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Relationships of the Host, Pathogen, and Environment: Implications for Diseases of Cultured and Wild Fish Populations

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Abstract.—Many effects of diseases on cultured fish are known; they are less clear in wild fish populations. Cultured fish represent captive populations that can be subjected to intense scrutiny with an increasing range of diverse and powerful tools. Disease represents a spectrum from acute mortality to rather benign or inconsequential syndromes, all sharing the common feature of a deviation from the normal structure or function of the host. Understanding these deviations among cultured and wild fish populations and balancing their implications against ecological, economic, and political concerns are challenges for both fish health scientists and fisheries managers. The severity of a given disease is dependent on the interaction of numerous variables of the host, the parasite, and the environment. To understand diseases and their impacts on fish populations, we must know which variables are important, how we measure them, and finally how we assess the results of our measurements. We have perhaps been most successful with variables associated with the pathogen. We often can more easily isolate and scrutinize the pathogen than either the host or the environment. The host variables of importance (for which we lack considerable knowledge) include actions of the immune system in general and specifically the influence of genetics and nutrition on host resistance–susceptibility to disease. Lastly, the contribution of the environment, a nebulous term encompassing everything other than the host and pathogen, is only partly appreciated. While we can measure certain physical and chemical parameters of the environment, we have a poor understanding of the biological–ecological variables that influence host–pathogen interactions. Ultimately, diseases of wild fish must be considered in the context of these complex interactions including numerous physical, chemical, biological, and ecological parameters, which may yet be discovered as integral parts of the aquatic habitat.

Diseases are an integral part of the existence of all animals including both cultured and wild fish populations. Elton (1931:435) illustrates a widely held misperception of the public and scientific community regarding diseases in wild animal populations. He stated, ''Up to the present time it has been customary to believe that wild animals possess a high standard of health, which is rigidly maintained by the action of natural selection, and which serves as the general, though unattainable, ideal of bodily health for a highly diseased human civilization. This belief is partly true and partly false.'' Although it is evident that human activities have directly altered the health of fish health populations by direct perturbation of habitats and ecosystems, diseases are natural phenomena in wild fish populations (Sindermann 1990:57; Whittington et al. 1997). Indeed, we must examine the complex interactions of numerous variables if we wish to understand diseases in both cultured and wild fish populations. It is therefore incumbent upon those charged with protecting our resources to understand these variables of the host, pathogen, and the environment in making sound decisions on fisheries management.

Diseases of Wild and Cultured Fish

The knowledge of diseases of captive fish is much greater than that of wild fish for both logistical and historical reasons. Aquaculture provides captive populations that we can scrutinize throughout their existence in a somewhat controlled environment. These cultured fish have been the subject of numerous investigations, many into the roles of pathogens and the environment in disease. These studies have employed an increasing range of diverse and powerful tools that exploit modern advances in molecular biology and human health.

The origins of the fish health sciences in North America can be traced to the development of federal and state hatchery systems. The first specialists in fish health worked directly with these captive fish populations, principally salmonids often raised in mitigation hatcheries in the eastern and western USA. This historic connection between the fish health sciences and captive fish propagation has continued to the present; state and federal agencies are the principal employers of fish health scientists. In contrast with captive fish, understanding diseases

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of wild fish was receiving considerably less attention during this period. Early investigations into diseases of wild fish dealt more with documentation of losses rather than mechanisms of why and how outbreaks occurred. Examples of these investigations include the occurrences of infectious hematopoietic necrosis virus in sockeye salmon *Oncorhynchus nerka* by Williams and Amend (1976) and fungal and viral infections associated with major losses among clupeids in Newfoundland and in Australia (Sindermann 1990:57; Hyatt et al. 1997; Whittington et al. 1997). More recent studies have attempted to integrate variables of the host and environment as they relate, for example, to the impacts of whirling disease on intermountain populations of wild rainbow trout *O. mykiss* (Nehring and Walker 1996; Vincent 1996). Despite these investigations and many others, our understanding of diseases in wild fish lags far behind species of fish with commercial value raised by aquaculture.

The promise of more cooperative studies among fisheries biologists, ecologists, and health specialists as demonstrated by recent investigations of whirling disease are encouraging. These studies can further benefit by additional participation of epidemiologists who, by virtue of their training, are prepared for disease investigations. Halpen (1975) points to the role of epidemiologists as those who exercise ‘‘lateral thinking, identifying connections between seemingly isolated observations of completely different natural phenomenon.’’ These approaches certainly will complement the existing studies aimed at understanding the roles of the host, pathogen, and environment in diseases among wild fish populations.

Diseases and Ecosystems

Diseases are inherent to aquatic ecosystems. Under certain conditions, they may be of major importance in controlling population abundance, exerting dominant selective pressure in the evolution of certain species of fish (Schafer 1968; McIntyre and Amend 1978). Why is this commonly overlooked? In part, fish health specialists (the author included) are largely at fault. Generally, we have done a poor job of documenting diseases in wild fish. We have perhaps overemphasized that diseases are tied to the effects of stressors that are abundant in the captive environment (Wedemeyer et al. 1976) and that wild fish free of these should enjoy good health.

What is Disease?

Disease is a process that is characterized by ‘‘any impairment that interferes with or modifies the performance of normal functions, including responses to environmental factors such as toxicants and climate, nutrition, infectious agents; inherent or congenital defects, or any combination of these factors’’ (Wobeser 1981). This differs somewhat from more classical definitions as found in medical dictionaries but illustrates better the range of factors that may cause disease. Clearly numerous factors are causes of disease, but how all of them interact is a complex situation for which we have yet to develop a full appreciation. The causes of diseases can be grouped into those associated with environmental, nutritional, and genetic factors of the host or infectious agents (e.g., microbial pathogens).

Diseases may be major controlling factors in the abundance of both cultured and wild fish and, therefore, should be an integral part of any assessment of these populations. Diseases can directly influence performance, susceptibility to predation, success of reproduction, and other critical factors required for survival and propagation of a species (Kinne 1984:9). These effects can be cumulative and have catastrophic consequences for wild fish populations (Nehring and Walker 1996). Similarly, diseases among cultured fish can cause death, poor growth and food conversion, increased production costs, and interrupted production schedules (Austin and Austin 1987:15).

Severity of Disease

Disease is a spectrum of responses dependent on the intensity of the interactions of variables defined for the host, the pathogen, and the environment. Numerous graphical representations of these variables are used to illustrate their interactions, the interconnecting three rings being the most popular. Often criticized is the overemphasis of the pathogen at the expense of the host or environment. The historical tie between the fish health sciences and the development of federal and state hatchery systems has been discussed. Interestingly, many of the fish health pioneers who worked with these hatchery programs were trained as, or by, microbiologists. Furthermore, a microbial pathogen, often as a separable entity, is more easily manipulated, studied, and altered than the host and environment. We can often propagate the microbial agent in vitro; study its physical, chemical, and genetic properties; and conduct controlled laboratory exposures to study its effects on the host (pathogenesis). Furthermore, we can manipulate, directly or indirectly, genes that alter virulence, which in turn may lead to attenuated or subunit vaccines (Leong and Fryer 1993). These advances in the understanding of the microbial pathogen are all possible because we can leverage the most current techniques and tools used in human and veterinary medicine. An unfortunate consequence of such rapid advancements in knowledge of the pathogen is that we often cannot interpret the new information in the context of the pathogen and disease continuum. This is probably best illustrated by the current controversy over the extreme sensitivity of DNA-based diagnostic tools and understanding how to interpret the results obtained from their use for control or regulation of diseases or pathogens.

Characteristics of the Pathogen, Host, and Environment

The Pathogen

Many characteristics of pathogens are directly relevant to the outcome of their interaction with the host and environment. These include whether the pathogen is always associated with infection of the host (obligate) or whether it has the ability to survive in the absence of the host (facultative). The virulence or the ability of pathogens to cause disease depends on the strain, biotype, serotype, or genotype of the agent (Engleking et al. 1991). Changes of simply a single amino acid in key proteins may greatly affect the virulence of the pathogen (Kim et al. 1994). The dose or the numbers of pathogens, how they are delivered to the host (route of entry), and duration of the exposure directly influence the severity of subsequent infection (LaPatra et al. 1989).

The Host

Several parameters associated with the host are directly related to the occurrence of disease upon interaction with the appropriate pathogen and environmental conditions. These include factors that are constantly present, or constitutive, such as the host species genotype, age, size, developmental stage (LaPatra et al. 1990), nutritional and reproductive statuses, and behavior and innate defenses related to immune competence (Anderson 1990). Additional factors that affect host susceptibility to disease include adaptive factors, which result from previous interactions with the pathogen or environment. Among the most important interactions is the acquisition of immunity after exposure to the pathogen.

The Environment

The environment is perhaps the least defined element of the host, pathogen, and environment paradigm. Certain components of the environment are evident; these chemical and physical characteristics can be measured, either continuously or more often at specific time points, often after a disease problem has arisen. The variables measured include, but are not limited to, dissolved gases, pH, temperature, flows, turbidity, and contaminants. The effects of biological processes, including those due to human intervention, must be considered because they will affect diversity and density of the biota, which may encourage certain hosts, pathogens, and other symbionts. Additional variables related to the geomorphology, limnology, and hydrology of the aquatic environment that are critical to fish health need to be evaluated as they change with time and with human intervention. The consciousness of human impacts on our aquatic environment has never been greater, and a major focus of fisheries biologists and ecologists is habitat and its restoration (Rahel 1997). Difficulties with changing our expectations and demands of our aquatic resources, however, often bring human activities in direct conflict with the health of our fish populations. Significant alterations of habitat due to power generation, flood control, irrigation, logging, grazing, mining, et cetera, have affected wild fish populations, often in a negative manner. Balancing the costs and benefits of these activities and human dependence on them with the health of our fish populations is the supreme challenge for fisheries managers.

Integrating the Variables

The complex nature of disease as illustrated by the interactions between the host, pathogen, and environment is perhaps best shown by a web of causation (Wobeser 1994:6) as modified for wild fish (Figure 1). Making sense of these complex interactions requires an understanding of many variables; some we have discussed, others we have not, and yet others are to be discovered. We must strive to understand these variables to respect new and diverse interactions that will certainly arise. New interactions may include appreciation of other hosts in the distribution and severity of parasites. The recent emphases on understanding the biology and ecology of oligochaetes, polychaetes, and perhaps other annelids, as they relate to the severity of myxosporean diseases like whirling disease and ceratomyxosis, are examples. Also,

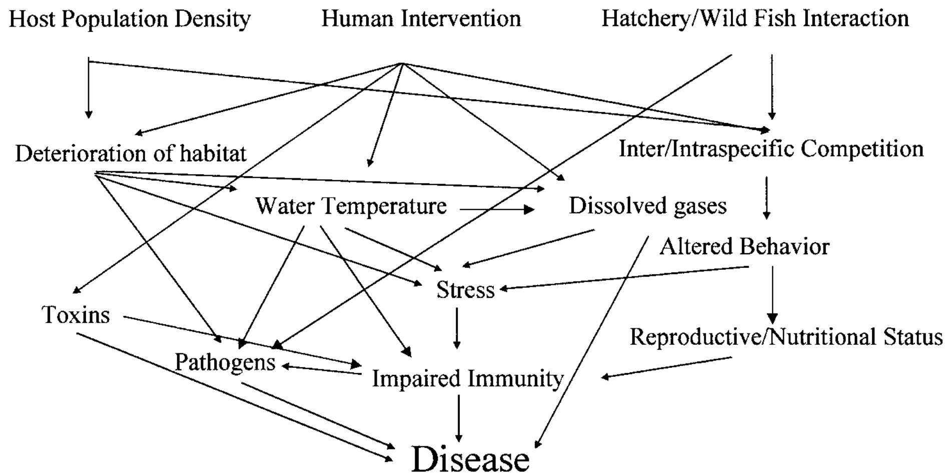

FIGURE 1.—A web of causation for diseases as they manifest themselves among wild populations of fish as adapted from Wobeser (1994:6) by the author. The interactions of water temperature, spawning stress, and the pathogen *Flavobacterium columnare* and the resultant columnaris disease in adult Pacific salmon is one example of how these factors are related.

understanding how pathogens and hosts evolve is critical to predicting the effectiveness of management and regulatory decisions. Recent studies have shown the similarities among iridoviruses in amphibians (Mao et al. 1997) and poxviruses in insects (Ono et al. 1986; R. P. Hedrick and others, unpublished data) with recent disease outbreaks in fish. Are we seeing the evolution of new viral pathogens as they cross from amphibians and insects into fish? Can we use this information to better shape our management decisions?

Conclusions

Diseases result from a series of complex interacting variables of the host, pathogen, and environment. Whereas wild fish are generally viewed as relatively free of diseases, we must appreciate that diseases are and will be an inherent and important component of aquatic ecosystems. The impacts of diseases on wild fish populations may range from seemingly insignificant to catastrophic. Estimating and then managing the effects of diseases on wild fish can only come from a better understanding of these complex interacting variables (those discussed and more). As fish health scientists we must more thoroughly investigate and document these variables. We must then integrate this information with that collected by fisheries biologists and ecologists and, together, employ epidemiological principles that have been applied with success in investigations and management of diseases of other wild animals (Wobeser 1994).

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