# SEA LICE PHYSICS WITHOUT THE MATH—UNDERSTANDING WHY SEA CAGE FISH CAUSE WILD FISH TO DECLINE

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**Summary**
An open cage net pen, often referred to as a *sea cage*, is an enclosure designed to prevent farmed fish from escaping, and to protect them from large predators, while allowing a free flow of water through the cage to carry away wastes. Sea-cage farmed fish thus share water with wild fish, enabling transmission of sea lice from wild to farm, and farm to wild. This paper concerns the compatibility of sea cages with organic aquaculture standards regarding damage to surrounding wild ecosystems. The position of the paper is this: (a) elementary physics shows that sea-cage finfish aquaculture causes the abundance of sea lice on sympatric wild fish to increase, and (b) elementary biology shows that increased sea lice abundance on wild fish causes their numbers to decline. In observational data, the year-on-year increase in lice and decline of wild fish can be difficult to distinguish from natural variability, which has been a source of confusion in the literature of aquaculture and fisheries. To understand the physics of sea lice, mathematics is helpful but not essential. In this paper, I explain without mathematics the *host density effect*, the *reservoir host effect* and why epidemics of sea lice on farmed fish occur in some localities and not others. The physics dictates that damage to wild fish can be partly, but not wholly, reduced by locating sea cages far from wild fish, by short grow-out times for farmed fish, by medicating farmed fish, and—most important—by keeping farm stocking levels below the level likely to precipitate epidemics of lice on farm fish.

## 1. Introduction

Sea cages have an undeniable appeal to people who worry that wild fish are being over-harvested, to businessmen seeking to make a profit, and to governments who wish to make nutritious sea food available to all. Unfortunately, there is now an overwhelming amount of data showing that wild fish usually decline—sometimes to near zero levels—in areas where sea cages have been allowed to proliferate. Often the decline is associated with a parasite that the wild fish and farm fish have in common. For example, in Scotland, Norway and Western Ireland stocks of wild salmon and sea trout have declined in areas with sea-cages containing farmed salmon.

Often the data regarding declines are difficult to interpret: In some areas, wild fish decline immediately after sea cages are introduced; in other areas, wild fish do not decline until years after sea cage farming has begun; some stocks of wild fish decline to near extinction while other stocks remain at pre-farm levels. These sources of confusion are compounded by obvious difficulties in counting wild fish, and by the tendency of stocks of wild fish to fluctuate due to unknown environmental factors.

In this situation it is necessary to use basic principles of science to try to understand the interactions between wild fish and sea-cage farmed fish. These principles can't predict exactly what will happen in any given situation—there are too many unknowns for that—but they can tell us how to bet. My goal in this brief essay is to introduce some of those principles and apply them to the exchange of sea lice between wild and farmed fish.

Scientists have found that understanding and communicating ideas about animal populations is much easier with the aid of mathematics such as differential equations and abstract diagrams. However, the most important parts can be communicated without mathematics, except for a very small amount of arithmetic, and I will try to do that here.

## 2. Predators large and small

Let's take salmon as an example. Salmon in the wild are subject to predation by a multitude of micro-predators (e.g., bacteria, viruses, parasites) and a few large predators (macro-predators) such as sharks, seals, sea lions and orcas. A predator that prevents prey populations from increasing indefinitely is said to regulate the prey. It is easy to see how this works: if there are many salmon, mother seals find salmon easier to catch, and so young seals have an increased chance of survival, and next year there are more seals searching for salmon. Micro-predators also proliferate when prey are plentiful, and for similar reasons: it's much easier to make a living and reproduce when prey are plentiful.

When an animal is preyed on by micro-predators it is referred to as a host rather than a prey. Thus, biologists talk about host-parasite systems and predator-prey systems. This nomenclature reminds us that in the first case the predator is very tiny and seldom kills its prey immediately, whereas in the second case the predator is comparable in size to the prey and usually kills the prey during capture.

With fish, we know that large predators are very good at sensing disease in their prey. Diseased fish are a little slower and weaker, and their schoolmates tend to shun them to the edge of the school. Accordingly, diseased fish are easier for large predators to capture. Capture of diseased fish by large predators has a regulatory effect on micro-predators because the micro-predators present on or in the prey get eaten right along with the prey and thus lose their chance to reproduce. This regulation of micro-predators by large predators isn't peculiar to fish; it is well documented in many predator-prey systems. The only exceptions seem to be parasites with life-cycles requiring multiple hosts.

One of the important things about a sea cage is that it excludes large predators while doing nothing to exclude micro-predators. Water flows freely through the mesh of the cage, carrying micro-predators in and out. Moreover, a sea cage confines the prey (farmed fish) at densities higher than those of wild fish. The regulatory effect of large predators on micro-predators is thus completely prevented by a sea cage, and it is not surprising to learn that disease is one of the greatest problems in sea cage aquaculture. In sea cage-farmed Atlantic salmon, for example, there are now well over 200 known infections, most of which were unknown or infrequent in wild Atlantic salmon. In one recent year, salmon sea-cage operators had costs exceeding US$100 million (twenty percent of revenues) due to sea lice alone.

**3. Sea lice**

Sea lice are parasitic copepods (tiny crabs) that graze on the surface of fish. They consume the tissue of their host fish, including the mucus layer of the skin, the skin itself, and the tissues beneath the skin. External layers of mucus and skin are very important to a fish, not only as barriers to infection, but also as part of the mechanism (called an osmoregulatory system) that a fish needs to maintain the concentration of salts in its body at an optimal level. When salmon begin their life cycle in fresh water, their skin works to prevent fresh water from entering tissues, and after they enter the ocean it works to prevent fresh water from leaving tissues. Punctures and lesions created by feeding sea lice compromise this system and lower the fitness of the host. Wounds created by sea lice require metabolic energy from the host in order to heal. More important, wounds provide a pathway into the host for bacteria and viruses in the surrounding water. When newly infected with sea lice larvae, juvenile salmon roll and flash, increasing their visibility to predators.

Biologists who study the population dynamics of parasites find it useful to distinguish two types of parasite: microparasites (including bacteria and viruses), which reproduce within the host fish, and macroparasites (including sea lice), which broadcast their offspring into the environment to find their own host or die. Most sea lice have roughly similar life-cycles, but to be specific I'll use the salmon louse *Lepeophtheirus salmonis* as an example. Leps, as they are often called by researchers, have a life cycle with eleven stages. Adult lice meet and mate on the host, and the female louse then generates a clutch of 200-800 eggs in paired strings. The eggs hatch into the water as larvae, called nauplii, which do not feed and are incapable of swimming or attaching to a host. After drifting around in the ocean for three to four days the nauplii transform into copepodids which also do not feed, but can propel themselves toward a close-passing host and attach to it. If a copepodid does not find a host within about five days, it dies. After capturing a host, the copepodid transforms into a chalimus stage, attached to the host by a small filament, around which it grazes. Eventually the chalimus stage transforms to the pre-adult stage, which can move around on the host to feed, and then to the adult stage in which it mates. Male lice leave females after mating, to seek other females, and females produce several clutches of eggs during their adult life. The complete life cycle takes from thirty to sixty days depending on factors such as temperature and salinity. Leps can survive for a while on hosts other than salmon, but can reproduce only on salmon. They cannot survive in fresh water for more than a few weeks.

The key to sea lice physics is that a female sea louse that completes her life cycle produces about a thousand larvae. Out of those thousand larvae, only two need to complete their life cycle in order to maintain the louse population. Biologists say that a sea louse is an R-strategist because it generates many offspring, of which only a few will survive. Sea lice researchers estimate that only half of sea lice larvae survive to the copepodid stage (infective stage), and that most copepodids die before capturing a host. To simplify the arithmetic needed later in this essay let's assume that each adult female louse produces 1000 larvae and that each larva that captures a host has a one fifth chance of completing its life cycle. Then only one in a hundred larvae must capture a host in order to maintain the sea lice population. To see that this makes sense, notice that (1/5)(1/100)=1/500, which is the chance each larva must have if two of the thousand larvae are to complete their life cycles and maintain the population.

Let's summarize the important facts about sea lice:

1. Sea lice steal metabolic resources from the host, compromise a host's osmoregulatory system, provide a pathway for secondary infections, and increase a host's risk of being eaten by large predators.
2. A mature female sea louse produces about a thousand larvae.
3. Sea lice larvae drift in the currents and cannot swim.

Now let's summarize the implications: From (1) it follows that sea lice increase, however slightly, the death risk (mortality rate) of their host. From (2) it follows that only two larvae out of every thousand must complete their life cycle in order to maintain the lice population. From (2) and (3) it follows that capture of a host by a larva is largely a matter of luck (randomness).

**4. The host density effect**

Suppose that the room in which you are reading this is a volume of ocean containing wild fish, but no farmed fish, and that you are a sea louse larva drifting about in it. This volume of ocean is closed, in the sense that you are unlikely to be carried outside of it by currents, which is why it does no harm to think of it as a room. The fact that the room in which you are reading is greatly different in shape from a volume of ocean defined by currents and probabilities doesn't matter; all that matters is that you will not be leaving it. Depending on the currents that carry you around the room, and the habits of the fish, you are more or less likely to have a fish pass near enough for you to capture it (infect it). If the fish all stay at one end of the room and the currents keep you at the other end of the room, your chances of capture will be poor. On the other hand, if the fish swim all through the room and the currents carry you all through the room, your chances of capturing a fish will be better. The important thing is that, in either of those scenarios, your chances of capture go up if there are more fish, and down if there are fewer fish. In other words, no matter what the environmental variables might be, your chance of capturing a fish is proportional to the number of fish. This is called the *host density effect*.

Continue to imagine yourself drifting around the room, hoping to find a host. Many other larvae are drifting too, with the same chance of survival as yours. After about five days your food stores will be exhausted. If the fish are so few that your chances of capturing one before you die are less than one percent, then the next generation of larvae is going to be smaller than your generation. On the other hand, if the fish are so numerous that your chances of capturing one are greater than one percent, the next generation of larvae will be larger than yours. You can see that for a small number of fish, sea lice will gradually die out, whereas for a large number of fish, sea lice will increase without bound.

Wait a minute, you might say. Sea lice have been in existence for a very long time without dying out, or filling up the ocean. What is going on to prevent either of those things from happening? The answer lies in the regulatory effect of sea lice under natural conditions. Recall that sea lice injure their hosts, and that although the injury is usually not great, it does reduce the chance that a wild fish will survive. If sea lice become very numerous, wild fish suffer higher mortality rates and their numbers decline; conversely, if sea lice become scarce, wild fish enjoy lower mortality rates and their numbers increase. Population levels of lice and fish fluctuate, but neither one of them grows without bound. In biology as in physics this situation leads to the concept known as *equilibrium*. Natural systems are never quite at equilibrium because of the time lag between input and response variables. However, it is still very helpful to remember that there *is* an equilibrium, and that if you have to bet on where the system is headed, it is much safer to bet that it is headed toward equilibrium rather than away from it.

**5. Sea lice epidemics on sea-cage farmed fish**

Once more, imagine that you are a larva and that the room in which you are reading this a the volume of ocean to which currents and other variables confine you. Now suppose that there are no wild fish in your room, only farmed fish in cages at the other end of the room. If currents carry you into one of the sea cages, you are likely to capture a farm fish, but if not, you are certain to die.

Suppose there are just a few sea cages with not many fish in them, so the chance of your capturing a host is just half a percent instead of the one percent needed to maintain the population. Then every generation of larvae will be half as large as the last. As a generation requires about two months, sea lice go through about six generations in a year. After a year, the number of larvae will have declined to (1/2)(1/2)(1/2)(1/2)(1/2)(1/2)=1/128 of its original level. This is known as an exponential decline. "Exponential" is now popularly used to mean a rapid increase of some quantity, but here I use the word in its exact technical sense.

Now suppose there are many sea cages, with many farmed fish in them, so the chance of your capturing a farm fish is two percent—twice as great as the one percent needed to maintain your numbers at their present level. After a year, the number of larvae will have increased to (2)(2)(2)(2)(2)(2)=128 times its original level—a phenomenon known as exponential growth. Large predators cannot get into the sea cages to eat infected farmed fish, and farmed fish are fed every day even if they are weak and slow, so farmed fish numbers are not regulated by lice.

You can see that sea cages and lice by themselves are an unstable system. If the number of farmed fish is greater than a certain level (the critical level), sea lice increase exponentially, but if the number of farmed fish is less than the critical level, sea lice decline exponentially. Unfortunately, the critical level depends on currents and temperature and harvest rates and treatment rates (the frequency at which farmers medicate their fish for lice), and many other variables that are impossible to calculate. The only way to tell that the critical level has been reached is that there is an epidemic of sea lice on farmed fish.

One thing that can be said about the critical stocking level of farmed fish is that it often moves in the opposite direction to water temperature and salinity. Sea lice thrive only within a definite range of temperatures and salinities. If temperature and salinity are outside those optimal ranges, sea lice do not reproduce as rapidly. What often happens in real-world sea-cage systems is that the stocking level of farm fish is sub-critical; then temperature or salinity suddenly increases into the optimal range causing the critical level to drop below the actual stocking level, and so a sea lice epidemic breaks out. Fish farmers understand this effect, qualitatively. What has not been appreciated is that the suddenness and severity of epidemics is explained by the exponential nature of the growth whenever the critical level is exceeded.

**6. Wild fish and sea-cage farmed fish together**

We saw above that in a model system consisting of wild fish and sea lice there is always an equilibrium to which the system slowly returns (or tries to return) when it is perturbed. In the real world, this equilibrium is a “moving target” because of exogenous variables such as weather, numbers of large predators, and so forth, and so the populations of fish and lice are constantly changing, trying to catch up with their changing equilibrium values. In order to understand the interaction of wild fish and farmed fish, we will assume that those exogenous variables are constant, and continue with the room analogy. As noted above, the room analogy can’t predict what will happen in every real-world situation, but it can tell us how to bet, which is sometimes enough to save us from disaster.

Imagine again that the room in which you are reading this is a volume of ocean containing wild fish, sea lice, and some seals that like to eat fish. Imagine that things are pretty much in equilibrium, which means that each larva drifting in the water has a one percent chance of capturing a fish. There is a lot of randomness because of the currents and the variable paths of the fish, so occasionally a lot of larvae get lucky at the same time, and lice numbers increase. Then the seals find those infected fish easier to catch, and so the number of fish declines. Then the larvae have correspondingly less luck finding a host, and so lice numbers decline toward their original level where each larva again has a one percent chance of finding a host. Although these fluctuations are interesting, we can ignore them because our goal is only to track the equilibrium point.

Now let’s put a sea cage at one end of the room, and put a few farm fish into it. The currents carrying larvae flow right through the mesh of the cage, so each larvae in the room now has a better chance of finding a host (host density effect), and lice numbers rise. The farmed fish are protected from the seals by their cage, so their number stays the same, even though they have more lice on them. The wild fish aren’t so lucky. With more lice on the wild fish, the seals find them easier to catch, so wild fish decrease in number. How far do they decline? Remember that the equilibrium point is the point at which each larvae has a one percent chance of capturing a fish; therefore the wild fish will decline until that is again the case. If the circulation in the room is such that the larvae have equal chances of capturing farm fish or wild fish, then the wild fish will decline by an amount equal to the number of farm fish.

To understand the increase in lice and decline of wild fish, it’s important to remember that a larva capturing a farm fish had a ninety-nine percent chance of failing to find a host if the farm fish wasn’t there. Thus, only a very tiny fraction of the larvae that capture farmed fish are larvae that would otherwise have captured wild fish—most of them would have died without finding a host. That is why farmed fish cause a rise in the level of larvae even when the numbers of lice on them are lower than the numbers of lice on wild fish. If you don’t mind arithmetic and high-school algebra, see the more detailed treatment of this important point in Appendix A.

So far, we have assumed that farm fish and wild fish have equal chances of being captured by a larva. What if the currents in the room are such that the wild fish and the larvae from their lice are mainly confined to one end of the room, and that the sea cage is at the other end of the room. In that case, the sea cage fish don’t much increase a larva’s chance of finding a host, so larvae numbers rise only slightly and wild fish numbers fall only slightly.

What effect does farm harvest rate have on the situation? If you harvest your farm fish and replace them with young fish at about the same rate that the wild fish die and are replaced, then from a larva's point of view a farm fish is much like a wild fish. However, if you leave your farm fish in the cage for only a fraction of a wild fish life-cycle, then the larva that capture those farm fish won't have as much time to reproduce, so lice levels won't rise quite as much and wild fish won't decline quite as much. Fish farmers refer to the time that their fish are in the cage as the grow-out time. Short grow-out times of farm fish are therefore good for wild fish.

Up to this point the imaginary sea cage at the far end of the room has held only a few farm fish. What if we fill it with farm fish, or add another sea cage beside it, and fill both of them? Recall from above that there is a critical level of farm fish. Below that critical level, if wild fish are not around to re-infect them, lice on the farm fish will decline exponentially to zero. However, above that critical level, lice on the farm fish will increase exponentially. You can see that if the stocking level of our farm fish is above the critical level there is no equilibrium point for wild fish. Lice just keep increasing, and wild fish keep declining, until the wild fish go extinct. That last wild fish, covered with sea lice, is easily caught by the seals. For the seals in our imaginary room, it is feast followed by starvation.

**7. The reservoir host effect**

To understand the reservoir host effect, it will be helpful to first consider the case where no sea cages are present, but this time with a slightly more complex room model. Where before we imagined one room with wild fish and sea lice, now we imagine two rooms connected by a hallway, with little movement of water between the rooms. Let's call them room A (for adults) and room B (for birth). The wild fish spend most of their time in room A, but every autumn some of them migrate to room B for a brief period to mate and spawn, then return to room A. The fish eggs in room B take about six months to hatch, and after they hatch in the spring, the juvenile fish slowly migrate down the hall to room A to join the adults.

Consider sea lice in the two-room model: When the adults in room A migrate down the hall to room B, the lice attached to the adults put larvae into the water, and soon Room B has almost as many larvae as room A. When the adult fish have finished mating and laying their eggs in room B, they leave on their return migration to room A. With no hosts left in room B, all the larvae left there soon die. When the fish eggs in room B hatch, the young fish enter an environment without larvae. This is fortunate for them, as the effects of sea lice on mortality are roughly proportional to body mass: a few lice on an adult fish increase the chance of death only very slightly, whereas the same number of lice on a tiny juvenile fish make its death nearly certain. As they grow, the juvenile fish slowly migrate down the hall toward room A. About halfway down the hall—a year has now elapsed since the migration of their parents to room B—the juveniles migrating toward room A meet another cohort of adults migrating in the opposite direction. By this time, the juveniles are large enough that a few lice do not dramatically increase their mortality rates. In the life-cycle of the fish, room B functions as a refuge from sea lice for juvenile wild fish.

Now suppose we put sea cages in room B. When the adult wild fish arrive there to mate and spawn, their lice will also be putting larvae into the water, and those larvae infect the farmed fish. If stocking levels are sub-critical, the lice on the farmed fish decline over the next six months while wild fish are absent, and when the juvenile wild fish hatch there are some larvae in the water, but not many. However, if farm stocking levels are above the critical level, lice increase exponentially on the farm fish over the winter, and the juvenile wild fish emerge into water full of larvae. Their mortality rates will be very high. The sea cage fish in room B are said to function as a *reservoir host* for sea lice.

The reservoir host effect is especially relevant to sea cages located on coasts with runs of wild salmon. When adult wild salmon migrate from the open ocean past the sea cages on their way to their natal rivers to spawn, larvae from the adult lice on the wild salmon infect the farmed fish in the cages. The farmed fish provide a reservoir host for lice over the winter when adult wild salmon are absent. In spring, the juvenile wild salmon must pass the sea cages on their out-migration to the open ocean, and while passing they become infected by larvae from the lice on the sea-cage fish. Pink and chum salmon are particularly vulnerable in this regard because they enter salt water very soon after hatching, weighing a gram or less.

**8. Conclusions**

It is well known that in order to minimize lice transfer between farmed and wild fish one should keep them as far apart as possible for as much of the year as is possible, perhaps by locating sea cages in places wild fish seldom go. However, it is widely imagined that keeping lice levels on farm fish at or below those on wild fish (by chemical treatment, for example) is sufficient protection for sympatric wild fish. What they fail to note is that most of the larvae that capture farmed fish are larvae that would have died if the farmed fish were not present. We have seen that this is a direct consequence of the randomness of larval capture and the great numbers of larvae produced by female sea lice. We also saw that in order to hold wild fish harmless from lice on farmed fish it is necessary to keep lice levels on farmed fish at surprisingly low levels. In Appendix A we estimated that if farm fish are equal in number to wild fish, lice levels on farmed fish need to be kept to less than 1/20 of their levels on wild fish.

Using basic physics, we showed that a system of farmed fish and sea lice is unstable because it has no regulatory feed back other than what farmers choose to provide by more frequent treatment and shorter grow-out times, both of which require financial sacrifice. The instability of the farmed fish-sea lice system is manifested in a critical stocking level of farmed fish. Above the critical level, epidemics of lice are nearly certain, and below it lice decline rapidly. In Appendix B we noted that an exponential increase in lice on farmed fish must eventually extinguish wild fish, and used this fact to derive a simple equation that estimates the equilibrium level of wild fish sympatric with sea-cage farmed fish.

**Appendix A. The probability a larva will capture a wild fish**

We noted above that when sea cages are placed in a system of wild fish and sea lice, and wild fish are assumed not to decline, the probability that an individual larva will capture a wild fish is reduced only slightly by the presence of the farmed fish. The reason for this is that most larvae die without finding a host, and so most of the larvae that capture farmed fish would otherwise have died. Here we show that this is so using elementary physics.

For an individual copepodid, the probability of capturing a host goes to zero when the number of hosts goes to zero, and to unity as the number of hosts goes to infinity. We express this by writing

$$p = H/(H_0 + H), \tag{A1}$$

where $p$ is the probability of capture, $H$ is the number of hosts in the system, and $H_0$ is called a filter. Notice that when hosts are scarce, the term $H$ in the denominator becomes insignificant compared to the filter, and the probability of capture is approximately $H/H_0$.

We noted above that in a system without farm fish, the equilibrium probability that a larva will capture a wild host is 1/100. Denoting the number of wild hosts by $W$, and the equilibrium number of wild hosts by $W^*$, it follows that

$$0.01 = W^*/(H_0 + W^*). \tag{A2}$$

Solving for the value of the filter, gives $H_0 = 99W^*$.

Now let's add some farm fish to the system. To keep things simple, we suppose that larvae from lice on the farm fish and larvae from lice on the wild fish are well mixed by ocean currents, so that the chance a larva will capture a farm host is the same as its chance of capturing a wild host. We also assume that wild hosts do not decline because of the excess larvae. Then, by equation (A1) the probability of capture must rise to the value

$$p(F,W^*) = (F + W^*)/(H_0 + F + W^*). \tag{A3}$$

By our mixing assumption, the probability a larva will capture a wild fish is equal to the probability of capture multiplied by the fraction of fish that are wild, $W^*/(F + W^*)$. Denoting this probability by $p_W$, we have

$$p_W(F,W^*) = W^*/(H_0 + F + W^*). \tag{A4}$$

From the situation where only wild are present, to the situation where farmed fish are also present, the probability that a larva captures a wild fish changes by

$$\frac{\Delta p_W}{p_W} = \frac{p_W(0,W^*) - p_W(F,W^*)}{p_W(0,W^*)} = \frac{-F/W^*}{100 + F/W^*}\ . \tag{A5}$$

This last equation shows that even when there are as many farm fish as wild fish, and wild fish are (somehow) held to their pre-farm equilibrium level, the probability that a larva will capture a wild fish declines by less than one percent. Clearly, most of the larvae that capture farm fish would otherwise have died. Without doing any more mathematics, you can guess that in order not to increase larval densities in the water it will be necessary to hold lice levels on farm fish at a very small fraction of their levels on wild fish, either by chemical treatment or short grow-out times. Recalling that only a fifth of larvae that capture a host are able to complete their life cycle, we infer that lice levels on farm fish must be held to less than (5)(1/100) = 1/20 of their levels on wild fish, in order that wild fish levels not decline.

**Appendix B. The equilibrium level of wild fish when farmed fish are present**

In Appendix A we assumed that the level of wild fish did not decline when farmed fish were added to the system. However, we know that wild fish must decline to the point at which the probability a larva will capture any fish is again 1/100, for otherwise the density of larvae will be so great that wild fish must decline further. Setting the capture probability to its equilibrium value gives

$$0.01 = (F+W)/(H_0+F+W), \tag{B1}$$

and substituting $H_0 = 99W^*$ gives the relation

$$W + F = W^*. \tag{B2}$$

In other words, the equilibrium number of wild fish is reduced by the number of farm fish in the system. This result assumes that water circulation is such that farm fish and wild fish are equally exposed to larvae. Obviously, when farm fish and wild fish are widely separated, the decline in wild fish will be smaller. We recognize this by introducing a coefficient of sympatry $\varepsilon$ for farm fish, and replacing *F* everywhere above by $\varepsilon F$ . In particular, (B2) becomes

$$W + \varepsilon F = W^*. \tag{B3}$$

in which $\varepsilon$ can have values between zero (zero mixing of larvae from farm and wild fish) and one (all larvae have equal access to farm and wild fish).

The value of $\varepsilon$ in a particular area can be found by noting the value of *F* at which lice epidemics become frequent in the associated farm system. To do this, first recall that lice epidemics are associated with exponential growth of lice in the farm system, and that exponential growth of lice on farm fish must eventually extinguish wild fish. Letting $F_x$ denote the level of *F* at which farm epidemics become frequent, equation (B3) gives $\varepsilon F_x = W^*$, hence $\varepsilon = W^*/F_x$. In other words, the sympatry index is the pre-farm, equilibrium level of wild fish, divided by the level of farm fish at which farm epidemics begin. Substituting this result into (B3) gives a more useful version of the relation between farm fish and wild fish.

$$W/W^* + F/F_x = 1. \tag{B5}$$