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Evolutionary Transitions of Parasites between Freshwater and Marine Environments

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Synopsis Evolutionary transitions of organisms between environments have long fascinated biologists, but attention has been focused almost exclusively on free-living organisms and challenges to achieve such transitions. This bias requires addressing because parasites are a major component of biodiversity. We address this imbalance by focusing on transitions of parasitic animals between marine and freshwater environments. We highlight parasite traits and processes that may influence transition likelihood (e.g., transmission mode, life cycle, host use), and consider mechanisms and directions of transitions. Evidence for transitions in deep time and at present are described, and transitions in our changing world are considered. We propose that environmental transitions may be facilitated for endoparasites because hosts reduce exposure to physiologically challenging environments and argue that adoption of an endoparasitic lifestyle entails an equivalent transitioning process as organisms switch from living in one environment (e.g., freshwater, seawater, or air) to living symbiotically within hosts. Environmental transitions of parasites have repeatedly resulted in novel forms and diversification, contributing to the tree of life. Recognizing the potential processes underlying present-day and future environmental transitions is crucial in view of our changing world and the current biodiversity crisis.

Introduction

Evolutionary transitions between terrestrial, marine and freshwater environments have long fascinated biologists (Little 1990; contributions to this volume). However, virtually all studies on such environmental transitions have centered on free-living organisms and the physiological and mechanical challenges such transitions would pose. This bias requires addressing because many organisms are parasitic, occurring within or attached to free-living individuals. Indeed, parasite species diversity may rival or exceed that of free-living organisms, although limited sampling and the hidden nature of most parasites hinder diversity insights (Dobson et al. 2008; Okamura et al. 2018). Parasites are ubiquitous and are components of food webs in marine, freshwater, and terrestrial environments (Lafferty et al.

2008). Here, we address this imbalance by focusing on evolutionary transitions between marine and freshwater environments of metazoan parasites that utilize animal hosts.

We define environmental transition to entail establishment of a species in an environment (freshwater, seawater, or air) not inhabited by ancestors. Establishment is initiated when individuals translocate to a new environment (Blackburn and Ewen 2017). Parasites must then establish viable populations and subsequently spread. Here, we explore transitions between freshwater and marine environments by highlighting constraints and potential mechanisms of parasitic transitions. We then consider evidence for transitions in both deep time and the present day, and how our changing world may impact transitions. The collective

arguments and evidence suggest that buffering by host environments particularly promotes endoparasite transitions, and we argue that adoption of endoparasitism involves a trajectory equivalent to undergoing environmental transition. Such exchanges of environments have repeatedly led to novel diversity. To provide context and background for our arguments, we first briefly review the nature of parasites, largely focusing on examples from aquatic environments.

The nature of parasites

Symbionts form intimate associations, living on or in another organism—the host. Hosts provide resources to symbionts, which may or may not provide services in return (Leung and Poulin 2008). Parasites and mutualists, by definition, are symbionts with harmful and beneficial impacts on hosts, respectively, while commensals have no impact. In reality, the nature of these intimate interactions can be highly variable and context-dependent, demonstrating that interactions vary along a continuum and may be heavily influenced by environmental regimes (Leung and Poulin 2008). Indeed, shifts in the nature of symbioses can entail transitioning from mutualism to parasitism and vice versa. It should be borne in mind that such complex dynamics underly our arguments and scenarios.

The repeated evolution of parasitism within Metazoa (Weinstein and Kuris 2016) has resulted in a diverse array of taxa at both higher and lower levels. A total of 15 of the 35 recognized animal phyla include parasitic members, and parasitism has been estimated to have evolved independently 223 times in Animalia (Weinstein and Kuris 2016). Some phyla are exclusively parasitic (e.g., Dycemida, Orthonectida). In others, parasitism has evolved repeatedly (e.g., Arthropoda, Mollusca, Rotifera, Annelida, Cnidaria) (Weinstein and Kuris 2016). Transitions to parasitism have been followed by both extensive (e.g., Myxozoa within Cnidaria, Cestoda/Trematoda within Platyhelminthes) and limited (e.g., Orthonectida, Dicyemida) diversification (Ruppert et al. 2004), contributing to biodiversity and the tree of life. The evolution of parasitism over time is thus demonstrated by both deep (e.g., De Baets et al. 2021) and shallow (e.g., Galbreath et al. 2020) branches in phylogenetic trees.

Helminth and arthropod parasites are relatively well-studied (Poulin 2011) as they infect humans and domestic animals. Helminths comprise a group of worm-like parasites, including nematodes, trematodes, cestodes, and monogeneans. Apart from monogeneans, helminths are endoparasitic in tissues and internal spaces (e.g., digestive tract) of hosts. Parasitic arthropods such as sea lice (copepods) and cymothoid isopods

are located on or attached to host surfaces as ectoparasites, while others are endoparasitic (e.g., rhizocephalan barnacles and pentastomids). Microscopic endoparasites include various protists and myxozoans (a large cnidarian clade; Okamura and Gruhl 2021).

Parasites display a diversity of life cycles and patterns of host utilisation. Some taxa have both free-living and parasitic stages. For example, many nematodes are parasitic as adults but have free-living larval stages. Parasites with simple or direct life cycles infect one host, and include monogeneans, some nematodes, and many arthropods. Parasites with complex life cycles use multiple hosts and include many helminths, *Plasmodium* species (causative agents of malaria), and myxozoans. Parasites display a range of fundamental niches defined by host use (Mestre et al. 2020). Some are specialists, at the extreme exploiting only a single host species. Others are generalists, exploiting a wide range of hosts (Poulin 2011). In addition, parasites with complex life cycles can be specialists at one stage in the life cycle but generalists at other stages (Benesh et al. 2021). It is important to note that poor sampling often obscures insights about host range (e.g., Wood et al. 2014).

Parasites employ a variety of transmission modes (Schmid-Hempel 2011). Some undergo direct transmission, infecting hosts via infective stages. For example, motile stages of trematodes penetrate intermediate and final (or definitive) hosts in the complex life cycle. Similarly, buoyant myxozoan spores released from annelid hosts infect fish upon contact. Trophic transmission occurs when parasites are consumed and characterizes several protists, some nematodes, many trematodes, most cestodes, and all acanthocephalans (Brown et al. 2001). Many parasites with complex life cycles are trophically transmitted when intermediate hosts are consumed by definitive hosts. Infectious stages may also be ingested during host feeding activities. For example, deposit-feeding annelids are infected when myxozoan spores released from fish hosts are ingested with sediments. Many parasite propagules are resistant to adverse environmental conditions and may remain dormant prior to infecting new hosts (e.g., eggs of some nematodes and cestodes, cysts of protozoans, spores of myxozoans released from fish hosts). Some parasites with complex life cycles achieve transmission indirectly via vectors that facilitate transport from one host to another (e.g., mosquitoes convey the causative agent of malaria to vertebrate hosts). As vector-borne parasites generally use terrestrial arthropods, this transmission mode is less relevant here. Finally, some microparasites achieve vertical transmission when infection is passed to host offspring. Examples include microsporidians infecting crustaceans (Kelly et al. 2003; Poley et al. 2017) and a myxozoan infecting dormant propagules

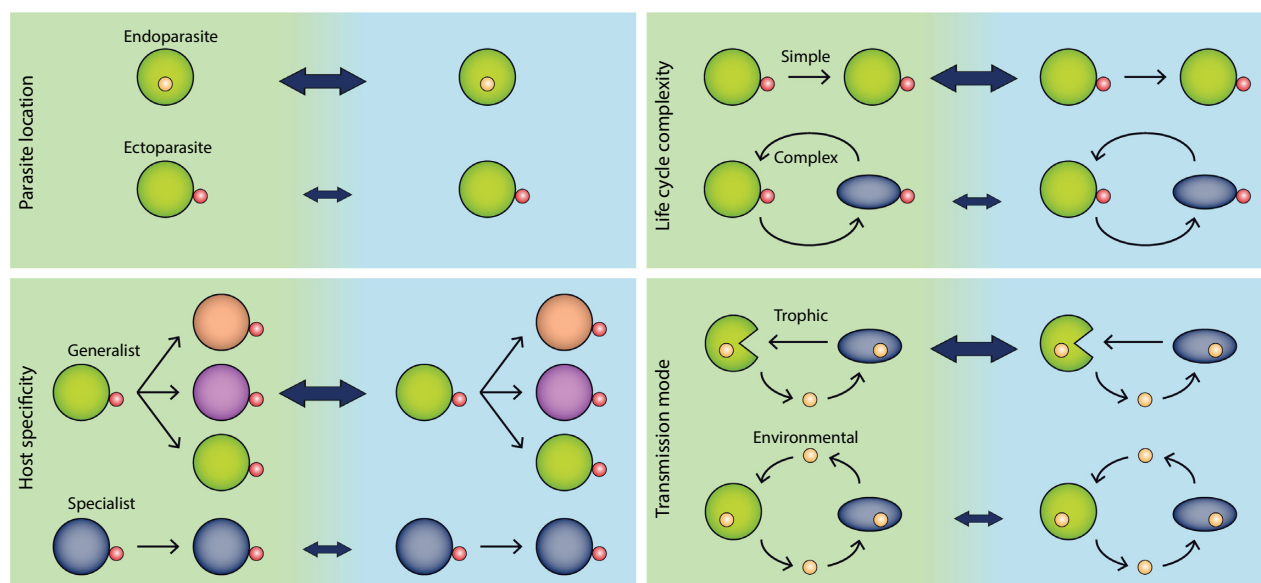


Fig. 1 Some inherent features of parasites and hosts that may influence likelihood of transitions (from left to right) from freshwater to marine environments or vice versa. Parasites denoted as small circles; other symbols = hosts. Thickness of arrows denotes likelihood of achieving transition. See text for further discussion and other features enhancing transitions.

(statoblasts) of a freshwater bryozoan (Abd-Elfattah et al. 2014).

Likelihood and constraints of environmental transitioning by parasites

Buffering against environmental challenges might promote range expansions of endoparasites because the host provides “environmental stability” (Mestre et al. 2020), a view that can be extended to environmental transitions (Fig. 1). Such buffering may particularly promote transitions of endoparasites that undergo regular movements with hosts between marine, brackish, and freshwater environments (e.g., diadromous fish). Challenges to unbuffered ectoparasites and free-living parasitic stages could include changes in salinity and temperature. Accordingly, intestinal parasites of estuarine fish were shown to be unaffected by changing water salinities, while reduced salinities impeded ectoparasite development (Möller 1978). Ectoparasite sensitivity to environmental challenge is also exemplified by management to reduce sea lice infections in Atlantic salmon aquaculture by exposure to challenging salinity and temperature regimes (Ljungfeldt et al. 2017; Sievers et al. 2019).

Parasite life cycles, host utilization patterns, and transmission modes may variously influence transition likelihood. For example, all being equal, generalist parasites may achieve transition more readily than specialists as they may be capable of utilizing a greater range of hosts in new environments (Fig. 1). Suitable hosts for specialists might be rare or absent. Life cycle plas-

ticity (adding or dropping hosts), which characterizes some parasites (Cable et al. 2017), should promote environmental transitions. Parasites with simple life cycles arguably have a greater facility to adapt to new environments than those with complex life cycles (Fig. 1), particularly if their free-living stages are resistant. Having a complex life cycle may make it more difficult for a parasite to establish itself in a new environment (Poulin 2011; Blakeslee et al. 2019). For example, infection of Hawaiian stream fish by a nematode introduced with non-native fish hosts (Font 2003) may have been facilitated by dropping intermediate copepod hosts (Levsen 2001). However, Fraija-Fernández et al. (2021) argue that the three-host life cycle along with host switching facilitated ancient environmental transitions of diphylobothriidean cestodes. Trophic transmission might also promote environmental transition as exposure to environmental challenge would be avoided (Fig. 1). Trophic transmission may particularly promote transitions of parasites with simple life cycles. For parasites with complex life cycles, trophic transmission may be achieved by certain life stages, but release of potentially vulnerable free-living stages at other times may hinder transition.

Mechanisms and directions of parasite transitions

Parasites may transition between environments when co-introduced with hosts naturally or via human activities. Such co-introduction may be followed by adopting native hosts in the new environment, as

demonstrated (albeit between separate freshwater systems) for an intestinal nematode introduced when humans released non-native freshwater fish into Hawaiian streams (Font 2003; Gagne et al. 2015). Resistant free-living stages of parasites could be introduced via feces excreted from mobile animals such as birds, fish, and otters. Accordingly, high throughput sequencing approaches have identified a range of parasites that produce such resistant stages in cormorant and gull feces, including parasites of the fecal producers themselves, parasites of food items, or those incidentally ingested (nematodes, digenean trematodes, acanthocephalans, and a myxozoan in cormorants; cestodes and nematodes in gulls [Briscoe et al. 2022]).

The annual migratory behavior of diadromous fish might particularly promote environmental transitions if parasites evolve tolerances to changing environmental conditions and undergo host switching. Transitions of endoparasites that are buffered by hosts might be particularly promoted. However, studies to identify treatments to reduce ectoparasite impacts on Atlantic salmon aquaculture suggest that transitions by some ectoparasites may be possible. For example, Sievers et al. (2019) found that early attached sea life stages tolerate very low salinities and therefore highlighted that further salinity tolerance might be promoted by exposure to lower salinities. Parasites themselves might also promote host tolerance to environmental challenge, thus providing first steps towards environmental transition. For example, an acanthocephalan parasite has been linked with enhanced salinity tolerance of a freshwater amphipod host (Piscart et al. 2007). Our considerations here highlight that environmental transitions may be promoted by both natural events (e.g., host migratory behavior) and human activities (e.g., host introduction). Other processes that may introduce parasites and promote transitions include flooding, tidal waves, hurricanes, the release of ballast water, and sewage outflow.

If life originated in the marine realm, then transitions were initially only possible from the sea to freshwater. However, ancient invasions of and radiations in freshwater environments eventually enabled transitions in either direction. The extant ray-finned (actinopterygian) fish are particularly notable here because they appear to have originated in freshwaters. Actinopterygians are highly diverse in both freshwater and marine environments, comprising the most species-rich clade of vertebrates and containing 96% of modern fish species (Carrete Vega and Weins 2012). Extensive radiation of some clades has entailed re-invasions of freshwaters from marine environments. Such environmental transitions and diversification of hosts will likely have influenced parasite transitions and diversification.

Finally, relative diversities may influence transition likelihood. For example, high abundances of marine microbial lineages may explain why many microbial transitions appear to have occurred from the sea to fresh waters and not vice versa (Logares et al. 2009).

Evidence of transitions

Phylogenetic analyses supported by oldest body fossils infer marine origins for Cnidaria, Annelida, Arthropoda, Nematoda, Nematomorpha, and Rotifera. In these phyla, parasitism is variously derived (De Baets et al. 2021; Okamura and Gruhl 2021), raising questions of where, when, and how many times it has evolved. Below we review how the fossil record and phylogenetic analyses jointly provide evidence for transitions of helminths in deep time across marine and freshwater/terrestrial environments. We then highlight environmental transitions of parasites that lack a fossil record.

Although rare, the oldest reported parasitic arthropod fossils are the worm-like pentastomids (currently placed in Crustacea) from Cambrian–Ordovician marine phosphatic Lagerstätten (Walossek and Müller 1994; Fig. 2). Their morphology implies parasitism, and co-occurrence with conodonts suggests early vertebrate hosts. Modern pentastomids are endoparasites of terrestrial tetrapods, thus at least one transition can be inferred from marine to freshwater/terrestrial environments at some time between the Ordovician and Triassic, likely tracking terrestrialization of vertebrate hosts (De Baets et al. 2015). A putative pentastomid ectoparasitic on a marine ostracod complicated this interpretation (Siveter et al. 2015), but recent work suggests misidentification (Boxshall and Hayes 2019).

Parasitic nematoids appear to have evolved repeatedly in marine and freshwater/terrestrial realms, including lineages comprising nematodes and the crown-group nematomorphs. Nematodes originating in the sea often exclusively parasitize marine hosts (e.g., echinoderms and octocorals; Westerman et al. 2021), and clear transitions to freshwater environments are lacking. Early lineages of terrestrial enoplid nematodes established at the latest in the Early Devonian (Fig. 2; Poinar et al. 2008). The major terrestrial parasitic lineages subsequently invaded marine environments (Blaxter and Koutsovoulos 2015). For example, ascaridoid nematodes within Chromadorea parasitizing terrestrial vertebrates adopted elasmobranch and teleost hosts (Fig. 2; Li et al. 2018). Divergence time estimates (Li et al. 2018) place the transition from freshwater to marine teleost hosts at the latest in the Cenozoic, but fossil finds attributable to ascaridoids in semi-aquatic crocodylians (Barrios-de Pedro et al. 2020) highlight an earlier Cretaceous transition to freshwater (Fig. 2). The success

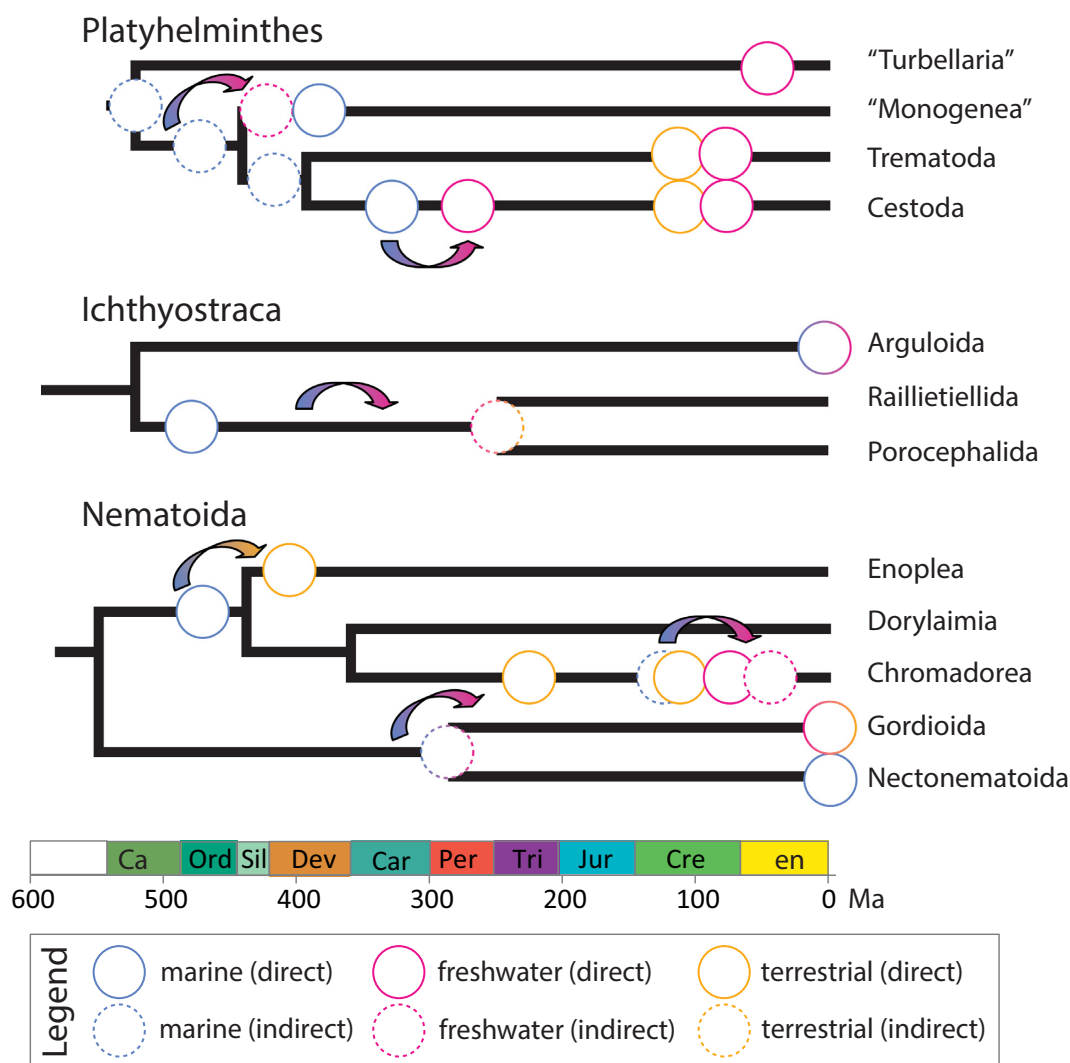


Fig. 2 Phylogenetic relationships and divergence time estimates of Platyhelminthes (modified from Perkins 2010), Pentastomida (Raillietiellida and Porocephalida; modified from Sanders and Lee 2010), Nematoida (modified from Blaxter 2009; Rota-Stabelli et al. 2013; Li et al. 2018), and constraints for colonization of particular environments (full circles = fossil or modern observations; stippled circles = inferred habitat based on modern clock or host constraints). Arrows denote ancestral environmental transitions. “ ” refer to paraphyletic lineages. Fossil constraints reviewed in De Baets et al. (2021).

of terrestrial/freshwater parasitic nematode lineages has been attributed to free-living ancestors in terrestrial environments that were preadapted for colonization of the vertebrate gut (Tchesunov and Ivanenko 2021). Molecular phylogenetic analyses demonstrate repeated transitions between marine and terrestrial environments (Holterman et al. 2019) in keeping with fossil evidence.

The monophyletic neodermatan flatworms include exclusively parasitic crown-group members, indicating parasitism evolved once. Recent molecular studies (Egger et al. 2015) support a simple ectoparasitic life cycle in basal neodermatans (monogeneans) with more derived endoparasitic forms (cestodes and trematodes) incorporating complex life cycles (Fig. 2). Monogeneans likely closely evolved with chondrichthyan and

osteichthyan hosts (Boeger and Kritsky 1997) and have been inferred to invade freshwater lungfish and lissamphibians as early as 425 and 250 Ma (Verneau et al. 2002). Basal lineages of cestodes and trematodes occur in marine environments (Littlewood et al. 2015). These observations suggest invasions (and re-invasions) of freshwater and terrestrial realms followed by host switches. However, some molecular phylogenetic analyses imply a freshwater habitat for the free-living sister-group of Neodermata (Laumer et al. 2015), and the fossil record places the original neodermatan habitat in marginal marine to deltaic environments (De Baets et al. 2015, 2021). Nevertheless, lineages of cestodes and trematodes parasitizing marine and freshwater fish and terrestrial tetrapods are clearly intercalated

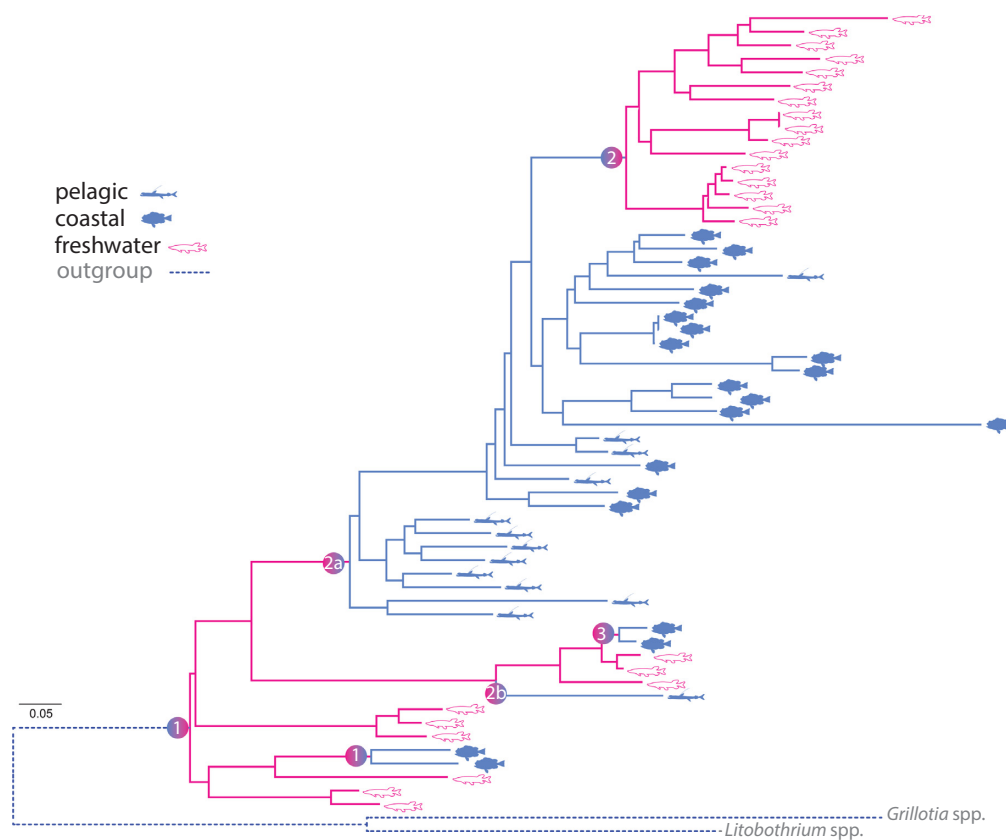


Fig. 3 Repeated transitions between marine and freshwater environments in cestodes belonging to the order Bothriocephalidea. Note propensity for more transitions from freshwater to marine hosts (modified from Brabec et al. 2015; permission to reproduce from Elsevier).

(Littlewood et al. 2015), indicating various transitions over deep time. In some groups with extensive molecular sampling (e.g., diphylobothriidean cestodes; Fraija-Fernández et al. 2021), transitions are seemingly non-directional. In others, a bias from freshwater to marine environments is suggested. For example, at least four transitions from freshwater to marine hosts versus one (two including the ancestral transition) in the opposite direction are inferred for bothriocephalidean cestodes (Fig. 3; Brabec et al. 2015). Trematodes have shifted at least once from freshwater to marine tetrapods in the Cyathocotylidae (Achatz et al. 2019), and various fossils place trematodes in freshwater Cretaceous environments (Rogers et al. 2018; Barrios de Pedro et al. 2020).

Evidence for a much more recent cestode transition is provided by *Schistocephalus solidus* in anadromous marine threespine sticklebacks that colonized freshwater lakes after Pleistocene glaciers receded. *Schistocephalus solidus* infects freshwater stickleback populations but is occasionally found at low prevalence in marine populations (Weber et al. 2017). The latter may reflect low encounter rates in the sea, effective host resistance in large, well-mixed marine populations, parasite specialization to lake sticklebacks, or a mixture of

these factors. These observations suggest that anadromous sticklebacks could introduce parasites to marine environments where they might become more fully established, for example, via host switching. The alternate interpretation—that tracking marine stickleback hosts to lakes has enabled *S. solidus* to greatly expand (e.g., due to release from competition with other parasites)—would imply transition from marine to freshwater environments.

Environmental transitions can also be inferred from molecular phylogenies of parasitic taxa with no fossil record, such as myxozoans. Myxozoa comprises a speciose and exclusively endoparasitic radiation within Cnidaria which is sister to Medusozoa. Myxozoans utilize invertebrates and vertebrates as definitive and intermediate hosts, respectively, in marine, freshwater, and terrestrial habitats (Okamura and Gruhl 2021). Molecular phylogenies based on 18S rDNA suggest myxozoans have undergone multiple environmental transitions (Fiala et al. 2015a; Fiala and Bartošová 2010; Holzer et al. 2018). The two main myxozoan lineages are the species-poor Malacosporea associated with freshwater environments, and the speciose Myxosporea that inhabit both freshwater and marine environments (Fiala

and Bartošová 2010). Fresh water has been identified as the ancestral myxozoan habitat based on the freshwater affinity of malacosporeans (Fiala and Bartošová 2010), although this trait may be derived. Malacosporean invertebrate hosts (phylactolaemate bryozoans) have marine ancestors, and at least one malacosporean is capable of infecting anadromous salmonid hosts (Feist et al. 2001).

Within Myxosporidia, molecular phylogenies identify three clades. The genus *Sphaerospora* is a sister to the remainder of myxosporidians, which comprises two large clades—one primarily freshwater and the other marine and using oligochaete and polychaete hosts, respectively. *Sphaerospora* contains a mainly marine lineage and a larger clade of mostly freshwater species (Patra et al. 2018). The latter contains a group of species that has returned to the sea. At least two independent transitions to freshwater have occurred in the otherwise entirely marine and polychaete-infecting clade. *Parvicapsula minibicornis* and the genus *Ceratonova* utilize one of the rare freshwater polychaetes, *Manayunkia speciosa*, as a definitive host (Bartholomew et al. 1997, 2006), while intermediate hosts are anadromous (salmon) or euryhaline (stickleback) fish. Co-introductions enabling such a transition may have involved either host. At least 10 species or groups have independently re-invaded the marine realm within the freshwater oligochaete-infecting myxosporidian clade (Fiala et al. 2015a, b; Holzer et al. 2018). Oligochaetes are primarily freshwater and terrestrial annelids; marine taxa are considered to have invaded the sea secondarily—a process that could have co-introduced myxozoan parasites. Myxosporidians in the freshwater clade also infect moles and ducks (Hallett et al. 2015) and thus indicate terrestrial transitions. We note that further sampling of diversity and genome-level analyses may reveal new insights about myxozoan environmental transitions.

Bråte et al. (2010) provide evidence of transitions between freshwater and marine environments for parasitic unicellular eukaryotes (perkinsid alveolates). As inferred for largely free-living eukaryotic microbial taxa (Logares et al. 2009), bacteria (Logares et al. 2010), and macroorganisms (Lee and Bell 1999), only a few transitions are evident over the entire history of Perkinsea. Logares et al. (2009) highlight that the interface between marine and fresh waters appears to constitute a significant barrier despite the often large and widely distributed populations that can characterize microorganisms (Logares et al. 2009). Whether the apparently greater frequency of environmental transitions inferred for myxozoans is a function of sampling or a more fundamental difference is of interest.

It is apparent that transitions between marine and freshwater environments have occasionally occurred

in the evolutionary history of many parasites. Parasitic species confined to either freshwater or marine habitats within a common genus may exemplify relatively recent such transitions. Examples here include species in the monogenean genus *Protogyrodactylus* (Mendlová et al. 2010)], the cestode genus *Acanthobothrium* (Alves et al. 2017), and the trematode genus *Eubothrium* (Brabec et al. 2015), although relationships may change with further taxonomic and molecular data. Current data for helminths and myxozoans suggest a bias for transitions from freshwater to marine environments. Parasites and hosts straddling marginal marine environments or movements of diadromous fish hosts may variously have promoted transitions, and earlier we highlighted other factors that might influence transition success. It is therefore likely that an interplay of factors prompted Pariselle et al. (2011) to suggest that ancestors of cichlids likely lost some parasites when crossing salinity gradients while retaining others—or even acquiring new ones. Parasites could also conceivably influence transition as they may be a cause as well as a consequence of migration (Poulin and de Angeli Dutra 2021). Further data are required, including for enigmatic early diverging lineages, life cycles, pre-adaptations, additional and more evenly sampled fossils, expanded sampling of parasite diversities, and genome-wide analyses, to understand the timing, mechanisms, frequency, and directionality of transitions.

We have been unable to find any bona fide examples of present-day transitions of parasites between freshwater and marine environments. Below we highlight cases of potential or incipient transitions.

American shad (*Alosa sapidissima*) is an anadromous fish native to rivers and nearshore regions along the Atlantic coast of North America. A riverine egg and larval period is followed by migration of juveniles to sea and then a return to natal rivers for iteroparous spawning. In 1871, American shad fry were introduced from the Hudson River in New York to the Sacramento River in California with subsequent spread northward (Hershberger et al. 2010). Gregg et al. (2016) determined that introduced American shad are infected by a large clade of the mesomycetozoan, *Ichthyophonus*, which infects a diversity of marine fish. Infection of native fish in the Columbia River system was thus a concern when record-high American shad abundance was linked with concurrently high *Ichthyophonus* infection prevalence. However, low *Ichthyophonus* prevalences in sympatric resident and anadromous fish in the system suggested that an efficient freshwater life cycle had not yet established (Hershberger et al. 2010). Subsequent demonstration of *Ichthyophonus* transmission to fish in both freshwater (LaPatra and Kocan 2016) and

marine (Kocan et al. 2019) settings suggests that resistant *Ichthyophonus* spores (schizonts) are functional in both freshwater and seawater—a trait that may facilitate transitioning between freshwater and marine environments.

Polymorphid acanthocephalans typically use intermediate crustacean hosts and infect final hosts (marine mammals, waterfowl, and fish-eating birds) often via paratenic fish hosts. The discovery of apparently viable *Profilicollis chasmagnathi* larvae in a freshwater fish suggests potential colonization of fresh waters, with ecotonal environments promoting such a transition (Levy et al. 2020). Nevertheless, it remains to be established that larvae of *P. chasmagnathi* in the freshwater host achieve transmission. This example highlights a common constraint of inferring environmental transitions and other aspects of parasite ecology imposed by our generally poor understanding of parasite life cycles, hosts, and distributions.

Transitions in our changing world

Biotic and abiotic changes can be anticipated to impact parasite transitions in our changing world. Variation in host abundances may impact parasite movement. In particular, populations of many migratory animals have greatly declined (Wilcove and Wikelski 2008), with relative abundances of 24 diadromous fish species in the northern Atlantic Ocean dropping by some 90% compared to historic levels (Limburg and Waldman 2009). Impacts of invasive alien species are of global concern (Early et al. 2016), and invasion of hosts and parasites may influence environmental transitions of parasites. Such invasions could entail spillover/spillback dynamics, competition with native hosts, or interference with parasite transmission (Goedknecht et al. 2016). For example, invasive bivalve hosts may act as pathogen sinks (dead-end hosts), prey on free-living infectious stages, or serve as carriers or reservoirs of disease (Costello et al. 2021). In addition, phenological changes may variously impact transition likelihood by offering more benign or more challenging conditions in new environments.

Abiotic factors may interact to influence parasite distributions, creating complex scenarios whose relative impacts are likely to vary over space and time. Hurricanes and storm surges may enhance dispersal of invasive propagules in the water column (Hellmann et al. 2008). Flooding may drive transitions from freshwater to marine environments, while transitions from marine to fresh waters might be anticipated with melting of ice sheets and rising sea levels (Marcogliese 2001). Storms and warmer temperatures are associated with marine disease outbreaks (Burge et al. 2014). Drought may also

limit or enhance transitions. For example, aerial transport of soil fungi across the Atlantic with Saharan dust particles has been linked with disease in Caribbean corals (Garrison et al. 2003), suggesting that increasing desertification could promote transitions of freshwater pathogens and parasites. Notably, ice sheet melting will reduce salinities in many marine habitats, while salinization may be driven by drought in freshwater habitats. These contrasting impacts could increase the likelihood of future transitions between the two habitats. Habitat fragmentation will almost certainly be influential as exemplified in rodent-helminth communities, with increasing habitat disturbance reducing connectance of parasite–host networks, thus diminishing parasite communities over space and time (Bordes et al. 2015).

Overall, there is evidence that our changing world is variously influencing parasite distributions and abundances. Nevertheless, impacts on parasite transitions between freshwater and marine environments remain poorly understood.

Conclusions

Potential constraints for parasites to achieve environmental transitions include life cycle complexity, host specificity and availability, transmission mode, translocation, and potential exposure to challenging conditions. Such constraints are shared with free-living taxa as they relate to transport, introduction, survival, establishment, and potential spread. We propose that endoparasites may undergo environmental transitions more readily than ectoparasites because hosts reduce exposure to physiologically challenging environments. However, many endoparasites also release free-living stages, which may limit such transition. Highly virulent parasites may reduce the chances of environmental transition as hosts (or parasites) may die in transit (Prenter et al. 2004; Strauss et al. 2012). We further suggest that adopting an endosymbiotic lifestyle is itself a form of environmental transition with organisms switching from living in one environment (freshwater, seawater, or air) to another (within hosts). Such transition may have been promoted by a close association of a symbiont with host surfaces as a commensal, followed by invasion by symbionts. Such endosymbionts may have initially been mutualists, but with rising fitness costs to hosts, transitioned to parasites.

Just as for the range expansion of parasites (Mestre et al. 2020), environmental transitions of parasites are likely to be driven by environmental changes that promote dispersal followed by host switching when encountering novel hosts. These processes can be expected to have contributed to parasite diversification historically and over deep time. In the present day,

however, anthropogenic activities and accelerating environmental change are jointly causing extensive biotic mixing, which can be predicted to promote biological invasions and emerging diseases and to impact ecosystem function and environmental transitions. Recognizing the potential processes underlying current and future environmental transitions is crucial in view of our changing world and the current biodiversity crisis. Extant sister lineages that exploit contrasting environments (marine versus freshwater) could offer model systems to explore constraints and adaptations associated with transitions revealed, for example, by characterizing environmental tolerances, performing experimental transmissions, or conducting comparative genomics.

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Data availability

No new data were generated or analyzed in support of this research.

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