

Infectious Diseases Affect Marine Fisheries and Aquaculture Economics

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ABSTRACT

Seafood is a growing part of the economy, but its economic value is diminished by marine diseases. Infectious diseases are common in the ocean, and here in aquaculture, which increasingly dominates seafood production as wild fishery production plateaus. For instance, marine diseases of farmed oysters, shrimp, pelagic and subtidal species. Farmed species often receive infectious diseases from wild species and can, in turn, export infectious agents to wild species. In other areas. The movement of exotic infectious agents to new areas continues to be the greatest concern.

Keywords

[fish \(/search?option1=pub_keyword&value1="fish"\)](#),
 [abalone \(/search?option1=pub_keyword&value1="abalone"\)](#),
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INTRODUCTION

An average person eats approximately half his or her weight in seafood each year. The 156 million metric tons (mmt) of total seafood from 2011 landings has declined because it takes more effort to maintain yield (**Willman et al. 2009**). With fisheries unable to keep up with the growing demand for seafood, aquaculture has become one major cost to aquaculture is marine infectious diseases.

In this review, we begin by considering the infectious diseases known or suspected to have economic impacts, and then ask what economic costs they impose. Studies for which information exists on economics and disease management: Dermo in oysters, various diseases in abalone, white spot disease in shrimp, bacterial

WHAT MARINE DISEASES HAVE ECONOMIC CONSEQUENCES?

Marine diseases are a natural part of ocean ecosystems, and many have economic consequences for fisheries or aquaculture. Of the 67 examples in **Table 1** are echinoderms. Most examples come from temperate waters, with a higher percentage from the Northern Hemisphere than from the Southern Hemisphere. See

Table 1
 Representative marine disease agents with known or potential economic significance
 Toggle display: **Table 1**

Host	Disease agent
Molluscs	
Viruses	
Abalone (<i>Haliotis laevis</i> and <i>Haliotis rubra</i>)	Abalone ganglioneuritis virus (Victoria)
Oysters (<i>Crassostrea angulata</i>)	<i>Crassostrea angulata</i> iridovirus
Oysters (<i>Crassostrea gigas</i>)	Ostreid herpesvirus 1 (including μ Var)
Bacteria	
Abalone (various)	Withering syndrome rickettsia-like organism (WS-RLO)
Abalone (<i>Haliotis tuberculata</i>)	<i>Vibrio harveyi</i>
Oysters (<i>Crassostrea gigas</i>)	<i>Vibrio tubiashii</i>

Host	Disease agent
Oysters (<i>Crassostrea gigas</i>)	<i>Nocardia crassostreae</i>
Clams (various)	<i>Vibrio tapetis</i>
Protists	
Molluscs (various)	<i>Perkinsus olseni</i>
Oysters (<i>Crassostrea virginica</i>)	<i>Haplosporidium costale</i>
Oysters (<i>Ostrea edulis</i>)	<i>Bonamia exitiosa</i>
Oysters (<i>Ostrea edulis</i>)	<i>Bonamia ostreae</i>
Bivalves (various)	<i>Marteilia refringens</i>
Oysters (various)	<i>Mikrocytos mackini</i>
Bivalves (various)	<i>Perkinsus marinus</i>
Oysters (various)	<i>Haplosporidium nelsoni</i>
Scallops (<i>Pecten maximus</i>)	<i>Perkinsus qugwadi</i>
Metazoan	
Abalone (various)	<i>Terebrasabella heterouncinata</i>
Unknown	
Clams (various)	QPX (quahog parasite unknown)
Crustaceans	
Viruses	
Shrimp (penaeid)	<i>Baculovirus penaei</i>
Shrimp (penaeid)	Infectious hypodermal and hematopoietic necrosis virus
Shrimp (penaeid)	<i>Aparavirus</i> spp.
Shrimp (penaeid)	<i>Penaeus monodon</i> -type baculovirus
Shrimp (penaeid)	<i>Whispovirus</i> spp.
Shrimp (penaeid)	<i>Okavirus</i> spp.
Lobsters (panulirid)	<i>Panulirus argus</i> virus 1
Bacteria	
Lobsters (homarid)	<i>Aerococcus viridans</i> var. <i>homari</i>
Shrimp (penaeid)	Necrotic hepatopancreatitis bacterium
Shrimp (penaeid)	<i>Vibrio parahaemolyticus</i>
Protist	
Crabs (various)	<i>Hematodinium</i> spp.
Metazoans	
Crabs (various)	Rhizocephalan barnacles
Crabs (Dungeness)	<i>Carcinonemertes errans</i>
Crabs (king)	<i>Carcinonemertes regicides</i> , <i>Ovicides paralithodis</i>
Echinoderm	
Protist	
Green urchins	<i>Paramoeba invadens</i>
Fishes	
Viruses	
Fishes (marine)	Nodaviruses
Fishes (herring)	Hemorrhagic septicemia virus
Red sea breams	Red sea bream iridovirus
Pilchards	Pilchard herpesvirus
Salmon	Infectious salmon anemia virus
Salmon	Infectious hematopoietic necrosis virus
Fishes (various)	Aquabirnaviruses
Bacteria	
Fishes (marine)	<i>Amyloodinium ocellatum</i>
Flounders	<i>Edwardsiella tarda</i>
Fishes (marine)	<i>Vibrio</i> spp.
Fishes (marine)	<i>Mycobacterium</i> spp.
Fishes (marine)	<i>Streptococcus</i> spp.

Host	Disease agent
Fishes (marine)	<i>Listonella anguillarum</i>
Fishes (marine)	<i>Moritella viscosa</i>
Fishes (marine)	<i>Photobacterium damsela</i>
Fishes (marine)	<i>Tenacibaculum maritimum</i>
Salmon	<i>Renibacterium salmoninarum</i>
Salmon	<i>Vibrio salmonicida</i>
Salmon	<i>Aeromonas salmonicida</i>
Yellowtail	<i>Nocardia seriolae</i>
Fishes (marine)	Chlamydia-like bacteria
Yellowtail	<i>Lactococcus garvieae</i>
Protists	
Fishes (marine)	<i>Ichthyophonus hoferi</i>
Fishes (marine)	<i>Cryptocaryon irritans</i>
Fishes (marine)	<i>Amyloodinium ocellatum</i>
Metazoans	
Fishes (marine)	<i>Kudoa</i> spp.
Salmon	<i>Parvicapsula</i> spp.
Fishes (marine)	<i>Enteromyxum</i> spp.
Fishes (marine)	Anisakid nematodes
Fishes (marine)	<i>Cryptocotyle lingua</i>
Fishes (marine)	Monogenea (various)
Salmon	<i>Eubothrium</i> spp.
Fishes (marine)	<i>Lepeophtheirus</i> spp., <i>Caligus</i> spp.

Nonseafood marine species can also have economic value that can be diminished by disease. For example, tropical aquarium fishes are marketed through retail services, such as supporting fisheries and protecting shorelines from erosion. Iconic marine species such as whales, dolphins, corals, sea stars, and sea otters are valued because of the absence of market prices or marginal harvest costs (Costanza et al. 1998, Peterson et al. 2003). Thus, although the infectious disease

ECONOMICS 101 FOR MARINE DISEASES

Economists use market data to estimate seafood's direct use value. Although the local economy that a fishery or aquaculture industry supports is important, the value of the fish to the owner or processing plant and therefore do not represent a fishery's true economic value. For example, money spent on processing infected fish fillets or vaccines increases the production cost.

Because fish stocks are exploited over time, a fishery has its highest economic value when it maximizes the discounted value of present and future net benefits. Infectious diseases could change the optimal strategy: If a healthy fish is going to die before it spawns, one might benefit from harvesting it (Conrad & Rondeau 2014).

Marine diseases can impact a species' economic value in two ways. The first comes from the reduction in potential catch resulting from decreased biological productivity. The second comes from a bad taste or appearance or from risks (or assumed risks) to human health. Not surprisingly, consumers avoid seafood if they can see or taste parasites. This reduces the total catch's net economic worth. Several infectious agents reduce the market value of infected muscle tissue, including sealworm larvae in the flesh of cod (Conrad & Rondeau 2013); and the hyperparasite *Urosporidium spisuli* in nematodes parasitizing surfclams (Perkins et al. 1975). Dealing with these infectious agents increases the cost of production.

Negative externalities interest economists and challenge management. A negative externality occurs when a firm or individual impairs the productivity or welfare of others. If fishery managers or decision makers face external costs, and thus they have no direct incentives to take corrective measures. Therefore, controlling or managing a marine disease is a challenge.

FISHERIES AND INFECTIOUS DISEASES

The most obvious way to reduce marine diseases is to increase the harvest. Fishing reduces host density and can break the transmission of host-specific, density-dependent diseases. This is a fishery's best interest; rather, as a fishery collapses, host-specific infectious diseases should, in theory, become a relatively minor problem.

Nonetheless, some fishing activities can increase infectious diseases. One example would be a fishery restoration effort that unknowingly outplanted infected crabs. Fishers can distinguish most healthy from infected crabs and, to avoid contaminating the catch, often throw infected crabs overboard while moving to a new area. This increases mortalities (Whittington et al. 1997). Fisheries should therefore assume that stocks carry infectious agents and be cautious about moving them.

Fisheries can also indirectly increase infectious diseases in nontarget species. An example is the California spiny lobster fishery: This fishery is profitable and commercially valuable species (**Lafferty 2004**). Here, the lobster fishery might benefit the red sea urchin fishery by reducing predation on urchins, but it also has effects on host population dynamics.

AQUACULTURE AND INFECTIOUS DISEASES

Wild stocks support many infectious agents, which can enter aquaculture farms through water intake, feed, or infected broodstock. As a result, most infectious species can be hit by series of infectious diseases over time. For instance, Japanese yellowtail (*Seriola quinqueradiata*) culture became industrialized around 1960, and is one of victories over diseases followed by new challenges.

Figure 1

Infectious disease interactions between wild and farmed stocks.

Yes
Export from farmed to wild species
Maybe
No

Lafferty
Annu.

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Infectious diseases that might not normally affect wild hosts can become problematic in aquaculture. Farmed stock is often not coevolved with local infectious agents (**2002**). Another factor that makes aquaculture susceptible to disease outbreaks is the high stocking density of monocultures, which increases host contact rates (**Sinderman 1984**). By contrast, infectious agents with complex life cycles should do worse in simplified aquaculture settings than in the wild, where intermediate hosts are available.

To stay profitable, farms must invest in prevention and treatment. Preventing opportunistic diseases requires good water quality and moderate stocking densities, which often require governmental approval combined with the small markets and potential health risks for consumers (**Friedman et al. 2003, Morrison & Saksida 2013**). Fortunately, for example, furunculosis and vibriosis were devastating to salmon cage culture in the 1980s and 1990s (**McVicar 1997**), but after vaccine use, these conditions were controlled. Separating wild-caught foundational stock from cultured offspring, and growing disease-resistant genetic stocks. With good management, the added mortality is reduced. In addition, the routine cost of using pesticides, vaccines, and therapeutics, for either prophylaxis or treatment, is substantial (**Asche & Bjørndal 2011, Dixon et al. 2011**).

WHEN MARINE DISEASES MOVE FROM AQUACULTURE TO WILD SPECIES

One promise of aquaculture was that it would relieve fishing pressure on declining wild stocks and help to restore ocean ecosystems. This has happened to some extent (**Diana 2009**). In **Figure 1**'s tabulation of marine diseases of economic importance, 45 of 57 infectious agents found in aquaculture are or might be exported to wild stocks with some tolerance.

Infectious agents can build up on farms with poor management, but good management can also foster infectious agents if farms manage for host tolerance. For example, transmission are low at these temperatures (**Braid et al. 2005, Friedman & Finley 2003**), tolerant red abalone might become sources of WS-RLO for wild (and

Where farming fosters disease transmission, infective stages should be higher in farm outflow than in farm inflow, making aquaculture a net exporter of infectious agents. A discharge pipe quickly dissipates within less than one to a few kilometers of the coastline (**Lafferty & Ben-Horin 2013**).

Whether farm effluent containing an infectious agent affects wild stocks depends on many factors. The extent to which an effluent plume reaches wild species is often adapted to their infectious agents, and the population-level consequences of increased exposure to most native pathogens should be mild (**Jackson et al. 2001**). For salmon, because there is not enough baseline information on infectious diseases in wild stocks to assess the net effect of disease export from aquaculture (Lafferty & Ben-Horin 2013), it can carry significant economic costs to aquaculture.

The stakes increase when aquaculture releases infectious agents that have evolved in culture (**Kurath & Winton 2011**). In farms, susceptible hosts are always present, but fish is highly pathogenic in farms (**Raynard et al. 2007**). On the one hand, adaptation to the water quality, host type, and treatment regime within a farm can help agents survive the farm environment and eventually establish themselves in the wild. Alternatively, culture-adapted infectious agents might cause suboptimal pathologies in wild stocks.

Impacts on wild species are easier to document when aquaculture moves farmed species and their infectious agents. One such infectious agent is *Bonamia orientalis*, which has moved into wild oysters (**Friedman et al. 1989**). The spread of these kinds of novel diseases has led to regulations on moving cultured species between different areas. Of the infectious agents that slip through the screening process, few will persist in wild stocks (**Kennedy et al. 1991**). For those that do, however, the local stocks can suffer. With better management, aquaculture still contributes to outbreaks of novel infectious agents (**Raynard et al. 2007**), such as *Haplosporidium nelsoni* (introduced to abalone) (**Kuris & Culver 1999**).

CASE STUDIES

Dermo in Oysters

The oyster culture industry has moved oyster diseases around the world, and several of these diseases have led to substantial mortality and economic impacts on oyster harvest (**FAO 2012**).

Perkinsus marinus is a parasite that causes Dermo disease in adult eastern oysters (*Crassostrea virginica*). This apicomplexan protozoan, which is related to *Perkinsus* species that infect other bivalves, has a complex life cycle. Their role in transmission under natural conditions is unknown. The parasites are acquired through feeding and often colonize digestive epithelia before entering the host's bloodstream. They can be transmitted to a new host when the host dies and decomposes (**Bushek et al. 2002**). Prevalence varies in time and space, but it is not unusual for most oysters to be infected.

Figure 2

Average Dermo prevalence for bays sampled in the winter, when prevalences are normally near yearly lows, by the NOAA Status and Trends Mussel Watch program from 1995 to 2010. For details of the sampling locations, see the text.

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Dermo was first identified in the late 1940s in the northwestern Gulf of Mexico (Ray & Chandler 1955) and shortly thereafter was recorded as far north as Chesapeake Bay. El Niño cycles in the Gulf of Mexico and Northern Atlantic Oscillation cycles in the Mid-Atlantic (Soniati et al. 2009), are implicated in triggering Dermo epizootics.

During epizootics, Dermo can reduce oysters' carrying capacity fivefold (Powell et al. 2009). In the Mid-Atlantic region, Dermo has absorbed at least two-thirds of the roughly 2,000 mt landed, the total potential ex-vessel economic loss to Dermo equates to approximately US\$6 million per year. Dermo is likely to be a long-term

Dermo impacts more than the oyster industry. Oysters build reefs that attract more oysters and reef-associated species that both support fisheries and contribute to coastal protection. The restriction on stock production imposed by Dermo can explain much of the oyster reef loss in the Gulf of Mexico and Mid-Atlantic (Beck et al. 2011). Only oyster

Dermo also complicates those oyster restoration efforts that focus on creating unfished oyster sanctuaries (Paynter et al. 2010). Most sanctuaries are in the lower estuary, where they recruit down-estuary, where they become infected with Dermo, helping the disease persist in the system (Munroe et al. 2012). If the evolution of resistant genotypes, this strategy is not an easy sell (Carlsson et al. 2008, Munroe et al. 2013).

Current and future research on Dermo is focusing on the development of disease-resistant genotypes in oysters and the identification of loci contributing to disease (Soniati et al. 2012), and the application of classic transmission dynamics models to investigate the influence of natural and anthropogenic changes on Dermo infection of 50% or more of the adult oysters in most East and Gulf Coast populations by *P. marinus* (Kim & Powell 2007).

Withering Syndrome Rickettsia-Like Organism, Sabellid Worm, and Herpesvirus in Abalone

Wild abalone fisheries are a high-value, high-cost, shallow-water endeavor, and these characteristics make abalone stocks vulnerable to overharvesting and depletion. Approximately 100,000 mt (FAO 2012). Although abalone grow slowly, farmed abalone production (400,000 mt) has a high farm-gate value worth approximately \$1.5 billion.

In the mid-1980s, WS-RLO caused a fatal withering syndrome in various California abalone species (Crosson et al. 2014). WS-RLO is an intracellular bacterium that the animal starves, catabolizing proteins from a withering foot before dying (Figure 3). All wild fisheries were closed as abalone populations crashed because of WS-RLO. In 1986, 100% of red abalone alive to market size if they were located in cooler-water sites or—for one farm that participated in the US Department of Agriculture's Investigative

were declared safe to sell only one year after the oxytetracycline treatment (**Friedman et al. 2007**). By 2008, abalone culture in California had risen to ~227 million abalones annually. A newly found phage hyperparasite of WS-RLO increases tolerance to WS-RLO in abalone farms and might signal a reprieve for wild populations as well (**Friedman et al. 2014**).

Figure 3

Red abalone (*Haliotis rufescens*) (a) without and (b) with withering syndrome. Note that the abalone with withering syndrome has an atrophied pedal muscle and is lethargic, whereas the uninfected abalone is active and has a large pedal muscle.



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In the early 1990s, California abalone farms became infested with a sabellid polychaete, *Terebrasabella heterouncinata* (**Kuris & Culver 1999**) that an abalone farm introduced from South Africa. The worm is a brood larva that can settle on nearby hosts. On the shells of their coevolved, wild South African hosts, the worms appear benign, but they slow growth and reduce fecundity. The California Department of Fish and Game established policies to eradicate the worm from farms and the wild, including cleaning up the stock, screening outflow, and halting shell-depositing (**Kuris & Culver 2004**). Volunteers eventually eradicated the worm by culling potential hosts (**Culver & Kuris 2000**).

Abalone viral ganglioneuritis (AVG) appeared in several abalone farms in Victoria, Australia, in December 2005. This virus is transmitted horizontally (individually or in groups) and is highly contagious. For virus latency in survivors is a concern. Then, in May 2006, AVG appeared in wild *Haliotis rubra* and *Haliotis laevigata* stocks next to an infected abalone farm. The outbreak spread into an area with 71 individual transferable quota (ITQ) holders in the well-regulated abalone dive fishery. The AVG outbreak was devastating, leading to a 90% loss in the present value of a fishery—that were trading for US\$5–6 million before the epizootic lost almost all their value (**Conrad & Rondeau 2014**). To help prevent a similar outbreak, the Australian government implemented a series of measures.

The spread of AVG illustrates the close biological and economic interdependence of wild fisheries and aquaculture, where farm decisions lead to risks and demands for prevention and remedial actions but also for the benefits of those actions for wild fisheries. If a disease in the wild responds to host density, then setting effort limits in wild fisheries. Recognition that a new disease is spreading leaves some time to modify harvesting policies, salvage the still-healthy stocks, and perhaps halt the spread of the disease. In wild fisheries, such as the Australian abalone fishery, it can be difficult to shift management policies in response to impending doom.

Successful management of wild and farmed abalone will require resolving several unanswered questions. For example, how long does WS-RLO survive in seawater? What is its range? Is an abalone more at risk near a wild or farmed population or near a developed area of coastline? Will the phage infecting WS-RLO be an efficient “natural enemy” of WS-RLO? What are the host-pathogen relationships? The sources of WS-RLO and AVG are still unknown, and understanding their origin will help elucidate disease introduction mechanisms.

White Spot Disease in Shrimp

Penaeid shrimp are the world's most valuable seafood. By the 1980s, declining wild fisheries could not keep up with the increased demand from wealthy consumers. Shrimp are now mostly captured 3 mmt of wild shrimp (**FAO 2012**). Shrimp fisheries use trawlers, whereas penaeid shrimp aquaculture requires inexpensive coastal land. These coastal areas are now used for shrimp farming. Shrimp farms have been hit by several infectious diseases, including white spot syndrome, yellow-head virus, hepatopancreatic parvovirus, mononucleocytopathic virus, and others (see **Lightner 2013** for communication).

The agent of white spot syndrome is *Whispovirus*, a new genus of double-stranded DNA viruses in the family Nimaviridae (**Sánchez-Mártinez et al. 2007**). The virus is highly contagious in shrimp farms, where the virus then spreads under high culture density (**Lotz & Soto 2002**) and warm temperatures (**Jiravanichpaisal et al. 2004**). During an outbreak, up to 100% of shrimp can die.

Figure 4

Carapace of a prawn with white spot disease. Photograph courtesy of D.V. Lightner.



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White spot syndrome outbreaks began in 1992 in Southeast Asia, where they devastated a thriving industry (**Flegel 2006**). In the 1990s, a shrimp pond could cause significant coastal environmental damage and economic loss (**Dierberg & Kiattisimkul 1996**). Losses from the 1992 and 1993 outbreaks throughout Asia were valued at \$1 billion in emergency when production plummeted by 65%, representing almost US\$1 billion in lost exports (**McClennon 2004**). Starting in 2002, disease outbreaks in Asia continued. The outbreaks in the 1990s and early 2000s changed shrimp farm management (**Lightner 2011**). In particular, using closed systems and culturing shrimp larvae in tanks reduced stress, and emphasizing biosecurity (**Lightner 2011**). As a result of these biosecurity practices, white spot syndrome is a far smaller problem now.

It might appear that exports of WSSV into the wild would have environmental impacts on wild crustaceans. After all, the virus enters the ocean through farm effluents. The virus kills stressed shrimp in farm conditions, which do not often apply to wild shrimp. The most compelling evidence for an economic impact of viral export is from the Gulf of Mexico and affected the fishery for a decade (**Morales-Covarrubias et al. 1999**). However, instead of being a net negative externality for shrimp farming, it benefited the fishery.

This example illustrates another interdependence between fishing and aquaculture. If consumers consider products from two sources (e.g., fished or farmed) and the price of products from one source is affected by diseases (or of any other economic problem, for that matter) to the sale value of products can be misleading. The true value of seafood is not the price at which it is sold, but the benefits capture fisheries and penalizes consumers by an identical amount. The real economic losses come from the diseased shrimp that are neither produced nor consumed.

Because there are no treatments for white spot syndrome, the focus of current research is on prevention through clean aquaculture protocols, new diagnostic tools, and vaccines (**Lightner et al. 2011**). The development of SPR strains amounts to breeding the survivors of experimental outbreaks. But these survivors are also locally adapted to particular environments. SPR strains of WSSV (**Cuéllar-Anjel et al. 2012**). Furthermore, it is important to distinguish whether SPR strains are tolerant or resistant because tolerant strains can act as reservoirs for the virus (**Huang et al. 2011**).

Betanodaviruses in Groupers

Tropical groupers (*Epinephelus* spp.) and sea bass (*Dicentrarchus* spp.) support valuable localized sport, commercial, and artisanal fisheries (**Seng 1998**). Tropical groupers are often raised in a hatchery.

Farmed and wild groupers are susceptible to diseases caused by generalist betanodaviruses that probably have both vertical and horizontal transmission (**Morales-Covarrubias et al. 1999**). Reassortment is highest in viral isolates from farmed fish, suggesting that farms create environments for viral evolution (**Panzarin et al. 2012**).

Most infected adult fish are resistant to these viruses but sometimes show bizarre disease symptoms (**Figure 5**). For instance, in the Gulf of Annaba, Algeria, groupers near a nearby beach, were infected with betanodavirus (**Kara et al. 2014**).

Figure 5

A living but moribund endangered dusky grouper in Italy infected with betanodavirus. The grouper has lost control of its swimming, causing it to crash into the bottom, which has led to severe trauma in



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The increasing number of reports of simultaneous but distant die-offs has led to the hypothesis that death in infected adult fish results from the stress of sp adapted and benign strains into novel culture settings could lead to unusual pathologies. Betanodaviruses are now a major threat to aquaculture in the Me Viral exchange between farms and wild fish seems probable and was proposed to explain a mass mortality of wild dusky grouper 15–20 km from sea bass fa whether farms are net virus exporters or simply victims of exposure from wild fishes is difficult to determine (Vendramin et al. 2013) but worthy of investig

Infectious Hematopoietic Necrosis Virus, *Kudoa*, and Sea Lice in Salmon

After years of decline resulting from river damming and overfishing, wild Pacific salmon stocks have stabilized, with landings totaling approximately 1 mmt

Infectious hematopoietic necrosis virus.

Infectious hematopoietic necrosis virus (IHNV) is a rhabdovirus endemic in the Pacific Northwest. This virus has efficient transmission in water, with acute d and septicemia. The disease severity depends on the pathogen genotype, host species, and stock, with the most susceptible being Atlantic salmon (Traxler ranging from 18% to 78%. Chinook salmon are less susceptible to the disease and have been identified as virus carriers when held near Atlantic salmon in n the Pacific salmon species, with a 48–85% death rate (Meyers et al. 2003).

IHNV has cost the salmon farming industry in several ways. In addition to lost production, carcass disposal has been an economic burden to farms. Many sm cumulative mortality on these farms reached 58%; more than 12 million Atlantic salmon, valued in the tens of millions of dollars, were killed or culled (Saks screen broodstock for IHNV at an annual cost of more than US\$200,000. Some farms reduce risk by vaccinating their Atlantic salmon against IHNV at an annu cost would outweigh the expected benefits. However, in 2012, an outbreak of an IHNV strain identical to an isolate from wild fish spread among unvaccinate ignored, leads to lower-than-optimal protection against disease among farms. Achieving optimal protection might require public policies that impose vacci

There has been one documented IHNV outbreak among wild sockeye salmon in the marine environment (Traxler et al. 1997), which is the most valuable w expense that IHNV management and prevention impose on stock enhancement. For example, using UV sterilization and modular facilities to help prevent o

Kudoa.

Kudoa is a common genus in the phylum Myxozoa that infects marine fishes. Based on our knowledge of other myxozoans, *Kudoa thyrsites* probably require their hosts, but several species infect commercially important fishes like yellowtail, mahimahi, Atlantic mackerel, and Pacific hake, causing visible pseudoc most abundant commercial fish species off the US West Coast (Kabata & Whitaker 1981).

Figure 6

A mackerel with myoliquefaction caused by infection with *Kudoa thyrsites*. Photograph courtesy of C. Whipps.



K. thyrstites was first documented in pen-reared Atlantic salmon industry in British Columbia in the early 1990s (**Whitaker & Kent 1991**), and by 2000 it was an economic problem, and one large company's 2011 annual report estimated that total costs related to discards and claims as a result of soft flesh caused by *K. thyrstites* on how consumers view farmed salmon quality. A few mushy *Kudoa*-infected fish can have a long-lasting impression, driving down demand and price.

Sea lice.

Small caligoid copepod crustaceans in the genera *Caligus* and *Lepeophtheirus* are called sea lice. Free-living nauplius larvae hatch from eggs of parasitic females, first into a parasitic preadult and then into an adult that can move about on the fish host. Sea lice feed on fish skin, mucus, and blood, causing lesions. The lice keep up with their energetic demands by feeding more, but this increases feed costs for penned salmon by 5% (**Sinnott 1998**). At high intensities, as is often the case in

Salmon aquaculture operations from Norway to Chile, Canada, the United Kingdom, and Ireland manage for sea lice. Best practices include separating age classes and reducing production costs by 5–20% (**Rae 2002**). Overall, sea lice increase farmed salmon costs by US\$0.15–0.30/kg, which translates to a global annual cost exceeding US\$1 billion.

The potential export of sea lice to wild stocks is controversial and leads to negative views of salmon farming. Some analyses have suggested that the increase in wild stocks in the Broughton Archipelago, British Columbia (**Krkošek et al. 2007**). This strong claim was contested by the salmon farming industry and has not been supported by eating sea lice, and that aquaculture does not need to protect wild stocks from sea lice (**Marty et al. 2010**). However, an independent analysis suggested that a lice-induced mortality between 20% and 30% could lead to sharp stock declines unless countered by reduced harvest rates or the closure of the commercial fishery.

Although salmon farms have a private interest in controlling sea lice in net pens, little incentive exists for farms to reduce hypothetical (and difficult-to-prove) management goals to reduce sea lice intensity on wild fish to 10 lice. Meeting this goal will be difficult because there are far more farmed salmon than wild salmon in the region.

A key research need for sea lice (and other marine diseases) is to collect baseline data on pathogen prevalence and distributions in wild species before establishing useful data for understanding the dynamics and risks of transmission of various marine diseases include the survival time of an infectious agent in the water column.

CONCLUSIONS

Marine diseases are common in the ocean and can reduce seafood's economic value by decreasing meat quality, increasing the marginal costs of harvest and increasing investment in disease management (**Sinderman 1984**). Because disease management has costs that weigh against profits, the economic effects of infectious diseases are often overlooked.

Aquaculturists try to control transfers and introductions. They also reduce stress-activated disease by maintaining water quality and limiting crowding. For many diseases, then, if it makes economic sense, hope to treat it. In worst-case scenarios, regulatory actions might require that farms cull stock to prevent spread to other farms.

The extent to which aquaculture exports infectious agents that in turn infect wild stock is controversial, drawing critiques from conservation biologists and ecologists. Documenting the extent to which aquaculture magnifies wild infectious agents has proven difficult given the sparse baseline information on their background prevalence and negative impacts of infectious agents accidentally moved around by aquaculture, such as when new infectious agents arrive with imported stock. The importation and evolution of new infectious strains is more speculative. The argument is that farms present a novel evolutionary environment for infectious agents (e.g., IHN in salmon), but new molecular tools will make it easier to identify novel genotypes of infectious agents associated with aquaculture.

Scientific studies could fill key knowledge gaps and mitigate the economic consequences of marine diseases in several ways. Given the continual onslaught of new diseases, developing best practices and strategies for maximizing the economic value of seafood in the face of disease pressures. However, a quantitative understanding of host–infectious agent interactions is a substantial need for basic research into the ecology and evolution of marine diseases.

Resolving the controversial issues surrounding the export of marine diseases from aquaculture will require understanding the background rates of disease in wild stocks and the sociological, behavioral, legal, and political issues that interact with the biology we review here. Given the staggering economic cost of marine diseases, resolving these issues is a high priority.

The most obvious economic impact of marine disease is the cost that aquaculture expends to manage infectious agents on farms. In addition, infectious diseases represent a negative externality that might affect wild fisheries and threaten biodiversity. However, the impact of infectious diseases on farms might also indirectly help stabilize seafood prices.

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