

Ecosystem consequences of fish parasites*

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In most aquatic ecosystems, fishes are hosts to parasites and, sometimes, these parasites can affect fish biology. Some of the most dramatic cases occur when fishes are intermediate hosts for larval parasites. For example, fishes in southern California estuaries are host to many parasites. The most common of these parasites, *Euhaplorchis californiensis*, infects the brain of the killifish *Fundulus parvipinnis* and alters its behaviour, making the fish 10–30 times more susceptible to predation by the birds that serve as its definitive host. Parasites like *E. californiensis* are embedded in food webs because they require trophic transmission. In the Carpinteria Salt Marsh estuarine food web, parasites dominate the links and comprise substantial amount of biomass. Adding parasites to food webs alters important network statistics such as connectance and nestedness. Furthermore, some free-living stages of parasites are food items for free-living species. For instance, fishes feed on trematode cercariae. Being embedded in food webs makes parasites sensitive to changes in the environment. In particular, fishing and environmental disturbance, by reducing fish populations, may reduce parasite populations. Indirect evidence suggests a decrease in parasites in commercially fished species over the past three decades. In addition, environmental degradation can affect fish parasites. For these reasons, parasites in fishes may serve as indicators of environmental impacts.

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This paper considers the extent that parasites of fishes can alter the ecological systems in which they occur. In addition, changes to ecosystems can alter parasitism. In some cases, fishing and other forms of environmental degradation will have a disproportionate effect on parasite diversity. This makes parasites of fishes a potentially valuable indicator of ecological impacts.

ECOSYSTEM EFFECTS OF PARASITES IN ESTUARIES

Most of the estuarine fishes in southern California estuaries (Table I) occur primarily in the intertidal channels that dissect salt marsh habitat. These fishes may hold a key to understanding the role of parasites in ecosystems. A good

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TABLE I. Predator and parasite diversity of common fishes in Carpinteria Salt Marsh (Lafferty *et al.*, 2006a). Trophic level (*e.g.* herbivorous species = 1, top predators = 6) is the maximum trophic level calculated (one level above the highest-level prey item). Predator richness is the number of species known to prey on a particular fish species. Parasite richness is the number of parasite species known to parasitize a particular fish species. Parasitic enemies represent the percentage of parasitic species out of the total number of natural enemies

Taxon	Common name	Trophic level	Predator richness	Parasite richness	Parasitic enemies (%)
<i>Atherinops affinis</i>	Topsmelt	1	17	11	39
<i>Mugil cephalus</i>	Striped mullet	1	4	10	71
<i>Clevelandia ios</i>	Arrow goby	2	19	9	32
<i>Fundulus parvipinnis</i>	California killifish	3	19	14	42
<i>Leptocottus armatus</i>	Staghorn sculpin	5	8	8	50
<i>Gillichthys mirabilis</i>	Long-jaw mudsucker	5	8	13	62
<i>Urolophus halleri</i>	Round stingray	5	0	4	100
<i>Triakis semifasciata</i>	Leopard shark	6	0	6	100
Mean		3.5	9.4	9.4	50

example is the most common parasite in the most common fish species. *Euhaplorchis californiensis* is a small trematode that lives in the intestine of several species of birds as a short-lived adult. The snail *Cerithidea californica* ingests the worm's eggs. After developing in the snail, the parasite produces and releases cercariae, which search for the next host in the life cycle, the common California killifish *Fundulus parvipinnis* Girard. For the worm to complete its life cycle, a bird, such as a heron or tern must eat the infected fish. In Carpinteria Salt Marsh, most *F. parvipinnis* ($\geq 95\%$) are infected with *E. californiensis* (Shaw, 2007) and, on average, an infected female fish contains 1700 cysts while infected male fish have 1200 cysts. The parasite cysts represent between 0.5 and 1.7% of the fish biomass in an estuary. There is evidence to suggest that the parasites do not passively wait for a bird to eat their host. Instead of encysting anywhere, the cercariae migrate along blood vessels or nerve tracts to the brain (McNeff, 1978). Inside the cranium, the metacercariae encyst on the pial surface. The sight of an apparently healthy fish with 1000s of parasite cysts coating its brain is both paradoxical and troubling.

The site of infection makes *E. californiensis* an obvious candidate for being able to manipulate host behaviour. In particular, the metacercariae might manipulate *F. parvipinnis* behaviour to make them easier for birds to catch. To investigate this, fish were captured from two locations, one where infection was common, and another where infection was absent (due to a lack of snails) (Lafferty & Morris, 1996). There were no obvious differences in physical health between the fish from the two populations. After acclimating to an aquarium, fish schooled normally, but would sometimes dart to the surface, spasm, roll on their sides or bend sharply. After categorizing the conspicuous behaviour, an individual fish was watched for 30 min, noting the conspicuous behaviour it exhibited. The fish was then netted and dissected to count the parasites. Infected

fish displayed a four-fold higher frequency of conspicuous behaviour compared to uninfected fish. The frequency of conspicuous behaviour in an infected fish increased linearly with the number of cysts on the brain, strongly suggesting that the parasite altered the behaviour of the fish (Lafferty & Morris, 1996).

It appears that *E. californiensis*, by settling on the brain, has the potential to steer its fish host towards a bird. But how does it steer? Recent research has investigated the mechanism by which *E. californiensis* alters *F. parvipinnis* behaviour (Shaw, 2007). In normal fishes, stress (being chased by a net) leads to physiological changes, including an increase in serotonergic activity in brain stem nuclei. Shaw (2007) found that infected fishes showed a suppressed stress response. Relaxing a fish in the face of danger may be a sophisticated adaptation by the trematodes to increase transmission to birds. It is unclear whether a reduced stress response relates to the observed conspicuous behaviour, or whether it is an independent behavioural change. Another difference Shaw (2007) observed in the brains of infected fishes could underlie conspicuous behaviour. Infected fishes had higher hypothalamic dopamine, which suppresses gonadotropin-releasing hormone. The resultant rise in sex hormones probably leads to spawning behaviour that might put fishes at risk to predation.

The manipulation of *F. parvipinnis* by *E. californiensis* is one of several fascinating stories about how parasites can manipulate host behaviour in ways that could make the host more susceptible to predation, thereby increasing the transmission of the parasite (Moore, 2002). Surprisingly little information exists to support the contention that behavioural manipulations increase predation in nature. A field experiment helped evaluate this possibility (Lafferty & Morris, 1996). Infected and uninfected fish were penned in a local lagoon. One pen was protected by plastic mesh to prevent birds from foraging. After a couple weeks of watching egrets and herons hunting fish in the open pen, the remaining fish were compared. Few infected fish, and very few heavily infected fish, survived in the open pen, whereas birds ate almost none of the uninfected fish. Comparing what was left in the two pens indicated that birds were 10–30 times more likely to eat infected fish than uninfected fish. The trematode, presumably by altering the neurochemistry of the *F. parvipinnis*, was able to influence its transmission.

Does parasite-increased trophic transmission have broader implications for fish population dynamics? Several mathematical models suggest parasites that alter the behaviour of their intermediate hosts can reduce the abundance of these hosts and this may result in a net benefit for definitive host populations (for which prey capture is made easy) (Dobson, 1988; Freedman, 1990; Lafferty, 1992; Fenton & Rands, 2006). Parasites, by strengthening predator–prey links, could be the glue that holds food webs together.

Although *E. californiensis* is the most abundant trematode in southern California estuaries, it is not the only parasite of fishes that uses birds as a final host (Table II). There are at least eight other trematodes that use fishes as second intermediate hosts, and all may be under a similar selective pressure to increase the chance that a bird eats a fish. A larval cestode that uses elasmobranchs as a definitive host also uses fishes as an intermediate host. Fishes serve as definitive host to three species of adult nematodes and one species of adult trematode. In addition, a leech, copepods and a monogenean occur

TABLE II. Distribution of fish parasite diversity by parasite taxon and life stage in Carpinteria Salt Marsh. One cestode species occurs twice (once as a larva in fishes and once as an adult in elasmobranchs). These data are probably underestimates of the true parasite richness in this system. For instance, protozoans are grossly understudied and viruses not studied at all in this system. Details on parasite species are in Lafferty *et al.* (2006a)

Taxon	Stage	Richness
Ciliate	Adult	1
Monogenean	Adult	1
Trematode	Adult	1
Trematode	Larval	9
Cestode	Adult	3
Cestode	Larval	2
Nematode	Adult	3
Leech	Adult	1
Copepod	Adult	2

on the skin and gills. Table II is an abbreviated list of the parasite community. It concerns only the most common parasites in the most common fishes, and the full range of diversity for several taxa, particularly the ectoparasites has not yet been quantified. Future work could triple this list of parasite species. Understanding how parasites manipulate their hosts and how this affects the estuarine ecosystem will take years.

One way to consider the broader role of parasites in this system is to look at their effect on food-web topology. Topology (the pattern of how nodes in a network are linked together) is a measure of the structure of a network. Of particular interest to ecologists is the extent to which species in food webs are interconnected (connectance) and how this changes with the diversity of species in a web; a question of considerable debate is how connectance and diversity affect food-web stability (Dunne *et al.*, 2002).

Historically, ecologists did not include parasites in food webs (Marcogliese & Cone, 1997). There are several reasons for this. Parasites are small, difficult to study and little studied compared to free-living predators (Lafferty *et al.*, 2008). Parasites, however, contribute a substantial component to biodiversity (Hudson *et al.*, 2006). Some estimates suggest that parasitism is the most frequent mode of life among animal taxa (Toft, 1986). Enough information has been accumulated on parasites and free-living species in estuaries to enable the construction of a food web with parasites for the Carpinteria Salt Marsh estuary (Lafferty *et al.*, 2006a).

An unexpected role for parasites in the food web was that they are often prey. Predators eat parasites every time they ingest infected prey (and most prey individuals are infected with at least one parasite species) or they may eat edible free-living stages of parasites. Kaplan *et al.* (in press) offered newly emerged free-swimming cercariae to several fishes in aquaria. They also captured wild fishes with cercariae in their gut. So long as the fishes were small (independent of species) and the species of cercaria was large, the fishes readily

engorged on them. This suggested that small fishes might serve as a source of mortality for cercariae and that cercariae might serve as a source of food for fishes. The cercariae shed from snails amount to 10–43 kg ha⁻¹ each year (Kuris *et al.*, 2008). Predation on cercariae alters the flow of energy through the estuary because primary productivity that would normally support snail growth and production of snail eggs (which may be eaten by crabs) instead leads to the production of cercariae available to zooplankton feeders. At least one trematode has taken advantage of the willingness of fishes to eat cercariae. *Renicola buchani* produces pink, fleshy cercariae. As individuals, the cercariae might not attract the attention of foraging fishes, so they cluster by linking their tails together in large groups called 'rat kings'. All fishes presented with rat kings feed until satiated. After ingestion, some cercariae escape from the intestine and migrate to the host's liver where they encyst as metacercariae (Martin, 1971). It is unknown if the nutritional gain obtained from the tails makes up for the cost of parasitism in a fish.

Comparing the topological properties of food webs, such as connectance, chain length and nestedness in the Carpinteria Salt Marsh food web before and after adding parasites shows parasites have dramatic effects on web topology (Lafferty *et al.*, 2006b). Hernandez & Sukhdeo (2008) also noted effects of parasites on connectance and nestedness in a pine-barrens food web and considered the extent to which this affects food-web stability. Parasites are involved in most links in the web, particularly those involving fishes. Fishes have, on average, as many species of parasites as they do predators (Table I). The ratio of parasites to predators tends to increase with trophic level, primarily because upper trophic levels (sharks and rays) have few predators but many species of parasites (Table I). This distribution of 'vulnerability' to natural enemies among trophic levels implies that top predators are not invulnerable. The consequences of these effects on community dynamics are not yet clear, but the data strongly suggest that, without parasites, no food web effectively represents the trophic dynamics of a system.

Although the estuarine food web indicates many parasites of many different species connected to many hosts, each parasite is small; perhaps, in total, parasites do not matter much to the energy flow within an ecosystem. To assess the importance of parasites on energy flow-through ecosystems, other measures are needed. For instance, one measure of the importance of fishes in estuarine ecosystems is their standing-stock biomass, and sampling indicates that the range in fish biomass is 17.8–32.1 kg ha⁻¹ (which includes the relatively large area of vegetated marsh where fishes are rare). How does the biomass of parasites, as a group, compare to the biomass of free-living groups like fishes? What proportion of the fish community is parasite tissue? Kuris *et al.* (2008) set out to count and weigh every free-living and parasitic animal and plant in three estuarine systems. The biomass range of all parasites was 6.4–11.6 kg ha⁻¹. These values suggest that, as a group, parasites (cumulative value for all animal hosts) have one-third the standing-stock biomass of the fish community. When computed as a percentage of the free-living species, parasites comprised 0.2–1.3% of all animal biomass. In fishes, parasites comprised 0.74–1.56% of the biomass. More impressive is that the total biomass of parasites was equivalent to 3.2–13.2% the biomass of other secondary consumers. Calculating this previously

unseen parasite biomass provides the first step towards understanding their role in the energetics of ecosystems.

ENVIRONMENTAL EFFECTS ON PARASITES

Because the fishes in local estuaries are too small to support fisheries, there is little public concern over their parasites. Nevertheless, there are plenty of parasites in commercial fish species. For instance, in recent history, parasites like 'sealworm' devalued the market price of *Gadus morhua* L. and other fishes. In Canada, seal culling was seen as a means of increasing *G. morhua* stocks and reducing the intensity of worm infections (McClelland, 2002). Mathematical models also indicate that intensive fishing should reduce parasitism in general (Des Clers & Wootten, 1990). Fishing has substantially reduced the abundance of many species (Jackson *et al.*, 2001; Myers & Worm, 2003). If a fished stock falls below the host density threshold for transmission, a fishery can fish out parasites (Dobson & May, 1987). For instance, experimental fishing substantially reduced the prevalence of a whitefish *Coregonus lavaretus* (L.) tapeworm (Amundsen & Kristoffersen, 1990), apparently extirpated a swim-bladder nematode from native lake trout *Salvelinus namaycush* (Walbaum) in the Great Lakes (Black, 1983), and dramatically reduced the prevalence of bucephalid trematodes in scallops (Sanders, 1966). Fishing out a parasite is most likely when the parasite has a recruitment system that is relatively closed compared with the recruitment of its host (Kuris & Lafferty, 1992).

Ward & Lafferty (2004) used reports of disease in fishes subject to commercial fisheries as a proxy for trends in infectious diseases in fishes and other marine species over the last three decades. Although the number of papers published on infectious diseases in fishes has increased steadily over time, this increase was a consequence of the overall growth of the scientific literature. To account for the overall increase in publication rates, reports of disease were normalized as a proportion of all reports on fishes (*i.e.* reports on disease of fishes divided by all papers about fishes). The normalized reports of disease decreased strongly in fishes (but not in some other marine taxa like corals, mammals and sea turtles). This decline suggests that exploitation has reduced diseases in fishes by making transmission more difficult (or that studying parasites of fishes, but not other marine taxa, has become relatively unfashionable among fisheries biologists; indeed, global funding for such studies declined in the 1990s). In contrast, aquaculture intentionally increases species densities, which should favour diseases such as sea lice (aquaculture species were excluded from the previous analysis). Although a decline in fish parasites might be a benefit of fishing, it may also indicate that fish stocks are in trouble (Marcogliese, 2002). A counter-intuitive negative association between parasitism and the 'health' of a fish stock suggests that parasites might be sensitive indicators of the status of a fishery.

Fishing can affect the structure of entire food webs and this may indirectly affect parasite communities. Coral atolls in the central Pacific vary strikingly in their food-web structure. Kiritimati Island has a large human population that heavily fishes the reef. Consequently, most of the large, top predators, *e.g.* sharks (Elasmobranchii) and jacks (Carangidae) are now rare. In comparison,

at Palmyra Atoll, there is no fishing pressure (there is no resident population), and large predators are strikingly abundant (Stevenson *et al.*, 2007; Sandin *et al.*, 2008). A comparison of parasites in five species of reef fishes from both sites suggests that the more complex food web at Palmyra Atoll has a richer parasite community (Lafferty *et al.*, in press). These results support the hypothesis that complex ecological networks can support more diverse parasite communities (Hudson *et al.*, 2006).

Like fishing, pollution is a stress that can affect the food web, indirectly altering parasite communities. Eutrophication and thermal effluent often raise rates of parasitism in aquatic systems. This is because the associated increased productivity can increase the abundance of intermediate hosts (Kennedy & Watt, 1994). Parasites that increase under eutrophic conditions tend to be host generalists with local recruitment; cestodes with short life cycles and trematodes seem to be particularly favoured (Marcogliese, 2001). The most dramatic examples include parasites whose intermediate hosts favour enriched habitats. Valtonen *et al.* (1997) found that eutrophication correlates positively with greater overall parasite species richness in two fish species. However, at high nutrient inputs, toxic effects may occur and parasitism may decline (Overstreet & Howse, 1977). Therefore, the association between eutrophication and pollution is not likely to be linear. The influence of pollutant stressors must be analysed in the context of natural history. Esch (1971) recognized that as invertebrate and fish abundance increases in response to eutrophication, birds and mammals increasingly feed at enriched sites. Hence, snails and fishes acquire increasing numbers of larval parasites that will be trophically transmitted to non-piscine top predators.

Other types of pollution affect the food web in ways that decrease parasitism. Parasites of fishes are generally negatively associated with toxic pollutants (Lafferty, 1997). In a recent example, parasites in Pacific sanddabs *Citharichthys sordidus* (Girard) are less abundant near municipal outfalls, presumably because contaminants alter the invertebrate community in a way that reduces the parasites that *C. sordidus* are exposed to when feeding (Hogue & Swig, 2007). Similarly, acid precipitation associated with air pollution can negatively affect parasites in waters with poor buffering capacity. Marcogliese & Cone (1996) found that yellow eels *Anguilla rostrata* (Lesueur) from Nova Scotia have an average of four parasite species at buffered sites, c. 2.5 parasite species at moderately acidified sites, and two parasite species at acidified sites. This decline in parasite richness with acidity is due to drops in the prevalence of monogeneans and digeneans. The latter require molluscs as intermediate hosts that cannot survive in acidified conditions. Some parasites, like ciliates and acanthocephalans, however, can perform better in acidic water (Halmetoja *et al.*, 2000).

Parasites may suffer directly from toxins in polluted water (MacKenzie *et al.*, 1995), and some toxins may even preferentially concentrate in parasite tissues (Sures *et al.*, 1997). Other parasites may benefit from toxins that suppress the host's immune system. Perhaps parasitic gill ciliates and monogeneans of fishes (Khan & Thulin, 1991) provide the best case for a link between toxic pollution and an increase in infectious disease. Intensities and prevalences of ciliates increase with a wide range of pollutants, presumably because toxins impair

mucous production, a fish's main defence against gill parasites (Khan, 1990). Overall, however, most parasites appear sensitive to toxic chemicals (Lafferty, 1997).

A relationship between fish parasites and pollution suggests that fish parasites could be used as environmental indicators (Lafferty, 1997; Sures, 2004). Parasites may do an even better job at reflecting the diversity of free-living species. Trematodes in snails correlate strongly with the community of birds at a site, presumably because birds directly transmit trematode eggs that infect the snail population; though establishing such a pattern requires repeated sampling to map the bird community (Hechinger & Lafferty, 2005). Trematodes may also indicate the distribution of other types of organisms. For instance, trematode diversity and prevalence in snails correlates with macro-invertebrate diversity and abundance (Hechinger *et al.*, 2007). This may result from birds being attracted to areas with diverse invertebrate prey communities (particularly if the invertebrates present also serve as intermediate hosts for trematodes). By this same reasoning, trematodes in snails might indicate aspects of the fish community. Associations between the fish community and trematodes in snails are apparent at large spatial scales, but at finer spatial scales (*e.g.* 10 m, where associations occur with the invertebrate community), the mobility of fishes makes it relatively difficult to establish fine-scale patterns without substantial sampling effort (Hechinger *et al.*, 2007). At very broad scales, historical events (recent glaciations) or geography (isolation in space) can lead to depauperate parasite communities in pristine aquatic systems (Kennedy, 1993). Controlling for such effects is important in interpreting the association between parasites in fishes and environmental health.

CONCLUSION

Studies of estuarine fishes indicate that common parasites can alter fish behaviour in profound ways, and that this increases predation rates on fishes by birds. Parasites also clearly affect food webs, both as parasites of fishes and food for fishes. Their diversity and abundance is high and their cumulative biomass suggests a role in ecosystem energetics that sometimes rivals fishes. These results all suggest that parasites affect fishes at the community and ecosystem level. Parasites are also dependant on the host communities that they live in and fish communities drive aspects of parasite communities. Because parasites may be sensitive to intensive fishing and pollution, their abundance may decline over time. For these reasons, parasites in fishes may be useful indicators of fish health and aquatic health in general.

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References

- Amundsen, P. A. & Kristoffersen, R. (1990). Infection of whitefish (*Coregonus lavaretus* L. s.l.) by *Triaenophorus crassus* Forel (Cestoda: Pseudophyllidea): a case study in parasite control. *Canadian Journal of Zoology* **68**, 1187–1192.
- Black, G. A. (1983). Taxonomy of a swimbladder nematode, *Cystidicola stigmatura* (Leidy), and evidence of its decline in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 643–647.
- Des Clers, S. & Wootten, R. (1990). Modelling the population dynamics of the sealworm *Pseudoterranova decipiens*. *Netherlands Journal of Sea Research* **25**, 291–299.
- Dobson, A. P. (1988). The population biology of parasite-induced changes in host behavior. *Quarterly Review of Biology* **63**, 139–165.
- Dobson, A. P. & May, R. M. (1987). The effects of parasites on fish populations – theoretical aspects. *International Journal of Parasitology* **17**, 363–370.
- Dunne, J. A., Williams, R. J. & Martinez, N. D. (2002). Food-web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America* **99**, 12917–12922.
- Esch, G. W. (1971). Impact of ecological succession on the parasite fauna in centrarchids from oligotrophic and eutrophic ecosystems. *American Midland Naturalist* **86**, 160–168.
- Fenton, A. & Rands, S. A. (2006). The impact of parasite manipulation and predator foraging behavior on predator-prey communities. *Ecology* **87**, 2832–2841.
- Freedman, H. I. (1990). A model of predator-prey dynamics as modified by the action of a parasite. *Mathematical Biosciences* **99**, 143–155.
- Halmetoja, A., Valtonen, E. T. & Koskenniemi, E. (2000). Perch (*Perca fluviatilis* L.) parasites reflect ecosystem conditions: a comparison of a natural lake and two acidic reservoirs in Finland. *International Journal for Parasitology* **30**, 1437–1444.
- Hechinger, R. F. & Lafferty, K. D. (2005). Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. *Proceedings of the Royal Society of London B* **272**, 1059–1066.
- Hechinger, R. F., Lafferty, K. D., Huspeni, T. C., Brooks, A. & Kuris, A. M. (2007). Can parasites be indicators of free-living diversity? Relationships between species richness and the abundance of larval trematodes and of local fishes and benthos. *Oecologia* **151**, 82–92.
- Hernandez, A. & Sukhdeo, M. (2008). Parasites alter the topology of a stream food web across seasons. *Oecologia* **156**, 613–624.
- Hogue, C. & Swig, B. (2007). Habitat quality and endoparasitism in the Pacific sanddab *Citharichthys sordidus* from Santa Monica Bay, southern California. *Journal of Fish Biology* **70**, 231–242.
- Hudson, P. J., Dobson, A. P. & Lafferty, K. D. (2006). Parasites and ecological systems: is a healthy system one with many parasites? *Trends in Ecology & Evolution* **21**, 381–385.
- Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. & Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–638.
- Kaplan, A. T., Halling, S. E., Lafferty, K. D. & Kuris, A. (in press). Small estuarine fishes feed on large trematode cercariae: lab and field observations. *Journal of Parasitology*.

- Kennedy, C. R. (1993). Introductions spread and colonization of new localities by fish helminth and crustacean parasites in the British Isles: a perspective and appraisal. *Journal of Fish Biology* **43**, 287–301.
- Kennedy, C. R. & Watt, R. J. (1994). The decline and natural recovery of an unmanaged coarse fishery in relation to changes in land use and attendant eutrophication. In *Rehabilitation of Freshwater Fisheries* (Cowx, I. G., ed.), pp. 366–375. Oxford: Blackwell Scientific.
- Khan, R. A. (1990). Parasitism in marine fish after chronic exposure to petroleum hydrocarbons in the laboratory and to the Exxon Valdez oil spill. *Bulletin of Environmental Contamination and Toxicology* **44**, 759–763.
- Khan, R. A. & Thulin, J. (1991). Influence of pollution on parasites of aquatic animals. *Advances in Parasitology* **30**, 201–238.
- Kuris, A. M. & Lafferty, K. D. (1992). Modelling crustacean fisheries: effects of parasites on management strategies. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 327–336.
- Kuris, A. M., Hechinger, R. F., Shaw, J. C., Whitney, K., Aguirre-Macedo, L., Boch, C., Dobson, A., Dunham, E. J., Fredensborg, B. L., Huspeni, T. C., Lorda, J., Mababa, L., Mancini, F., Mora, A., Pickering, M., Talhouk, N., Torchin, M. E. & Lafferty, K. D. (2008). Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* **454**, 367–550.
- Lafferty, K. D. (1992). Foraging on prey that are modified by parasites. *American Naturalist* **140**, 854–867.
- Lafferty, K. D. (1997). Environmental parasitology: what can parasites tell us about human impacts on the environment? *Parasitology Today* **13**, 251–255.
- Lafferty, K. D. & Morris, A. K. (1996). Altered behavior of parasitized killifish increases susceptibility to predation by bird final hosts. *Ecology* **77**, 1390–1397.
- Lafferty, K. D., Hechinger, R. F., Shaw, J. C., Whitney, K. L. & Kuris, A. M. (2006a). Food webs and parasites in a salt marsh ecosystem. In *Disease Ecology: Community Structure and Pathogen Dynamics* (Collinge, S. & Ray, C., eds), pp. 119–134. Oxford: Oxford University Press.
- Lafferty, K. D., Dobson, A. P. & Kuris, A. M. (2006b). Parasites dominate food web links. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 11211–11216.
- Lafferty, K. D., Allesina, S., Arim, M., Briggs, C. J., DeLeo, G., Dobson, A. P., Dunne, J. A., Johnson, P. T., Kuris, A. M., Marcogliese, D. J., Martinez, N. D., Memmott, J., Marquet, P. A., McLaughlin, J. P., Mordecai, E. A., Pascual, M., Poulin, R. & Thielges, D. W. (2008). Parasites in food webs: the ultimate missing links. *Ecology Letters* **11**, 533–546.
- Lafferty, K. D., Shaw, J. C. & Kuris, A. M. (in press). Reef fishes have higher parasite richness at unfished Palmyra Atoll compared to fished Kiritami Island. *Ecohealth* (in press).
- MacKenzie, K., Williams, H. H., Williams, B., McVicar, A. H. & Siddall, R. (1995). Parasites as indicators of water quality and the potential use of helminth transmission in marine pollution studies. *Advances in Parasitology* **35**, 85–144.
- Marcogliese, D. J. (2001). Implications of climate change for parasitism of animals in the aquatic environment. *Canadian Journal of Zoology* **79**, 1331–1352.
- Marcogliese, D. J. (2002). Food webs and the transmission of parasites to marine fish. *Parasitology* **124**, S83–S99.
- Marcogliese, D. J. & Cone, D. K. (1996). On the distribution and abundance of eel parasites in Nova Scotia: influence of pH. *Journal of Parasitology* **82**, 389–399.
- Marcogliese, D. J. & Cone, D. K. (1997). Food webs: a plea for parasites. *Trends in Ecology & Evolution* **12**, 320–325.
- Martin, W. E. (1971). Larval stages of renicolid trematodes. *Transactions of the American Microscopical Society* **90**, 188–194.
- McClelland, G. (2002). The trouble with sealworms (*Pseudoterranova decipiens* species complex, Nematoda): a review. *Parasitology* **124**, S183–S203.

- McNeff, L. L. (1978). Marine cercariae from *Cerithidea pliculosa* Menke from Dauphin Island, Alabama; life cycles of heterophyid and opisthorchiid digenea from *Cerithidea Swainson* from the Eastern Gulf of Mexico. Master's Thesis, University of Alabama, Mobile, AL, USA.
- Moore, J. (2002). *Parasites and the Behavior of Animals*. Oxford: Oxford University Press.
- Myers, R. A. & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature* **423**, 280–283.
- Overstreet, R. M. & Howse, H. D. (1977). Some parasites and diseases of estuarine fishes in polluted habitats of Mississippi. *Annals of the New York Academy of Sciences* **298**, 427–462.
- Sanders, M. J. (1966). Parasitic castration of scallop *Pecten alba* (Tate) by a bucephalid trematode. *Nature* **212**, 307.
- Sandin, S. A., Smith, J. E., DeMartini, E. E., Dinsdale, E. A., Donner, S. D., Friedlander, A. M., Konotchick, T., Malay, M., Maragos, J. E., Obura, D., Pantos, O., Paulay, G., Richie, M., Rohwer, F., Schroeder, R. E., Walsh, S., Jackson, J. B. C., Knowlton, N. & Sala, E. (2008). Baselines and degradation of coral reefs in the northern Line Islands. *Public Library of Science One* **3**, e1548.
- Shaw, J. C. (2007). Neural mechanisms of behavior modification in killifish (*Fundulus parvipinnis*) by a brain parasite (*Euhaplorchis californiensis*) and the ecology of the host-parasite relationship. PhD Dissertation, University of Santa Barbara, CA, USA.
- Stevenson, C., Katz, L. S., Micheli, F., Block, B., Heiman, K. W., Perle, C., Weng, K., Dunbar, R. & Witting, J. (2007). High apex predator biomass on remote Pacific islands. *Coral Reefs* **26**, 47–51.
- Sures, B. (2004). Environmental parasitology: relevancy of parasites in monitoring environmental pollution. *Trends in Parasitology* **20**, 170–177.
- Sures, B., Taraschewski, H. & Rydlo, M. (1997). Intestinal fish parasites as heavy metal bioindicators: a comparison between *Acanthocephalus lucii* (Palaeacanthocephala) and the zebra mussel, *Dreissena polymorpha*. *Bulletin of Environmental Contamination and Toxicology* **59**, 14–21.
- Toft, C. A. (1986). Communities of parasites with parasitic life-styles. In *Community Ecology* (Diamond, J. M. & Case, T. J., eds), pp. 445–463. New York, NY: Harper and Row.
- Valtonen, E. T., Holmes, J. C. & Koskivaara, M. (1997). Eutrophication, pollution and fragmentation: effects on parasite communities in roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) in four lakes in central Finland. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 572–585.
- Ward, J. R. & Lafferty, K. D. (2004). The elusive baseline of marine disease: are diseases in ocean ecosystems increasing? *Public Library of Science Biology* **2**, 542–547.