

# A mathematical model of biological resource dynamics, using Caspian/Ural sturgeon as a case study

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Some of the general principles involved in constructing mathematical models of biological resource dynamics are presented along with some of the requirements of such models for them to have value in terms of management application. A case study of sturgeon population dynamics in the Caspian Basin, using physical and biological parameters, is used to show theoretically how such a model can be developed and applied. The results of the case study are presented in graphic form, and the influence of different processes on the outcome of the calculation is discussed.

**Keywords:** bioresources, decision-making, mathematical model, sturgeon.

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## Introduction

Mathematical models of population dynamics are balance equations that characterize the rate of population change as a consequence of “inflow” and “outflow” of quantities of the population per unit of time. The complexity of a model depends on the number of accountable factors that influence the process it describes. Different methods, which may or may not use such models, can be used to estimate stock size, the most common ones being:

- (i) analysis of acoustic data;
- (ii) analysis of fishery-independent (generally research) time-series of swept-area trawl data;
- (iii) modelling catch per unit effort (cpue) and surplus production;
- (iv) estimating mortality and stock–recruitment;
- (v) age-based assessment such as virtual population analysis (VPA);
- (vi) comparisons of biomass in open and closed fishing areas;
- (vii) simple models based on landings data only.

All these methods provide the state of a fish population at time  $t$  with varying degrees of accuracy. Similarly, their ability to forecast or to provide a prognosis for the future varies and often requires an additional number of assumptions to those used for the estimation of the current stock size. Our main objective was to try to develop a model that could potentially increase the accuracy in forecasts of future dynamics of the stock and hence to contribute to the ongoing attempts of many others to improve the forecasting capability of the currently available suite of population dynamics models. We consider our exercise to be theoretical rather than

practical, but use a case study based on a valuable fish population that has not been subject to date to the same level of rigorous stock assessment as many other commercial fish stocks, simply to exemplify the output possible from a model of this type.

To develop a model of biological resource dynamics, it is necessary first to define the factors that make up a model's general structure (such factors are therefore called structural). They include factors such as the environment or the system in which the population exists, its age groups, inter-group competition, and sex. The structural factors determine the numbers of equations and variables in the model. For example, if the population inhabits two environments, there should be two equations with two unknown variables that characterize the number of fish in each environment. If there are three age groups within the population, then there need to be three equations for the number of individuals in each age group, etc.

The next step is to define the non-structural factors that influence the numbers in a population, and these factors determine the number of terms in each equation. Such factors are natural reproduction, intra-group competition, perhaps the artificial enhancement (seeding) of a population, the migration of fish between different environments, the transition from one age group to another, and natural mortality. The influence of all these factors can be expressed mathematically as specific terms with associated coefficients in the second part of a balance equation.

The significance of a model is determined by its completeness and level of realism in the simulation of the specific properties of the domain it models (i.e. its ability to take into account the basic factors that influence population size). For long-living species, the influence on population size of any factor usually becomes evident only after several years, so the model should allow one to forecast the influence of different factors over a long period of time. That is why simple models giving just a qualitative pattern of dynamics are

no longer considered adequate for quantitative research. To account more completely for basic factors, it is necessary to add into the equation additional terms that characterize the influence of those factors.

Development of mathematical models of the dynamic processes that characterize bioresources requires the following (Ricker, 1975):

- (i) the model should be flexible, i.e. it should be able to take into account all the basic factors that influence the process;
- (ii) it should be dynamic, i.e. all its parameters should clearly depend on time;
- (iii) it should be possible to solve the model on a computer, i.e. mathematical algorithms should converge sufficiently to allow solution of the model with the required precision;
- (iv) the model should be applicable in practice, i.e. there should be provisions for using statistical information to solve specific practical tasks.

To meet these requirements, we suggest the use not of a specific model of biological resource dynamics, but a general approach to the development of a series of models. As some factors may relate only to specific populations, this approach will allow models to be developed for each population separately. We use this approach to develop models of sturgeon (*Acipenser* spp. and *Huso huso*) population dynamics in the Caspian Sea and its rivers (the Caspian Basin). The Caspian sturgeon stocks, which provide probably the most valuable caviar available on world markets, are currently massively depressed (Karayev, 2006), so any contribution to understanding their unusual (in commercial fish stock terms) resource dynamics is crucial to improving management decision-making and stimulating any recovery in future.

### Mathematical model of sturgeon population dynamics

To develop a mathematical model of sturgeon population dynamics, we need first to make several assumptions that take into account the different factors known about the preferred environment and life history of the various sturgeon species:

- (i) The basic assumption of the model is that sturgeon return to their natal river and site, i.e. they “home”. This assumption allows our model to be limited to the part of the population that relates to a single river;
- (ii) Juvenile fish that reach the sea do not return to their natal river before they mature.

Factors in the model need to include the structural ones that influence the dynamics of each sturgeon species, i.e. its preferred environment (in the sea and in rivers), and the age of the fish. Other structural factors influence the dynamics of all sturgeon species. They include inputs to the populations through natural and artificial reproduction, and the outflows through fishing mortality (legal and illegal catches), migration from the sea to the river and back, and natural mortality (including predation).

To model the dynamics of sturgeon, we suggest considering separately the dynamics of the populations in the sea and in rivers. The two are very different environments for sturgeon, in terms of both catch and hydrodynamics. The sturgeon also need to be differentiated by age, and we propose four age groups:

group 1, up to 3 months of age; group 2, from 3 months to 2 years old; group 3, from 2 years of age to maturity; and group 4, sexually mature fish. The choice of these age groups is influenced by knowledge of their life history: newly hatched sturgeon generally reach the sea within 3 months; sturgeon aged between 3 months and 2 years have a greater natural mortality than older (2+ year old) fish, so need to be considered separately from older fish; sturgeon of 2+ years to maturity live only in the sea; then when they are close to sexual maturity, the fish return to the rivers to spawn, so taking up residence in a very different environment. The different species of sturgeon caught in the Ural River, after the Volga one of the main riverine inputs to the Caspian Sea, mature at different ages, beluga (*H. huso*) at 18 years, Russian sturgeon (*Acipenser gueldenstaedti*) at 16 years, and stellate sturgeon (*Acipenser stellatus*) at 14 years (data from the Republic of Kazakhstan Scientific Production Centre of Fishing). Fishing (commercial and illegal) generally targets just the spawning components of the population, those in the rivers.

Newly hatched sturgeon, i.e. younger than 3 months, suffer heavy natural mortality through predation, but no fishing mortality. Sturgeon only spawn in the rivers that flow into the Caspian Sea, a statement that applies to both natural and artificial reproduction. In the latter case, fish farms grow the fry to optimal size (3–5 g, according to the operators of the sturgeon hatchery at Atyrau, western Kazakhstan) and release them into the spawning rivers. Regardless of whether hatched naturally or artificially, the fry feed and grow in the rivers and, at ~2–3 months old, they enter the sea. Different estimates have been made of the extent of natural mortality of the young fish in the rivers, but the range is generally some 60–80% (Atyrau fish hatchery data). For groups 2 and 3, fishing mortality can be ignored in the model, because the fish are in the sea where their capture is currently not allowed (in reality, very few fish are caught in the sea itself, those that are caught being taken primarily for scientific research). Also, for groups 2 and 3, predation is not a very important parameter, except perhaps for the smallest fish in each group; there are not many predators of sturgeon in the Caspian Sea once they reach that size. The fourth group consists of sexually mature fish, a portion of which migrate from the sea into the rivers to spawn. Predation is then virtually zero, because the fish are very large and immune to attack, even by the other top predator of the Caspian, Caspian seal (*Phoca caspica*), which is not very abundant anyway. Only death through natural causes (e.g. old age) needs to be covered by the model.

To determine the number of fish in each group, the groups in the sea for more than 1 year were further subdivided into subgroups, the number in each subgroup being determined as a proportion of the total number of fish in each group. For each group of sturgeon in the model, we took into account only the factors specific to that group, and as stressed above, the unknown variables in the model are the quantities of fish in each group. The notations for these variables are given below.

### Variables and equations

To develop the model, we define the following functions, which are unknown, depend on time, and represent their corresponding quantities:

$M_1(t)$ —the quantity of fish of group 1 in the river at time  $t$ ,

$M_2(t)$ —the quantity of fish of group 2 in the river at time  $t$ ,

- $M_3(t)$ —the quantity of fish of group 3 in the river at time  $t$ ,
- $M_4(t)$ —the quantity of fish of group 4 in the river at time  $t$ ,
- $N_1(t)$ —the quantity of fish of group 1 in the sea at time  $t$ ,
- $N_2(t)$ —the quantity of fish of group 2 in the sea at time  $t$ , i.e.  
 $N_2(t) = \sum_{i=0}^2 N_{2,i}(t)$ ;
- $N_3(t)$ —the quantity of fish of group 3 in the sea at time  $t$ , i.e.  
 $N_3(t) = \sum_{i=3}^{S-1} N_{3,i}(t)$ ;
- $N_4(t)$ —the quantity of fish of group 4 in the sea at time  $t$ , i.e.  
 $N_4(t) = \sum_{i=S}^L N_{4,i}(t)$ ;

where  $i$  is age,  $S$  the initial age at maturity, and  $L$  the maximum age of each species of sturgeon. The  $\Sigma$  sign in the last three lines defines the population size in these groups as the sum of the quantities of sturgeon in each subgroup of that group.

If there were more groups, the number of variables would also increase. To define such unknown variables, the law of conservation of matter needs to be expressed in the form of a law of conservation of a number of fish. Mathematically, this is expressed as a system of ordinary differential equations. Therefore, for each environment (river and sea), four differential equations model the dynamics of the population in each group. Nevertheless, fish of groups 2 and 3 do not live in the river, spending all their time in the sea. Thus,  $M_2(t) = 0$  and  $M_3(t) = 0$  for any  $t$ . That is why we ultimately arrive at just six equations with six unknown variables:

$$\frac{dM_1}{dt} = \varepsilon M_4 + C - \beta M_1 - \varepsilon_1 M_1^{\alpha_1} - \text{fix}(t, \tau_{M_1}, \lambda_{M_1}, M_1); \quad (1)$$

$$\begin{aligned} \frac{dN_1}{dt} &= \beta M_1 - \gamma N_1 - R_{N_1} N_1^{\alpha_2} - \text{fix}(t, \tau_{N_1}, \lambda_{N_1}, N_1) \\ &+ \text{sign}(M_1) \times \text{fix}(t, \tau_{M_1}, \lambda_{M_1}, M_1); \end{aligned} \quad (2)$$

$$\begin{aligned} \frac{dN_2}{dt} &= \gamma N_1 - \text{kol}N_{2,2} \varepsilon_3 N_2 - R_{N_2} N_2^{\alpha_3} + \text{sign}(N_1) \\ &\times \text{fix}(t, \tau_{N_1}, \lambda_{N_1}, N_1) - \text{kol}N_{2,2} \times \text{fix}(t, \tau_{N_2}, \lambda_{N_2}, N_2); \end{aligned} \quad (3)$$

$$\begin{aligned} \frac{dN_3}{dt} &= \text{kol}N_{2,2} \varepsilon_3 N_2 - R_{N_3} N_3^{\alpha_4} + \text{kol}N_{2,2} \times \text{sign}(N_2) \\ &\times \text{fix}(t, \tau_{N_2}, \lambda_{N_2}, N_2) - \text{kol}N_{3,S-1} \varepsilon_4 N_3; \end{aligned} \quad (4)$$

$$\begin{aligned} \frac{dM_4}{dt} &= \rho_{N_4} N_4 - \rho_{M_4} M_4 - (K_{6p} + K_{KB}) \\ &- \text{fix}(t, \tau_{M_4}, \lambda_{M_4}, M_4); \end{aligned} \quad (5)$$

$$\begin{aligned} \frac{dN_4}{dt} &= \text{kol}N_{3,S-1} \varepsilon_4 N_3 + \rho_{M_4} M_4 - \rho_{N_4} N_4 - rN_4 + \text{sign}(M_4) \\ &\times \text{fix}(t, \tau_{M_4}, \lambda_{M_4}, M_4). \end{aligned} \quad (6)$$

$$\begin{aligned} \text{At } t = t_0; M_1 = M_{10}; N_1 = N_{10}; N_2 = N_{20}; N_3 = N_{30}; \\ M_4 = M_{40}; N_4 = N_{40}. \end{aligned} \quad (7)$$

Differential Equations (1)–(6) and the corresponding initial conditions [Formulations (7)] constitute our mathematical model of the dynamics of sturgeon populations in the Caspian Sea.

The initial conditions are defined for calculation, proceeding from the statistical data for the retrospective period. To solve

them, one needs to define the values of the coefficients on the right side of each equation. These coefficients may be determined either from statistical data or empirically through experiment. In the equations,  $M$  and  $N$  are the positive function of  $t$ , i.e. they are written for a given moment in time. The coefficients (except for  $C$ ) generally also depend on  $t$ . An explanation of the physical meaning of each term of the equations is given below.

The first term of the right side of Equation (1) represents the natural growth of a population of given age in a river at time  $t$ . As is obvious from the term, natural growth depends on spawning by sturgeon of group 4. The second term represents the increase in population size attributable to artificial reproduction.  $C$  is the number of newly hatched fish released down the river in a single day. The third term of Equation (1) reflects the reduction of the fish population in the river as a consequence of part of the population entering the sea (primarily at an age of 2–3 months). The fourth part of the equation represents the rate of reduction of the population of newly hatched fish through their being consumed by predators, a rate that is directly proportional to the number, raised to a certain power. Thus, the relationship is generally non-linear. A similar relationship, but with a different level of non-linearity, is present in the other equations. The last term of Equation (1) represents final migration of newly hatched fish from the river into the sea at age 2–3 months, i.e. through the function  $\text{fix}(t, \tau_0, \lambda, M(t))$ , expressed as

$$\text{fix}(t, \tau_0, \lambda, M(t)) = \begin{cases} 0, & \text{if } t < \tau_0 \\ M(\tau_0)/\lambda, & \text{if } \tau_0 \leq t < \tau_0 + \lambda \\ 0, & \text{if } t \geq \tau_0 + \lambda. \end{cases}$$

This function guarantees total transition of the newly hatched fish of a given age in the river to their new environment, the sea. Here,  $\tau_0$  and  $\lambda$  are, respectively, the initial time and the number of days needed for complete transition to the next group. This term was introduced because of the properties of the differential equation, namely that if all the terms on the right side of the equation equal zero, there is no change in population size. However, at a certain time, all newly hatched fish should enter the sea, i.e. the number in the river should become zero, which is ensured by having this term in the equation.

On the right side of Equation (2), modelling a similar process in the sea as for group 1 in the river, the first term characterizes the increase in newly hatched fish arriving in the sea through gradual migration from the river, the reverse process to that shown by the third term of Equation (1). The second term in Equation (2) represents the intensity of transition of newly hatched fish from group 1 to group 2. The third term is the rate of reduction of the population of such fish through predation, and the fourth term represents the complete transition of newly hatched fish at an age of 3 months into the sea and hence into group 2. The last term addresses the population growth rate attributable to migration of the remaining portion of newly hatched fish from the river into the sea.

In Equation (3), the first and fourth terms represent increases in the number of each group as a consequence of transitions from group 1. The factor “sign” in the fourth term provides a precise balance between sturgeon moving from group 1 to group 2. The second and the last terms represent the transition of sturgeon from group 2 to group 3. As group 2 spans fish from 3 months to  $\sim 2$  years of age, i.e. almost 2 years, though only

those fish that reach 2 years of age enter group 3, there is a coefficient  $\text{kol}N_{2,2}$  which determines the proportion of fish 1–2 years of age entering group 3. The third term refers to a decrease in the population attributable to predation, which is greatest on small species and individuals than on larger ones, something that needs to be considered when determining the coefficient.

The right side of Equation (4) is determined in a manner similar to the same side of Equation (3). The equation describes the dynamics of group 3 in the sea. The dynamics of group 4 are described by two equations: Equation (5) for river existence and Equation (6) for sturgeon living in the sea. The first and second terms of the right side of Equation (5) represent migration of some sturgeon from the sea into the river, and from the river into the sea, respectively. The rates of inflow of sturgeon into the river and into the sea are directly proportional to their number in each environment at a given time. For sturgeon of this group, therefore, the equation has an additional term (with a negative sign), representing the catch rate according to quota  $K_{KB}$  and the illegal catch rate  $K_{6p}$ . The last term of the equation refers to the complete transition/migration from the river into the sea, i.e. sturgeon that enter the rivers to spawn and are not caught legally or illegally.

The first term of the balance Equation (6) for group 4 in the sea represents the intensity of transition into group 4 from group 3. The second and the third terms of this equation refer, respectively, to the rates of inflow of some group 4 sturgeon into the sea from the river after spawning and of outflow from the sea into the river to spawn of the same group. The fourth term represents the death by natural causes of some group 4 sturgeon through, for instance, old age. It is assumed that such old fish do not spawn, but live only in the sea.

The last term of the balance Equation (6) refers to the growth rate of the population of group 4 sturgeon through migration of the rest of the population from the river into the sea.

**Physical and biological meaning of equation coefficients**

The coefficients of the age distribution introduced for each group denote the proportion of each subgroup (of each age) of each group. For sturgeon of group 1 in the river and the sea, as well as for sturgeon of group 4 in the river, the coefficients are equal to one, i.e.  $\text{kol}M_1=1$ ;  $\text{kol}N_1=1$ ;  $\text{kol}M_4=1$ . For other groups, the variables  $\text{kol}N_{2,i}$ ,  $\text{kol}N_{3,i}$ ,  $\text{kol}N_{4,i}$  have the values

$$\text{kol}N_{2,i} = \frac{N_{2,i}}{N_2}, i = \overline{0, 2}; \text{kol}N_{3,i} = \frac{N_{3,i}}{N_3}, i = \overline{3, (S-1)};$$

$$\text{kol}N_{4,i} = \frac{N_{4,i}}{N_4}, i = \overline{S, L}.$$

There is an additional age potential associated with reproduction, referring to the readiness of sturgeon to spawn, denoted as  $d_i$ . It is measured as a percentage (or a proportion of 1) of the total number of fish of each group.

To take into account any seasonality in the influence of some of the factors (i.e. the equation coefficients), the Heaviside function  $\chi(t, t_1, t_2)$  is used:

$$\chi(t, t_1, t_2) = \begin{cases} 0, & \text{if } t < t_1 \\ 1, & \text{if } t_1 \leq t \leq t_2 \\ 0, & \text{if } t > t_2, \end{cases}$$

where  $t_1$  and  $t_2$  are initial and final values of the time interval associated with each factor (coefficients are not equal to zero). Outside this interval, the factors do not act (i.e. the coefficients are equal to zero).

The equation  $\varepsilon = A\chi(t, t_0, t_1, t_2)/(t_2 - t_1)$  refers to the innate natural reproductive rate of newly hatched fish, where  $A$  is the number of newly hatched fish per adult fish in the river. The division by  $(t_2 - t_1)$  means that the reproductive process is viewed by time unit, i.e. per day. The coefficient  $A$  is defined on the basis of the influence of such factors as spawning ground and reception capacity of an ecological niche.

$C$  is the number of newly hatched fish released daily by fish hatcheries.

$\beta = \chi(t, t_0, t_1, t_2)/(t_2 - t_1)$  refers to the proportion of newly hatched fish of group 1 in the river entering the sea before attaining an age of 3 months.

$\varepsilon_1 = B\chi(t, t_0, t_1, t_2)$  represents the proportion of newly hatched fish of group 1 in the river suffering predation mortality, where  $B$  is the proportion dying in 1 day. This value is estimated, and can be corrected once real data become available.

$\gamma = \chi(t, t_0, t_1, t_2)/(t_2 - t_1)$  refers to the proportion of newly hatched fish of group 1 that have entered the sea attaining group 2 status (3 months old) daily.

$R_{N_1} = D\chi(t, t_0, t_1, t_2)$  takes account of the proportion of newly hatched fish of group 1 in the sea suffering predation mortality, where  $D$  is the proportion of group 1 sturgeon dying each day.

Coefficients  $\varepsilon_3 = \chi(t, t_0, t_1, t_2)/(t_2 - t_1)$ ,  $R_{N_2}$  represent, respectively, the rates of transition into group 3 and suffering predation mortality. Similarly, coefficients  $\varepsilon_4 = \chi(t, t_0, t_1, t_2)/(t_2 - t_1)$ ,  $R_{N_3}$  represent, respectively, the rates of transition into group 4 and suffering predation mortality.

$\rho_{M_4} = \chi(t, t_0, t_1, t_2)/(t_2 - t_1)$  is the daily rate of migration of a specific group from the river into the sea, and  $\rho_{N_4} = \sum_{i=S}^L (d_i \text{kol}N_{4,i}) \chi(t, t_0, t_1, t_2)/(t_2 - t_1)$  is likewise the daily rate of migration of a specific group from the sea into the river.

$K_{6p}$  and  $K_{KB}$  are, respectively, the intensity of illegal capture and the legal catch by quota (each per day).

In our model, sturgeon are not disaggregated by sex, so the coefficient of fishing mortality is derived as the ratio of females caught to the number of females in the population.

$r$  is the proportion of old fish dying through natural causes per unit of time, recalculated per individual fish. The value of this coefficient is defined on the basis of the influence on the number of adult sturgeon of factors such as fluctuations in sea level, anthropogenic influence (oil and gas removal from the Caspian Basin), and competitors for food.

Values of all these coefficients are defined based on statistical data/information to hand, and each coefficient is set precisely or defined with some probability using the data available. For example, the factor describing the number of young fish released by the hatcheries can be defined precisely, but the factor that characterizes the portion of young fish of group 2 in the sea that die by predation can only be defined with some probability.

When defining the factors in the model, it is necessary to take into account all issues that may influence their value. Therefore, a separate model is constructed for each factor, and on the basis of those models, the most appropriate value is deduced.

**Model results and discussion**

Figures 1 and 2, and 3 and 4 show, respectively, the results of two calculations done by the Adams method with changing

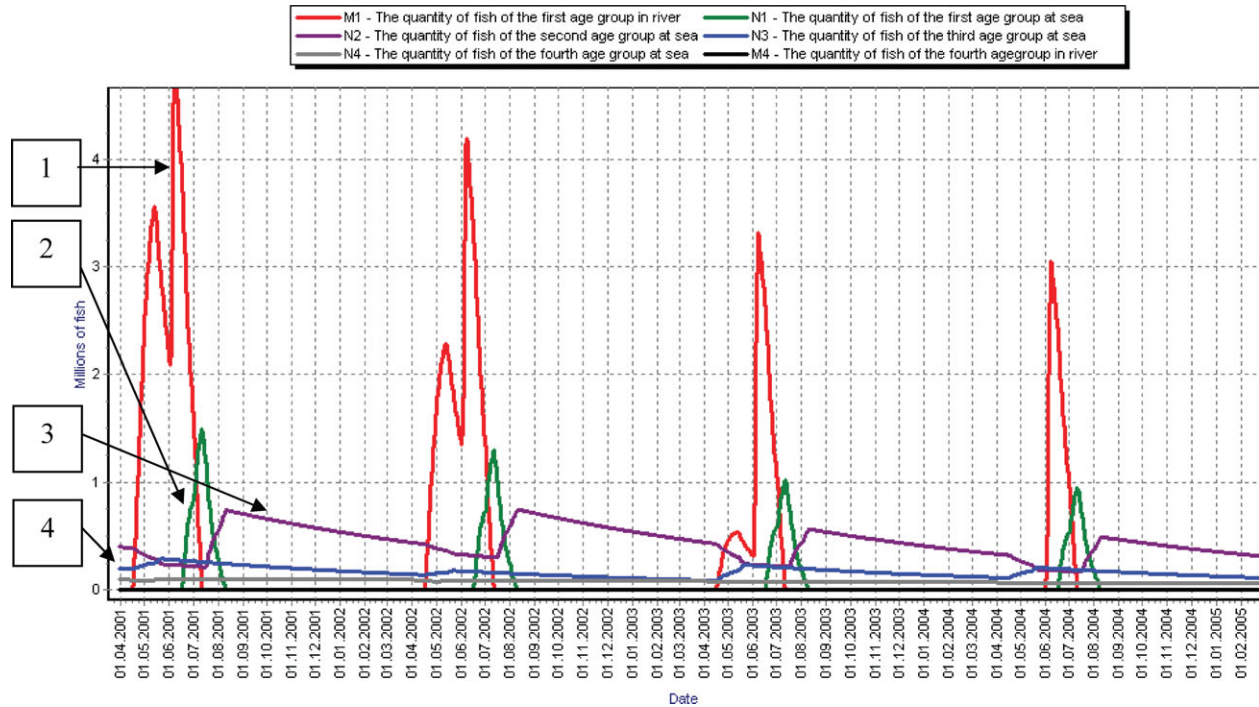


Figure 1. Change in the numbers of fish with time under an illegal catch of 95% of the total estimated catch.

steps (Bahvalov, 1974), in the form of relationships between fish numbers and time for different age groups. The calculations differ from each other in terms of the illegal catch proportion, Figures 1 and 3 corresponding to an illegal catch of

95% of the total catch, and Figures 2 and 4 to 50% of the total catch. All other parameters, which are listed in Table 1 and written in the form of the program's identifiers, were the same for both calculations. In Figures 1–4, the quantity of

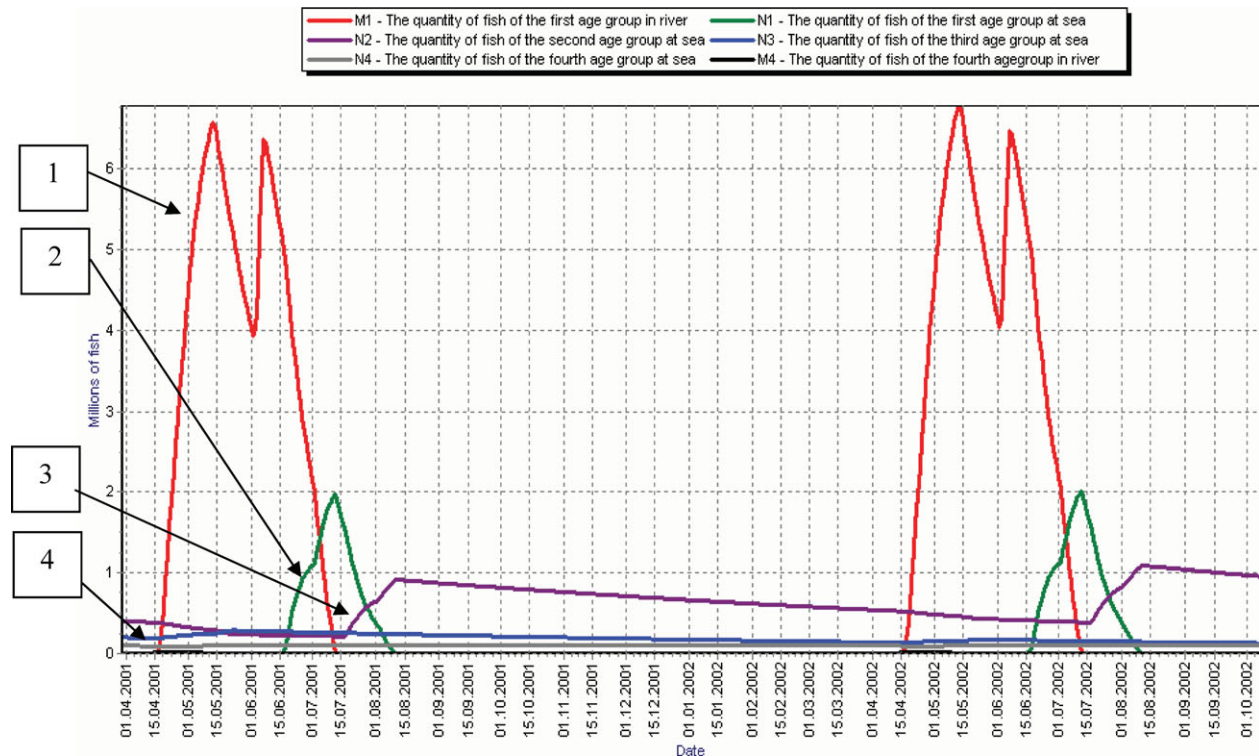


Figure 2. Change in the numbers of fish with time under an illegal catch of 50% of the total estimated catch.

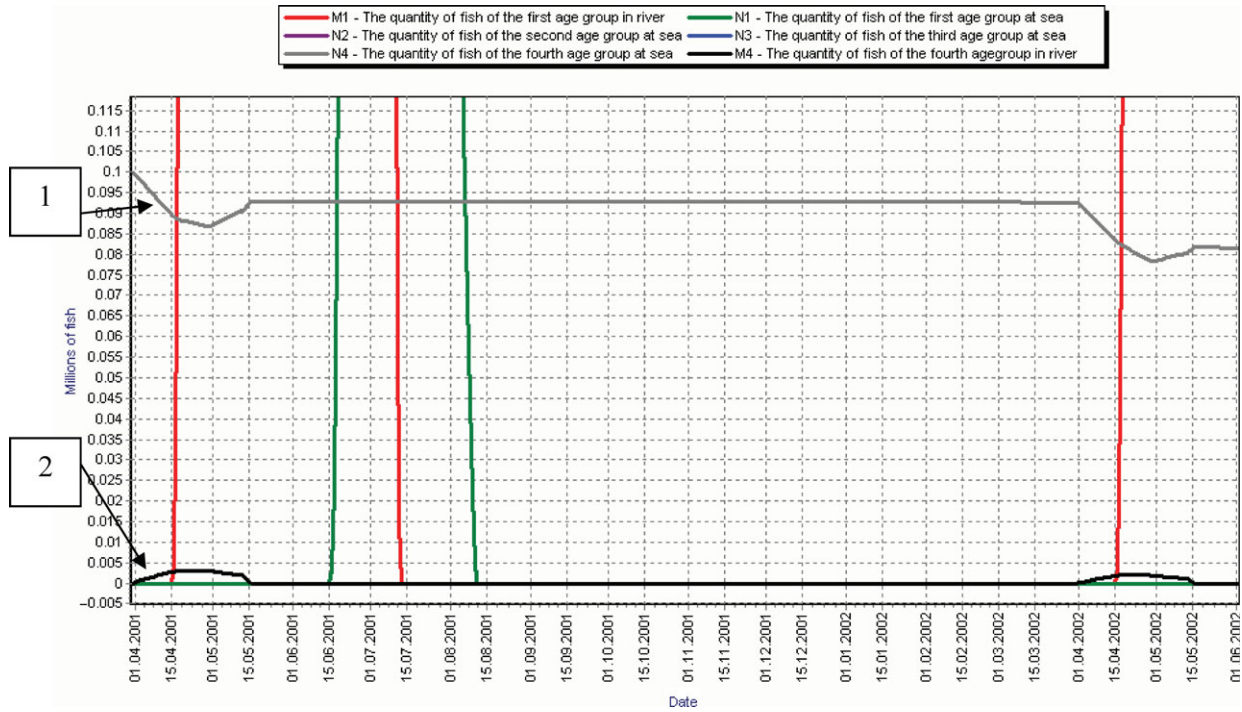


Figure 3. Change in the numbers of adult fish in the sea and river with time under an illegal catch of 95%.

fish is shown on the *y*-axis in millions of fish, and time is shown on the *x*-axis using a scale of 1 day. Figures 1 and 2 refer to the dynamics of the population of newly hatched fish in the river (shown by the line identified as 1) and in the sea

(line 2), and also the dynamics of groups 2 (line 3) and 3 (line 4) in the sea. Figures 3 and 4 represent the dynamics of adult fish in the sea (line 1) and the number of adult fish returning to the river to spawn (line 2).

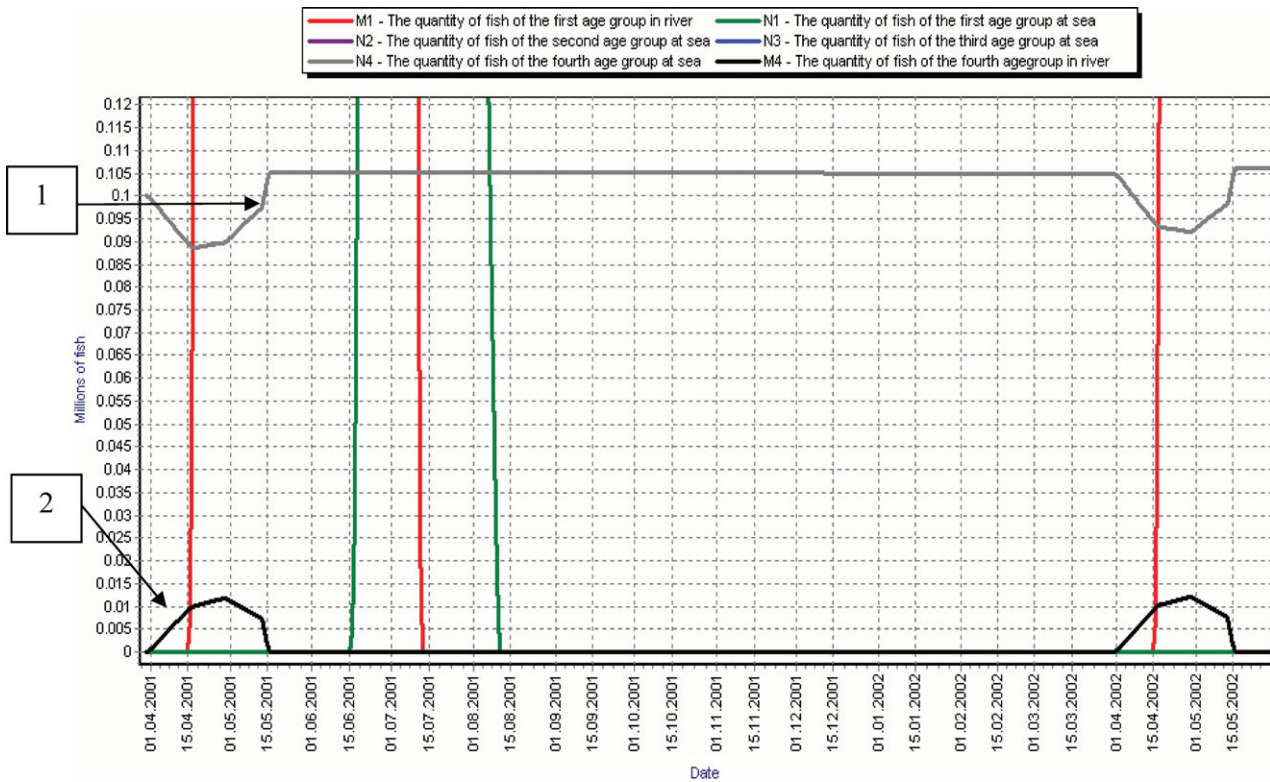


Figure 4. Change in the numbers of adult fish in the sea and river with time under an illegal catch of 50%.

**Table 1.** Parameters of the models, their description, and values.

Parameter	Description	Expression
$K_{KB}$	Number of sturgeon of group 4 caught legally in the river per unit of time (individuals/time)	$0.0013 * \text{HevObto}(t, t_0, '30.03', '02.04', '27.04', '30.04') / 30$
$K_{Gp}$	Number of sturgeon of group 4 caught illegally in the river per unit of time (individuals/time)	$0.0013 * \text{HevObto}(t, t_0, '30.03', '02.04', '27.04', '30.04') / 30$
$\varepsilon$	The rate of natural reproduction of sturgeon of group 4 in the river recalculated per individual (1/time; number of newly hatched fry derived from a single sturgeon/assumed maximum number of spawning sturgeon in the river/time)	$3000 * \text{HevObto}(t, t_0, '15.04', '18.04', '12.05', '15.05') / 30$
$R$	The proportion of older sturgeon of group 4 in the sea ( $N_4$ ), dying of natural causes per unit of time (1/time)	0.00001
$C$	The quantity of newly hatched sturgeon released by fish farms down the river (individuals/time)	$0.8 * \text{HevObto}(t, t_0, '1.06', '3.06', '5.06', '7.06')$
$\rho_{N_4}$	The proportion of sturgeon of group 4 in the sea ( $N_4$ ) migrating from the sea to the river to spawn, per unit of time (1/time)	$\text{HevObto}(t, t_0, '30.03', '02.04', '27.04', '30.04') / (30)$
$\varepsilon_3$	The proportion of sturgeon of group 2 in the sea ( $N_2$ ) transitioning to group 3 ( $N_3$ ) per unit of time (1/time)	$\text{HevObto}(t, t_0, '15.04', '18.04', '12.05', '15.05') / 30$
$\varepsilon_4$	The proportion of sturgeon of group 3 in the sea ( $N_3$ ) transitioning to group 4 ( $N_4$ ) per unit of time (1/time)	$\text{HevObto}(t, t_0, '15.04', '18.04', '12.05', '15.05') / 30$
$\varepsilon_1$	The proportion of newly hatched sturgeon of group 1 in the river ( $M_1$ ) subject to predation mortality per unit of time (1/time)	$0.025 * \text{HevObto}(t, t_0, '15.04', '18.04', '12.07', '15.07')$
$\rho_{M_4}$	The proportion of sturgeon of group 4 in the river ( $M_4$ ) migrating from the river back to the sea per unit of time (1/time)	$\text{HevObto}(t, t_0, '15.04', '17.04', '12.05', '15.05') / 30$
$\beta$	The proportion of newly hatched sturgeon of group 1 in the river ( $M_1$ ) transitioning to group 1 in the sea ( $N_1$ ) per unit of time (1/time)	$\text{HevObto}(t, t_0, '15.06', '18.06', '12.07', '15.07') / 30$
$\gamma$	The proportion of newly hatched sturgeon of group 1 in the sea ( $N_1$ ) transitioning to group 2 in the sea ( $N_2$ ) per unit of time (1/time)	$\text{HevObto}(t, t_0, '15.07', '18.07', '12.08', '15.08') / 30$
$R_{N_1}$	The proportion of newly hatched sturgeon of group 1 in the sea subject to predation mortality per unit of time (1/time)	$0.05 * \text{Hevobto}(t, t_0, '15.06', '18.06', '12.08', '15.08')$
$R_{N_2}$	The proportion of sturgeon of group 2 in the sea subject to predation mortality per unit of time (1/time)	0.002
$R_{N_3}$	The proportion of sturgeon of group 3 in the sea subject to predation mortality per unit of time (1/time)	0.002

The values used are determined on the basis of the statistical data/information available.

These results, shown for a period of four years (2001–2004), show that the number of newly hatched fish produced naturally is small (~3.4 million) when the illegal catch is 95%, and that the total reduces significantly in the second year of spawning (~1.5 million; Figure 1), and to virtually zero in the third and the fourth years; this factor also negatively impacts the population sizes of the other groups. However, when the illegal catch is 50%, the number of naturally hatched fingerlings is significantly higher (at ~6.3 million), and it then increases during the second year of spawning and subsequently (Figure 2). The second peak in the population of newly hatched fish (line 1) on both Figures 1 and 2 represents output from artificial reproduction carried out at the hatcheries. Some of the decreases shown by lines 3 correspond to the transition of some fish of group 2 in the sea (i.e. between 3 months and 2 years of age) to group 3 (from 2 years old to maturity) in the sea, the consequence of which is a slight increase in the population in the corresponding portion of line 4. A similar factor comes into play between lines 1 and 2 of Figures 3 and 4, i.e. sturgeon leave the sea to spawn in the rivers (line 2), so the adult population in the sea declines (line 1).

This modelling exercise was carried out on a purely theoretical basis in an attempt to demonstrate the dynamics of sturgeon populations in the Caspian Basin. Applying it to the true

population and new sturgeon life data observed scientifically is the next step in the process, along with further attempts to ensure biological realism in the model, but what has come out of the exercise thus far shows that a critical parameter in the model is the extent of the illegal catch. That there is an illegal catch is not questioned by the Caspian littoral states, but efforts to control it, and indeed the penalties for those caught, are not equitable or harmonized between the five states (Azerbaijan, Iran, Kazakhstan, Russia, and Turkmenistan). As Karayev (2006) points out, control of the illegal catch, which burgeoned following the break-up of the former Soviet Union, is crucial, but it may not be feasible given the socio-economic realities in many of the coastal regions of the Caspian Sea. There is also the question of the extent (if any) of illegal catching of sturgeon in the sea, given the lack of rigorous fisheries control currently.

Notwithstanding the above, this exercise forms, in our opinion, a necessary first step in demonstrating to decision-makers how the dynamics of sturgeon stocks are impacted by the various factors that have been identified. Hopefully, therefore, the results can be used with other inputs by managers and decision-makers to make educated decisions on such important issues as the extent of artificial propagation needed to sustain the currently stressed stocks, and on how much more to invest in control systems.

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