

PARASITES IN MARINE FOOD WEBS

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ABSTRACT

Most species interactions probably involve parasites. This review considers the extent to which marine ecologists should consider parasites to fully understand marine communities. Parasites are influential parts of food webs in estuaries, temperate reefs, and coral reefs, but their ecological importance is seldom recognized. Though difficult to observe, parasites can have substantial biomass, and they can be just as common as free-living consumers after controlling for body mass and trophic level. Parasites have direct impacts on the energetics of their hosts and some affect host behaviors, with ecosystem-level consequences. Although they cause disease, parasites are sensitive components of ecosystems. In particular, they suffer secondary extinctions due to biodiversity loss. Some parasites can also return to a system after habitat restoration. For these reasons, parasites can make good indicators of ecosystem integrity. Fishing can indirectly increase or decrease parasite populations and the effects of climate change on parasites are likely to be equally as complex.

Food webs are ecological maps of species interactions. For instance, a recent investigation found that in an estuarine food web there were 505 feeding interactions among 87 free-living species (Lafferty et al. 2006). The addition of 47 parasites to this food web revealed a further 615 host-parasite or parasite-parasite interactions. Furthermore, there were 1093 interactions where parasites were eaten by free-living species. This accounting indicates that parasites are frequent, if not dominant aspects of species interactions in marine communities. In addition to acting as consumers or prey, parasites can alter predator-prey interactions, sometimes strongly, and with considerable consequences. Here, I review the literature to consider six questions about the importance of parasites in species interactions, using examples from marine systems.

The phrase “invisible fabric of nature” describes parasites well. They are small and often hidden within their hosts. As a result, discussion of infectious disease agents (typical parasites, pathogens, parasitic castrators, parasitoids, etc.) has traditionally been excluded from marine ecology courses. Nevertheless, close inspection of any marine species will typically reveal parasites. This raises questions about the degree to which ecologists should consider parasites. For instance, how many parasite species are there? What do they do to their hosts? How might parasites affect host populations? Are they abundant enough to affect energy flows through systems? Are parasites important parts of food webs? How do human impacts like fishing, climate change, species invasions, and habitat degradation affect the role of parasites in marine systems? In this brief review, I discuss these questions, drawing heavily on work with several colleagues in a variety of marine systems.

HOW MANY PARASITES ARE THERE?

Whether or not parasites are important for species interactions hinges, to a degree, on their contribution to marine biodiversity. Parasites are ubiquitous in examined hosts (Dobson et al. 2008). Unfortunately, few marine species have been examined for parasites.

Of the fish species listed in Fishbase (www.fishbase.org), only 12% have parasite records (Strona and Lafferty 2012) and, of these, usually just a subset of the potential parasite taxa has been considered. For instance, Cribb et al. (2002) looked closely at the parasite literature for groupers (*Epinephelinae*), one of the best studied fish groups, and found investigations of trematodes (one of the best studied parasite groups) from only 62 of the 159 grouper species and nine of the 15 grouper genera. Most sampled grouper species were studied at just a single location, leading to a substantial underestimate of trematode richness per host species.

We can make only gross estimates about the number of parasite species and our estimates are best for terrestrial vertebrates. Not counting the many protozoan, bacterial, and viral pathogen species, Poulin and Morand (2004) estimated that there are 75,000 helminth parasite species in 45,000 terrestrial vertebrate host species. Many of these parasites are not strictly host specific, so there are about nine helminth species infecting a given bird or mammal species. In food-web studies of estuarine systems, there are just as many parasite species feeding on a host as there are predators consuming that host (Lafferty et al. 2006). All this indicates that parasites are a considerable, if not overwhelming, part of biodiversity and that there are far more parasites than are currently described (Dobson et al. 2008).

When thinking about the contribution of parasites to biodiversity, it is important to consider that parasites and free-living consumers have a diversity of consumer strategies. One classification system of consumers considers factors such as their effect on the host and whether that effect is intensity dependent or intensity independent (Kuris and Lafferty 2000, Lafferty and Kuris 2002). For example, free-living predators can be divided into typical predators (e.g., trumpet fish, sharks), social predators (e.g., orcas), and micropredators (e.g., leeches). Detritivores (e.g., hagfish, sea cucumbers) are an important free-living consumer strategy in marine systems and are similar to predators that feed on dead material. The two most familiar types of parasites are typical parasites (e.g., intestinal tapeworms), which have intensity-dependent pathology, and pathogens (e.g., gill ciliates), which build up by reproducing on their host.

Other types of parasite consumer strategies are less well known. Parasitic castrators (e.g., rhizocephalan barnacles, larval trematodes) are common in aquatic systems, and reduce fecundity to zero, but do not kill their host. Parasitoids always kill their host as part of their life cycle. Parasitoids are more common in terrestrial systems, but do occur in the ocean (e.g., hyperiid amphipods in ctenophores). Several parasites use predator-prey interactions to complete their life cycles, and such trophically transmitted parasites have different relationships with their hosts than do other types of parasites, as described below.

WHAT DO PARASITES DO TO THEIR HOSTS?

The importance of species interactions can be defined as interaction strengths among species (Wootton 1994). Parasites can affect their hosts because, as consumers, parasites drain energy. From medical studies, we know that the energetic drain of some parasites can cause anemia, stunt growth, and impair learning in humans. For macroparasites (i.e., worms that do not multiply within a host), the cost to the host will be related to the number of parasites (and their size), which is a function of exposure rates and defense. For pathogens (infectious agents that multiply within their host), the cost to the host will depend on how the host caps parasite multiplication through immune defense (Lafferty and Kuris 2002).

Parasite fitness (i.e., reproductive output) is a function of consumption rate and life span. These will be in conflict if energy drain shortens the host's life span (because this also shortens the parasite's life span), leading to the classic virulence trade off. For example, parasitic castrators (e.g., parasitic rhizocephalan barnacles in crabs) deal with this trade off by maximizing their energy drain on the host while minimizing host mortality (Lafferty and Kuris 2009).

Hosts also face trade-offs with respect to parasites. In particular, defense against parasites takes resources away from other purposes. For example, the energetic cost of immune defense against bot fly parasitism can exceed the direct energetic consumption of the parasite by an order of magnitude in chipmunk hosts (Careau et al. 2010).

However, the effect of parasites is not solely energetic. Many parasites live in specific organs (hearts, brains, gills, eyes), and their targeted energy drain, though small, can impair essential organ systems. A classic example is a copepod parasite that infects the eye of flatfish (Kabata 1969). Losing an eye is far more costly to the fish than if the energy taken by the parasite was broadly distributed.

Sometimes parasites end up in the wrong hosts, where they can wander about or have maladaptive behaviors. A classic example is intestinal acanthocephalan worms that use crabs as intermediate hosts and birds as final hosts. If a sea otter eats the crab, the sea otter intestine is sufficiently different from a bird's that the parasite often bores through the intestinal wall instead of into it, leading to peritonitis and death (Thomas and Cole 1996).

ARE PARASITES SUFFICIENTLY ABUNDANT TO BE IMPORTANT?

Species abundance affects the importance of species interactions at the ecosystem level. Parasites are small compared to most predators, but are they sufficiently abundant to counter the difference? One way to consider the importance of a species at an ecosystem scale is in units of biomass density. Kuris et al. (2008) looked at the biomass density of all free-living and parasitic species in three estuaries. Parasites species combined were about 1% the biomass density of free-living animals. Although this might seem small, some parasite guilds, such as larval trematodes in snails, exceeded the biomass of birds (Kuris et al. 2008). If birds, as top predators, are important consumers in estuarine ecosystems, perhaps trematode parasites are as well.

Another way to consider the importance of species in ecosystems is to plot their abundance vs their body size. According to many studies, small-bodied species are, on average, more abundant than large-bodied species (Brown 1995). For example,

one would expect to see more silversides than groupers on a reef. Part of this is basic geometry; the total mass of a species can be divided into more small bodies or fewer larger bodies. In addition, metabolism affects the slope of the body size-abundance relationship. Small bodies have less efficient metabolism because they spend more metabolic energy per unit mass. Kleiber's Law predicts that the slope of the size-abundance relationship should scale inversely with the shallow $\frac{3}{4}$ slope that describes how metabolism changes with body mass (Brown 1995). Plotting body mass and abundance for free-living and parasitic species from three estuaries reveals that parasites are less common than expected given their body size (Hechinger et al. 2011). However, this difference can be explained by the high trophic level of parasites. After controlling for trophic level, all species, parasitic and free-living, fall on the same line with a $-\frac{3}{4}$ slope that describes the decline of abundance with body mass (Hechinger et al. 2011). In short, parasites are just as abundant as similar free-living consumers.

HOW DO PARASITES AFFECT HOST POPULATIONS?

If parasites are abundant and affect their hosts, they have the potential to affect host populations. Parasites can regulate host populations (keep the host population near an equilibrium; i.e., not extirpating it or allowing it to grow unchecked) if transmission is density dependent (Tompkins and Begon 1999). For directly transmitted parasites, host contact is expected to increase with host density. For example, bacterial epidemics in California sea urchins are more likely in situations where sea urchin populations are at high density; mortality after intense epidemics then reduces sea urchin densities (Lafferty 2004). If host population regulation occurs, it means that host-specific parasites can mediate the outcome of competition between free-living species because the parasite will disproportionately affect the numerically dominant species, leading to greater coexistence among competitors (Mordecai 2011).

Not all parasites regulate host populations. Some parasites drive host populations to low densities. For social species, like schooling fishes, transmission occurs even at low host density (Johnson et al. 2011), making classic regulation less likely. Furthermore, when parasites are generalists, regulation is less likely because the parasite can persist on other hosts when one of the hosts becomes rare. This is especially true if host species vary in the extent that they suffer from a parasite. For example, withering syndrome, a novel rickettsial pathogen, infects all California abalone, but is most pathogenic in black abalone, causing mass mortalities (Lafferty and Kuris 1993, Altstatt et al. 1996). Normally, such a pathogen would go extinct before its host (de Castro and Bolker 2005), but the pathogen is able to persist in other more tolerant abalone species, staying in the system even after black abalone disappear (Ben-Horin et al. in press).

Fortunately, parasite-induced mass mortalities are relatively rare (Lafferty et al. 2004). One hypothesis for mass mortalities, as seen in black abalone, is a lack of coevolution between host and parasite (Lafferty and Gerber 2002). We do not know the origin of the rickettsial pathogen that led to mass mortalities of black abalone in southern California, but it had not been reported previously, so it seems possible that international movements of abalone for aquaculture could have brought the pathogen from elsewhere. Other examples are better documented. Morbilliviruses have presumably crossed from dogs to seals, and this has led to mass mortalities of seals

(Bengston and Boveng 1991). A spectacular mass mortality of Australian pilchard, *Sardinops neopilchardus* (Steindachner, 1879), was linked to viruses in imported frozen pilchards fed to captive tuna (Jones et al. 1997). Despite these examples, most parasite species probably do not have detectable effects on host populations (Scott 1988).

Scales of recruitment can greatly affect host-parasite dynamics in the ocean (Kuris and Lafferty 1992, Gaines and Lafferty 1995). Most free-living marine species have broadly dispersing larval stages. On local scales, recruitment rates are not usually tied to the reproductive output of the local adult population and host populations continue to recruit even when parasitism in a population is high. Parasites also vary in how broadly their larvae disperse. Classic host population regulation, as described above, is most likely to happen on the scale where both parasite and host recruitment are closed (i.e., offspring recruit locally). Parasites will do best when their recruitment is closed and the host's recruitment is open (i.e., offspring disperse widely; because there will be a continual supply of uninfected hosts). Parasites can extirpate hosts when host recruitment is closed and parasite recruitment is frequent and open (and parasites are pathogenic). Here, other populations of the host act as reservoirs for the parasite species. When both parasites and hosts have open recruitment, the relationship between parasitism and host density is more complicated. A higher proportion of parasites will succeed at high host density, but ironically, high host density could lead to a lower prevalence of infected hosts due to an absolute limit on the number of parasite propagules. Open recruitment in marine systems means that models of infectious diseases designed for terrestrial systems might not be suitable for marine parasites (McCallum et al. 2004).

HOW DO PARASITES AFFECT FOOD WEBS?

The food web is a conceptual framework for understanding complexity in ecology. It is also a formal way to consider the architecture of species interactions. Recent studies indicate that parasites are pervasive components of food webs and greatly increase their complexity. For instance, including parasites in food webs increases species richness, connectance (a measure of complexity), and alters the distribution of natural enemies among trophic levels such that large predators, due to their tendency to have many species of parasite, are no longer the top of the food chain (Lafferty et al. 2006). Our view of food webs is certainly incomplete without parasites (Lafferty et al. 2008a).

Surprisingly, free-living stages of parasites can be important sources of food in food webs (Johnson et al. 2010). For instance, cercarial stages of trematode parasites must swim from their mollusk host into the water to search for a second-intermediate host. Here, the naked fleshy larvae become prey for fishes that normally feed on zooplankton of a similar size (Kaplan et al. 2009). Parasites must also adapt to being in food webs. A common fate for a parasite is for its host to be eaten. Many parasites die this way, but others are able to survive their host's death and transfer to the predator (Lafferty et al. 2006).

Some parasites manipulate the behavior of their intermediate hosts in ways that appear to increase predation rate (Moore 2002). The magnitude of such behavioral effects can be notable. A common trematode metacercarial stage found on the surface of the brain of killifish alters neuromodulators in ways that attenuate stress

responses (Shaw et al. 2009). This may be the mechanism driving the pattern that conspicuous behaviors are four times more frequent in infected fish than in uninfected fish (Lafferty and Morris 1996). In addition, infected killifish are 10–30 times more likely to be eaten by wild birds that are the final host for the parasite, with heavily infected fish being the most likely to be eaten (Lafferty and Morris 1996). Presumably, this increase in predation rates on fishes changes the flow of energy through the estuarine ecosystem where the fishes occur.

Parasite manipulations can have unexpected indirect effects. One of the best examples is from the mudflats of New Zealand, which are vast expanses of soft sediment, suitable mostly for burrowing invertebrates, including bivalves such as cockles. Trematodes that encyst in the foot of New Zealand cockles reduce their burrowing ability, thereby stranding infected cockles on the surface where they become easy prey for oystercatchers, which are the final host for the worms (Thomas and Poulin 1998). Cockle shells that protrude from the sediment also create a habitat for several epibionts, including anemones, chitons, barnacles, amphipods, and serpulid worms (Thomas et al. 1998). Exposed shells are also substrates for algae that support a small limpet. In the bays of New Zealand, there are few alternative natural substrates for this rich and distinctive epibiont community (Thomas et al. 1998). The trematodes, therefore, are the mechanism by which the cockles increase the available substrate for epibionts to colonize. Furthermore, by digging less, infected cockles modify properties of the sediment, which alters infaunal communities (Mouritsen and Poulin 2005). New Zealand mudflats would have less biodiversity without these manipulative parasites.

Food webs can also affect parasites. Consider again bacterial epidemics in sea urchin populations from the California Channel Islands (Behrens and Lafferty 2004, Lafferty 2004). A key source of variation in sea urchin density (the factor that drives epidemics) is the density of spiny lobsters. Lobsters prey on urchins, but lobsters are also heavily fished. As a result, fishing initiates a trophic cascade because where lobster abundances are reduced, urchin densities increase and algal densities decrease. With lobsters no longer depressing sea urchin density, the transmission of bacterial pathogens becomes more efficient. In marine reserves, where lobsters are abundant due to protection, bacterial epidemics in sea urchins are rare. Reports of disease in sea urchins around the world have increased over time, suggesting that the release of sea urchins from their predators could be a general phenomenon with broad-scale effects (Ward and Lafferty 2004).

In the Galápagos Islands, there is a similar food web to the California kelp forest. Predators like fishes and lobsters eat sea urchins, which may prevent sea urchins from over-grazing algae (Sonnenholzner et al. 2009). Two species of eulimid snails also parasitize sea urchins. However, due to an additional complexity in the Galápagos food web, fishing does not increase the abundance of these parasites the same way that it increases the frequency of bacterial epidemics in California. The web is more complex because small crabs shelter under the spines of pencil urchins to escape predation from fishes and lobsters. These crabs feed on the parasitic snails, reducing the number of snails on urchins that host crabs. Because fishing decreases the abundance of fishes and lobsters, fished sites have more crabs per urchin, which leads to a net indirect reduction in parasitism of urchins, despite the larger number of urchin hosts available to snails (Sonnenholzner et al. 2011).

Fishing on coral reefs disproportionately affects top trophic levels and simplifies food webs. Because most coral reefs are heavily fished, there are few places to study parasites in intact coral reef food webs. One exception is Palmyra Atoll, a US Fish and Wildlife refuge in the Line Islands chain of the central Pacific (part of the Pacific Remote Islands Marine National Monument), which is neither fished nor does it have an indigenous population. For this reason, the food web at Palmyra is dominated by top predators; in comparison, nearby populated coral reefs, such as Kiritimati Atoll, have intensive fishing pressure and few top predators (Sandin et al. 2008). A study of the parasites in five species of coral reef fishes found consistently higher parasite diversity at Palmyra compared to Kiritimati atolls (Lafferty et al. 2008b). In particular, larval cestodes that use sharks as final hosts are more prevalent in coral reef fishes at Palmyra Atoll due to the high density of sharks at Palmyra Atoll and their near absence at Kiritimati Atoll.

Invasive species alter marine food webs and have complex interactions with parasites. On average, every invader brings with it only 12% of its parasite species (Torchin et al. 2003). This means that invasions are more complex additions to biodiversity than generally appreciated. In the new region, invaders pick up a few more parasites, but on average, they host fewer parasite species than they did in their native range.

Leaving parasitic enemies behind is one of the oldest hypotheses for why invaders sometimes do so well in introduced locations (Elton 1958). One example is the European green crab, *Carcinus maenas* (Linnaeus, 1758), which has been introduced from Europe to South Africa, Japan, Australia, and both coasts of North America. In the introduced locations, green crabs reach larger-than-normal sizes and can obtain high densities; these populations are much less parasitized than populations in Europe, which are parasitized by rhizocephalan barnacles that castrate the crab and stunt their growth (Torchin et al. 2001). Invaders that arrive with few parasites might out-compete hosts with many parasites, leading to a net reduction in parasitism. The clearest example involves a mud snail from Japan that arrived on the west coast of the United States with only two of its several trematode parasite species. Although this invasion led to an increase in the trematode fauna for the region, on a local scale, the invading snail was able to outcompete a native snail with more than a dozen trematode species, leading to overall reductions in parasite diversity in estuaries where the invader replaced the native (Torchin et al. 2005). Invasions will continue to alter host-parasite interactions, but it is difficult to predict if invasions will lead to net increases or decreases in parasitism.

WHAT DO PARASITES INDICATE ABOUT THE ENVIRONMENT?

Although we might expect a healthy and robust ecosystem to have few infectious diseases, an argument exists for the opposite association. For instance, environmental stressors that increase host susceptibility can also increase parasite mortality and reduce host abundance, leading to net decreases in parasite transmission (Lafferty and Holt 2003). Furthermore, host depletion due to fishing or habitat degradation reduces the transmission efficiency of parasites that have density-dependent transmission (Wood et al. 2010). Parasites, particularly those with complex life cycles (Rudolf and Lafferty 2011), require a diversity of hosts to be present (Lafferty 1997). Therefore, as hosts are extirpated from a system, host-specific parasites will likely fail to find alternative hosts, at least on ecological time scales, and go extinct. In

degraded systems, we should expect to find mostly generalist parasites, parasites on hosts that somehow increase in abundance in response to degradation, and opportunistic parasites that take advantage of weakened immune systems. Most other parasite species will probably be lost.

The popular literature on climate change has implicated that parasites will thrive as the globe warms, but this is a vast over simplification that helps sound the alarm about climate change more than it helps reveal what will happen with parasites. Parasites, like all ectotherms, are sensitive to their thermal environment and have a temperature range where they do best. This means that warming in the oceans will shift the distributions of species, including parasites, generally toward higher latitudes (Lafferty 2009). However, a shift implies that regions that currently support a parasite could become too warm for the parasite to persist. Or, indirectly, parasite transmission will collapse if warming disrupts communities of free-living species that parasites depend on to complete their life cycles (Lafferty 2012).

Parasites should also respond to habitat degradation and restoration. For example, in southern California estuaries, there are fewer species of trematodes parasitizing snails at degraded sites than in an adjacent nature reserve (Huspeni and Lafferty 2004). These trematodes use birds as final hosts and their diversity and abundance is driven directly by the diversity and abundance of birds at a site (Hechinger and Lafferty 2005). Restoration of degraded sites creates more food and habitat for birds so that, after a few years, trematode diversity returns to normal (Huspeni and Lafferty 2004). Similar effects can be seen when hurricanes eliminate trematodes, but the parasite community recovers gradually (Aguirre-Macedo et al. 2011). For these reasons, some parasites can be counterintuitive indicators of healthy ecosystems (Huspeni et al. 2005). For example, marine mammal recoveries in the last century have been spectacular, particularly for pinnipeds. This might explain why we have seen a significant increase in reports of infectious diseases in this group (Ward and Lafferty 2004).

CONCLUSION

Parasitism is a type of species interaction that should not be ignored when studying marine communities or fisheries. Parasites are normal components of the complexity of nature. They are both a common and potentially important type of species interaction and they also affect interactions among species. From the perspective of a host individual, parasites range from an annoyance to a significant cause of disease and death. Parasites can affect host populations through energy drain, reproductive loss, or mortality, and if they have density-dependent transmission, they can regulate host populations. At the ecosystem level, parasites may be important. Parasites are integrated into food webs both as consumers and prey. They are subject to top-down and bottom-up effects, and can have indirect effects via trophic cascades. Those parasites that use the food web in their life cycles can manipulate prey behavior, with indirect consequences for ecosystems. Parasites, due to their strict dependency on hosts, are sensitive members of communities. They are likely to disappear before their hosts and therefore can make good indicators of ecosystem complexity, decreasing with degradation. Due to their ubiquity in marine systems, we can expect them to influence and be influenced by fisheries.

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DATE SUBMITTED: 17 November, 2011.

DATE ACCEPTED: 15 November, 2012.

AVAILABLE ONLINE: 20 December, 2012.

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