

REVIEW

Fish as parasites: an insight into evolutionary convergence in adaptations for parasitism

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Introduction

There are over 32 000 known living species of fish and they have adapted to a wide variety of habitats and ecological niches. Some fish have evolved close ecological associations with other species in their environment, such as the relationship between cleaner fish with their clients (Grutter, 1999; Bshary, 2003), anemone fish with anemones (Szczebak *et al.*, 2013 and reference therein), or the more recently documented protective partnership between gobies and *Acropora* corals – which has been likened to the protective mutualism of ant-plant symbioses (Dixon & Hay, 2012).

Given their ubiquity and diversity, perhaps it should not be surprising that at least some species have evolved parasitic lifestyles. While fish are often the subject of parasitological studies as hosts to parasites, fish themselves (or simply just vertebrates in general) are not usually thought of as being parasitic. Yet there are some species of fish that live as parasites of some kind at different stages of their life cycle. Far from being merely natural history curiosities, these taxa can provide remarkable insights into the process of adaptation, functional morphology, species interaction, coevolution and the limits of morphological and behavioural adaptations.

In this review, the term ‘fish’ refers to the group of vertebrate as defined by Nelson (2006) as aquatic vertebrates with

Abstract

Fish are the most diverse group of living vertebrates on the planet with 32 000 living species. They have diversified to fill a wide variety of ecological niches. Some species have formed close ecological interactions with other aquatic species that can be best described as symbiotic or even parasitic. Some fish species have evolved different ways to exploit invertebrates, ranging from using their body as a site for depositing their eggs and larvae to actually sheltering inside the invertebrate themselves and feeding on the organs of their host. Other fish species are frequently associated with larger aquatic vertebrates, attaching to them for either phoretic or feeding purposes or both. The aim of this review is to provide an overview of some general patterns in these symbiotic or parasitic relationships, comparing them with more ‘traditional’ parasites and symbionts, and discuss the insight they can offer on both the evolutionary process that leads to parasitism, as well as the evolutionary pathways of fishes as a whole.

gills throughout their life and limbs, when present, in the form of fins. The definition of ‘parasite’ will follow that of Esch & Fernández (1993) and Zelmer (1998) which emphasizes a sustained and extended period of interaction between the parasite and host, whereby the parasite takes nutrient or utilizes some other resource while staying in physical contact with the host at some point of its life cycle. As such, this definition excludes fish such as cookie cutter sharks, sabre blennies or lepidophagous (scale-eating) fish which are micropredators that have very brief interactions with their prey through taking small (but usually non-lethal) bites. While some authors have categorized such feeding style as parasitism (Keenleyside, 1979; Wootton, 1998; Woodland, 2005; Poulin, 2011), it is more comparable to predation (Sazima, 1977, 1983; Grubh & Winemiller, 2004; Lima *et al.*, 2012) and can be considered as a modified form of piscivory rather than parasitism.

While the males of deep sea ceratioid anglerfish, which spent most of its life attached to the female fish, have sometimes been cited as an example of a ‘parasitic’ fish (e.g. Woodland, 2005), such a relationship is not parasitism. Rather, this is an example of a cohabiting dwarf male which provides the female with sperm in return for sustenance (Vollrath, 1998; Pietsch, 2005). From an ecological and evolutionary perspective, the ceratioid male cannot be considered

as a parasite in any sense as it does not impose a fitness cost on the female ‘host’ (which would not be able to reproduce at all without it).

There are a number of different ways that fish can be parasitic (see Figs 1 and 2, Table 1). Some species are free-living as adults but have parasitic eggs or larvae, whereas other species, such as lamprey, only become parasitic as adults, and there are some such as pearlfish which are parasitic for their entire lives. However, they all share a feature which they have in common with all parasites – they are dependent upon their hosts to complete their life cycle, which is a key feature of parasitism. It should not be surprising that some of the adaptations which have evolved in these fish share parallels with more ‘tradi-

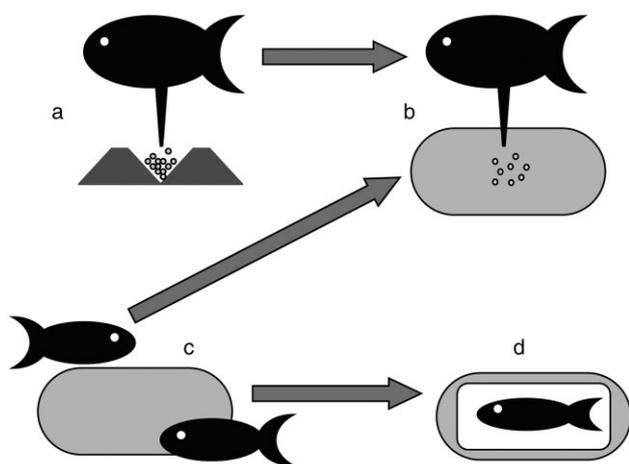


Figure 1 Interactions between fish and invertebrates; (a) fish that oviposit in crevices leading to the evolution of (b) ovipositing in invertebrates (Ostracophils), or it may evolve from (c) fish which closely associate with invertebrates. Such fish may also evolve to (d) live inside the body of invertebrates.

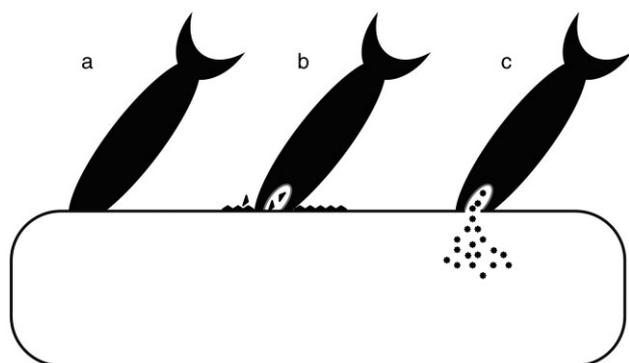


Figure 2 Interaction between fish and larger aquatic vertebrates; (a) using the host mostly as a mean of dispersal (e.g. remora), (b) attaching to the host and feeding non-invasively on superficial tissue, such as mucus (e.g. stegophiline), (c) attaching to host and feeding invasively on host tissue, such as blood (e.g. lamprey, vandelliine catfish).

tional’ parasites as they face similar challenges when establishing on or in their host; these selection pressures have led to evolutionary convergence in morphology and function in different parasite taxa (Poulin, 2011). The aim of this review is to provide a synthesis of the literature on fishes with parasitic lifestyles, compare them with parasites in other taxa and discuss what they can tell us about the evolutionary transitions and adaptations associated with parasitism.

Fish–invertebrate interactions

By far the most numerous and diverse range of interspecific interactions involving fish are those with aquatic invertebrates. Many fish are known to be closely associated with invertebrates at some stage of their lives. Juvenile cusk eels (*Barathrites* sp.) have been observed to forage around the periphery of pancake urchins, *Hygrosoma petersi* and *Phorosoma placenta*, and take refuge at their base and among their long spines (Moore & Auster, 2009). The so-called man-of-war fish, *Nomeus gronovii*, live among the tentacles of the Portuguese man-o-war siphonophore (*Physalia* spp.) for protection (Jenkins, 1983) and additionally many larval and juvenile fish associate closely with medusae and other pelagic gelatinous species for much the same reason (Purcell & Arai, 2001). One of the more well-known fish–invertebrate relationships is that of anemone fish and their mutualistic relationship with sea anemones (Szczebak *et al.*, 2013 and references therein). These relationships are often obligate and the sheltering involved may have led to the evolution of some fish that originally only remained in close physical proximity with invertebrates, but became gradually more closely associated with invertebrates and eventually physically lodged themselves within their host at some stage of their life either as eggs, larvae or as adults (Fig. 1).

Ostracophils

Fish that have a preference for spawning in live invertebrates are also known as ‘ostracophils’ (Balon, 1975). Of the fish species that have been documented as ostracophils, all display some degree of host specificity and varying degrees of morphological and behavioural adaptations for ovipositing in their host. These fish are remarkable examples of convergent evolution as they are phylogenetically dissimilar but have independently evolved morphological and behavioural adaptations for depositing their eggs inside invertebrates (see Fig. 3). On a functional level, as ostracophils are only parasitic as eggs and larvae, they are comparable with organisms such as unionid mussels which have larvae (called glochidia) that temporarily parasitize the gills of fish but are free-living for most of their life (Kat, 1984).

Of the fish species which lay their eggs in the body of invertebrates, the bitterling–mussel system is most well studied. Female bitterlings have long ovipositors which allow them to deposit eggs in the gills of freshwater mussels. While the relationship between bitterling and mussels has been considered by some to be commensalistic or even mutualistic, several lines of evidence indicate that the relationship is

Table 1 Parasitic fish taxa discussed in this review including their families, mode of parasitism, representative species/genera and their hosts

Common name and family	Mode of parasitism/ association	Representative genera/species	Host(s)	Key references
Bitterling (Cyprinidae: Acheilognathinae)	Ostracophil	<i>Rhodeus</i> spp.	Freshwater mussels	Mills & Reynolds (2003)
Snailfish (Liparidae)	Ostracophil	<i>Careproctus</i> spp.	Lithodid crabs	Akagawa <i>et al.</i> (2004, 2008)
Tubesnout (Hypoptychidae)	Ostracophil	<i>Aulichthys japonicus</i>	Ascidian	
Pearlfish (Carapidae)	Endoparasitic	<i>Carapus</i> spp., <i>Encheliophis</i> spp., <i>Onuxodon</i> spp.,	Various benthic marine invertebrates	Trott (1970) Parmentier & Vandewalle (2005)
Lamprey (Geotriidae, Mordaciidae, Petromyzontidae)	Ectoparasitic/invasive tissue-feeding	<i>Eudontomyzon</i> spp., <i>Lampetra</i> spp., <i>Petromyzon marinus</i>	Various aquatic vertebrates	Hardisty & Potter (1971) Gill <i>et al.</i> (2003)
Candiru (Trichomycteridae: Stegophilinae)	Phoretic/superficial grazing	<i>Ochmacanthus</i> spp.	Various freshwater fishes	Adriaens <i>et al.</i> (2010)
Candiru/Vampire fish (Trichomycteridae: Vandelliinae)	Ectoparasitic/ blood-feeding	<i>Vandellia</i> spp.	Various freshwater fishes	Zuanon & Sazima (2005) Adriaens <i>et al.</i> (2010)
Remora (Echeneidae)	Phoretic/superficial grazing	<i>Echeneis</i> spp., <i>Remora</i> spp.	Various large marine vertebrates	O'Toole (2002) Brunnschweiler & Sazima (2006)

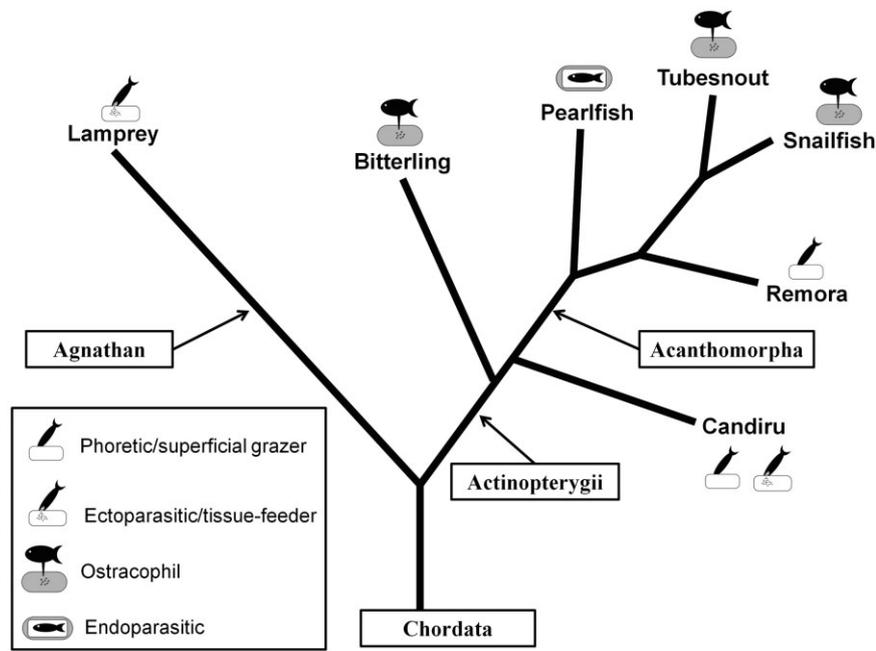


Figure 3 A simplified phylogeny of the parasitic fishes discussed in this review and their mode of parasitism.

parasitic, and the hypotheses for the mussels benefiting from the interaction (such as the bitterling serving as host to the mussel’s own glochidia larvae or obtaining additional nutrients from bitterling sperm) are not supported by evidence (Mills & Reynolds, 2003). Compared with other fish which live in sympatry with mussels, bitterlings are actually more resistant to infection by glochidia, and bitterling sperm does not enhance mussel growth (Mills & Reynolds, 2003). Bitterling embryos impose a significant cost on their host by robbing them of oxygen and nutrient and can be considered as parasites (Reichard *et al.*, 2006; Spence & Smith, 2013).

Bitterlings have different levels of host preferences based on ventilation rate of the host mussel (reviewed in Mills & Reynolds, 2003). Female bitterlings are known to spend time inspecting the quality of a mussel before deciding whether or not to oviposit in the bivalves (Candolin & Reynolds, 2001; Smith *et al.*, 2001) in a manner which can be compared with how an adult parasitoid wasps examine potential hosts using cues, such as host size and chemical profile, to determine whether or not to parasitize that host (Vinson, 1976; Kouamé & Mackauer, 1991). A bitterling’s ovipositor length and egg shape vary depending on the species’ host preference but both

are selected independently and may not evolve in parallel because of shifts in host preference and/or because of host availability (Kitamura *et al.*, 2012). Female bitterlings also avoid ovipositing in mussels that are already carrying bitterling embryos. This aversion to superparasitism can be due to the fact that the survival rate of bitterling embryos is strongly density dependent and this behaviour varies depending upon the host mussel species (Smith *et al.*, 2000). Once again, this is comparable with behaviour exhibited by some species of parasitoids that actively avoid ovipositing in already parasitized hosts (Rogers, 1972; Outreman *et al.*, 2001) (N.B. however for parasitoids, superparasitism may be adaptive under certain circumstances: Hubbard *et al.*, 1987; Hubbard, Harvey & Fletcher, 1999).

As well as behavioural and morphological adaptation of the adult female, the eggs and embryos of bitterlings also have a number of adaptations for parasitizing mussels. Not only does the ellipsoid shape of bitterling eggs increase the surface area to volume ratio which enhances oxygen diffusion in low-oxygen conditions that can sometime occur inside the mantle cavity of a mussel, but it also allows the eggs to wedge themselves more securely within the host's gills. Indeed, the egg shape of bitterlings appears to be under selection pressure from the mussel hosts (Kitamura *et al.*, 2012) and mussels which have lived in sympatry with bitterling are better able to reject their eggs (Reichard *et al.*, 2010). Once hatched, the embryos also have adaptations for securing themselves in the gills of the mussel against the host's exhalant current. The embryos of some bitterling species are covered in minute spine-like tubercles or dermal scales which may help them to stay lodged in the gills (Balon, 1975; Smith *et al.*, 2004; Kim *et al.*, 2008). Those spines are reminiscent of the tegument spines on some digenean flukes that live in the intestine of vertebrates (for example Hong, Chai & Lee, 1991; Abdul-Salam & Sreelatha, 2000; Simões *et al.*, 2006). Additionally, the yolk sac of bitterling embryos has wing-like protuberances which help them lodge in the gill lamellae (Smith *et al.*, 2004). Apart from such morphological features, they also have physiological adaptations that enable them to tolerate anoxic conditions that occur within the host's mantle cavity when the mussel closes its valves (reviewed in Mills & Reynolds, 2003). In addition, the embryo is also capable of obtaining nutrient from the mussel's inhalant current, thus taking both oxygen and nutrient from its host (Spence & Smith, 2013).

There is a considerable body of work which indicates a strong and ongoing coevolutionary relationship between bitterling and their mussel host. There is significant interspecific variation in the range of host species used by bitterlings, with some host species being more preferable (Reichard *et al.*, 2007) and the geographic variability in the ability of mussels to resist parasitism by bitterling suggests a geographic mosaic pattern of coevolution (Reichard *et al.*, 2007, 2010, 2012; Kitamura *et al.*, 2012).

Bitterlings are not the only fish which lay eggs that parasitize the body of invertebrates, merely the best studied system. A few other species are also known to lay their eggs inside other animals. Liparid snailfishes from the genus

Careproctus lay their eggs in the gill chamber of deep sea crabs using a long ovipositor similar to that found in bitterlings. The eggs of snailfish place considerable mechanical pressure on the gills of the crab and can sometimes fill up an entire side of the crab's gill chamber, causing mechanical damage (Hunter, 1969; Love & Shirley, 1993; Somerton & Donaldson, 1998; Poltev & Mukhametov, 2009). Their presence alone must cause substantial respiratory hindrance to their host crab, and parasitism by snailfish eggs can be very widespread in some crab populations (up to 97% on the east coast of North Kurils, Russia) (Poltev & Mukhametov, 2009).

Many of the questions which have been studied with the bitterling–mussel system would also similarly apply to the snailfish–crab system. This includes: the nature of the interaction between snailfish eggs or larvae with their crab host, whether there has been any coevolutionary interactions and how it varies over geographical regions.

Snailfish eggs are adhesive and can stick to the host crab's gill filaments. However, it is currently unknown whether they also have other morphological or physiological adaptations such as those found in bitterlings to help them stay in the gill chamber. It is also unclear if the crabs themselves have means of ejecting the eggs from their gill chamber as freshwater mussels do for bitterling eggs in their mantle cavity (Reichard *et al.*, 2010). Most crabs found infected with snailfish eggs only harbour egg masses in one gill chamber (Poltev & Mukhametov, 2009) – this is comparable with bitterlings which are known to adaptively select the site of egg deposition within the host's gills to maximize embryo survival based on the size and the sex of the host (Kitamura, 2006). This asymmetrical distribution is also reminiscent of other host–parasite systems such as the moth ear mite *Myrmonyssus phalaenodectes* which unilaterally occupies only one of their host's ears (Treat, 1965) or the metacercarial cysts of the fluke *Echinostoma* which overwhelmingly prefer to encyst in the right kidney of *Rana clamitans* tadpoles (Thiemann & Wassersug, 2000). The presence of multiple egg clusters from different species of *Careproctus* seems to indicate that unlike bitterlings, snailfishes do not avoid superparasitism (Somerton & Donaldson, 1998), but they are selective about the size of their host (Poltev & Mukhametov, 2009).

While observations on snailfish eggs in crabs have revealed some sex bias in the preferred host, the pattern varies between different studies. Somerton & Donaldson (1998) reported greater numbers of male crabs were infected with *Careproctus* eggs, but other studies have found egg infestations to be more common in female crabs (Love & Shirley, 1993; Poltev & Mukhametov, 2009). This might reflect geographic variation as those studies took place in the Bering Sea (Somerton & Donaldson, 1998), east coast of North Kurils (Poltev & Mukhametov, 2009) and south eastern Alaska (Love & Shirley, 1993). Further sampling and studies are necessary to verify whether this pattern represents actual geographic variation in host use or merely a spurious sampling artefact.

It is currently unknown how liparids are able to deposit eggs in the gill chambers of crabs which are fairly well-protected and presumably able to defend themselves against

an intruding snailfish. It has been suggested that the snailfish deposits eggs in the crab during periods of vulnerability such as moulting or mating when the host crab is weakened or otherwise preoccupied (Poltev & Mukhametov, 2009). However, this needs to be verified with *in situ* observation and manipulative experiments, which can be logistically challenging given the habitat of the snailfish and their crab host. Prior *in situ* observation has already yielded some interesting insight into this symbiosis. It appears that the relationship between liparids and crabs goes beyond oviposition of eggs in the crab's gill chamber; *Careproctus* from the Southern Ocean have been observed attaching themselves to the carapace or limbs of crabs via a ventral suction disc (Yau, Collins & Everson, 2000), possibly using the crab as a vehicle for dispersal. Perhaps, this behaviour habituates the crab to the presence of the snailfish, and the relationship switches from commensalism to become parasitic during the snailfish's reproductive periods.

The snailfish–crab system is difficult to study because of their habitat in the deep sea. But aside from bitterlings, there are other systems we can turn to in order to study fish with ostracophil habits. Akagawa *et al.* (2004) documented that female Japanese tubesnouts *Aulichthys japonicus* lay their eggs in the peribranchial cavity of ascidians (see also Akagawa, Hara & Iwamoto, 2008) but much less is known about their ecology and if there has been any coevolution between the tubesnout and their ascidian hosts. This system may present a good alternative model to bitterlings for studying the evolution of ostracophils.

Given that the known examples of ostracophil fish are from such different orders (bitterlings in Cypriniformes, snailfish in Scorpaeniformes, Japanese tubesnout in Gasterosteiformes) (Balon, 1975), it must be expected that much like how parasitism has evolved independently a number of times in other taxa (Poulin, 2011), this might have also occurred in fishes so perhaps other ostracophil species are yet to be documented. So what are the ecological factors that have driven the evolution of such oviposition behaviour in these different groups of fish?

Akagawa *et al.* (2008) presented a scenario for the evolution of oviposition in ascidians by the Japanese tubesnout as a mean of guarding the eggs against male cannibalism. Fish in the ostracophil guild may have originally evolved from other brood-hiders that deposited eggs in shelters (Balon, 1975), but sessile and slow moving invertebrates provide the added benefit of their ventilation current, a potential supplementary source of nutrients (see Spence & Smith, 2013) and additional protection from the defensive morphology of the host. Indeed, Thompson (1976) suggested that such egg-depositing behaviour had evolved in response to egg predation. In turn, this style of oviposition also selects for a specific set of morphological and behavioural adaptations which have convergently evolved in the different lineages of ostracophil fishes, much like in other forms of parasitism (Poulin, 2011).

Fish as endoparasites

Beyond laying eggs in the body of invertebrates, some fish are known to shelter within the body of various invertebrates, and

interactions which are more intimate and dependent may evolve from such behaviour. The cardinalfish *Astrapogon stellatus* are reported to shelter during the day in the mantle cavity of the penshell *Pinna carnea* (possibly due to overharvesting of its other host, the queen conch *Strombus gigas*: Aucoin & Himmelman, 2010). Juvenile red hake *Urophycis chuss* are known to shelter inside the mantle cavity of sea scallops *Placopecten magellanicus* (Steiner, Luczkovich & Olla, 1982; Garman, 1983), although this relationship is not necessarily obligate as juvenile hake are also found in the empty shells of dead bivalves (Steiner *et al.*, 1982). Of these, the carapids – pearlfishes – are best adapted to life inside invertebrates. Pearlfishes can be found living in various benthic marine invertebrates, mostly echinoderms such as sea cucumbers and sea stars, but also in bivalve molluscs and ascidians (Parmentier & Vandewalle, 2003).

Pearlfish and other fish with similar lifestyles have sometimes been referred to as 'inquilines', but as Trott (1970) pointed out, this is an incorrect label as inquilinism refers to animals that live in the *nest* of other animals, as opposed to living in their body as pearlfishes do in their host. This should be more broadly described as symbiosis, although the nature of this relationship varies between different species as with other symbioses (Leung & Poulin, 2008). While some pearlfish use their host simply as shelter and may be considered as commensals, other species also feed on host internal organs, such as gonads, and should be considered as parasitic (Parmentier & Das, 2004).

Experiments by Trott (1970) showed that carapids rely on a combination of visual and chemical cues to locate their host, and the sight of a holothurian must also be accompanied by chemical cues for the fish to make an approach. This is supported by a subsequent study which found that pearlfish are able to find hosts via odour cue, use exhalation currents to locate sea cucumber cloaca through which they enter the host, and have stronger resistance to holothurian toxins than other reef fishes (Parmentier & Vandewalle, 2005).

Different species of carapids living in sympatry have different breeding cycles, which minimize cohabitation of the same host (Orphal *et al.*, 2008). Carapids are also known to devour heterospecifics or conspecifics coinfecting the same host (Meyer-Rochow, 1977; Smith, Tyler & Feinberg, 1981; Parmentier & Das, 2004), with the exception of *Carapus boraborensis* which tolerates the presence of other pearlfish (same or different species) and do not cannibalize juvenile conspecifics (Orphal *et al.*, 2008). Despite what appears to be potential for strong inter- and intraspecific antagonism, they do not show preferences for either vacant or inhabited hosts, although this may be due to temporal variability in their settlement period which minimizes the need to distinguish if the host is already occupied (Parmentier & Vandewalle, 2005). *Echeliophis gracilis* – a parasitic species known to feed on their host's gonadal tissue – has a larval settlement period which corresponds with the gonadal maturation period of two host species (*Holothuria cabra* and *Thelenota ananas*); this is possibly a life history strategy that has evolved to provide larvae with food immediately after settlement (Orphal *et al.*, 2008). This strategy of having a phenology which matches that of the

host has also evolved in many other parasitic taxa (Tinsley & Jackson, 1988; McCurdy, Forbes & Boates, 1999; Hilsing, Anderson & Nayduch, 2011).

Trott (1970) proposed that the ancestors of pearlfish were accidental commensals that used the body of holothurians as convenient makeshift shelters, which then became both a shelter and food source as some species of pearlfish evolved into obligate parasites. Herald (1953) noted that ophidiids, the sister group to the carapids, have a tendency to enter crevices, so perhaps the commensalism or parasitism lifestyle of pearlfish evolved from a more general tendency to enter dark crevices to evade predators, much like how ostracophils may have arisen from more general brood-hiding behaviour.

As with other forms of symbioses, there is a gradient in the nature of the interactions these fish have with invertebrates. This extends from merely being in close proximity to each other, to being able to physically attach to the host, to physically depositing eggs or even themselves within the body of the host, to directly drawing nutrients from the host's body (see Fig. 1).

Fish as ectoparasites

Some fish have evolved to attach themselves to larger aquatic vertebrates. Much like those that interact with invertebrates, they also show a gradation in their interactions, mainly in relations to their dependency on the host as a food source and the type of material that they ingest from the host (Fig. 2). Of these, the lamprey is the most widely known and recognized example of an ectoparasitic fish. There are 18 species of parasitic lampreys (Gill *et al.*, 2003). While juvenile lampreys are filter feeders, adult lampreys are parasitic, attaching themselves to the body of their host with suction mouthparts, which are armed with rasping teeth (Hardisty & Potter, 1971).

In terms of their functional ecology, they are broadly comparable with leeches and cymothoid isopods that stay attached to the host for an extended period while feeding, but can detach to feed upon other hosts. But unlike those invertebrate parasites, lampreys are comparatively larger and thus cause greater damage to the host. Much like leeches and cymothoids which have been reported to both attach to the skin and from within the branchial chamber of their host (Noga, Bullis & Miller, 1990; Marks *et al.*, 1996; Mladineo, 2003; Saglam *et al.*, 2003; Bakenhaster, McBride & Price, 2006; Schulz *et al.*, 2011), lampreys have also been reported to attach to the interior of the branchial chamber more often than expected by chance given the relative surface area of that site compared with the rest of the host's body (Cochran & Lyons, 2010). Attachment within the branchial chamber can provide two main benefits to the lamprey. First, the parasite is protected against dislodgement from either hydrodynamic drag or the host's attempts at detaching it, and secondly it also facilitates feeding as arterial blood under pressure would flow directly into the lamprey's mouth (Cochran & Lyons, 2010). The gill is a common site of attachment for other blood-feeding ectoparasites; for example blood-feeding monogeneans and copepods tend to attach to the gill or gill chamber of their host, whereas epidermal or mucus feeders usually attach to the

skin (Kearn, 1963; Einszporn, 1965; Halton & Jennings, 1965; Kabata, 1974, 1982; Gao, Nie & Yao, 1999).

Lampreys have been reported from a range of aquatic vertebrates ranging from teleost fishes (Kearn, 2004) and elasmobranchs (Wilkie *et al.*, 2004; Gallant *et al.*, 2006) to cetaceans (Nichols & Tschertter, 2011; Samarra *et al.*, 2012). They have both morphological and physiological adaptations for their parasitic lifestyle. Among different species of lampreys, the structure of the buccal region is reflected by their diet (Renaud, Gill & Potter, 2009). They also have physiological and biochemical adaptations for eliminating toxins that are present in the blood of elasmobranch hosts (Wilkie *et al.*, 2004). In addition to specialized mouthparts, lampreys can also produce secretions from buccal glands that have anticoagulant properties (Baxter, 1956), much like leeches (Kvist, Min & Siddall, 2013). They can also secrete peptides during feeding that mimic host hormones and modulate host immune responses in order to minimize the possibility of immune-rejection by the host (Wong, Sower & Takei, 2012).

The parasitic lifestyle of lampreys is an ancient one; blood-feeding appears to be the ancestral condition in this group (Potter & Hilliard, 1987) and the mouthpart of the fossil lamprey *Priscomyzon riniensis* indicates that it most likely had a parasitic lifestyle (Gess, Coates & Rubidge, 2006) and that parasitism had already evolved in lampreys by the late Devonian some 360 million years ago.

Kearn (2004) has suggested that *Petromyzon marinus* attaches to basking shark as a form of phoresy as the scarring incurred by lamprey attachment on these sharks appears too superficial to be feeding marks. Phoresy is a type of interspecific interaction whereby an organism attaches on to a larger, more mobile animal (considered here as the 'host') which acts as a mean of dispersal for the phoretic species (Farish & Axtell, 1971). Wilkie *et al.* (2004) later demonstrated that lampreys do indeed feed on basking sharks, although there is no reason why they cannot also engage in a phoretic relationship with their hosts and use them for both feeding and dispersal, especially when attaching to comparatively larger and wide-ranging hosts such as cetaceans and elasmobranchs.

The use of the host both as a feeding site and a mean of dispersal bears some parallels to the relationship between mites and their bird hosts, with some phoretic species using birds as a mean of dispersal, others feeding on superficial (non-invasive) tissue such as feather oils and skin flakes, while others still feed directly on skin tissue and blood (Proctor & Owens, 2000). In fact, this gradation from merely attaching to the host to feeding on superficial tissue or actively feeding on host blood is even better demonstrated in another group of parasitic fish known as the candiru.

Parasitism from phoresy

Blood-feeding is not restricted to agnathans and has also evolved in jawed fishes. The most widely known example of this is the candiru catfish. The candiru are a group of parasitic catfish from the Amazon in the subfamilies Stegophilinae and Vandellinae, both from the family Trichomycteridae. In par-

ticular, some species of vandelliines have become rather well-known because of their supposed habit of occasionally penetrating the urethra of human bathers, although evidence supporting this commonly touted claim is lacking (Bauer, 2013).

Trichomycterid catfishes occupy a variety of trophic and ecological niches. One of the most distinct characteristic of that group is the enlarged integumentary teeth on the opercular system. According to Adriaens, Baskin & Coppens (2010), this feature is a basal condition in trichomycterids and is believed to be an adaptation for living in torrential rivers. These enlarged opercular teeth, which in some species are used for clinging to substrate under high-flow conditions, have been suggested to be an exaptation which allows parasitic taxa such as a stegophilines and vandelliines to cling to swimming hosts (Adriaens *et al.*, 2010).

Zuanon & Sazima (2005) documented candiru attached to the skin of giant catfish, and suggested candiru originally had a phoretic relationship with their host which subsequently evolved to be parasitic. The transition from phoresy to parasitism is likely to broadly resemble those seen in other taxa. Phoretic relationships have also been suggested as a key innovation for transitions to more physiologically dependent symbioses such as parasitism in both mites (Houck & Cohen, 1995; Holte, Houck & Collie, 2001) and insect-infecting nematodes (Sudhaus, 2008).

The thin elongated body of stegophilines and vandelliines greatly facilitates their parasitic lifestyle. Candiru catfish of the *Vandellia* genus feed by inserting themselves into the gill chamber of their hosts (Kelley & Atz, 1964; Spotte, Petry & Zuanon, 2001; Zuanon & Sazima, 2004). There, the fish anchors itself into position with its opercular teeth and makes an incision at one of the major gill arteries or gill vessels (depending on the size of the host) with its teeth, allowing the blood pressure of the host to pump blood directly into its gut (Zuanon & Sazima, 2004).

A phylogenetic study on trichomycterid catfish indicates that parasitism has arisen once in that group, giving rise to the stegophilines which live as ectoparasites that attach to the skin of their host and feed on superficial tissue, such as mucus, scales, and skin, as well as the vandelliines which attach directly to the interior of the branchial cavity and feed on blood (Fernández & Schaefer, 2009). This association between host attachment site and diet parallels that of monogeneans and parasitic copepods as mentioned above. In one of the species found within this clade, *Pareidon microps* which is predatory and/or necrophagous, full parasitism has either not evolved or has otherwise been reversed. Parasitism in trichomycterids is considered to have arisen from facultative or semiparasitic feeding habits, such as eating scales and/or mucus from the surface of their host, as exhibited by some stegophiline species (Baskin, Zaret & Mago-Leccia, 1980), which may be an intermediate step towards obligate parasitism as seen in the vandelliines (Sazima, 1983; Fernández & Schaefer, 2009).

Winemiller & Yan (1989) documented a species of obligate mucus-feeding stegophiline catfish – *Ochmacanthus alternus*. It possesses small opercular teeth that are similar to

those found on other candiru catfishes, and pectoral fins which secrete a possible adhesive. *Ochmacanthus alternus* presents a model for a potential intermediate form in the evolution of blood-feeding/parasitism in catfish. The ancestors of these catfish might have initially attached to larger fish as a mean of dispersal (similar to remoras) and from there, it is only a short step towards grazing on superficial tissue of their host fish such as mucus. Mucus is a good source of amino acids and lipids (Wessler & Werner, 1957; Lewis, 1970) which can easily be harvested by any animal already attached to the skin of a fish. Such a step presents a gateway to feeding on other host tissue such as scales and blood (Sazima, 1983).

The feeding style of *Ochmacanthus alternus* is not unlike that of remoras (Echeneidae). Also called sharksuckers, these fish attach themselves to a wide variety of marine animals including teleosts, elasmobranchs, turtles, cetaceans, sirenians (O'Toole, 2002; Williams Jr *et al.*, 2003; Brunnschweiler & Sazima, 2006) and they are even known to attach to conspecifics (Brunnschweiler & Sazima, 2006), although different species show varying degrees of host specificity (O'Toole, 2002). They attach to their hosts with a large, segmented suction disc which is in fact a highly modified dorsal fin (Britz & Johnson, 2012). A recently described fossil of an early remora from the Oligocene shows how this remarkable transformation might have taken place (Friedman *et al.*, 2013). The relationship between remoras and their host is generally thought to be a phoretic one, with remoras hitchhiking on other marine animals as a mean of transport and reducing energy expenditure. In addition, remoras also feed on the material that they can glean non-intrusively off their host including faeces (Williams Jr *et al.*, 2003) and ectoparasites (Strasburg, 1959; Cressey & Lachner, 1970). In the latter capacity, they are considered as mutualists because they remove ectoparasites from their hosts. Their feeding mode of gleaning non-invasively on the host's bodily products or material found on host skin shares some parallels with *Ochmacanthus alternus*. While considered commensals or even mutualists, some hosts appear irritated when carrying attached remoras and will make attempts to dislodge them as their suction disc can abrade host skin and cause irritation, as well as imposing hydrodynamic drag (Ritter, 2002; Brunnschweiler, 2006; Brunnschweiler & Sazima, 2006; Fish, Nicastro & Weihs, 2006); therefore, their presence is not entirely without its cost to the host.

From the lifestyles of these disparate taxa (lamprey, candiru catfish, remora), it is possible to see a series of gradation in the type of interactions fish have with large vertebrates. While these taxa are not at all closely related to each other, nor do they represent 'transitional' or 'intermediate' forms in the process of evolving from or into one of the lifestyles described above, they do nicely illustrate the potential range of symbiotic interactions with larger vertebrates which has evolved in fish; from mere hitch-hiking, to non-intrusive feeding on material superficially attached to or produced by the host, to feeding directly on host tissue and fluid such as blood (see Fig. 2).

Evolutionary relationships of parasitic fishes

At this point, there does not seem to be any consistent broad evolutionary patterns in the appearance of parasitism in fish; ostracophils and ectoparasitism both have independently evolved in lineages that are taxonomically very disparate from each other, whereas endoparasitism is only known in the specialized carapids (see Fig. 3). The few smattering of examples currently known to us are not enough to draw any firm conclusions. However, it is worth noting that aside from the agnathan lamprey, all the parasitic fishes discussed in this review are actinopterygians (ray-finned fishes) which contains over 30 000 living species (Nelson, 2006; Near *et al.*, 2012). Furthermore, most of those are acanthomorphs, or the spiny-rayed fishes – an extremely diverse group with a wide range of body plans, comprising of over 18 000 living species which makes up almost one-third of all living vertebrates, and are present in almost all known marine and freshwater habitats (Near *et al.*, 2013). So it should not be surprising that some species have evolved to be parasitic in one way or the other. Given their morphological and ecological diversity, perhaps it should be more surprising that so few have evolved to be parasites, considering that parasitism is one of the most common modes of life on Earth (Poulin & Morand, 2004). This may indicate that fish as a group have not been sufficiently examined for potentially parasitic behaviours and lifestyles, or that fish, or indeed vertebrates in general, are ill-suited for a parasitic way of life.

Conclusion and future directions

Currently, there is a lack of data on the likely negative impact(s) most parasitic fishes may (or may not) have on their hosts. Aside from the injuries caused by lampreys (King Jr, 1980; Beamish & Neville, 1995; Swink, 2003) and the interactions between bitterling and freshwater mussel (Mills & Reynolds, 2003; Mills, Taylor & Reynolds, 2005; Reichard *et al.*, 2006; Spence & Smith, 2013), both of which are fairly well documented, the level of harm in terms of fitness cost caused by most parasitic fishes upon their respective host, as well as other aspects of such host–parasite interactions, are still largely unknown. Furthermore, apart from the bitterlings, there have not been any studies on the coevolutionary histories between these parasitic fishes and their hosts. Have the hosts evolved mechanisms or strategies for evading or defending themselves against these parasites? And if so, how has this in turn affected the evolution of these parasitic fishes? Investigating various aspects of host–parasite interactions and the coevolutionary history between parasitic fishes and their respective hosts would be a fruitful avenue for research.

Additionally, unlike other parasites which because of their small size and soft body parts, do not leave much of a fossil record, fish lineages do have a tractable fossil record and may provide clues to potential intermediate forms (such as the early remora described by Friedman *et al.*, 2013), making them good candidates for studying the evolutionary transition from a free-living to symbiotic lifestyle over geological time.

Such studies can also address questions such as whether the evolution of various parasitic fish taxa had coincided with the appearance of their respective host taxa in the fossil record.

Apart from fossils, studies on living taxa can also be useful for investigating the evolution of parasitism in fishes. Some of the taxa discussed in this review (remora, bitterling, pearlfish) have relatives which exhibit similar behaviour with non-living substrates/objects. The family Rachycentridae, which include fish such as Cobia, are sister group to the echeneids (Gray *et al.*, 2009) and tend to school near floating objects in the open sea (O'Toole, 2002). Some cyprinids have ovipositors which allow them to deposit their eggs in crevices (Freyhof, 1997 cited in Mills & Reynolds, 2003), and ophidiids have a tendency to seek shelter from predators in crevices (Herald, 1953). The behaviour of these species provides insights into potential scenarios for the evolutionary origins of various types of symbiotic lifestyles. Further and more detailed studies on the behaviour and lifestyles of other fish taxa may uncover more species that also have parasitic lifestyles.

Because parasitism is so rare in vertebrates, the fish species discussed here provide a unique perspective on its evolution. Further studies on these fish and similar parasitic taxa will reveal much about the morphological, functional and behavioural traits that facilitate the evolutionary transition into parasitism, as well as the selection pressures involved and how they resemble or differ from those of other parasitic organisms.

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