Gasterosteus and host response. Journal of Parasitology, 58: 717-722.*
Miller, Jr. G. (2004). *Essentials of Ecology. Second edition. Thomson Learning Academic Resource Center, Canada.*
Mo, T. A. (1994). *Status of Gyrodactylus salaris problems and research in Norway. In.: Parasitic Diseases of Fish (ed. By A. W. Pike & J. W. Lewis), pp. 43-58. Samara Publishing/BSP, London.*
Mohamed, A. M.; Ismaiel, M. M.; Kenawy, A. K. and Abd El-Ghany, O. A. (2010). *Impact of experimental infection with Gyrodactylus species on the density of skin mucous in fries of catfish (Clarias gariepinus) with emphasis on the pathological changes. Global Veterinaria, 4(1): 67-73.*
Olstad, K.; Cable, J.; Robertsen, G. and Bakke, T. A. (2006). *Unpredicted transmission strategy of Gyrodactylus salaris (Monogenea: Gyrodactylidae): survival and infectivity of parasites on dead hosts. Parasitology, 133(1): 33-41.*
Paperna, I. (1964). *Competitive exclusion of Dactylogyrus extensus by Dactylogyrus vastator (Trematoda: Monogenea) on the gills of reared carp. Journal of Parasitology, 50(1): 94–8.*

Prudhoe, S. (1957). *Trematoda. In: Exploration du Parc National de l'Upemba. I. Mission G. F. De Whitte en collaboration avec W. Adam, A. Janssens, L. Van Meel et R. Verheyen (1946-1949) 48: 1-28.*
Rohde, K. (1991). *Intra- and interspecific interactions in low density populations in resource-rich habitats. Oikos 60, 91-104.*
Rohde, K. (2002). *Niche restriction and mate finding in vertebrate hosts. In: The Behavioral Ecology of Parasites, pp. 171-197 (eds. Lewis, E.E., Campbell, J.F. and Sukhdeo, M.V.K.). CAB International, Wallingford, Oxon.*
Rohde, K. (2005). *Nonequilibrium Ecology. Cambridge University Press, Cambridge.*
Rohde, K. (2011). *Niche restriction and segregation. What makes species different? Ecology and Evolution.*
Sahney, S.; Benton, M. J. and Ferry, P. A. (2010). *Links between global taxonomic diversity, ecological diversity and the expansion of vertebrates on land. Biology Letters 6 (4): 544–547.*
Simková, A.; Desdevises, Y.; Gelnar, M. and Morand, S. (2000). *Co-existence of nine gill ectoparasites (Dactylogyrus: monogenea) parasitizing the roach (Rutilus rutilus l.): history and present ecology. International Journal for Parasitology, 30(10):1077-88.*
Simková, A.; Kadlec, D.; Gelnar, M. and Morand, S. (2002). *Abundance-prevalence relationship of gill congeneric ectoparasites: testing the core satellite hypothesis and ecological specialization. Parasitology Research, 88(7):682-686.*
Soleng, A. and Bakke, T. A. (1997). *Salinity tolerance of Gyrodactylus salaris (Platyhelminthes, Monogenea): laboratory studies. Canadian Journal of Fisheries and Aquatic Sciences, 54: 1837–1845.*
Sterud, E.; Harris, P. D. and Bakke, T. A. (1998). *The influence of Gyrodactylus salaris Malmberg, 1957 (Monogenea) on the epidermis of Atlantic salmon, Salmo salar L., and brook trout, Salvelinus fontinalis (Mitchill): experimental studies. Journal of Fish Diseases, 21: 257-263.*
Tinsley, R. C. (2001). *Population dynamics of Gyrodactylus on sticklebacks. In: Halton, D.W.; Behnke, J. M. and Marshall, I. (eds.) Practical exercises in parasitology. Cambridge University Press, Cambridge, p 147–160.*
Watson, N. A. and Rohde, K. (1994). *Two new sensory receptors in Gyrodactylus sp. (Platyhelminthes, Monogenea, Monopisthocotylea). Parasitology Research, 80 (5): 442-445.*
Wells, P. R. and Cone, D. K. (2006). *Experimental studies on the effect of Gyrodactylus colemanensis and G. salmonis (Monogenea) on density of mucous cells in the epidermis of fry of Oncorhynchus mykiss. Journal of Fish Biology, 37 (4): 599-603.*
Witmer, G. W. and deCalesta, D. S. (1986). *Resource use by unexploited sympatric bobcats and coyotes in Oregon. Canadian Journal of Zoology, 64: 2333- 2338.*
Yamaguti, S. (1963). *Systema Helminthium IV. Monogenea and Aspidocotylea. Interscience Division, John Wiley and Sons Incorporation, New York pp. 699.*

Table (1). Mean nearest–neighbour distance of G. rysavyi and M. congolensis infrapopulations on the skin surface and fins of the Nile catfish host C. gariepinus under experimental conditions.

	First week		Second week		Third week		Fourth week		Fifth week
	G. rysavyi	*M. congolensis*	*G. rysavyi*	*M. congolensis*	*G. rysavyi*	*M. congolensis*	*G. rysavyi*	*M. congolensis*	*G. rysavyi*
Maximum	3	4	2	3	1.5	2	0.5	0.75	0.08
Minimum	1	1	0.5	1	0.3	1	0.25	0.05	0
Mean	1.75	2.7	1.2	2	0.77	1.6	0.34	0.51	0.03
± SD	0.72	0.82	540.	0.67	0.40	0.52	110.	0.32	0.03