

## A new class of predator prey models with interactions described by thresholds

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### *Abstract*

There exists an urgent need in fisheries science for simple models for assessing the impact of fishing on the dynamics of fish communities. We present a new class of predator prey models that describe the relationship between predators and their prey by piecewise-linear differential equations. Interactions are governed by threshold values for population abundances. The simplest model has four distinct cases with different asymptotic stable states. The model allows for fishing mortality on both predator and prey. If fishing mortality on either the predator, the prey or both are varied, the system might move to new stable states. The threshold values act as reference points for fishing exploitation, as they indicate a structural change in the predator-prey relationship. The model is demonstrated for several predator-prey couples in the Celtic Sea.

**Key words:** predator-prey model, reference points, differential equations

### *1 Introduction*

While there is a growing interest in ecosystem-based fisheries management, it is recognised that the required system-level knowledge and models are not yet well developed (Anonymous 2000; Hall and Mainprize 2004). Two categories of food web models are currently widely used, namely MSVPA (Magnússon 1995) and Ecopath-Ecosim models (Pauly et al. 2000). The former describes the age-structured dynamics of the main (usually target) species in the food web, the remainder of the species being treated as forcing variables. The latter rely on a system-equilibrium hypothesis and consider stable-state transfers between generally large compartments encompassing several systems. There is room for additional models with intermediate levels of complexity, based on different assumptions. Due to the scarcity of data on marine ecosystems, especially for non-target species, these models need to be parsimonious but still capture the effects of fishing on predator-prey dynamics as well as the structure of such dynamics. In the marine environment everybody eats anybody provided it is small enough. Many marine communities consist of unspecialised and opportunistic food webs/chains. Ideally such models should allow to set reference points for management purposes, which would indicate if changes in the functional predation dynamics were happening or expected to happen if fishing pressure continued or increased.

We propose a class of dynamic predator-prey models that allows for intermediate modelling of predator-prey relationships. The models are based on piecewise-linear systems with thresholds. These thresholds can then serve as reference points for management. In this paper we present in details a simple model with one predator and one prey and provide a description of the asymptotic properties of the model. An example application for some predator-prey couples in the fish community of the Celtic Sea serves to outline model fitting and interpretation.

## 2 A class of predator-prey models

### 2.1 Outline

The model describes the changes in population abundances (or densities)  $x_i$  of species  $i$  belonging to a community of  $n$  species interlinked by trophic relationships, according to:

$$\dot{x}_i = f_i(x) - F_i x_i, i=1, \dots, n \quad (1)$$

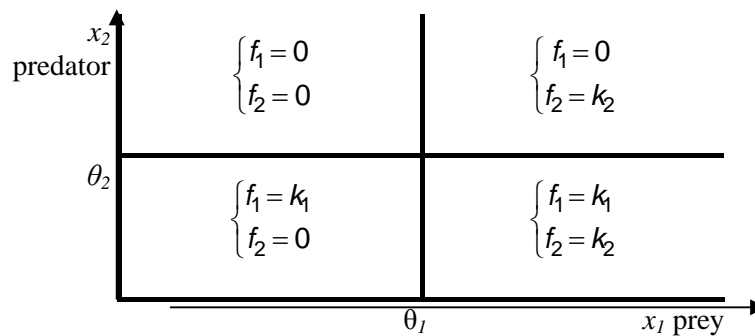
where:

- $f_i$  is the surplus production of species  $i$ , encompassing both population growth by recruitment and natural mortality;  $f_i$  is positive and piecewise constant
- $F_i$  is the rate of fishing mortality of species  $i$

The dynamics of the system depend on thresholds  $\theta_i$ ,  $i=1, \dots, n$ , which define boxes in the  $n$ -dimensional population abundance (density) space. Within each box the  $f_i$  functions can be either 0, or a positive constant  $C_i$ .

### 2.2 Two species: one prey, one predator

Let  $x_1$  be the abundance of the prey and  $x_2$  of the predator. Three crucial assumptions are then made by the model: i) there are always enough prey to maintain predator abundance and conversely there are never too many predators to jeopardize prey abundance; ii) if prey abundance is high (above threshold value  $\theta_1$ ), there will be predator surplus production; iii) if predator abundance is low (below threshold value  $\theta_2$ ), there will be prey surplus production. Any surplus production means that the population would be increasing unless the surplus is removed by fishing. The two threshold values on population abundances underlying the three assumptions lead to four model states which are summarised in Figure 1. In the SW quadrant there are few predators, which allows a constant prey surplus production of  $C_1$  (every year recruits exceed deaths by a constant number, which implies density-dependent mechanisms either in recruitment or in mortality, or both); there are also few prey, consequently predators have no surplus production ( $f_2 = 0$ ). Hence predator numbers remain constant, recruitments exactly matching deaths every year, which again implies constant or compensatory processes. In the SE quadrant there are also few predators but many prey to feed these predators which have a constant surplus production of  $C_2$  (again meaning density-dependence in predator dynamics). In the NW and NE quadrants by contrast, there are many predators, which consume any prey surplus production, effectively keeping the prey population stable ( $f_1=0$ ).



**Figure 1:** Production functions for the model with one prey, one predator.

We now describe the asymptotic dynamics of this simple model. In the absence of fishing and starting with predator numbers below the threshold,  $x_2 < \theta_2$ , the system asymptotically tends towards an equilibrium point at the intersection of the lines defined by the threshold values:

$$(x_1(t), x_2(t)) \xrightarrow{t \rightarrow +\infty} (\theta_1, \theta_2).$$

Starting with predator abundance above the threshold but prey abundance below,  $x_2 > \theta_2$  and  $x_1 < \theta_1$ , the system will remain invariant (no population growth). The situation that both the predator and prey

abundances are above the respective thresholds,  $x_2 > \theta_2$  and  $x_1 > \theta_1$ , will not occur in unexploited systems, as it would be unstable.

When fishing mortalities are applied to both the predator and prey, then depending on the ratio surplus production to fishing mortality,  $g_1 = \frac{C_1}{F_1}$  and  $g_2 = \frac{C_2}{F_2}$ , the asymptotic dynamics are as follows:

- a) if  $g_1 > \theta_1$  and  $g_2 > \theta_2$   $(x_1(t), x_2(t))_{t \rightarrow +\infty} \rightarrow (\theta_1, \theta_2)$ .
- b) if  $g_1 < \theta_1$   $(x_1(t), x_2(t))_{t \rightarrow +\infty} \rightarrow (g_1, 0)$
- c) if  $g_1 > \theta_1$  and  $g_2 < \theta_2$   $(x_1(t), x_2(t))_{t \rightarrow +\infty} \rightarrow (g_1, g_2)$

This means that:

- a) a light exploitation of both predator and prey will not alter the equilibrium state of the system.
- b) if fishing mortality on the prey exceeds its surplus production, then the predator will starve and go extinct.
- c) if fishing mortality exceeds surplus production on the predator but not on the prey, the system will be driven to an alternative equilibrium point with less predators and more preys than the unfished equilibrium.

Note that only the predator but never the prey can go extinct in this model (case b).

### 3 Celtic Sea application

The Celtic sea is a shelf sea bordered by Ireland, Wales and Brittany. Several national fisheries exploit its groundfish community. Two predator-prey pairs have been identified among the interacting groundfish populations based on stomach content studies (du Buit and Merlinat 1987; du Buit 1996; Trenkel et al. 2004) and the general biology of the species (Quéro 1984). The pairs are hake (*Merluccius merluccius*) feeding on horse mackerel (*Trachurus trachurus*) and whiting (*Merlangius merlangus*) feeding on horse mackerel. Annual scientific surveys in the Celtic sea in the years 1997-2003 provided population abundance estimates. Swept area estimates were raised to the total survey area assuming a catchability of one for all species. Fishing mortality rates, denoted  $F_{\text{surv}}$ , were estimated directly using total catch data (discards + landings) for 1997 see (Trenkel and Rochet 2003). Average fishing mortalities for the years 1990 to 2003 were also derived from ICES 2003 stock assessment reports. Note that these fishing mortality estimates apply to the whole stock and not only to the part in the Celtic Sea. These fishing mortality estimates are denoted  $F_{\text{ices}}$ . Annual surplus productions  $C_i$  were estimated using estimated population numbers and mortality rates, based on equation (1). Using the approximation  $\dot{x}_{i,t} \approx x_{i,t+1} - x_{i,t}$ , a simple estimator of  $C_i$  is

$$\hat{C}_i = \frac{1}{t_2 - t_1} \sum_{t=t_1}^{t_2} (F_{i,t} x_{i,t} + (x_{i,t+1} - x_{i,t})).$$

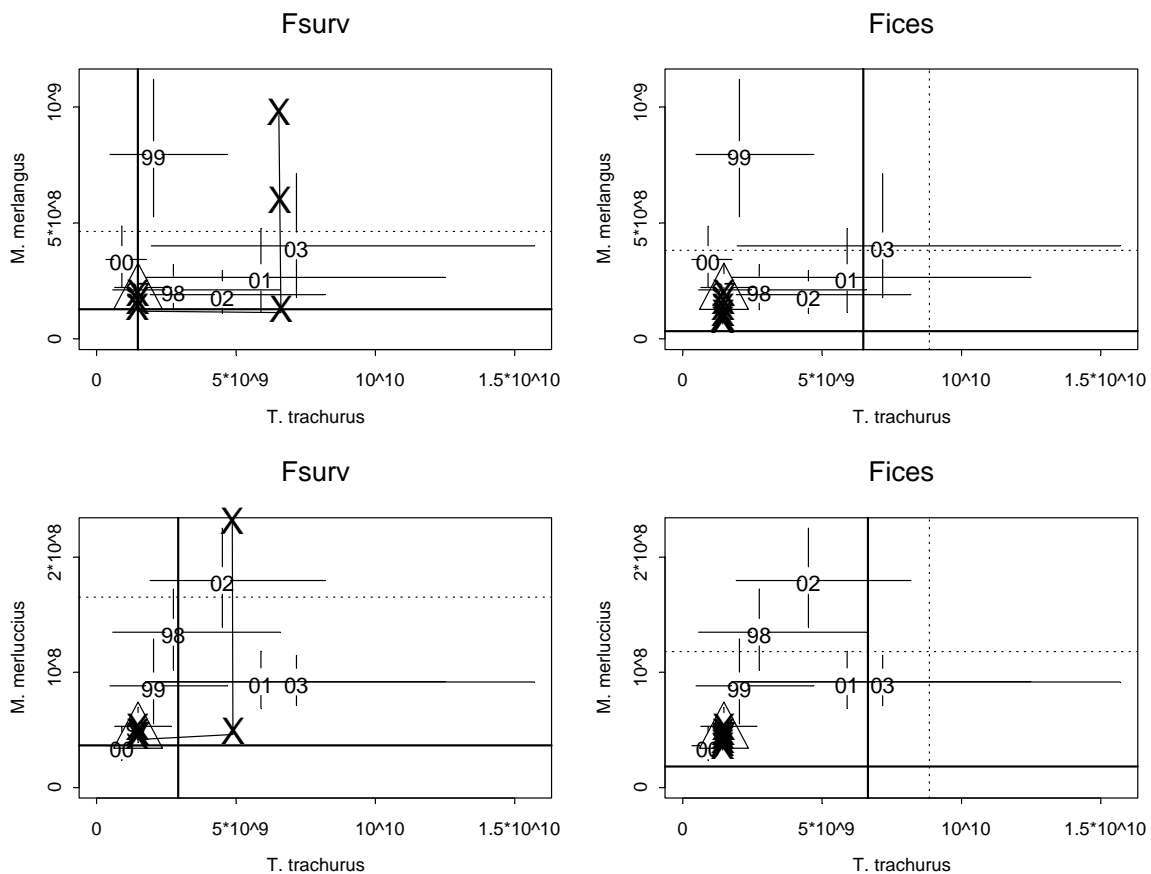
Surplus production was estimated for both sets of fishing mortality rates (Table 1). Threshold values  $\theta_i$  were obtained by fitting simulated model trajectories to observed predator-prey abundance dynamics, starting from the 1997 abundance estimates and using the 1998-2003 estimates in a least squares minimisation procedure (systematic grid search). Note that the same average fishing mortality rates,  $F_{\text{surv}}$  and  $F_{\text{ices}}$ , were used for all years.

Table 1. Input model parameter estimates for Celtic Sea application.

Species	Common name	$F_{\text{surv}}$	Surplus $C_{\text{surv}}$	$F_{\text{ices}}^*$	Surplus $C_{\text{ices}}$
<i>Merluccius merluccius</i>	hake	0.09	$1.6 \cdot 10^7$	0.31	$3.7 \cdot 10^7$
<i>Merlangius merlangus</i>	whiting	0.24	$11.0 \cdot 10^7$	0.68	$26.0 \cdot 10^7$
<i>Trachurus trachurus</i>	horse mackerel	0.007	$96.7 \cdot 10^7$	0.16	$141.6 \cdot 10^7$

\* ICES stock assessment estimates average 1990-2003: hake  $F_{bar}(2-6)$ , whiting  $F_{bar}(2-5)$ , horse mackerel  $F_{bar}(1-10)$

The first studied pair, hake feeding on horse mackerel, presented situation a) and was moving towards the stable point defined by the threshold values (intersection of solid lines in Figure 2 a & b). Depending on the assumed fishing mortality rates,  $F_{surv}$  (Figure 2a) or  $F_{ices}$  (Figure 2b) the location of the stable point changed somewhat. Lower stable hake abundances are expected at the higher fishing mortality rate ( $F_{ices}$ ). Assuming lower fishing mortality rates (scenario  $F_{surv}$ ), the system had nearly reached the stable state. The same situation a) was found for the other pair, whiting feeding on horse mackerel (Figure 2 c & d). This time the system seemed to be moving away from the stable state defined by the threshold values. The model assuming the lower fishing mortality rates, scenario  $F_{surv}$ , provided a somewhat better model fit for both predator-prey pairs: hake/horse mackerel (objective function  $6.0 \cdot 10^6$  for  $F_{surv}$  and  $9.6 \cdot 10^6$  for  $F_{ices}$ ) and whiting/horse mackerel (objective function  $13.2 \cdot 10^6$  for  $F_{surv}$  and  $9.7 \cdot 10^6$  for  $F_{ices}$ ). This might indicate better agreement of the lower fishing mortality rates with the model assumptions. The fact that the threshold values for the prey horse-mackerel were estimated to lie within the range of observed values would be interpreted as meaning that prey abundance has been limiting for the predators in the past if it was the only prey species. Of course in reality both hake and whiting prey on other species.



**Figure 2:** Observed predator-prey dynamics (labelled by year of observation) and simulated model trajectories (crosses and bold lines) for two trophic pairs of the Celtic sea groundfish community. Prey abundances on x-axes, predator abundances on y-axes. 95% confidence intervals of the abundance estimates are shown. Continuous lines:  $\theta_i$ , dashed lines:  $g_i$ . Starting values (1997) are surrounded by open triangles. top: Whiting (*Merlangius merlangus*) preying on horse mackerel (*Trachurus*

*trachurus*); bottom hake (*Merluccius merluccius*) preying on horse mackerel. Left column using fishing mortality rates  $F_{surv}$ ; right column with  $F_{ices}$  (see Table 1).

#### 4 Discussion

We have proposed a new class of predator-prey models for assessing the status and the dynamics of exploited marine systems. We have discussed in details a simple model with one predator preying on a single prey. Extensions to several predators and preys are straight forward, although finding their asymptotic properties is less so. For example, in a model with two predators and one prey, both predators would produce surplus production when the prey was above its threshold value. Conversely the prey would have surplus production only if both predators were below their respective threshold abundances. Thus some characteristics of this model class might seem strange to users of classical Lotka-Volterra predator-prey models.

First, in this model *the axes are non-invariant*: in some boxes prey or predator can be produced even if their current quantity is zero. This will seem impossible to people familiar with Lotka-Volterra models or experimentations in closed systems. However, this is not surprising in the marine environment. Most of marine communities are open and new individuals might migrate into the community even if the local population went extinct.

Second, in a model with two predators several possible steady states include coexistence of both predator species. This is inconsistent with the competitive exclusion paradigm, which states that there should be a winner in a competition for a common resource. Depending on the condition, one or the other of predators should drive the other one to extinction. This theory results from the assumptions of the Lotka-Volterra model. Here the predators share a common resource but do not really compete for it: the presence of one predator is not harmful to the other one. This may be a realistic model of field situations. Alternative versions of the model including a competition for the prey might be studied to check the robustness of the paradigm.

In terms of actually fitting the model to real cases, we note that all model parameters can be estimated without too much data. The application of even the simple model to fisheries is obvious. The threshold values of the model serve as reference points, which indicate a change in the predator-prey dynamics. For the two Celtic Sea examples, the predator-prey dynamics might have changed states in recent years as horse mackerel prey abundance moved above the threshold value while predator abundance of both hake and whiting might have been above it during the whole series. As the results depend to a certain degree on the assumed fishing mortalities, any such interpretation has to be taken with caution. The example was mainly intended as an illustration and more work is needed to evaluate the practical usefulness of the proposed models and to develop the theory for more complicated predator-prey relationships.

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