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Parasites: Small Players with Crucial Roles in the Ecological Theater

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Abstract: Effective management of our natural resources requires an understanding of ecosystem structure and function; effectively, an ecosystem-based approach to management. Parasites occur, albeit cryptically, in almost all ecosystems, yet they are usually neglected in studies on populations and communties of organisms. Parasites can have pronounced or subtle effects on hosts affecting host behavior, growth, fecundity, and mortality. Furthermore, parasites may regulate host population dynamics and influence community structure. Many parasites have complex life cycles and depend for transmission on the presence of a variety of invertebrate and vertebrate intermediate hosts. Often transmission involves predator–prey interactions. Thus, parasites reflect the host's position in the food web and are indicative of changes in ecosystem structure and function. Parasites can provide information on population structure, evolutionary hypotheses, environmental stressors, trophic interactions, biodiversity, and climatic conditions. I use examples from diverse freshwater and marine systems to demonstrate that parasites should be incorporated into research and monitoring programs to maximize information gathered in ecosystem-based studies and resource management.

Key words: parasitism, stress, parasite-induced host mortality, food webs, ecosystems, fresh water, marine, indicators

INTRODUCTION

Parasitic organisms are often neglected in the management and conservation of biological resources and ecosystems. They are analagous to “extras” in a theatrical production who do not have speaking parts, yet are crucial to a deeper comprehension of the ongoing scene. They are most often small, short-lived, and rarely observed in the external environment, or more commonly hidden within organisms during their parasitic phase. Their effects on their hosts may be obvious and profound, or more subtle, reflecting principal characters or supporting players on the ecosystem stage. Typically, they attract attention only when they cause pathology and disease, or somehow degrade biological products, thus reducing production yields and economic benefits. This is a role where they are only temporarily prominent on the scene and always panned by their critics. Yet, virtually all species are host to at least one parasite species, with the remitting probability that parasitic organisms outnumber free-living species (Price, 1980). Thus parasites comprise an important component of the cast of organisms in ecological theaters throughout the world, including freshwater and

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Supplementary Tables 3, 4, 5, 6 and additional references for this article are available for viewing by subscribers only at http://www.springerlink.com

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marine, whose effects can be manifested in the evolutionary play of life (with apologies to Hutchinson, 1965).

Research on parasites can provide a great deal of information about their host organisms and habitats. A population or ecosystem-scale approach to parasitology can be applied not only to the control of disease, but to the proper management and conservation of aquatic resources, be they species targeted for harvest or areas designated as protected. In this article, I summarize basic parasitic life-styles and transmission patterns and review the various applications of this information to species management in aquatic ecosystems. I outline a holistic approach whereby knowledge of parasites can be applied to conservation of multispecies systems to aid in conservation management. Examples are given from freshwater and marine ecosystems including plants, invertebrates, and vertebrates, for the implications of parasitism extend beyond commercially exploited species to include all trophic levels and organisms within habitats. The goal is to foster an appreciation for the role played by parasites as the drama of life unfolds on the global ecosystem stage.

LIFE-STYLES AND TRANSMISSION PATTERNS

For epidemiological purposes, parasites are traditionally divided into microparasites and macroparasites (Anderson and May, 1979; May and Anderson, 1979). Microparasites consist of small organisms that are primarily unicellular, including viruses, bacteria, and protozoans, but also multicellular organisms of small size (< 50 μm) such as myxozoans. These organisms typically multiply in or on the host and are often associated with disease. Transmission is usually direct but may be indirect, involving alternate hosts (e.g., myxozoans), or vectors (e.g., many protozoans). Macroparasites are larger, multicellular organisms such as monogeneans, digeneans, cestodes, nematodes, acanthocephalans, arthropods, leeches, and others. These typically undergo sexual reproduction in or on a host, but do not normally proliferate there (the production of cercariae by digeneans in molluscan intermediate hosts is an exception). They often possess complex life cycles, with one or more intermediate hosts required for development or growth (Figs. 1 and 2). These parasites are sometimes clearly detrimental to their hosts, but in many cases their effects are more subtle and difficult to measure.

For those parasites with complex life cycles, a variety of transmission modes has evolved. Transmission may involve one or more free-living infective stages, where the infective stage is passively ingested by the next host in the parasite's life cycle, for example, certain larvae of digeneans (metacercariae) that encyst in the external environment; free-swimming cestode larvae (coracidia) that are preyed upon by crustacean intermediate hosts; or parasite eggs of many groups. Free-living infective stages also may be transmitted actively by penetrating the next host in the life cycle, as with the larval cercariae of many digeneans in fish and other organisms, and nematode larvae in moist soil. Parasite life cycles may involve a parasitic infective stage in one precursor host that must be ingested for transmission to occur. Examples can be found among all the principal helminth groups (except monogeneans) including many digeneans, and all species of cestodes, nematodes, and acanthocepahalans. In these cases, occurrence of a parasite in a host reflects predator–prey interactions between the host and its prey and predators. The diversity of parasites within a host reflects the presence of diverse intermediate and definitive hosts in the ecosystem participating in the parasites' life cycles. Thus, by the nature of their different life cycles, the parasites in a host population provide information on that organism's role in the food web (Marcogliese and Cone, 1997a; Marcogliese, 2001b, 2002, 2003).

IMPACTS ON HOSTS AND COMMUNITIES

By their very nature, parasites have a variety of impacts on their hosts. They impose energetic demands, alter behavior, affect morphology and appearance, reduce fecundity and growth, and cause mortality. These effects are well documented in numerous host–parasite systems in both freshwater and marine habitats. Behavioral alterations may lead to increased vulnerability to predation. In some cases, this is a pathological side effect, but in others it may enhance transmission to the next host in the life cycle. Thus, parasites can affect the diet of predators, influencing predator–prey dynamics (Fig. 1) and competitive interactions between that host and other organisms (Price et al., 1986; Lafferty et al., 2000). Parasites can affect sex ratio and mate choice (Minchella and Scott, 1991). Taken together with the effects listed above, it seems likely that parasites can have an impact on host fitness, and thus, play a role in natural selection of host characteristics. A list of parasites that affect commercial fish stocks through parasite-induced host mortality, reduction in fecundity, or reduction in market value or weight appears in Dobson and May (1986).

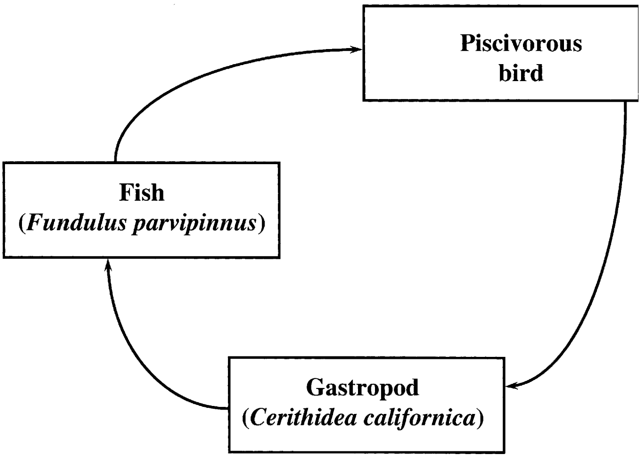

Figure 1. Life cycle of a typical digenean (*Euhaplorchis californiensis*) in a salt marsh. Piscivorous birds such as egrets or herons serve as definitive hosts. Eggs are passed with feces, which are ingested by the first intermediate host (horn snail, *Cerithidea californica*). Cercariae are asexually produced in the snail and released into the water, infecting a suitable second intermediate fish host (Pacific killifish, *Fundulus parvipinnus*) upon contact. The parasite then encysts as a metacercaria in the brain. The life cycle is completed when the bird eats the infected fish. The parasite impacts upon the ecosystem at multiple trophic levels. Infected snails are castrated, possibly affecting snail population levels. Infected fish display behavioral alterations such that they become 30 times more susceptible to predation. Conceivably, the presence of the parasite permits the persistence of piscivorous waterfowl by facilitating predation (Lafferty and Morris, 1996).

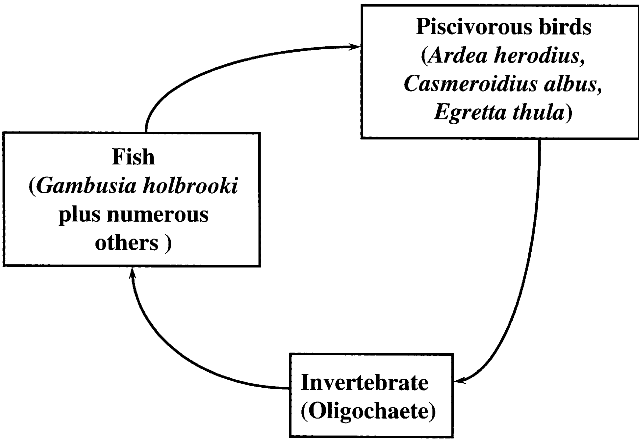

Figure 2. Life cycle of a typical nematode (*Eustrongylides ignotus*) in the aquatic environment. Piscivorous birds, including great blue herons (*Ardea herodius*), great egrets (*Casmeroidius albus*), and snowy egrets (*Egretta thula*), are definitive hosts. Eggs are passed into the water with the feces and are ingested by oligochaetes, the first intermediate hosts. Numerous fish species, including mosquitofish (*Gambusia holbrooki*) may function as second intermediate hosts, acquiring the parasite by eating infected oligochaetes. The avian definitive hosts become infected when they consume the fish, thus completing the life cycle. This parasite causes pathology in piscivorous fish hosts and renders smaller forage fish more susceptible to predation (Coyner et al., 2001). In addition, the parasite causes significant mortality among nestling birds. Furthermore, the parasites' abundance is amplified in eutrophic conditions, probably via effects on oligochaete populations. Thus, this parasite has impacts at different trophic levels, and these impacts are substantially amplified by anthropogenic nutrient enrichment.

Pathology caused by parasitism is widespread in all organisms (Kinne, 1980–1990; Woo, 1995; Bondad-Reantaso et al., 2001), and virtually all organs and tissues can be damaged by a plethora of parasitic organisms. Examples of parasites of a range of invertebrate and vertebrate aquatic organisms that have different negative impacts on their hosts are listed in Table 1. Infection with many types of parasites causes sublethal effects in virtually all types of organisms, including ctenophores, cnidarians, molluscs, crustaceans, insects, echinoderms, chaetognaths, fish, and plants (see supplementary Table 3, available for viewing by subscribers only at http://www.springerlink.com), as well as amphibians, waterfowl, and aquatic mammals Though most parasites do not normally kill their hosts, death can result from infection. Parasites of numerous different types of organisms, from algae through vertebrates, have been shown to cause parasite-induced host mortality (see supplementary Table 4, available for viewing by subscribers only at http://www.springerlink.com). Clearly, the effects of parasites are manifest throughout the food webs of aquatic systems, and not confined to well-studied commercial species. These lists of host–parasite associations represent a variety of invertebrate and vertebrate taxa at different trophic levels, along with different types of impacts. Virtually all types of parasites manifest some sort of effect and all types of organisms are impacted in some way, no matter where they occur within a food web.

Parasites also function as ecosystem engineers by directly or indirectly modifying the environment of other organisms (i.e., the host phenotype). A parasite may alter host biology such that new habitat for other species is formed (Thomas et al., 1999; Lafferty et al., 2000).

If prevalence and abundance are high, parasites can have a significant impact on the host population, and regulate its numbers (Anderson and May, 1979; May and Anderson, 1979). If that particular host population is a dominant species in an ecosystem, then the presence of the parasite may have consequences for the entire food web

Table 1. Selected Examples of Sublethal and Lethal Impacts on Aquatic Hosts by Parasites in Freshwater and Marine Environments

Host species	Common name	Parasite species	Parasite group	Ecosystem	Impact	Reference[a]
Mollusca						
Hydrobia ulvae	Gastropod	Microphallids	Digeneans	Intertidal mudflats	PIHM	Jensen and Mouritsen, 1992
Illyanassa obsoleta	Gastropod	Numerous species	Digeneans	Intertidal mud flats	Castration; alter vertical distribution	Curtis, 2002
Arthropoda						
Cyclops strenuus	Copepod	*Triaenophorus* spp.	Cestodes	Lab (freshwater)	Alter activity, decrease depth, reduce fecundity, feeding, PIVP	Pasternak et al., 1999; Pulkkinen et al., 2000
Daphnia spp.	Cladocerans	*Ordospora colligata* (= *Pleistophora intestinalis*), *Flabelliforma magnivora*, *Octosporea bayeri*	Microsporidians	Freshwater pools, lab	Reduce fecundity, reduce competitive ability, PIHM	Ebert, 1994; Ebert et al., 2000; Salathé and Ebert, 2003
Gammarus pulex	Amphipod	*Pomphorhynchus laevis*	Acanthocephalan	Freshwater rivers, lab	Reduce respiration, altered drift, increase phototactism and activity, alter appearance, PIVP, increase sensitivity to acid conditions and cadmium, decrease feeding, reduce lipid in gravid females	Rumpus and Kennedy, 1974; Brown and Pascoe, 1989; McCahon and Poulton, 1991; McCahon et al., 1991; Bakker et al., 1997; Plaistow et al., 2001
Echinodermata						
Strongylocentrotus droebachiensis	Sea urchin	*Paramaoba invadens*	Amoeba	Nova Scotia coast	PIHM	Hagan, 1996
		Echinomermella matsi	Nematode	Norwegian coast	PIHM, castration	
Pisces						
Clupea harengus	Herring	*Ichthyophonus hofferi*	Fungus	North Sea	PIHM	Patterson, 1996
		Scolex pleuronectis	Cestode	Lab (marine), marine	PIHM, reduce larval feeding	Rosenthal, 1967; Heath and Nicoll, 1991

		Hysterothylacium aduncum	Nematode	Lab (marine)	PIHM	Balbuena et al., 2000
		Lernaeocera sp.	Copepod	Lab (marine)	PIHM	Rosenthal, 1967
Gasterosteus aculeatus	Threespine stickleback	*Diplostomum gasterostei*	Digenean	Freshwater	PIHM	Pennycuick, 1971
		Schistocephalus solidus	Cestode	Freshwater, lab	Reduce growth, affect foraging ability, diet choice and appearance, reduce mobility, avoidance behavior, nutrient reserves and liver size, delay maturation, stop reproduction, increase sensitivity to cadmium, decrease depth distribution, PIVP, PIHM	Pennycuick, 1971; Pascoe, and Cram, 1977; Barber and Huntingford, 1995
Lepomis macrochirus	Bluegill	*Allacanthochasmus* sp.	Digenean	Mississippi River	PIHM	Fischer and Kelso, 1988
	Sunfish	*Uvulifer ambloplitis*	Digenean	Freshwater pond, lab	PIHM	Lemly and Esch, 1984
Oncorhynchus mykiss	Rainbow trout	*Cryptobia salmositica*	Hemoflagellate	Lab (freshwater)	Reduce respiration and swimming	Kumaragura et al., 1995
		Myxobolus cerebralis	Myxozoan	Freshwater	Deformities, abnormal swimming, lower leuckocyte and lymphocyte counts	Densmore et al., 2001
		Gyrodactylus spp.	Monogenean	Lab (freshwater)	Induce cortisol	Stoltze and Buchmann, 2001
		Crepidostomum farionis	Digenean	Lab (freshwater)	Reduce hemoglobin and hematocrit	Klein et al., 1969
		Nanophyetis salmincola	Digenean	Lab (freshwater)	Reduce swimming speed, reduce immune response	Butler and Milleman, 1971; Jacobson et al., 2003

PIVP, parasite-induced vulnerability to predation; PIHM, parasite-induced host mortality.

[a] References are chosen to represent diverse host and parasite taxa from different habitats and to illustrate a variety of potential impacts of parasitism. Viruses and bacteria are not included.

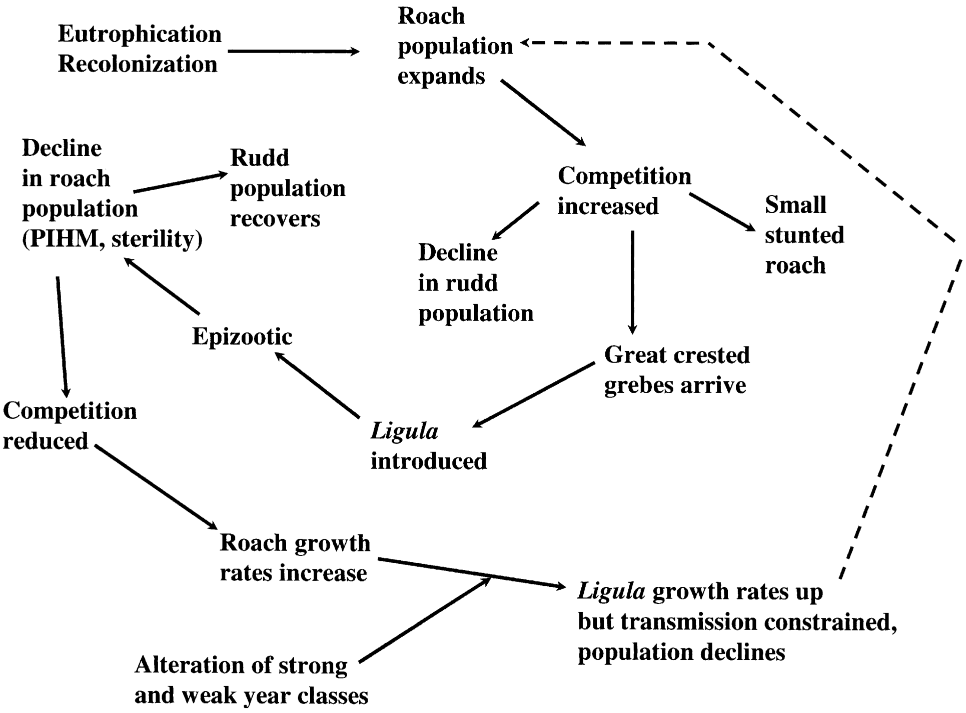

Figure 3. Schematic displaying role of the cestode *Ligula intestinalis* in population cycles of the roach, *Rutilus rutilus* (direct interactions) and rudd, *Scardinius erythrophthalmus* (indirect interactions) in Slapton Ley, United Kingdom. In the first phase of the epizootic cycle, roach population dynamics are controlled by the parasite population. In the second phase, roach population dynamics determine infection levels of *L. intestinalis*. Initiation of a new cycle (dashed line) may depend on local conditions and is not obligatory (after Kennedy et al., 2001). PIHM, parasite-induced host mortality.

and ecosystem structure (Dobson and Hudson, 1986; Minchella and Scott, 1991; McCallum and Dobson, 1995). Such parasites are termed “keystone parasites” by Minchella and Scott (1991). For example, two different parasites are known to control local populations of the green sea urchin (*Strongylocentrotus droebachiensis*) which can overgraze kelp beds and completely alter coastal ecosystems. In Norwegian waters, populations of sea urchins are limited by the nematode *Echinomermella matsi*, while in Nova Scotia by the protozoan *Paramoeba invadens* (reviewed in Hagen, 1996). Outbreaks of the microsporidian *Cougourdella* sp. reduce populations of the dominant grazer in the system, the caddisfly *Glossosoma nigrior*, thus permeating increases in the production of periphyton and the abundance of other invertebrate grazers in Michigan streams (Kohler and Wiley, 1997). The parasitic plant *Cuscuta salina* preferentially infects the dominant competitor *Salicornia virginiana* over three other subordinate salt marsh plants, thus affecting community composition and dynamics (Pennings and Callaway, 2002). Parasites may actually drive plant succession, with very small effects on competitive ability being translated into community-wide consequences (Dobson and Crawley, 1994). These few examples illustrate the broad range of communities that can be influenced by parasitic infections in key species.

Depending on the location within the food web of a species infected by parasites, impacts may permeate through a bottom-up or a top-down cascade on the rest of the web. It should be stressed that organisms found throughout the food web are subjected to the impacts of parasitism. These impacts strongly suggest that it is imperative to consider parasites in management and conservation of their hosts.

Parasites may exert more subtle effects on host communities. For example, epizootics of plerocercoids of the cestode *Ligula intestinalis* in their intermediate host, the roach (*Rutilus rutilus*), clearly determine not only the population structure of the roach via parasite-induced host mortality and sterility but of another sympatric cyprinid fish, the rudd (*Scardinius erythrophthalmus*) in Slapton Ley via roach–rudd interactions (Fig. 3; Kennedy et al., 2001). Such interactions only became apparent after collection of long-term data and may generally be more common than previously assumed in other host–parasite systems.

In terms of conservation, the introduction or elimination of a parasite may affect interactions between a variety of species within a community (Dobson and Hudson, 1986; Kennedy et al., 2001). Furthermore, parasites and disease are a major threat to endangered species (McCallum and Dobson, 1995), especially if those species are maintained at high densities in small, fragmented areas that promote transmission and parasite exchange across species (Scott, 1988; McCallum and Dobson, 1995; Holmes, 1996). In addition, introductions and other emerging infectious diseases, including parasites, are a potentially serious threat to endangered species and biodiversity at large (Cunningham et al., 2003; Daszak and Cunningham, 2003).

PARASITES AS INDICATORS OF HOST BIOLOGY

Numerous studies in aquatic systems have effectively used parasites as indicators of host stocks and their ontogenetic or seasonal migrations. For some recent reviews, consult in Williams et al. (1992), Arthur (1997), and MacKenzie and Abaunza (1998) for rationale, examples, and guidelines. Most of the studies to date involve marine species of fish, but some work in fresh waters has successfully used parasites to discriminate among stocks (Marcogliese et al., 2001, and references therein). Because many parasites are transmitted via predator–prey interactions, and parasites possess a variety of complex life cycles with different intermediate hosts, parasites are excellent indicators of host diet (Williams et al., 1992; Marcogliese and Cone, 1997a). In fact, for numerous reasons, parasites provide complementary information to that obtained through stomach content analysis. Parasites reflect trophic interactions over weeks or months, whereas gut contents provide details of the animal's diet only over the last 24 hours or less (Williams et al., 1992; Curtis, 1995). They can indicate ontogenetic shifts in diet, whether hosts feed on more than one trophic level, niche shifts due to competition or other factors, individual feeding specializations within a population, seasonal changes in diet, and temporary links in a food web such as periodic migrants into a system (reviewed in Williams et al., 1992; Marcogliese and Cone, 1997a; Marcogliese, 2003). When combined with other techniques used in fisheries science such as meristics and population genetics, research managers have at their disposal a very powerful array of tools to study the biology of virtually any organism. Moreover, and not insignificantly, parasites are used as indicators of historical biogeography and phylogenetics of their hosts (Brooks and Hoberg, 2000).

PARASITES AS INDICATORS OF ECOSYSTEM STRESS, FOOD WEBS, AND BIODIVERSITY

A number of reviews summarize existing knowledge of the relationship between parasites and pollution, and parasites as indicators of stress (Overstreet and Howse, 1977; Overstreet, 1988, 1993, 1997; Khan and Thulin, 1991; Poulin, 1992; MacKenzie 1993, 1999; MacKenzie et al. 1995; Lafferty, 1997; Lafferty and Kuris, 1999). Basically, parasites can be used as indicators of environmental stress in a way analogous to their employment to differentiate among host populations or stocks. Many parasites possess complex life cycles and depend on the presence of one or more intermediate or paratenic hosts for transmission. Should the abundance of any of these hosts decline, for example, by exposure to chemical contaminants, then transmission of the parasite may be impaired. Similar results occur if infected hosts are more sensitive to effects of contaminants and are selectively removed (MacKenzie et al., 1995). Furthermore, free-living stages of parasites or those inhabiting the external surface or gastrointestinal tract are directly exposed to toxicants, and those parasites may be directly susceptible to pollution (Poulin, 1992; Overstreet, 1997; MacKenzie, 1999). See Table 1 in Pietrock and Marcogliese (2003) for a list of various endohelminths where survival and infectivity of their free-living stages are susceptible to toxicological effects caused by environmental contaminants. Parasites demonstrate different types of sensitivity to contaminants and environmental stress in aquatic hosts and ecosystems (see supplementary Table 5, available for viewing by subscribers only at http://www.springerlink.com). In terms of other relationships with pollutants, intestinal parasites appear to be more sensitive bioaccumulators of heavy metals than their fish hosts, and may serve as excellent indicators of heavy metal pollution (Sures et al., 1999; Sures, 2001, 2003). Alternatively, if a host's immune response is compromised by toxin exposure, its parasite burden may increase. Such a situation is often observed for monogeneans and protozoans that proliferate in hosts that inhabit polluted habitats (Overstreet, 1997). Commonly parasites that increase in abundance in contaminated habitats often possess direct life cycles (see Table 1 in MacKenzie et al., 1995, for numerous examples). Interpreted another way, abundance of infections with endoparasitic helminths tends to decrease, while those of ectoparasites tend to increase with pollution (MacKenzie, 1999). Moreover, many facultative parasites such as pathogenic viruses and bacteria also proliferate under these circumstances. Guidelines for selecting the most appropriate host–parasite combinations and the most vulnerable stages as indicators are provided in MacKenzie (1993, 1999) and MacKenzie et al. (1995).

Just as entire communities of free-living organisms are affected by environmental stress, so are the communities of parasites that infect any particular host species. Diversity

Table 2. Studies that Indicate Reductions or Increases in Parasite Species Richness and Abundance, or Changes in Species Composition for Parasite Communities in Hosts Exposed to Various Types of Environmental Stress in Aquatic Habitats[a]

Host species	Common name	Ecosystem	Contaminants or stress	Observations	References
Buccinum undatum	Common whelk	Firth of Clyde, UK	Sewage	Decline in prevalence of digeneans toward source	Siddall et al., 1993
Stagnicola emarginata	Snail	Lakes, northern Michigan	Human development	Decline in species richness and total prevalence	Cort et al., 1960; Keas and Blankespoor, 1997
Anguilla rostrata	American eel	Rivers, Nova Scotia, Canada	Acidification	Decline in species richness, loss of digeneans, change in species composition (acanthocephalans), with acidity	Cone et al., 1993; Marcogliese and Cone, 1996, 1997b
Bairdiella chrysura	Silver perch	Estuaries, Florida	Contaminants	Decrease in prevalence of crustaceans and parasites with indirect life cycles	Landsberg et al., 1998
Gambusia affinis	Western mosquitofish	Mississippi and Texas	Organic toxicants, heavy metals	Decline in species richness (heteroxenous species)	Overstreet, 1997
Gambusia holbrooki	Eastern mosquitofish	Florida	Sewage	Increase in prevalence of *Eustrongylides ignotus*	Coyner et al., 2003
Leuciscus cephalus	Chub	Moravia River, Czech Republic; rivers, Italy	Eutrophication, domestic and industrial	Change in abundance of acanthocephalans, decline in species richness	Dusek et al., 1998; Galli et al., 1998, 2001
		Moravia River, Czech Republic	Industrial and domestic	Decline in species richness downstream of source	Gelnar et al., 1997
Limanda limanda	Common dab	Firth of Forth, UK	Sewage	Change in prevalence and abundance of certain species	Siddall et al., 1994
Notropis hudsonius	Spottail shiner	St. Lawrence River, Quebec, Canada	Sewage	Increase in myxozoan prevalence and species richness	Marcogliese and Cone, 2001
Perca fluviatilis	Perch	Lakes, Finland	Pulp and paper, eutrophication	Decline in species richness, variable effects on species	Valtonen et al., 1997
			Acidification	Decline in species richness and digeneans	Halmetoja et al., 2000
Platichthys flesus	Flounder	SE Baltic; North Sea	Domestic and industrial	Decline in species richness	Sulgostowska et al., 1987; Broeg et al., 1999
Gobies	Fish	Baltic Sea	Eutrophication	Decline in species richness	Zander, 1998

[a] For further examples, please consult Tables 2 and 3 in MacKenzie et al. (1995).

and species richness may increase under stressful conditions, but more often a decrease occurs, at least for endoparasites with indirect life cycles. Reductions in parasite species richness have been observed following acidification, eutrophication, and chemical contamination (Table 2; see also supplementary Table 6 for a more comprehensive list, available for viewing by subscribers only at http://www.springerlink.com). These reductions in parasite diversity are believed to parallel diversity loss in free-living species, because populations of intermediate hosts are impacted by environmental changes. Furthermore, parasite communities may recover concomitantly with free-living communities when conditions improve (Cone et al., 1993).

However, resource managers must be aware that parasite taxa respond differently to environmental perturbations (Curtis, 1995; Lafferty, 1997; Marcogliese and Cone, 1997b; Lafferty and Kuris, 1999; MacKenzie, 1999), depending on the life cycle of the parasite, the concentration and type of contaminant, and the exposure time (Overstreet and Howse, 1977; Khan and Thulin, 1991; Poulin, 1992). Thus, generalizations about the relationship between parasitism and pollution cannot be made without taking into account the biology of individual species. Kennedy (1997) further highlights the intrinsic difficulties to using parasites as indicators of pollution, but concludes that they can be excellent, nonspecific, early-warning indicators of environmental change.

Because many parasites depend on predator-prey relationships for transmission, parasites are sentinels for food web interactions. One species of parasite may depend on the presence of only one or a few intermediate and paratenic hosts for transmission, however, the total parasite diversity within a host represents a diversity of life cycles that utilize numerous different organisms as hosts at some point in their life cycles (Figs. 4 and 5). Not only do parasites provide information on a host's diet, but this information is complementary, and in many ways superior, to gut content analysis (see above). Furthermore, information on a host's predators can also be derived from a host's parasites. Thus, the parasite fauna within a host population provides information about the role of the host in the food web, and the variety of predator–prey relationships in which it participates (Marcogliese and Cone, 1997a, b; Marcogliese, 2002, 2003).

Parasite life cycles evolve in tandem with the evolution of their hosts' life history traits, and have adapted to long-standing predator–prey interactions. Thus, the presence of particular parasites in a host may also tell us something about the stability of the ecosystem (George-Nascimento, 1987; Marcogliese and Cone, 1997a; Marcogliese, 2003). Moreover, parasites may actually maintain the stability and integrity of ecosystems (Brooks and Hoberg, 2001). Environmental changes resulting from global warming, for example, may disrupt synchronous population cycles of predators and their prey in aquatic habitats, interfering with parasite transmission between those organisms (Marcogliese, 2001a). The climate change-related environmental perturbations that can affect parasitism include alterations in temperature regimes, precipitation, host range, water levels and flow rates, eutrophication, stratification, extent of ice cover, acidification, oceanic circulation patterns, and UV radiation (Marcogliese, 2001a).

Parasites may be excellent, economical, early-warning indicators of changes to environmental conditions and ecosytem health (MacKenzie, 1993, 1999; Overstreet, 1993, 1997; Lafferty, 1997; Marcogliese and Cone, 1997b; Marcogliese, 2003). This concept can be expanded to changes in biodiversity by taking into account the nature of parasites, their life cycles, and transmission. Biodiversity and its measurement have been an increasing concern for research managers and conservationists. By definition, biodiversity includes not only species diversity, but the ecological complexes of which they are a part (Glowka et al., 1994). Developing appropriate indicators for biodiversity has been a difficult task. The idea that certain taxa can be used as surrogates is popular, but few indicators have proven reliable, especially across different ecosystems. Because parasites respond to environmental stressors and track food webs via their transmission processes, it is logical to extend their use to indicators of biodiversity. They have the further advantage that they belong to many distinct and unrelated taxa. Thus, there are no phylogenetic constraints such as those imposed when specific taxa are used as indicators. In addition, because they infect hosts on different trophic levels, their usage is not trophically constrained (Marcogliese and Cone, 1997b; Marcoglies, 2003).

Those organisms in the middle of the food web such as small fish may be best suited as biodiversity indicators. They tend to be more heavily infected than top piscivores, because they prey upon intermediate and paratenic hosts and thus acquire parasites that may or may not mature in them (George-Nascimento, 1987). They, in turn, are preyed upon by larger piscivores and pass on larval parasites to these organisms, where they may or may not mature. In addition, predators on small fish include not only larger fish, but other vertebrates such as birds and mammals.

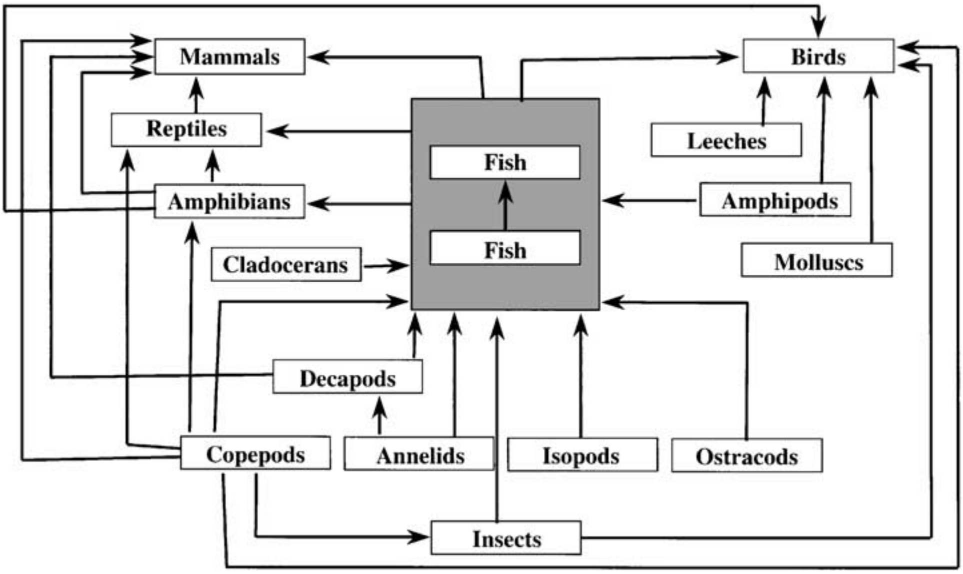

Figure 4. Potential transmission pathways involving predator–prey interactions for helminth parasites in freshwater environments. In this figure and in Figure 5, other types of parasites are not shown for simplicity's sake, nor are interactions involving free-living infective stages depicted (e.g., cestode coracidia and digenean miracidia and cercariae). For both this figure and Figure 5, specificity for the intermediate and definitive hosts within any one life cycle (and any one compartment in the diagrams) will vary with individual parasite species. Routes of trophic pathways will also vary with parasite species, with some being obligate and others facultative, depending on the nature of the host–parasite interaction. In addition, within each life cycle, parasites may follow more than one path to reach the definitive host, again depending on the specificity of the host–parasite interaction. Reprinted in adapted form from Marcogliese and Cone (1997a), copyright 1997, with permission from Elsevier Science.

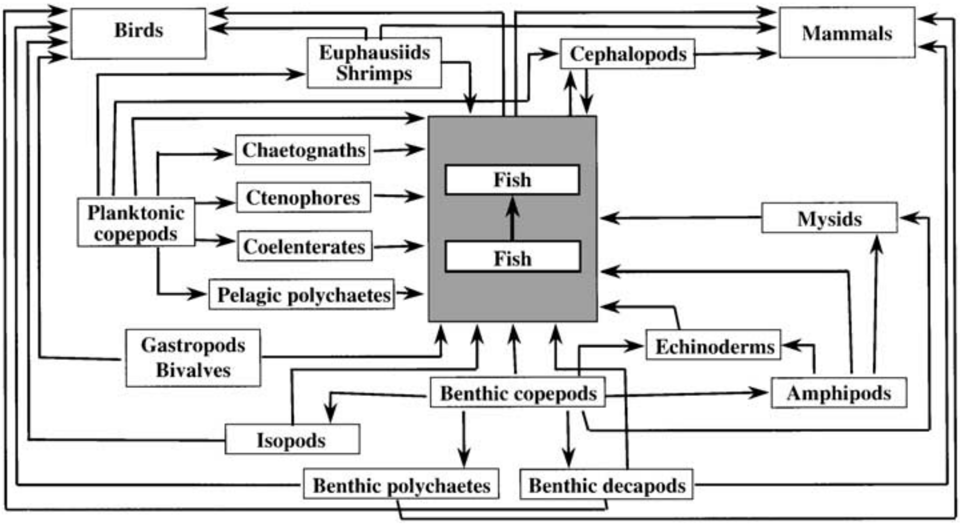

Figure 5. Potential transmission pathways involving predator–prey interactions for helminth parasites in marine environments (see Fig. 4 for details about the food web diagram). Note that the marine food web appears more complex than the freshwater web. This is a result of the presence of an additional trophic level in marine systems, that of large invertebrate predators, which play a relatively greater role in marine food chains than in freshwater food chains. Reprinted in adapted form from Marcogliese and Cone (1997a), copyright 1997, with permission from Elsevier Science.

Thus, it is possible to obtain information on food web pathways linking the aquatic and terrestrial milieux.

In summary, parasites are ubiquitous in the aquatic environment. They have impacts ranging from the subtle, to the sublethal, to the lethal. Their impacts on hosts are propagated up and down food webs and thus are manifested throughout entire communities. Like free-living organisms, they are affected by biotic and abiotic changes to the environment. Parasites are effective indicators of many aspects of host biology and thus extremely useful as management and conservation tools. Moreover, they are uniquely situated within food webs, and their transmission processes may permit their usage as indicators of environmental stress, food-web structure, and biodiversity. Indeed, far from being mere extras without speaking parts in the ecological theater, parasites may be bit players but with incredibly important roles who should step forward and take a bow as the curtain goes down on the ecosystem stage. Critics must acknowledge the significance of their wonderfully complex roles that are intricately woven into the scripts of virtually all the principal players in the theater of life.

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