Size structured fish populations

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17 March 2017

Introduction

Fish grow several orders of magnitude during their life. They start out as tiny eggs and larvae with a weight around 1 mg, and grow to adult sizes between 1 g and about a ton (Figure 1). Because of the big difference in size, they change fundamentally physically and in physiological ability: their growth rate decreases during life – small organisms double in size with a faster rate than large organisms. Their mortality risk also declines as small organism are much more likely to be eaten than large ones. Their size are also important for their risk of being caught by fishing gear – all fishing gear is size selective, and size also determines their commercial potential – large individuals typically obtain a high per kg price than smaller individuals. Considering therefore the physiology and the exploitation of fish (from fishing or farming), body size of individuals is a key variable. It is therefore obvious to organise a mathematical description of a fish population according to their size distribution.

The size distribution $n(x)$, where x is the body mass, is a "density function" representing the density of number of individuals per size range. In other words, the number of individuals in the size range x_1 to x_2 is:

$$\int_{x_1}^{x_2} n(x,t)\,\mathrm{d}x, \tag{1}$$

and the biomass in the same size range is:

$$\int_{x_1}^{x_2} n(x,t)x\,\mathrm{d}x. \tag{2}$$

We can determine the size distribution $n(x,t)$ if we know the growth rate $g(x)$ and the mortality rate $\mu(x)$ of individuals. The size distribution follows from the fundamental conservation equation derived in Box 1:

$$\frac{\partial n(x,t)}{\partial t} + \frac{\partial g(x)n(x,t)}{\partial x} = -\mu(x)n(x,t). \tag{3}$$

In steady state the conservation equation is reduced to an ordinary differential equation:

$$\frac{\mathrm{d}g(x)n(x)}{\mathrm{d}x} = -\mu(x)n(x). \tag{4}$$

BOX 1: THE MCKENDRIC-VON FOERSTER EQUATION

The conservation equation can be derived by considering a small range of body sizes from x to $x+\Delta x$ (Figure 2). We assume a size distribution $n(x)$, which represents the abundance density, i.e., number of individuals per weight. The number of individuals within that size range is $\approx n(x)\Delta x$. The rate at which individuals from the size class of smaller individuals is growing into the range, the "flux" of individuals, is $g(x)n(x)$. During a short time interval, Δt, the number of individuals growing into the size range is then $g(x)n(x)\Delta t$. Similarly, the number of individuals growing out is $g(x+\Delta x)n(x+\Delta x)\Delta t$. In the same time interval some individuals within the size range will die. The number of deceased individuals is approximated by the total number in the interval $n(x)\Delta x$ multiplied by the mortality $\mu(x)$ and the length of the time interval: $n(x)\Delta x\mu(x)\Delta t$. Combining the growth in and out of the interval with the mortality gives the total change in the number of individuals within the size range $\Delta n\Delta x$ as:

$$\Delta n(x,t)\Delta x = g(x)n(x,t)\Delta t - g(x+\Delta x)n(x+\Delta x,t)\Delta t - n(x,t)\mu(x)\Delta x\Delta t. \tag{B1.1}$$

As the size range is short, the growth at $x+\Delta x$ can be approximated by a Taylor expansion: $g(x+\Delta x) = g(x)+g'(x)\Delta x+\mathscr{O}(\Delta x^2)$, where $g'(x)$ is the derivative with respect to x, and similarly for the size distribution at $n(x+\Delta x,t)$. Inserting the expansions in (B1.1) and simplifying gives:

$$\frac{\Delta n(x,t)}{\Delta t} = -g'(x)n(x,t) - n'(x,t)g(x) - n'(x,t)g'(x)\Delta x - n(x,t)\mu(x). \tag{B1.2}$$

When we consider the limit $\Delta x \to 0$, the third term disappears. Taking the limit $\Delta t \to 0$, and recognizing that $g'(x)n(x,t)+n'(x,t)g(x) = \partial(g(x)n(x,t))/\partial x$, gives the conservation equation (3).

In the biological literature the conservation equation is referred to as the "McKendric-von Foerster equation". It is however a very standard equation that occurs in problems involving transport process: the field $n(x,t)$ is advected (transported) along the x axis with velocity $g(x)$, and at the same time it is lost with a rate $\mu(x)$.

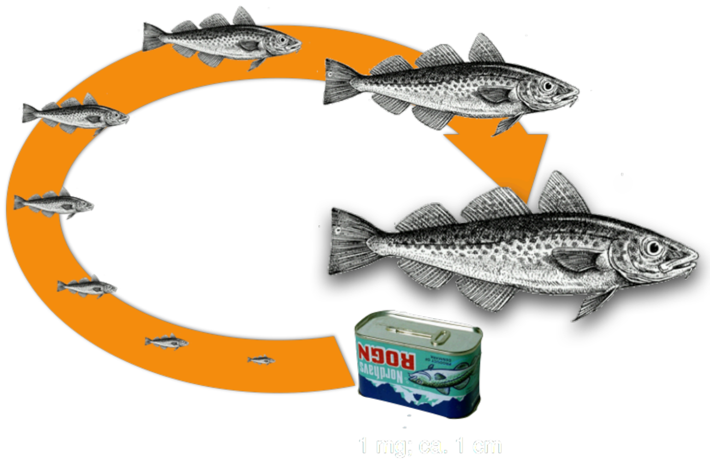


Figure 1: Fish grow over a large size range during their life, from eggs around 1 mg to adult sizes between 1 g and 1 ton. The cod shown in the figure matures at a size around 3 kg but continues to grow to around 20 kg.

1 Solving the conservation equation

First, solve the conservation equation (4). Assume that the growth rate (mass per time) and the mortality rate (per time) are power law functions:

$$g(x) = Ax^b \quad \text{and} \quad \mu(x) = \alpha x^{b-1}, \tag{5}$$

where $b = 3/4$ and A and α are positive constants. The solution is of course only given up to an unknown integration constant – we'll return to that constant in the last exercise. Introduce now the constant $a = \alpha/A$ into the solution and write it the simplest possible form. Plot the abundance distribution $n(x)$ (Use logarithmic axes wherever appropriate).

Using equation (2), calculate and plot the biomass of individuals in exponentially increasing size groups, i.e., in the size range x to cx where c is an arbitrary positive constant larger than 1 (try "octave" groups $c = 2$ or base-10 groups $c = 10$). Remember that $n(x)$ is the abundance distribution; the biomass is formed by multiplying with x. Plot the biomass as function of size x. A typical value of a is around 0.3.

2 What is the biomass of a cohort of fish?

A cohort of fish (or any other organisms) are those individuals born at the same time or in the same batch. Let us assume that a cohort is born within a time interval Δt. What is the biomass of this cohort? How does it increase with size? – and with age?

A simple approximation of the cohort biomass can be made as:

$$c(x) = \int_x^{x+\frac{dx(t)}{dt}\Delta t} n(\xi)\xi \, d\xi \approx n(x)x\frac{dx(t)}{dt}\Delta t. \tag{6}$$

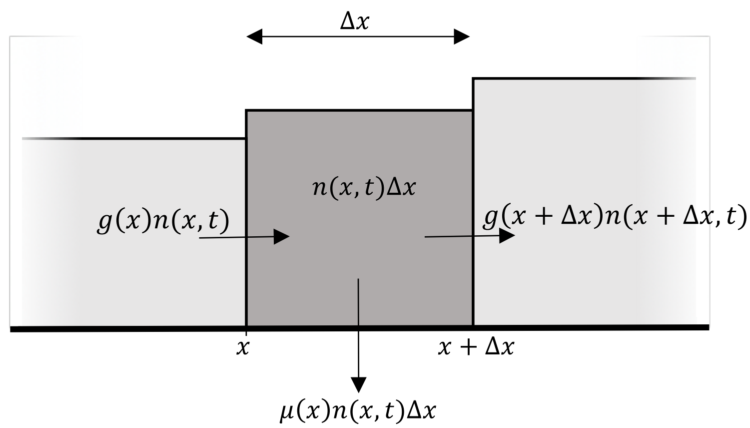


Figure 2: Sketch of the balance between growth and mortality in a size group containing $n\Delta x$ individuals in the size range x to $x+\Delta x$. The flux of individuals growing into the group (numbers per time) is the growth rate multiplied by the abundance at the boundary $g(x)n(x,t)$, and likewise the flux of individuals growing out is $g(x+\Delta x)n(x+\Delta x,t)$. The flux of individuals disappearing from the group is given by the mortality multiplied by the abundance $\mu(x)n(x,t)\Delta x$.

How does this solution match up with the exact solution?

3 Now add fishing

How does the population respond to fishing – and how should we fish to optimize the production of biomass? Assume that a species has a maximum body size x_∞ and that fishing acts on all sizes $x_F \leq x \leq x_\infty$. Then we can write the mortality in the fished size range as:

$$\mu(x) = \begin{cases} \mu(x) = \alpha x^{b-1} & x_0 < x < x_F \\ \mu(x) = (\alpha+\alpha_F)x^{b-1} & x \geq x_F \end{cases} . \tag{7}$$

Plot the mortality for various values of α/α_F and starting at different sizes w_F.

Write the piece-wise solution for $n(x)$ in a log-log plot. Introduce the new fishing constant $a_F = \alpha_F/A$ and write the solution in a simple form. Plot the solution for a species with offspring size $x_0 = 1$ g (they are really much smaller, but it does not matter for these calculations), and maximum size $x_\infty = 1000$ g, and for various values of the fishing constant a_F. Choose a suitable value of the size where fishing starts x_F.

The yield from the fishery (mass per time) is the integral of the abundance $n(x)$ multiplied by the weight x and the fishing mortality $\alpha_F x^{b-1}$:

$$Y = \int_{x_F}^{x_\infty} n(x) x \alpha_F x^{b-1}\,\mathrm{d}x \tag{8}$$

Solve for the yield. Plot the yield as a function of fishing mortality and as a function of the size where fishing start. How should we fish a stock to get the highest yield?

Extra: solve it for a fishing mortality that is constant with size, i.e., $\mu(x) = \alpha x^{b-1} + \mu_F$.

Extra: the size-selectivity of fishing gear varies greatly between different gear types (Box 2). How is yield maximized with different types of gear? Answering this question involves developing numerical solutions to the conservation equation. See here for an interactive demonstration of a numerical solution.

4 How fast can a fish stock recover?

A central issue in fish stock management is the rate at which a fish stock is able to recover from over-fishing. Assume that we have a depleted fish stock. How fast will it increase in abundance? To answer that question we need to solve the time-dependent conservation equation 3. Since this equation is a partial differential equation, it is not easy to solve right away. However, we can solve it by making an inspired *ansatz*. Let us assume that the solution can be written in the form:

$$n(x,t) = e^{rt} f(x). \tag{9}$$

This solution assumes that the population will grow exponentially with growth rate r and with a size-distribution $f(x)$.

Insert the ansatz 9 in 3 and solve it for $f(x)$. How does this solution compare with the equilibrium solution found earlier? Why are the two solutions not identical?

The solution $f(x)$ gave the size distribution, but not the population growth rate r. To find the growth rate we need to know the reproductive output of the fish population. Assume now that when fish become mature, at a size x_m, they stop growing further and instead invest their energy in reproduction. The reproductive output then becomes (measured in biomass per time):

$$R = \varepsilon g(x_m) n(x_m,t) x_m, \tag{10}$$

where $\varepsilon \approx 0.01$ is an efficiency of the reproduction that accomodates the costs of reproduction, mortality of eggs etc.. The new offspring enters the size distribution at the smallest size x_0. We can then write a boundary condition to the conservation equation (3) as:

$$g(x_0) n(x_0,t) x_0 = R. \tag{11}$$

Insert the ansatz (9) and the solution to $f(x)$ in the boundary condition (11) and solve for the growth rate r. Plot the population growth rate as a function of the size of the adult fish x_m. How long time will it take a population of herring-like fish ($x_m \approx 100$ g) to recover a factor of 10 in biomass? And cod ($x_m \approx 10000$ g)? What is the smallest adult body size that gives a viable population?

Extra: how large a fishing pressure can the population withstand before it collapses (at $r = 0$)?

BOX 2: SIZE SELECTIVITY OF FISHING GEAR

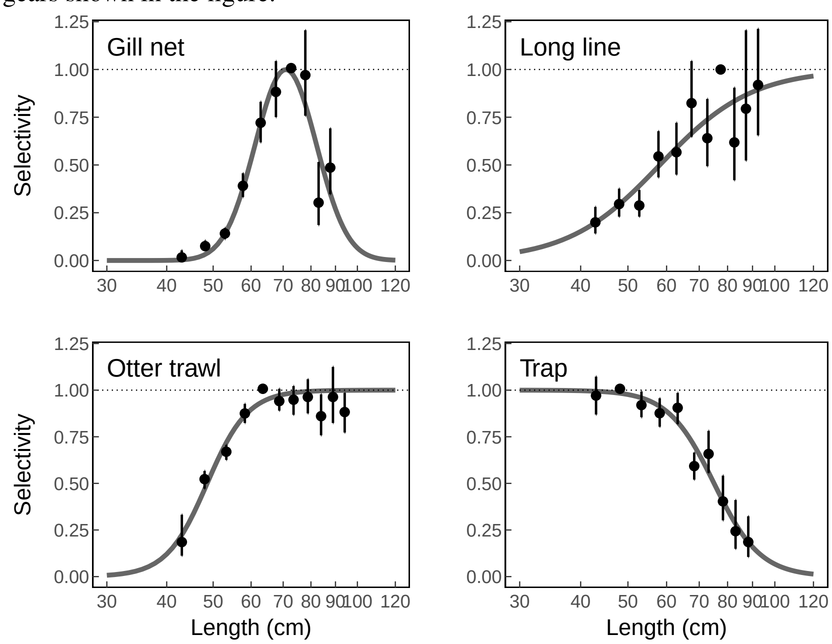
The selectivity of a trawl is a sigmoidal function:

$$\psi_{\text{trawl}} = (1 + (x/x_F)^{-\sigma_F})^{-1}, \tag{B2.1}$$

where x_F is the inflection point at the size with 50% retainment, $u = 3$ is a non-dimensional parameter describing the sharpness of the selection around the size of 50% retainment; $u \to \infty$ gives a "knife-edge" selectivity. Fisheries employ a mesh size suitable for the targeted species: the larger the species, the larger the mesh size is used, and therefore the larger the value of x_F. I assume that x_F is proportional to x_∞: $x_F = \eta_F x_\infty$ with $\eta_F \approx 0.05$. Gill net selectivity is described by a log-normal function:

$$\psi_{\text{gillnet}} = \exp\left[-\log^2(x/x_F)/\sigma_F^2\right] \tag{B2.2}$$

where x_F is at the maximum and $\sigma_F \approx 1.5$ characterizes the width.
The figure below shows the selectivity of various fishing gear on cod. Gill nets are fitted with a log-normal selection curve (B2.2) and the other gears with a sigmoidal function. (B2.1). The values of σ_F are 1.5, 2, 3 and 3 for the four gears shown in the figure.



5 Why do fish make small eggs?

Fish have a peculiar life-history strategy: they make very many, very small eggs. A typical egg size of a fish is 1 mg: small herring make eggs of around 1 mg, cod make many eggs of around 1 mg, and even several 100 kg large tuna make tremendous amounts of eggs of around 1 mg. Why do they do that? Most eggs and small fish die before they reach maturity and can themselves have a go at reproducing (the Bob Dylan principle: "I'm bound to get lucky, or I'm bound to die trying"). What is the chance of survival of an egg to a certain size? The survival is:

$$P_{x_0 \to x} = \exp\left[-\int_{x_0}^{x} \frac{\mu(x)}{g(x)} \mathrm{d}x\right]. \tag{12}$$

Calculate and plot the survival. Clearly, the chance of survival is slim for a small egg from a large tuna. The upside for the tuna is that once they are adults, they have a capacity to make very many eggs, as given by (10). We can form a proxy of the a populations fitness as the product of the survival from eggs to adults and their reproductive rate R. Plot the fitness for a tuna ($x_m = 100000$ g) as a function of the egg size x_0. What is the approximate solution (*asymptotic solution?*) for $x_0 \to 0$? Speculate why fish do not make eggs even smaller than 1 mg [1].

6 Solutions to the size distribution with realistic growth rates

Previously we have used a simple power-law function to describe growth. However, fish do not continue to grow, rather growth slows down as they reach maturity. The typical way to describe growth of fish (and many other organisms [2]) is with a von Bertalanffy growth function:

$$g(x) = \frac{\mathrm{d}x}{\mathrm{d}t} = Ax^b - Bx. \tag{13}$$

Find the maximum size x_∞ when growth stops, i.e., when $g(x_\infty) = 0$. Reformulate (13) in terms of x_∞ instead of B. Solve the differential equation to find weight-at-age $x(t)$ (hint: do not do it for general values of b but enforce $b = 3/4$). Plot the size as a function of age, $x(t)$ for different values of x_∞, and compare it with a solution of the simple growth equation $g(x) = Ax^b$ (a typical value of A is 5 $\mathrm{g}^{0.25}$/year.

Solve the conservation equation with von Bertalanffy growth rate (13). Write it in a simple form. How does this solution compare to the simple solution derived earlier? What is the asymptotic limit of the size spectrum as $x \to x_\infty$?

References

[1] Erik A Martens, Navish Wadhwa, Nis Sand Jacobsen, Christian Lindemann, Ken Haste Andersen, and André Visser. Size structures sensory hierarchy in ocean life. *Proceedings of the Royal Society B*, 282:20151346, 2015.

[2] G B West, J H Brown, and B J Enquist. A general model for ontogenetic growth. *Nature*, 413:628–631, 2001.