Sea lice physics without the math
(why sea-cage fish cause wild fish to decline)[1]

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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. Here I use elementary physics to explain why sea-cage finfish aquaculture causes the abundance of sea lice on sympatric wild fish to increase, and why increased sea lice abundance on wild fish causes their numbers to decline. Physics is important for this question because 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 concept of *equilibrium*, the *host density effect*, the *reservoir host effect* and why epidemics of sea lice on farmed fish occur in some localities and not others. 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 physics 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 arcana such as flow diagrams and differential equations. 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.

In all systems that have been studied, it has been found that large predators are good at detecting weakness in their prey. Diseased fish tend to be slower and weaker than healthy fish, 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, or if they escape that fate, they may die without finding another host. The only exceptions to this rule are parasites with life-cycles requiring multiple hosts; for them, being eaten is part of the plan. Sea lice are not in this category since they require only one host fish to complete their life-cycle.

One of the important things about a sea cage is that it excludes large predators but not 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 are infrequent or rare in wild Atlantic salmon. In one recent year, salmon sea-cage operators had sea-lice related costs exceeding twenty percent of revenues.

3. Sea lice
Sea lice are parasitic copepods (tiny crabs) that graze on the surface of fish. They consume 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 about two months depending on factors such as temperature and salinity. Under optimal conditions the life-cycle can be as short as a month, while under extreme conditions it can stretch to four months. Leps can survive for a while on hosts other than salmon, but can reproduce only on salmon and closely related species, collectively known as salmonids. Leps and other sea lice cannot survive in fresh water for more than a few weeks.

The key to sea lice physics is to focus on larvae. A female sea louse that completes her life cycle produces about a thousand larvae. Assuming equal numbers of males and females, only two of those thousand larvae must complete their life cycle in order to maintain the population. Animals that generate many offspring, of which only a few survive, are known in biology as reproductive-strategists, or simply R-strategists, and sea lice are an example. Sea lice researchers estimate that less than half of sea lice larvae survive to the copepodid stage (infective stage), and that most of those copepodids die before capturing a host. To simplify the arithmetic let's assume that each larva that captures a host has a one fifth chance of completing the remainder of its life cycle, and that there are an equal number of males and females. 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 original larvae are to complete their life cycles.

If you had trouble with that last paragraph, don't worry. All scientific writing contains bits that require thought, and perhaps re-reading on another day, which is why most scientists read with pencil in hand. In science, that is what you pay to play, and even having a PhD doesn't get you a discount.

Let's summarize the important facts about sea lice:

1. Sea lice steal metabolic resources from the host, damage the host's osmoregulatory system, provide a pathway for secondary infections, and increase the 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 very different in shape from a volume of ocean defined by currents and probabilities doesn't matter; all that matters is that you, the larva, 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. 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 roughly 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 essay is 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 your 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 in this essay 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 tends to return when it is perturbed. In the real world, this equilibrium is a moving target because of exogenous variables such as climate, 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 larva 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 larva 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 exposure to farm fish and 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 recall that each larva has only a one percent chance of capturing a wild fish. Ninety-nine percent of the larvae would die without ever capturing a host if the farm fish weren't present. This large number of surplus larvae means that the probability of capture is proportional to the total number of fish present. If we double the number of fish by adding as many farm fish as there are wild fish, then, to a very good approximation, the number of larvae that capture a host will double. In other words, to a very good approximation, the number of larvae that capture farm fish is not subtracted from the number of larvae that capture wild fish. Put another way, the lice on farm fish are surplus lice, and the larvae they produce are surplus larvae.

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 increase a larva's chance of finding a host by much, so larvae numbers rise only slightly and wild fish numbers fall only slightly.

What effect does farm harvest rate have on the situation? If we harvest the 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 we leave the 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 stocking 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 the critical stocking level, lice on the farm fish will increase exponentially. You can see that if the stocking level of 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. Of course, in real situations farmers do not allow the lice levels on their fish to grow without bound, so wild fish may or may not go extinct; it depends on how many farm fish are present. If enough farm fish are present, then even very low levels of lice on farm fish can be enough to extinguish wild fish.

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, after which they 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: As the adults in room A migrate down the hall to room B, their lice release 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, the larvae left there die without finding a host. When the fish eggs in room B hatch, they enter an environment without sea lice 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 would 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 a 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 wild fish, room B functions as a refuge from sea lice for juveniles.

Now suppose we put sea cages in room B. The farm fish in the cages initially have no lice. When the adult wild fish arrive there to mate and spawn, their lice are releasing larvae into the water, and those larvae infect the farmed fish. If farm 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 while adult wild salmon are absent. In spring, the juvenile wild salmon must pass the sea cages on their out-migration to the open ocean, so they are 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, many people imagine 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. This is a direct consequence of the randomness of larval capture and the large numbers of larvae produced by female sea lice. The lice on farmed fish thus generate extra larvae in the water, and higher levels of infection on sympatric 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. We saw that the instability of the farmed fish-sea lice system is manifested in a critical stocking level of farmed fish. Above the critical stocking level, lice increase exponentially, and below the critical level lice decline. The critical level depends on conditions such as ocean currents, that are poorly known, and conditions that can change rapidly, such as temperature and salinity. Thus, a fixed stocking level in a farm system can be sub-critical under some conditions and super-critical under others.

As sea lice are harmful to fish, they must regulate fish populations, at least to some extent. Thus increased levels of sea lice cause wild fish to decline. As increased farm fish cause increased sea lice, it follows that increased farm fish cause wild fish to decline. At sub-critical stocking levels, mathematics are needed to estimate the magnitude of the decline. However, mathematics are not needed to understand that when a farm system is super-critical, sympatric wild fish decline toward extinction.

Acknowledgment

Some of the material above is adapted from:
Frazer, L.N. (2007), Comment on “Sea lice on adult Pacific salmon in the coastal waters of British Columbia, Canada” by R.J. Beamish et al., *Fisheries Research*, **85**, 328–331.
