## Mathematical models can help to better manage fishing

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Fishing provides an important part of the food for people in some developing countries. This can lead to a worrying cascade of overfishing, collapsing catches and rising market prices, and the extinction of many species. How can we prevent this situation from becoming catastrophic and, on the contrary, stabilize it?

Mathematical modelling, by coupling ecological and economic dynamics, provides a better understanding of the dynamics of
fisheries systems. It is presented here in a basic way and illustrated by the particular case of thiof, an emblematic species threatened in Senegal.

## 1. Trophic interactions within marine ecosystems



Figure 1. Engraving "big fish eat small fish" inspired by Bruegel the Elder. [Source: From Harris Brisbane Dick Fund, 1917, Pieter van der Heyden (ca. 1525-1569). Metropolitan Museum of Arts, New York]

A particularly structuring element of marine ecosystems is that trophic interactions depend on the size of individuals [1]: large fish eat small fish (Figure 1). As a result, an operation targeting large species, or small species, will have different cascading effects on all trophic levels of a marine ecosystem. Broadly speaking, in the first case, the decrease in the abundance of large species, such as tunas, leads to an increase in the abundance of smaller species on which tunas feed, such as sardines. This increase itself leads to the decrease of species on which sardines feed, such as zooplankton, and finally to the increase of zooplankton prey, phytoplankton (Figure 2, left part) [2].


Figure 2. Schematic representation of the effect of a fishery targeting large (left) or small (right) species, cascading along trophic levels. [Source: Reproduced with permission from Cury et al. 2001, reference [2]]

In the second case where the fishery directly targets sardines, the decrease in their abundance results in both a decrease in tuna and an increase in zooplankton, resulting in a decrease in phytoplankton (Figure 2, right part). In this simplified vision, the strategy would be to exploit species of increasingly smaller size, and therefore trophic level, leading to the phenomenon of " fishing down the food web" [3]. In reality, food webs are more complex, but there are many examples corroborating this pattern of exploitation of species high in the food chain that has led to the disruption of the structure and functioning of marine ecosystems (Figure 3) [4].


Figure 3. Simplified representation of an estuarine food web before (left) and after (right) fishing exploitation. [Source: Reproduced with permission from Jackson et al., 2001, reference [4]]

## 2. Basis of the fishing economy

In theory, the exploitation of a species can lead to its extinction if its price increases faster than the cost of its exploitation when the level of abundance decreases_[5], or if its distribution area contracts as a result of exploitation, without a significant increase in cost [6]. In practice, while global extinctions of marine species are rare, their local extinction, or the disappearance of their ecological or economic role, is not [7]. To achieve the ecologically and economically sustainable exploitation of marine resources, the application of fisheries management measures using a multidisciplinary [8] and ecosystem [9] approach is the recommended approach. The spatialization of the marine environment and its uses, including fishing, is a major challenge. In particular, economic zoning, such as exclusive economic zones, and areas dedicated to conservation, such as marine protected areas, must be ecologically coherent.


Figure 4. Evolution of "thiof" catches in Senegal at different landing ports. [Source: Reproduced with permission of Thiao et al. 2012, reference [10]]

A large part of commercial fish species are overexploited. The main species affected by overfishing are cod in Newfoundland, sardines in California, anchovies in Peru, herring in the North Sea and Epinephelus aeneus, better known as "thiof", along the Atlantic coast of West Africa. This grouper is called thiof in Senegal, a word borrowed from Lebou and Wolof vocabulary. Thiof was traditionally used in the preparation of the Senegalese national dish, thiep bou dien, composed of fish, various vegetables and rice. Thiof catches only decreased in Senegal until 2006 (CRODT data [10], Figure 4).


Figure 5. A, Artisanal fishing fleet, Soumbédioune beach, Senegal. B, Industrial fishing off Seychelles. [Source: Photos: left: © IRD Joëlle Vincent; right: © IRD - Jean-Pierre Hallier]

Fishing is essential for the economies of many developing countries. Local commercial species are exploited by artisanal fishing fleets (Figure 5A). Intensive exploitation is also carried out by industrial fishing under fisheries agreements with developing country governments (Figure 5B). Fish are an important source of food for local populations. When catches collapse due to overfishing, market selling prices increase, making it increasingly difficult for the poorest populations to access the resource.

## 3. A simple mathematical model of the evolution of the biomass of an exploited species

It is therefore important to understand the mechanisms that govern the dynamics of commercial fisheries. The management of marine resources must be based on decision-making tools that enable managers and decision-makers to take measures for the conservation and optimal exploitation of fisheries. Mathematical modelling makes it possible to develop such tools in order to predict the effects of coastal development and fisheries control measures.

Mathematical models in fisheries are based on assumptions about the production and extinction mechanisms of harvested species.

We will now present a classical model with only one variable $x(t)$, the biomass of the exploited species, depending on the time variable $t$. The left member of the equation is the derivative of biomass as a function of time (dx/dt). It represents the rate of variation of biomass. The right-hand side of the equation has two terms, a biomass production term and an extinction term. The production term represents the growth of the biomass of the fish stock. The extinction term refers to capture by fishing. These two terms involve parameters ( $\mathrm{r}, \mathrm{K}, \mathrm{q}, \mathrm{E}$ ) that are constants. For commercial fish species, it is usual to choose for the production term the logistic growth law that has been tested on many animal species. Parameter $r$ represents the rate of growth of the fish population.

When biomass is very low, logistical growth is exponential. When biomass becomes more important, resulting from intra-specific competition for resources, growth is slowed to reach an equilibrium value K , called carrying capacity, for which production is cancelled, as shown in Figure 6A (curve with $\mathrm{E}=0$ ).

The carrying capacity therefore represents the equilibrium biomass towards which the stock would tend in the absence of fishing. The second negative term of the second member of the equation below represents the catch by fishing with a catch rate q called "catchability". It is common in fisheries to assume that the catch is proportional to the product of the biomass of the resource by the fishing effort $E$. This fishing effort represents the investment in fishing. It is proportional to the number of vessels in the fleet, or it is obtained by calculating the number of hours of fishing at sea. With these assumptions, the model is written:

$$
\frac{d x}{d t}=r x\left(1-\frac{x}{K}\right)-q x E
$$



Figure 6. (A) Evolution over time of fish biomass with a constant fishing effort $E, q=1, r=0.1$ and $K=20$. When fishing effort is too high, the resource goes to extinction. Otherwise, it is moving towards a sustainable fishing equilibrium. (B) Evolution over time of fish biomass with a constant fishing quota, $Q=4, r=1$, and $K=20$. Fishing with a constant quota generates an "Allee" effect. Below a threshold (here $x=5$ ), the resource goes to extinction in a sustainable finite time. [Source: Reproduced with permission from Auger et al., 2015, reference [11]]

Figure 6A [11] illustrates the results of the model by showing the evolution over time of the total fish biomass for different fishing efforts.

This very simple model, with fishing effort maintained at a constant level, predicts two cases [12]:
if the fishing effort is too high ( $\mathrm{qE}>\mathrm{r}$ ), the resource goes to extinction. In this case, the fishery has a higher harvest rate than the fish reproduction rate, which disappears (Figure 6A with $\mathrm{E}=2$ ).
if fishing pressure is moderate ( $\mathrm{qE}<\mathrm{r}$ ), the resource will tend in the long term towards a positive biomass equilibrium below the limiting capacity K and which is generally stable (Figure 6A with $\mathrm{E}=0.2$ ).

In the event that the resource is maintained despite exploitation, it is also possible to choose a "good" fishing effort to optimize the catch at equilibrium. This optimum corresponds to the Maximum Sustainable Yield (MSY). In our case, the "MSY" is reached when the fishing pressure is chosen equal to half the growth rate of the species being harvested ( $\mathrm{qE}=\mathrm{r} / 2$ ). An abundant literature exists on this subject, particularly by using optimal control methods [13]. A species is said to be overexploited when fishing effort is maintained at a level above MSY. Biological overfishing occurs when the proportion of spawning fish becomes too low to ensure the renewal of the species and threatens its survival.

Another method of exploitation is to set a fishing quota per unit of time. The previous model, assuming a catch with constant quota represented by parameter Q , becomes [14]:
$\frac{d x}{d t}=r x\left(1-\frac{x}{K}\right)-Q$

The study of this model shows that even a low quota can generate an "Allee" effect, i.e. below a threshold, the population quickly goes into extinction. Figure 6B [11] shows the evolution over time of the biomass of the resource under different initial conditions. With an initial condition chosen below a threshold, the population disappears. The great variability of environmental conditions in the marine environment from one year to the next can induce a passage below a threshold and irreparably lead the exploited species to extinction. In the 1970s, whaling was allowed freely, with the effect of causing a very significant drop in its numbers. These mathematical models have alerted decision-makers to the risks of fishing with a fixed quota.

## 4. Taking economic aspects into account: bio-economic models

It is also crucial to take into account economic aspects in fisheries management models, particularly investment and price variations. The model then includes three variables: the biomass of resource $x$, the fishing effort $E$ and the price $p$ of the resource on the market [15]. The first equation is the same as the first model presented. The second equation describes the variation in investment. Fishing effort increases if the fishery is profitable and vice versa. Thus, the second equation makes the difference between the net profit of the fishery, corresponding to the catch multiplied by the price, minus the operating costs of the fishery. The c costs per unit of fishing effort result from the purchase of fuel oil, fishermen's salaries, minimum expected profit and various taxes. The third equation gives the variation in the price of the resource as a result of supply and demand. Supply is represented by instant capture and demand is represented by a monotonous function $D(p)$ decreasing in price. In other words, if the price increases, demand decreases, and vice versa. Under these assumptions, the model is written:

$$
\begin{aligned}
& \frac{d x}{d t}=r x\left(1-\frac{x}{K}\right)-q \times E \\
& \frac{d E}{d t}=p q \times E-c E \\
& \frac{d p}{d t}=\alpha(D(p)-q \times E)
\end{aligned}
$$

The first two equations correspond to Lotka-Volterra's predator-prey model [11],[12] where the prey is the fish and the predator the fishing fleet. This classic model provides for two possible cases:
the extinction of fishing effort when the operating costs of the fishery are high,
otherwise a stable equilibrium of sustainable fisheries.
In order to obtain overfishing equilibria leading to the extinction of the fish stock, it is necessary to add the third equation with a variable price. The simplest case of demand function is that of a negative slope line whose study has been carried out and predicts the case of fisheries in a state of overexploitation with prices soaring while catches are falling [16].

The choice of a linear demand function is questionable because it implies the existence of a maximum price beyond which no demand exists. However, for some rare species, prices can increase until they reach considerable values. For example, some very rare tunas have been auctioned in Japan for more than $\$ 1$ million, showing that, even at a very high price, there was residual demand. It is therefore wise to consider the more general case of a positive non-linear demand function for any price, even very high.


Figure 7. Changes over time in fish biomass (black), fishing effort (red) and price (blue). The resource is going to extinction with fishing remaining at a high level and with a price that only increases with the scarcity of the resource.

The study of this type of model predicts situations of overfishing with the extinction of the resource while continuing to fish to the last fish, with fishing effort remaining high and a price that is only increasing (Figure 7).

The available data are often partial and incomplete. These mathematical models make it possible above all to predict the qualitative evolution of the fishery, in particular major trends such as the collapse of the stock or its maintenance, the variation in fishing effort, or the soaring or stabilization of prices on the market.


Figure 8. Evolution over time of the price of "thiof" (false cod) in Senegal. [Source: Reproduced with permission from Thiao et al (2012), reference [10]]

Figure 8 shows the variation in the price of thiof on the market in Senegal with a significant increase in the price from the 1980s until 2006 in a period when catches collapsed. The previous model is therefore able to "explain" the data for the thiof fishery by predicting the extinction of the species resulting from overfishing with a price that only increases. Other authors had mentioned the possibility of causing the extinction of species that are becoming rare and whose market prices are increasing significantly [17].

Versions of the bio-economic fishing model with stronger non-linear terms, in particular with a catch term with a fishing saturation effect for a large fish biomass, lead to periodic solutions such as boundary cycles or more complex attractors [18].


Figure 9. Fish concentrated under a Fish Aggregating Device (FAD). [Source: Photo © IRD - Marc Taquet]

In reality, fisheries are active on several fishing sites that are regularly visited by boats. One fishing technique consists in placing floating objects at sea, which exert a significant attraction power for certain pelagic species [19]. These objects are called fFish Aggregating Devices (FADs, Figure 9). Fishermen come to visit them regularly to catch the fish that aggregate there.

Most recent mathematical models take into account the spatialization of fisheries to allow the control of a multi-site fishery to be studied (Figure 10) [20]. Is it possible to leave an overfishing situation that would eventually lead to the extinction of the overexploited species? A recent study has shown that it is possible to move from a state of overfishing to a state of sustainable fishing without risk of extinction for the species exploited, by varying the number of fishing sites and the operating costs of the fishery [21]. The latter study could explain the change in trend observed for the thiof fishery in West Africa where landings began to increase again after a significant decline, and prices to decline after a period of strong growth. The shift from overfishing to sustainable fishing could therefore result from the decision of Senegalese fishermen to fish for thiof from increasingly distant fishing sites in Mauritania, Gambia, Guinea and Sierra Leone, with increasingly high operating costs.


Figure 10. Diagram of a multi-site fishing model. The sites are Fish aggregating Devices (FADs). [Source: Modified from Auger et al (2010), reference [20]]

Many other aspects can be taken into account in bio-economic fisheries models, including the structure of fish in the stage (egg, larva, juvenile, adult) or interactions with other species in the ecosystem. However, the existence of an overfishing equilibrium leading to the extinction of the commercial species and the cessation of fishing is a result that remains robust for a wide range of mathematical and computer models.

## 5. Messages to remember

Trophic interactions within marine ecosystems depend on the size of individuals.
An exploitation targeting species according to their size will have cascading effects on all trophic levels of a marine ecosystem.
Global extinctions of marine species are rare, but their local extinction, or the disappearance of their ecological or economic role, is frequent.

A large proportion of commercial fish species are overexploited.
The management of marine resources must be based on decision-making tools that enable managers and decision-makers to take measures for the conservation and optimal exploitation of fisheries.

Mathematical modelling makes it possible to predict the effects of coastal development and fisheries control measures.
A fixed quota fishery is more risky than an unconstrained fishery because it can lead to the extinction of the species.

The coupling of ecological and economic dynamics predicts situations of overfishing causing the extinction of the resource with a high fishing effort remaining and a rising price.

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Cover image. Fish bank. [Source: Andrepiazza[CC BY-SA 3.0], via Wikimedia Commons]
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