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Environmental Stress and Colonization Time as Predictors of the Susceptibility of Fish Communities to Introduced Parasites

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The introduction of non-indigenous fish has been a worldwide phenomenon for over a thousand years,[1] but scientific interest in its consequences and utility is relatively recent.[2] Despite the important benefits which introductions may have, it is now widely accepted that they can also bring about significant alterations in aquatic community structure at all trophic levels. The most obvious changes may be in the fish fauna itself, where exotics act as new sources of predation, food, or competition. However, recent attention has also been focused on the concomitant introduction of parasites and its associated problems.[3-7] One of the most interesting and innovative approaches to this issue is the analysis of helminth communities in terms of richness[8-10] and saturation.[10] This research indicates that exotic parasites may have fewer immediate consequences on the systems to which they are introduced than might be expected, primarily due to high pre-introduction degrees of parasite community saturation and the resultant scarcity of suitable niches available to new arrivals. However, it also appears to be difficult for indigenous parasites to colonize exotic fish, perhaps due to parasite-host coevolution.

With the rapidity and reliability of modern air transportation, live fish may now be transported worldwide in several days. Most of these fish supply the pet trade and individual stocking, which remain important consumers of exotic fish. However, translocation of fish over shorter distances is regularly performed by fisheries agencies, fish farms, and the fishing bait industry for the purposes of sport fishing, ornament, food, or ecological manipulation.[1,4,11] In either case, when these fish are placed in their new habitats, they often produce stress within the fish community by competing for space, food, or spawning sites.[11] In some situations, they may extirpate local populations or disappear themselves; a significant proportion of introduced fish will probably be unable to colonize.[6] Stressed fish, both exotic and native, may also suffer heightened susceptibility to parasites and predators, thereby exacerbating the direct effects of introductions on individual- and community-level ecology.

Parasite taxa are often spread by non-endemic fish. This may occur by the stocking of infected fish, the natural spreading of an established fish population into new reaches of a system,[5] or the importation of contaminated water or infected vector organisms, though the former two mechanisms predominate.[3,6] The only method of stocking parasite-free fish seems to be by using fertilized eggs rather than juveniles or adults.[7] Although susceptibility to parasites decreases with age.[12,13] there is also an established, if weak, correlation between body size and parasite diversity.[8] Parasite life cycles may be complex, requiring certain birds, fish, invertebrates, or other animals as vectors during various life stages, or simple, necessitating only a single suitable host. In either case, parasite species may be specialized for hosts or vectors of a single species, or very flexible in their choice of carrier.[7,12]

Helminths are an ideal parasitic group to use as an index of both parasite community richness and the spread of introduced parasites. Their relatively large sizes make them popular study specimens, particularly for taxonomic purposes,[8] and they are one of the most diverse groups of aquatic parasites. There are an immense number of helminths parasitic or commensal to fish, including the Turbellarians, monogenetic trematodes, digenetic trematodes, Cestoda, Acanthocephala, and nematodes.[14] Helminths include organisms both with multi-vector (e.g., digenetic nematodes) and single host (e.g., monogenetic nematodes) life cycles.[13] These worms may be relatively harmless to their host while feeding on "surplus" tissue in small numbers,[12] fatal in very large infestations,[7] or anything in between.[13] There are both ecto- and endoparasitic helminths, and many are relatively easy to treat when necessary.[12]

Three factors must be considered to understand the effectiveness of parasitism or disease in fish: the susceptibility of the host, the virulence of the pathogen, and the environmental conditions under which they interact.[13,15] If one or more of these factors are altered, the balance between host and parasite will change accordingly. Parasite populations will often exist at low densities under all non-optimal environmental and host conditions,[12] then explode when conditions become optimal. This sometimes results in a severe reduction in the host population size. Thus an unstable balance is struck between parasite and host, and any alteration in one or more of the determinant conditions may radically alter this equilibrium.

There are at least two ecological factors whose effects on the survival and spread of parasites introduced with exotic fish have been documented: stress (both of the parasite and of the potential hosts/vectors) and existing parasite community richness. Environmental stresses are critical in determining the rapidity of parasite propagation and the risk of parasitism for fish. For fish, common sources of natural stress include seasonal and stochastic fluctuations in temperature, dissolved oxygen, and other water conditions, as well as competition for resources and predator avoidance. Anthropogenic stresses such as chemicals, heat, exotic fish, and new pathogens can completely change the relative importance of each factor, and thus the position of the parasite-host equilibrium. Fish have been shown to be far more susceptible to disease under stressful conditions,[13,15] and if those conditions happen to overlap significantly with a parasite's optimal ones, one or more parasite populations are likely to grow explosively.[15,16]

The changes in competition and predation which exotic fish may cause in an aquatic community can significantly change the population sizes, age-structures, and growth rates of the native flora and fauna (e.g., koi carp in Lake Conroe, Texas, USA; personal observation). In fact, this may be the most important form of stress placed on the system by the introduction of exotic fish. Both exotic and indigenous

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fish populations may become dramatically more vulnerable to parasitism following introductions, thereby creating unoccupied niche space available for either newly introduced or resident parasites. Parasites of both types which act as inferior competitors under pre-introduction conditions may do particularly well following such a disturbance. The availability of susceptible hosts, both native and introduced, may afford them opportunity to expand their relative importance within the parasite community. However, all other things being equal, pre-introduction parasite populations will probably have an advantage over introduced parasites by virtue of their adjustment to local conditions, both biotic and abiotic, and be conserved on this basis. The small initial population sizes of introduced parasites also reduces the likelihood that they will become established within a host-parasite community. Therefore, invaders will be less fit in the context of these conditions, and should theoretically have a low chance of survival and colonization.[6]

The above remarks are largely based on ecological theory; in reality, researchers have come to conflicting conclusions about the actual chances of colonization by parasites introduced by exotic fish. Kennedy states that parasites "generally possess the attributes of good colonists and are thus always well placed to extend their distributions if opportunities arise."[6] Yet he also concludes that invasion is much simpler than colonization, and that most attempts at colonization fail. Why does this seemingly paradoxical situation occur? The answer seems to be based both on environmental factors and the maturity of the parasite community into which an exotic is introduced. As stated earlier, environmental conditions often determine growth rate and population size among parasites, though small relict populations may be ubiquitous.[15] This conclusion is supported both by studies of parasite assemblages on migratory fish and the spread of a monogenaean trematode in a Norwegian river.[7] For example, shad, whose anadromous habits and lengthy coastal migrations result in exposure to a wide geographic range of parasites, exhibit diverse parasite assemblages when sampled near the center of their range on the eastern coast of the U.S. Members of these assemblages can reflect the migration patterns of the shad or of their prey, which may also act as vectors for parasite dispersal. However, most of these parasites have not extended their ranges as reproducing populations, but instead occur only on individual shad which have been parasitized during migration.[5] This may reflect intolerance for environmental conditions or some other sort of competitive disadvantage, or both. In the case of the trematode dispersal, it was found that the parasite, which had been introduced inadvertently from a nearby fish farm, remained localized for four months before spreading into the river system very rapidly. This may have been associated with host activity, but more likely the environmental conditions were not suitable for the initial spread of the parasite.[7]

As Guegan and Kennedy point out, theories of island biogeography were used until very recently to explain patterns of parasite distributions in relation to host range.[8,9] However, they propose that colonization time (i.e., elapsed time since introduction) is a more reasonable explanation for helminth distributions in the U.K. By comparing helminth diversity in truly indigenous fishes to that seen in fish introduced within the last 1000 years, they found that helminth richness was explained as well by time since introduction as by host range, and that the former was a less biased and more powerful correlation. Thus they hypothesize that the number of helminth species per host species is best predicted by colonization time of the host species.[9]

This theory may agree well with the concept of environmental limitations on distribution, as tolerance ranges can be modified over time to allow colonization of empty niches. Guegan and Kennedy add that colonization is difficult under any circumstances.[9] While contradictions to their theory may be common, these situations are probably due to host specificity and small propagule size. The potentially radical change in environmental conditions may also contribute to the disadvantage which exotic parasites face when competing with their indigenous counterparts. Conversely, it is possible, though unlikely, that introduced parasites might be competitively superior to native species and thus might colonize an area quickly. Stress upon hosts of both exotic and indigenous parasites might also reduce host quality, particularly in the exotic fish. This might either reduce the chance of colonization by invading parasites or force them to abandon the hosts on which they were introduced in favor of healthier, native hosts.

More evidence that helminth distribution limitations are imposed by both colonization time and environmental factors is presented by Kennedy and Guegan in their comparisons of local and regional species richness.[10] They found that introduced fish are helminth poor, and they predict that saturation of helminth communities will be attained as time since colonization increases. The data given by Kennedy indicate that, for five of eight introduced fish, 50-100% of their current helminth parasites were those carried at the time of introduction, indicating competitive advantage of parasites on the hosts to which they have adapted.[6] This may be an illustration of parasite success in a coevolutionary "arms race" against its host. Even in indigenous fishes, however, local species richness is far lower than that observed at the regional level,[10] indicating that local environmental characteristics such as host and vector types, temperature ranges, and water quality probably play a significant role in determining helminth distributions.

This conclusion may have important implications for the potential use of parasite introductions in eradicating or controlling the spread of undesirable, introduced aquatic organisms (*e.g.* koi carp, zebra mussels). If introduced parasites are unlikely to colonize any host group except the one to which they were originally adapted, then this may provide a safe, powerful method for returning aquatic systems to their natural, pre-introduction state. However, the long-term effects of parasite introductions are unpredictable, and this approach should be scrutinized on a case-by-case basis before it is used. Furthermore, the methods used to assess the applicability and potential effectiveness of parasite introductions in controlling exotic insect populations are being debated at present,[17,18] and consideration of this approach for use in aquatic systems should be postponed until its real costs and benefits become more clear. In any case, parasite communities present a continuing challenge to ecologists, microbiologists, parasitologists, evolutionary biologists, and conservation biologists as they try to understand species distributions. For now, it appears that both environmental factors and colonization time limit the richness of parasite communities on their individual hosts.

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