To appear in MEPS

Nonlinear response of Black Sea pelagic fish stocks to over-exploitation

Temel Oguz
Institute of Marine Sciences, Middle East Technical University,
P. O. Box 28, Erdemli 33731, Mersin, Turkey
E-mail: oguz@ims.metu.edu.tr

ABSTRACT: A three trophic levels prey-predator model investigates the underlying nonlinear dynamics governing the long-term (1960 - 1999) changes in pelagic fish stocks of the Black Sea. The model first explores the quasi-steady state dynamics of the system under various combinations of the consumption, harvesting and mortality rate values and identifies the critical parameters and their ranges that control equilibrium characteristics of the system. This knowledge is then used to describe progression of the stocks under temporally varying harvesting conditions. Albeit idealized structure of the model, the simulations reproduce the observations reasonably well. The model possesses different single equilibrium solutions during different phases of the system and associated regime shift dynamics. The late 1960s characterized the disruption period of heavily-exploited top predator stock and the successive proliferation of weakly-exploited small and medium pelagic stocks. The high stock regime of small pelagics persisted for a decade and then rebounded back and forth between the low and high abundance regimes. The 1990s ecosystem represents a gradual switch to their high stock regime, whereas other groups preserve their low stock regimes. Simulations further explore optimum harvesting conditions for balanced stocks of small and medium pelagics by the end of next decade. The present study highlights how a simple model, when carefully tuned, may provide detailed information on fish stock dynamics and realistically reproduce the observations. The model also illustrates the value of a minimalist deterministic approach for multi-species fishery management strategy development.

KEY WORDS: Black Sea, pelagic fish populations, prey-predator model, abrupt transitions, quasi-stable states, over-exploitation.

RUNNING HEAD: Modelling Black Sea pelagic fish stock variations

INTRODUCTION

An extensive body of literature documents dramatic changes in marine food web structures and functioning under climatic or human-induced perturbations over the globe. Overfishing is one of the serious ecological concerns. Many of the world's fish stocks, especially large predatory fishes, were severely depleted within the past 50 years (Hutchings 2000, Jackson et al. 2001, Myers & Worm 2003). In intensively fished ecosystems, decline in abundance of top predatory fish populations has shifted fisheries to target species at lower trophic levels (Pauly et al. 1998). The Black Sea is by no means an exception. Successive over-exploitation of fish stocks (i.e., "fishing down the food web") together with intense eutrophication, strong decadal-scale climatic cooling/warming, and population outbursts of opportunistic species and gelatinous carnivores have concomitantly introduced stresses on the ecosystem far more severe than those encountered in many other semi-enclosed, marginal and shelf seas within the second half of the previous century (Zaitsev & Mamaev 1997, Gucu 2002, Kideys 2002, Daskalov 2003, Bilio & Niermann 2004, Oguz, 2005a, Oguz 2005b, Oguz et al. 2006). Utilizing a long-term ecological data, Oguz & Gilbert (2007) recently diagnosed sharp transitions between quasi-stable states of various ecological properties during the reorganisation of ecosystem under synchronous climatic and anthropogenic forcing. They noted a switch from large predatory fish to small planktivore fish-controlled system in the early 1970s, the transition to a gelatinous-controlled system at the end of the 1980s, and to small planktivore-controlled system again at the end of the 1990s.

Daskalov (2002) and Oguz & Gilbert (2007) further noted inevitable role of the trophic cascade process in the food web under marked changes in the higher trophic level structure in response to excessive and continual harvesting of stocks at different periods of the recent past. Therefore, the quantitative understanding of likely response of the pelagic fish stocks to over-exploitation constitutes one of the key issues to gain a deeper insight into the mechanisms that govern the long-term organisation of ecosystem. The present study employs a simple deterministic model to explore underlining nonlinear dynamics associated with the long-term stock variations under differing harvesting conditions.

So far simple prey-predator type population dynamic models dealing with multiple states generally focused on the equilibrium (i.e., steady-state) properties of fish and plankton populations under different parameter ranges and for various functional representation of the consumption and predation mortality mechanisms (May et al. 1979, Steele & Henderson 1984, Hastings & Powell 1991, Abrams & Roth 1994, Spencer & Collie 1995, Edwards & Yool 2000, Scheffer & Rinaldi 2000, Kemp et al. 2001, Lima et al. 2002, Gibson et al. 2005, Morozov et al. 2005). In a rather idealized way, some models incorporated impacts of stochastic climatic variability on long-term fish population fluctuations (e.g., Steele & Henderson 1984, Spencer & Collie 1995, Collie et al. 2004). The present study extends these efforts to testing capability of a minimalist model for the simulation of multi-decadal behaviour of pelagic fish populations within a heavily exploited marine environment (i.e. the Black Sea). The subsequent sections provide (1) a qualitative interpretation of the available catch data to set a basis for the modelling studies, (2) a brief overview of the regime shift concept in ecological systems, (3) the equilibrium analyses of the model for elucidating the mechanisms controlling abrupt stocks changes and identifying the optimum parameter ranges that are critical to model dynamics, (4) simulations of the long term (1960-1999) stock and catch variations and possible stocks development under different harvesting scenarios during the next decade.

INTERPRETATION OF CATCH OBSERVATIONS

The catch observations are the only available systematic long-term data set to make inferences on the fate of Black Sea fish stocks during the recent past. The fact that the fishing effort was quite high during the 1970s and 1980s (Gucu 2002) justifies the link between the catch and stock variations and thus to develop a conceptual view which forms a basis for the present modelling studies. The data set (Fig. 1), retrieved from http://www.seaaroundus.org/lme/ lme.aspx, comprises the total annual landings of small pelagics (anchovy *Engraulis encrasicolus,* sprat *Sprattus sprattus,* horse mackerel *Trachurus* spp*,* Pontic shad *Alosa pontica*), of medium size pelagics (Atlantic bonito *Sarda sarda*, mackerel *Scomber* spp, blue fish *Pomatomus saltator*), larger pelagics (> 90 cm) and the total annual landings of small and medium demersals (turbot *Scopthalmus rhombus*, red mullet *Mullus barbatus*, whiting *Merlangius m. euxinus*). The data set also includes the annual dolphin catch in the Former Soviet Union countries prior to the banning of its harvesting in 1966 (Zemsky 1996) and the annual Turkish catch that continued extensively in the 1970s (Yel 1996).

The first phase in the data covers the 1950s and the early 1960s. It is characterized by low catches of small and medium pelagics and relatively high catches of dolphins and demersal fish community (Fig. 1). Large pelagic fish catches, on the other hand, maintain a steady level around 20 ktons throughout the study period. It likely suggests the prevalence of low stocks of large pelagics under their intense harvesting and thus their weak predation control on the food web. This system appears to suggest domination of the higher trophic level by large predatory and demersal fish stocks with respect to small and medium pelagics. The total catch of the former group varied between 100 - to - 200 ktons, whereas that of the others was below 200 ktons (Fig. 2).

Dolphin catch declined dramatically by the mid-1960s and reached almost complete extinction towards the end of 1970s. It was accompanied with a large reduction in demersal fish catches as well. Their total low catch level (< 50 ktons) in the subsequent decades implies a continuous high fishing effort on these stocks. On the contrary, first the small pelagic catch and then the medium pelagic catch increased in the 1980s up to a total of 800 ktons (Fig. 2) primarily in response to rapid development in Turkish fishing fleets (Gücü 2002). This period therefore should be able to sustain high stocks of faster-growing species of small and medium pelagics following declines of large predators and demersals. Interestingly, similar shifts have been observed on global scale during the same period (Myers & Worm 2003).

The catches of small and medium pelagics declined dramatically and concomitantly at the end of the 1980s. In particular, anchovy stocks that used to be the most abundant fish species of the 1980s collapsed rapidly from more than 800 kilotonnes to ~ 200 kilotonnes (Ivanov & Panayotova 2001, Daskalov et al. 2002). This phase, however, lasted for only four years and the small pelagic catch started increasing gradually by 1993 up to about 400 ktons during the early 2000s. The medium, large predatory and demersal fish catches, on the other hand, persisted at their background levels during this period.

The catch data may have the following implications in regards to the reorganization of stocks within the last 50 years: (1) a major shift from a demersal and top predator dominated system to a small and medium pelagic dominated system at the end of the 1960s, (2) the existence of two successive quasi-persistent low and high stock regimes of the small plus medium pelagic groups and the top predator plus demersal groups (Fig. 2) each lasts approximately for two decades during 1950 - 1990, (3) a transition towards high stock regime of small pelagics during the 1990s at the expense of low stock regimes of medium and large pelagic predators, (4) two distinct short-term transitional periods of the lowest stocks for all populations at the end of the 1960s and the 1980s. The model simulations presented in the subsequent sections seek a quantitative support for these assertions.

AN OVERVIEW OF REGIME SHIFTS IN ECOLOGICAL SYSTEMS

One of the objectives of the present study is to identify the mechanisms responsible for marked changes (i.e., regime shifts) that likely occurred in the Black Sea fish stocks during the second half of the last century. A brief overview of the regime shift concept is therefore appropriate here for the sake of completeness. The ecological properties may alternate their stable states (also referred to as regimes) when an ecosystem looses its internal resilience under strong environmental stressors (both natural and human-induced) and subsequently some internal and/or external properties of the ecosystem reach critical thresholds (May 1977, Scheffer et al. 2001, Petraitis & Dudgeon 2004). Transitions between the stable states occur in two different forms depending on the equilibrium characteristics of the system. In the case of multiple equilibria, the strongly nonlinear systems possess alternative stable states (e.g., the low and high stock regimes) for a particular set of internal or external conditions (e.g., fishing mortality rate, temperature). The properties alternate their states abruptly via forward and backward transitions at two different thresholds (c.f., Fig. 2 in Petraitis & Dugdeon 2004). The transitions are referred to as “discontinuous” regime shifts and the phenomenon is called “hysteresis” (Scheffer et al. 2001). The George Bank haddock stock variations due to marked changes in harvesting rates (Collie et al. 2004) fall into this category. Discontinuous regime shifts impose strong constraints on reversibility of the states. They are traced by abrupt changes in the time series data.

Ecosystems are more often characterized by a single equilibrium in which a stable state characterized by specific internal and external conditions may alternate to a new stable state as conditions change (c.f., Fig. 3 in Petraitis & Dugdeon 2004). The states are therefore identified by two different ranges of conditions on both sides of thresholds (instead of the same range between two different thresholds in the discontinuous shifts). They resemble sinusoidal-type fluctuations in the time series data as in the case of low frequency, multi-decadal scale, climate-driven fluctuations observed in open ocean fish populations (de Young et al. 2004). A well-known example is the successive transitions between a warm “sardine regime” and a cool “anchovy regime” in the Pacific Ocean since the early 1950s (Chavez et al. 2003). Following Scheffer et al. (2001) and Collie et al. (2004), they are referred to as "smooth" regime shifts here. The discontinuous and linear shifts represent two end-members of nonlinear bifurcations depending on the degree of nonlinearity of the system. Scheffer et al. (2001) and Scheffer & Carpenter (2003) provide the theoretical framework of regime shifts as well as some case studies from marine and aquatic ecosystems.

The definitions of regime shifts given above formally apply to the systems controlled by one variable (e.g., the consumption rate or harvesting rate). In reality, more than one internal and/or external factor often impose simultaneous controls on ecological systems, and therefore make the regime shift interpretations ambiguous in terms of identification of the threshold values and the equilibrium characteristics (single or multiple equilibrium). As described in the following sections, this ambiguity also arises in the present study.

MODEL FORMULATION

The model comprises the small pelagic (resource or prey), medium pelagic (consumer) and large pelagic (top predator) groups; the latter involving both large pelagics and dolphins. The small pelagic group grows using resources provided by the lower trophic level, and is consumed by both medium pelagic and top predator groups. As the top predator and the consumer groups compete for a single resource, the predator group feeds on the consumer group as well. The model resembles an intraguild omnivory system such as phytoplankton (resource), microzooplankton (consumer) and mesozooplankton (predator). For simplicity, demersal stock variations and their interactions with small pelagics are not explicitly taken into account because of their negligible role on the Black Sea fishery after the 1960s. All groups are subject to a linear harvesting, and the system is closed by the quadratic mortality terms for the top predator and medium pelagic groups. A higher degree of complexity introduced by nonlinear couplings between the consumption, mortality and harvesting mechanisms of these three groups make the model more sophisticated than the earlier one prey-one predator models (e.g. Spencer & Collie 1995) and three trophic level food chain models (Powel & Hastings 1991, Abrams & Roth 1994). In essence, the model complexity conceptually resembles the one presented by May et al. (1979) that investigated the dynamic response of the Antarctic ecosystem to changes in harvesting regimes of different fish species. The governing equations, in their dimensional form, are expressed by

$$\frac{dS_1}{dt^*} = R_1 S_1 \left(1 - \frac{S_1}{K_1}\right) - R_2 S_2 \frac{S_1^2}{K_2^2 + S_1^2} - R_3 S_3 \frac{a_1 S_1^2}{K_3^2 + a_1 S_1^2 + a_2 S_2^2} - f_1^* S_1 \tag{1a}$$

$$\frac{dS_2}{dt^*} = \varepsilon_2 R_2 S_2 \frac{S_1^2}{K_2^2 + S_1^2} - R_3 S_3 \frac{a_2 S_2^2}{K_3^2 + a_1 S_1^2 + a_2 S_2^2} - D_2 S_2^2 - f_2^* S_2 \tag{1b}$$

$$\frac{dS_3}{dt^*} = \varepsilon_3 R_3 S_3 \frac{a_1 S_1^2 + a_2 S_2^2}{K_3^2 + a_1 S_1^2 + a_2 S_2^2} - D_3 S_3^2 - f_3^* S_3 \tag{1c}$$

In eq's (1a-c), the operator d/dt^* represents the time derivative, S_1, S_2, S_3 denote respectively small, medium and top predator pelagic fish abundances, R_1 defines growth rate of small pelagics, K_1 is their carrying capacity, R_3 is consumption rate of top predator group on small and medium pelagic populations with respective percent feeding preference rates of a_1 and a_2, R_2 is consumption rate of medium pelagics on small pelagic population. K_2 and K_3 are prey abundances where consumption rates are half of their maximum values, ε_2, ε_3 are food conversion efficiencies (i.e., the proportion of food assimilated by consumers), f_1^*, f_2^* and f_3^* are harvesting rates, D_2 and D_3 denote mortality rates.

In general, the quadratic mortality term used in the consumer and predator equations parameterizes the consumption by higher predators that are not explicitly incorporated in the models, and the natural mortality is often considered a part of this loss term. Its nonlinear form, which in biological sense implies a density dependent mortality, is preferred to the linear representation in order to suppress unstable oscillations in the models and to stabilise solutions (e.g., Edwards & Yool 2000). The density dependent mortality (d_kF_k), however, goes to zero as the top predator stock vanishes. A better choice may be to use both density dependent and independent terms (Caswell & Neubert 1998). The quadratic mortality term is omitted in eq.1a since the predation mortality by the medium pelagic and top predator groups have already been explicitly taken into account in the model. On the other hand, because of the presence of linear fishing mortality term in eq. 1a, a separate linear natural mortality loss term would be redundant within the framework of this simplified model. The natural mortality is simply assumed to be a fraction of the linear loss term. Low rates of natural mortality of adult fishes, which form the main stocks for fishery, justify this approximation.

The model incorporates neither age-structure of populations nor seasonal variability and spatial structure. The model is further simplified by assuming no active biological and physical processes regulating population sizes. The lower trophic structure is not explicitly represented but its contribution is parameterized by the carrying capacity in the logistic growth term. Based on these simplifications, the model offers the first-order dynamical behaviour of the system and forms a basis for building up more sophisticated models that allow complex interactions among different trophic levels. Equations are solved by the fourth order Runge-Kutta numerical algorithm with a time step of 60 seconds. A time step up to one hour, however, gives comparable results.

Nonlinear dynamics of these systems are well known. The combination of a logistic growth functional form together with sigmoidal type III consumption, the quadratic natural and/or unparameterized predator mortality and the linear fishing mortality functions imply either single high or low stable equilibrium of stocks or three equilibria (two stable equilibria separated by an unstable equilibrium) for different combinations of parameter values. In the case of multiple equilibria, a slight change in one of the parameters can cause bifurcation of prey-predator stocks to their alternative domains of attraction (May et al. 1979, Steele & Henderson 1984, Spencer & Collie 1995, Caswell & Neubert 1998, Edwards & Yool 2000, Scheffer & Rinaldi 2000, Kemp et al. 2001, Lima et al. 2002, Gibson et al. 2005, Morozov et al. 2005). The system may also provide single equilibrium, limit cycles and chaotic fluctuations for some parameter ranges (Hastings & Powell 1991, Abrams & Roth 1994, Caswell & Neubert 1998).

In order to make the analysis more tractable, eq's 1a-c are made nondimensional by scaling S_1 with K_2, S_2 and S_3 with K_3, time t with R_1^{-1}, and other dimensional parameters as shown in Table 1. Eq's 1a-c then transform to

$$\frac{dF_1}{dt} = F_1\left(1 - \frac{F_1}{K}\right) - \frac{r_2}{\gamma} F_2 \frac{F_1^2}{1+F_1^2} - \frac{r_3}{\gamma} F_3 \frac{a_1\gamma^2 F_1^2}{1 + a_1\gamma^2 F_1^2 + a_2 F_2^2} - f_1 F_1 \tag{2a}$$

$$\frac{dF_2}{dt} = \varepsilon_2 r_2 F_2 \frac{F_1^2}{1+F_1^2} - r_3 F_3 \frac{a_2 F_2^2}{1 + a_1\gamma^2 F_1^2 + a_2 F_2^2} - d_2 F_2^2 - f_2 F_2 \tag{2b}$$

$$\frac{dF_3}{dt} = \varepsilon_3 r_3 F_3 \frac{a_1\gamma^2 F_1^2 + a_2 F_2^2}{1 + a_1\gamma^2 F_1^2 + a_2 F_2^2} - d_3 F_3^2 - f_3 F_3 \tag{2c}$$

The values for dimensional growth rate and carrying capacity of small pelagics are taken from the available literature as $R_1 = 0.9$ y^{-1}, $K_1 = 2000$ ktons; the latter approximately corresponds to twice the maximum observed stock value of small pelagics. The nondimensionalisation of equations introduces a new parameter $\gamma = K_2 / K_3$ that defines the ratio of half saturation constants of consumer and top predator abundances. Thus, γ sets the value of K_3 relative to K_2 in the model. The stocks are scaled by K_2 and K_3 and the value of K_2 is set to 50 ktons, whereas the value of K_3 depends on the choice of γ. The feeding preference rate of top predator and medium pelagic groups are $a_1 = 0.7$ and $a_2 = 0.3$, respectively. This setting suggests more efficient prey consumption of the top predator group on small pelagics with respect to the medium pelagic group. The food conversion efficiencies ε_2, ε_3 are taken as 0.7. These parameter values are kept fixed in all simulations because the model is not critically sensitive to their changes under their expected range of variations for the Black Sea. Other parameter values, particularly the parameter γ and the consumption rates r_2 and r_3, are not precisely known and preliminary sensitivity experiments suggested their critical importance on structuring the long-term observed stock and catch variations. Their optimum values that reproduce the observed stocks and catches during different phases of the system are assessed by the equilibrium analyses of model instead of choosing them from a broad range of observed values reported for different species. The alternative and/or complementary approach could be their estimation with a nonlinear parameter optimization technique if the data set would be more complete.

EQUILIBRIUM ANALYSES

I refer to Fig. 2 to reiterate the hypothesis put forward on the existence of two distinctly different regimes of the fish stocks before and after 1970. The existence and equilibrium characteristics of these two quasi-steady phases of the system are now examined under various combinations of the harvesting, predation and mortality parameter values. For this purpose, an extensive set of experiments are performed by systematically altering the parameter values within their dynamically feasible ranges. A sample from this set that specifically applies to the Black Sea conditions is presented below. More general aspects of the prey-predator dynamics given by this relatively complex three-trophic levels model will be reported elsewhere.

Response of the system to the ratio of half saturation constants

I first focus on the response of pristine system (1950s and 1960s) to the parameter γ. The equilibrium solutions are sought for its values changing between 0.5 and 5.0 at an increment of 0.5 for different choices of r_2. The solutions are obtained from an initial state representative of the pristine conditions with $F_1 = F_2 = 3.0$ (the low stock states of small and medium pelagic groups; 150 and 60 ktons, respectively) and $F_3 = 10.0$ (the high stock state of top predator group; 200 ktons) and running the model for 20 years that is long enough to achieve the steady state solution. The subsequent equilibrium solutions for other γ values are obtained by every 20 years of integration as well starting from the former steady state solution. Other parameters are chosen as $K = 40, f_1 = 0.25, f_2 = f_3 = 0.30, d_2 = d_3 = 0.01$ (the rest is given above). The K and f values reflect low harvesting and moderate carrying capacity of the pristine system during the 1950s and 1960s.

The equilibrium solutions are obtained for its both increasing and decreasing values in order to identify whether the system possesses single or multiple equilibrium states. The solutions indicate that the small and medium pelagic stocks are not sensitive to the choice of γ up to its value of 4.0 and permanently reside in their low stock regimes. The stocks however flip to their high stock regimes when $\gamma \geq 4.0$. The top pelagics change gradually from the low to high stock regime for increasing γ values.

The cases with $\gamma \geq 4.0$ (i.e., $K_2 = 50$ and $K_3 \leq 12.5$) represent a condition that the prey group has an efficient growth, supplies high resource for the consumer and predator groups and gives rise to high stocks for the entire system. Conversely, the cases with $\gamma \leq 1.0$ (i.e., $K_2 = 50$ and $K_3 \geq 50$) possess severe food limitation and exhaustion of stock at all trophic levels. The choices of γ between 1.0 and 4.0 introduce strong top-down control by top predators on the prey and consumer groups. Among all these combinations, $\gamma = 2.5$ reveals the top pelagic stock and catch values consistent with the observations during the 1950s and 1960s. This value is therefore adopted for the rest of the analyses.

Response of the system to consumption rates

The sensitivity of the system to the values of r_2 and r_3 is searched next in order to identify the range of their values which adequately describe the dual-mode structure of the observed fish stocks. The equilibrium solutions are obtained for changing the values of r_3 from zero to 2.0 at an increment of 0.1 for different choices of r_2. The stock variation of each group versus r_3, depicted in Fig. 3a-c for three different consumer consumption rates $r_2 = 0.5, 0.7, 0.9$, reveals single equilibrium of the system. Either the small pelagic group or medium pelagic group or both, depending on the value of r_2, lay in the state which is opposite to the state of top predator group for any value of r_3. The transition between the stable states occurs at slightly different threshold values of r_3 for all groups. For example, for $r_2 = 0.5$ the small pelagic group possesses the high stock regime up to $r_3 = 0.7$, shifts to the low stock regime in the range $0.7 < r_3 < 0.9$, and remains stable thereafter for increasing values of r_3 (Fig. 3a). The top predator group shows an opposite characteristics (Fig. 3c). The medium pelagic group remains permanently in the low stock regime for the entire range of r_3 (Fig. 3b) suggesting that its consumption rate on small pelagics is not sufficiently strong for their net growth. During its decreasing values, the states alternate at a slightly lower range $0.4 < r_3 < 0.5$ (Fig. 3a, c). The small and top predator groups therefore acquire both low and high stock regimes for a narrow range of r_3 during the transition phase of stocks. The top predator group exhibits limit cycle solutions during the transition as evident by the peak at $r_3 = 0.8$ in Fig. 3c.

For $r_2 = 0.7$, the structures of small pelagic and top predator stocks resemble those already presented for $r_2 = 0.5$ but, in addition, the medium pelagic stock acquires two different stable states on both sides of the same threshold range of r_3. The high stock regime of medium pelagics occurs at the expense of reduced small pelagic stock while the top predator group retains its former stock size. For decreasing r_3 values, the transition of medium pelagic stock takes place more gradually from 0.7 to 0.4. For $r_2 = 0.9$, the small pelagic stock is exhausted completely irrespective of the value of r_3 due to a stronger consumption pressure exerted by medium pelagics. The reduction in medium pelagic stock size with respect to the case for $r_2 = 0.7$ reflects relatively weaker growth due to the exhaustion of small pelagic stock under their high consumption rate by medium pelagics and points to a feedback mechanism between the consumption and growth characteristics of the prey-consumer system. The structure of top predator stock generally remains unchanged during the transition phase except weaker oscillations. Under the present parameter setting, the equilibrium analysis indicates that the consumption rate values of $r_3 > 0.7$ and $0.5 < r_2 < 0.9$ are the most appropriate for the Black Sea prey-consumer-predator system. Beyond these ranges, the solutions are not relevant for the Black Sea.

A closer focus to Fig. 3a-c may help to further constrain the optimum choices of r_2 and r_3. For example, the values of r_3 much larger than 0.7 stabilise the small and medium pelagic stocks in their low stock regimes and can not alternate their states when the system is perturbed by other environmental parameters (e.g., increasing fishing mortality rate of the top predator group). Therefore, the optimum choice of r_3 should be around 0.7. The choices of $r_2 > 0.7$ for decreasing r_3 values drastically reduce the small pelagic stock abundance at the expense of a compensatory increase in the abundance of medium pelagics. The predicted small pelagic stock size is $F_1 \sim 26$ (1300 ktons) for $r_2 = 0.5$ and ~ 16 (800 ktons) for $r_2 = 0.7$ (Fig. 3a). Thus, the choices of r_2 around 0.6 should predict the small pelagic stock size consistent with the observations (~ 1100 ktons), and also support the low stock regime of medium pelagics at the time of abrupt stock increase of small pelagics. The time-dependent simulations described in the next section provide further examples of stock variations using various combinations of r_2 and r_3 values between 0.6 and 0.7.

Response of the system to mortality rates

The equilibrium characteristics of first phase of the Black Sea fish stocks are also sensitive to the values of top predator mortality rate d_3. Higher values of d_3 result in the alternation of states; the top predator stock switches to the low equilibrium state and the small and medium pelagic stocks jump into their high equilibrium states at progressively lower thresholds of f_3. They even permanently reside at the high equilibrium state for $d_3 \geq 0.05$ independent of the value of f_3. As expected, higher values of d_3 reduce more effectively the top predator stock when it is at the high stock regime (i.e., at low f_3 values). The analysis suggests the optimum choices of d_3 between 0.01 and 0.04.

The model dynamics are altered by the presence/absence of medium pelagics mortality closure term in eq. 2b. In the absence of this term (i.e. $d_2 = 0$), the small and medium pelagic stocks exhibit more dominant low frequency oscillations within the threshold range of f_3. The period of oscillations is about 31.1 years for $f_3 = 0.40$, 26.6 years for $f_3 = 0.45$, and around 20 years for $f_3 = 0.5$ prior to stabilization of the solution after 30 years of integration. On the other hand, setting d_2 to a small value around 0.005-0.01 stabilizes the solution, and this range is adopted in our simulations. The relatively low values of d_2 are justified because consumption of the medium pelagic stocks by the top predator group is already included in the model. The present contribution mainly represents the natural mortality that is as expected to be small for adult populations.

Response of the system to harvesting rates

Analysis for the first phase: Having constrained the critical ranges of r_2 and r_3, the equilibrium analyses next explore how the first phase of the system responds to the variations of f_3. The primary interest is to locate the range of f_3 values which exhausts the top predator stock and proliferates to the others. Keeping the previous parameter setting ($\gamma = 2.5$, $K = 40$, $f_1 = 0.25$, $f_2 = 0.30$, $d_2 = d_3 = 0.01$) and letting $r_3 = 0.7$, equilibrium solutions are obtained for increasing and decreasing f_3 values between zero to 1.0 at an increment of 0.05 for different r_2 values. As in the previous case, the small and medium pelagic stocks respond nonlinearly to the top predator fishing mortality rate variations (Fig. 4a, b). For $f_3 \leq 0.35$, these stocks exist at their low stock regimes but they flip to the high stock regime at different stock sizes depending on the value of r_2 when $f_3 \geq 0.4$. The choice of $r_2 = 0.5$ allows only the small pelagic stock to switch to the high stock regime ($F_1 \sim 28$; 1400 ktons) whereas the medium pelagic stock remains at its former state ($F_2 \sim 3$; 60 ktons). The choice of $r_2 \geq 0.9$ permanently gives rise to the low (high) equilibrium state of small (medium) pelagic stock for the entire range of f_3 (Fig. 4a, b). The choice of $r_2 = 0.7$ switches both the small and medium pelagic stocks to their high stock regimes at the same threshold value of f_3 (0.35 - 0.45) and results in a more realistic solution for the Black Sea. Moreover, setting $r_3 \sim 0.7 \geq r_2$ favours small pelagics to dominate the high equilibrium state of system with respect to medium pelagics as in the observations (Fig. 3). The optimum values of r_2 that makes both small and medium pelagic stocks to change their stable states lay between 0.6 and 0.7. They agree with the former analysis of stock variations with respect to the consumption rates.

At a first glance, the choice of $r_3 \geq r_2$ contradicts with the general view that smaller fish species consume at a higher rate and grow faster with respect to larger ones. In the model, the only way that the top predator stock dominates that of medium pelagics is to have comparable to or slightly greater effective annual consumption rate of top predators (ktons y^{-1}) on the annual basis. The choice of $r3 \geq r2$ accommodates this effect during low harvesting rate conditions of the first phase. In reality, the top predator group consumes small pelagics for almost entire year, whereas the medium pelagic group consumes them most effectively for only a certain part of the year when young fish species of this group migrate from the neighboring Aegean and Marmara Seas. Moreover, the stock size of migrating young medium pelagic species is much smaller than their actual annual standing stock sustained in the Black Sea and therefore is not explicitly incorporated in the model. This simplification is verified by the model simulations.

Contrary to nonlinear response of f_3 on the small and medium pelagic groups, the top predator stock displays a linear response (c.f., eq. 1c). It decreases from its maximum values around 15 (= 300 ktons) for increasing f_3 and vanishes at $f_3 \sim 0.55$

(Fig. 4c), which is roughly equal to $\varepsilon_3 r_3$ (i.e., the maximum value of effective growth rate of the top predator group). The threshold range $f_3 \sim 0.45 - 0.55$ remains the same for different choices of d_3 or f_1, f_2.

A striking feature of the steady-state solutions is the existence of both single equilibrium and multiple equilibria of the system for different ranges of f_3. For $f_3 >$ 0.4, the system possesses one stable state for both its increasing and decreasing values. It is, however, characterized by two alternative stable states for the values f_3 between zero and 0.4 for all choices of r_2. During the decreasing phase of f_3, the stocks do not shift back to their former states; instead they all reside permanently at their present states. The system thus shows a strong resistance (hysteresis) to the recovery of top pelagic stock and the collapse of other stock groups under decreasing f_3 as long as the harvesting rates of the small and medium pelagic groups are small (~ 0.3). This is indeed a desirable fishery management option. The top pelagic stock may however recover under different harvesting conditions, an example of which is described further below.

Analysis for the second phase: The equilibrium analyses are further extended to elucidate the form of stock variations under different combinations of three harvesting rates that likely apply for the second phase of long-term stock variations (1970-1985) following the first regime shift event. The consumption rates are set to $r_2 = 0.6$ and $r_3 = 0.7$ as deduced from the previous analysis and the other parameters are taken as before. Fig. 5a-c display stock variations for both increasing and decreasing values of f_1 for three different choices of $f_3 = 0.3, 0.5, 0.7$ and two choices of $f_2 = 0.3, 0.5$. Under low harvesting conditions of the medium and top predator pelagic groups ($f_2 = 0.3$ and $f_3 = 0.3$), the small and medium pelagic stocks reside persistently at their low stock regimes for all choices of f_1 (curve 1). They are however identified by their high stock regime when $f_3 \geq 0.5$ and $f_3 = 0.3$ (curves 2 and 3), as shown previously in Fig. 4a. For $f_3 \geq 0.5$ and increasing f_1, the small pelagic stock diminishes first gradually in the high stock regime and then more steeply during the transition to the low stock regime at the threshold range of $f_1 = 0.55 - 0.60$. Increasing f_1 does not affect stability of high stock state of medium pelagics up to the threshold value of f_1. But once the small pelagic stock starts decreasing for the values of f_1 beyond its threshold, the medium pelagic stock also alternates gradually to the low stock regime as their growth becomes limited due to the food shortage (Fig. 5b). The top predator stock, that is in the low stock regime for $f_3 \geq 0.5$, is subject to a linear decrease for increasing f_1 due to the resource limitation as well (Fig. 5c).

In the case of higher values of f_2 (e.g., 0.5 and 0.7) and f_3 (e.g., 0.7), small pelagics switch from high to low stock regime along a linear trajectory in response to weaker predation pressure of the medium pelagic group (curve 4 in Fig. 5a). Small pelagics can thus maintain a relatively higher stock size as they are simultaneously harvested but place eventually in the low stock state at $f_1 \sim 0.8$ together with the other groups (Fig. 5b, c). The entire pelagic stocks collapse at moderate f_2 and f_3 values and $f_1 \geq 0.8$, as observed in the Black Sea at the end of 1980s prior to the recovery of small pelagic stock (see the next section for details).

Analysis for the third phase: For decreasing f_1 (as harvesting conditions of the small pelagic group are restored to those before the shift), the stocks generally revert to their previous conditions along the same trajectories (see the curves shown by broken lines in Fig. 5a-c). The thresholds of f_1 for the forward and backward transitions are almost the same within the range of 0.5 – 0.6, and the transitions are thus classified as "smooth" regime shifts. For low f_2 and f_3 (~0.3), the return trajectory of small pelagic stock (curve 1) however exhibits unstable oscillations at high f_1 but the solutions are eventually stabilised prior to the shift to the high equilibrium state. Similar oscillations also appear for the case of $f_2 = 0.3$ and $f_3 = 0.5$. The return trajectories of small and medium pelagics follow different paths with respect to their forward trajectories up to the threshold range of f_1, but merge with the forward trajectories once the stocks alternate the states at lower f_1 values. As discussed below, the solutions for decreasing f_1 describes the conditions of stocks recovery after the early 1990s.

The solutions with decreasing f_1 also display an interesting top predator stock recovery case that offers an alternative to the previous no-recovery case under low harvesting conditions of small pelagics $f_1 \sim 0.3$ (Fig. 4c). The recovery case requires initially relatively high f_1 and f_3 values ($f_1 > 0.6, f_3 \geq 0.5$) that move small pelagics to their low stock regime at any value of f_2 (curve 1 Fig. 5a, c). Once small pelagics are settled in the low stock regime and the harvesting rate of top predators is low ($f_3 \sim 0.3$), reduction in f_1 does not alter the state of small pelagics but promote the top predator stock to flip into the high stock regime. Progressively lower f_1 values give rise to higher stock size of top predators.

TIME-DEPENDENT STOCK VARIATIONS

Having identified the optimum ranges of critical model parameters and the underlying dynamics of precipitous stock variations by the steady-state analysis, three groups of time-dependent simulations are presented next to describe the progression of stocks under temporally varying harvesting conditions. The first group shows how the observed catch variations can be simulated as closely as possible within the framework of this simplified model. The second group highlights a dynamically different stocks progression under somewhat different temporal variations of the top predator harvesting rate. The third group of experiments offers alternative stocks development scenarios within the next two decades.

Simulations of observed stock and catch variations

Parameter setting: Among large number of prognostic simulations only three almost identical ones, which are consistent with the available observations, are presented here. The values of r_i and d_i (i = 2, 3) are given in Table 2 and other parameters are taken as before; $\gamma = 2.5$, $a_1 = 0.7$, $a_2 = 0.3$, $\varepsilon_1 = \varepsilon_2 = 0.7$. The time integration of model starts from the initial state at 1960 and continues for 40 years (36 nondimensional time units) until 1999. The initial state is described by low stocks of the small and medium pelagic groups at $F_1 = F_2 = 3.0$ (150 and 60 ktons, respectively), and high stock of the top predator group at $F_3 = 10.0$ (200 ktons). The carrying capacity increases linearly by 1980 from its constant value of 40 (2000 ktons) up to 50 (2500 ktons) in 1985 and retains this value until 1993. Its 20 % increase during the period of intense fishing represents the concomitant higher resource availability from the lower trophic level in conjunction with the nutrient enrichment and more intense plankton production in the Black Sea during the 1980s (c.f., Fig's 2 and 3 in Oguz & Gilbert 2007). It helps to sustain the high stock regime of small pelagics somewhat longer during the early 1980 at the time of most intense stock exploitation. Otherwise, the small pelagic stock would start decreasing earlier and wouldn't be able to support high catches observed during the 1980s. Starting by 1993, the carrying capacity reduces linearly to its original value in 1999 in accordance with the decreasing trend of observed phytoplankton production.

Specification of harvestion rates: The temporal variation of small pelagic fishing mortality rate resembles the one given by Daskalov et al. (2006) with some adjustments (Fig. 6). It attains fairly stable values of f_1 ~ 0.3 up to 1978, increases linearly to 0.95 in 1986 and then declines first steeply to 0.6 in 1990 and then more gradually to 0.3 in 1999. Temporal variations of other fishing mortality rates are adjusted, in an idealized sense without introducing too many details, to the observed catch values. The medium pelagic fishing mortality rate retains a low steady value of 0.3 up to 1982 and varies similarly to f_1 afterwards; it first increases up to 0.95 in 1989, then decreases to 0.4 in 1994 and keeps this value for the rest of simulation period (Fig. 6). The fishing mortality rate of top predator group alters between 0.4 and 0.7 during 1964-1970 and remains constant afterwards (Fig. 6). Setting $f_3 = 0.7$ allows a relatively higher small pelagic stock prediction as indicated by the equilibrium analysis (Fig. 5a), but the solutions are not overly sensitive to to its exact choice as long as it is above the threshold value of about 0.5.

Temporal variation of stocks: The simulated stock and catch variations are depicted in Fig. 7 and Fig. 8, respectively. The small pelagic stock possesses three distinct successive transitions between its low regime (< 350 ktons) and high regime (> 950 ktons) (Fig. 7a). The first transition (TR1) comprises the period from 1969 to 1973, during which the small pelagic stock switches to the high stock regime (HSR). Consistent with the former equilibrium analyses, the shift occurs at the large pelagic fishing mortality threshold rate of $f_3 \sim 0.5$ at which the top predator stock drops below 40 ktons (Fig. 7c). Upon increasing f_3 to 0.7, the top predator stock decreases further and vanish by the mid-1970s that coincides with the transition of small pelagics from the low to high stock regime (Fig. 4a-c). The harvesting rates of small and medium pelagics during the transition are $f_1 = 0.32 – 0.35$ and $f_2 = 0.3$, respectively.

The transition of medium pelagic stock from the low stock regime (< 60 ktons) to the high stock regime (> 180 ktons) follows that of small pelagics with some time lag (Fig. 7b). It also starts at the same threshold value of top fishing mortality rate ($f_3 \sim 0.5$) during the late 1960s. It is initially a slow process during 1970-1975 at the time of rapid increase of small pelagic stock. Once this shift is completed, the medium pelagic stock more rapidly alternates its state during the second half of the 1970s.

The complementary steady-state analysis of the model, performed using the parameter values of first simulation in Table 2, further elucidates dependence of TR1 to the harvesting rates of small and medium pelagic groups. According to the equilibrium analysis (Fig. 9a), the small pelagic stock remains permanently in the low stable state for $f_2 = 0.2$ (not shown). The choices of $f_2 \geq 0.4$, on the other hand, keep the medium pelagics permanently in the low stock state for all values of f_1 (Fig. 9b). The only favourable ranges of f_1 and f_2 that must accompany the f_3 threshold rate ~ 0.55 for the existence of transition TR1 of small and medium pelagics to their high stock regimes appear to be $f_2 < 0.4$ and $f_1 \leq 0.4$. The values of $f_1 = 0.32 – 0.35$ and $f_2 = 0.3$ used in the time-dependent simulations during the transition TR1 are compatible with the ranges provided by the equilibrium analysis. These ranges of f_1 and f_2 will also alternate the medium pelagic stock to its high equilibrium state (Fig. 9b).

The HSR of small pelagics persists until 1982, after which the second transition (TR2) during 1983 - 1986 brings the stock back to its low stock regime (LSR). TR2 initiates at $f_1 \sim 0.6$ that again is in harmony with the equilibrium analysis (curve 4 in Fig. 5a). Above this threshold value of f_1, the small pelagic stock is continually depleted at the expense of maintaining a steady catch level around 600 ktons (Fig. 8a). As the stock approaches to the low stock regime at higher values of f_1, the catch then drops dramatically to ~ 150 ktons within few years.

Prior to their collapse, small pelagics can temporally support medium pelagics to sustain their high stock level up to 250 ktons until 1985 under relatively low fishing mortality rates around $f_2 \sim 0.3$ - 0.4 (c.f., Fig. 9b). Thereafter, as the fishing mortality rate f_2 exceeds 0.6 and food supply from small pelagics reaches a critical level following the collapse of their stock, the medium pelagic stock starts declining within the high stock regime and finally switches back into the low stock regime during 1988 - 1989 concurrently with small pelagics (Fig. 7b). At $f_2 \sim 0.6$, the catch becomes as high as 120 ktons and then drops abruptly to less than 60 ktons (Fig. 8b) as the stock tends to approach the low stock regime. Thereafter, the medium pelagic stock remains within the low stock regime until the end of simulation period for decreasing fishing mortality rate to 0.4.

The LSR of small pelagics lasts only for four years. Once its fishing mortality rate reduces below the threshold value of 0.6 by 1993, the stock starts increasing gradually (the third transition, TR3) and moves into the high stock regime at 1998 when $f_1 < 0.6$ and $f_2 \sim 0.4$. As suggested by the equilibrium analysis (see the broken lines representing the return trajectories for decreasing f_1 in Fig. 9a-c), the crucial factor which promotes the switch is the specific choice of f_2 values during the transition. The values $f_2 \sim 0.4$ support the increase in F_1 when $0.45 < f_1 < 0.60$ and keeps F_2 depleted (curve 4 in Fig. 9a, b), which is the case in the time-dependent simulations (Fig. 7b). The smaller values of f_2 shift F_1 to the high stock regime at lower f_1 threshold values. It also shifts F_2 to high stock regime and thus would be a better stock recovery option for the small and medium pelagic stocks as further studied in the next subsection.

Comparison with observations

When simplicity of the model bears in mind, it reproduces adequately all major features of the multi-decadal fish stock and catch variations. Contrary to a prolonged high stock phase up to 1987 in the data (Fig. 7a) the small pelagic stock however starts decreasing by the early 1980s. One possible explanation for the difference is the composite representation of anchovy and sprat stocks in the model. According to the data (c.f., Fig. 11 and 12 in Oguz et al. 2006), the anchovy stock declines by the early 1980s whereas the sprat stock that is less commercial and thus less exploited retains its high stock level somewhat longer. This difference is reflected in the total stock estimate data (Fig. 7a) by a short-term peak at 1986-1987. Because the temporal variations of fishing pressure, f_1, was primarily set to that of anchovy in the model (since its catch was predominant), the total small pelagic stock variations follow more closely to those of the anchovy. Nevertheless, an extended high stock regime can be reproduced under somewhat lower fishing mortality rates of small pelagics. But, in this case, the total catch is underestimated by the model.

The difference in sprat and anchovy stock fluctuations may be partly related to the climate-induced changes impacted on their temperature dependent growth characteristics. Sprat is a cold water species spawning in autumn and winter months. Sprat abundance and growth are therefore expected to be more favourable during the cold years such as in the mid-1980s known to be the coldest period of previous century in the Black Sea (Oguz et al. 2006). A separate modeling of the anchovy and sprat stocks together with their temperature-controlled growth parameterizations may provide a more realistic total small pelagic stock estimate.

The simulations predict depletion of top predators by the mid-1970s whereas a low level catch was always maintained in the data (Fig. 8a). The difference likely arises due to an idealized (i.e., temporally uniform) specification of the top predator mortality rate ($f_3 = 0.7$) until the end of simulation period. As depicted in Fig. 4c and 5c, setting $f_3 \sim 0.5$ could be a more realistic choice but, in this case, the small pelagic stock and catch would be underestimated to some extent (c.f., Fig. 5a). Nevertheless, the difference between the observed and computed catches is not critical in terms of model dynamics and does not alter the interpretations.

Long-term stock variations under different harvesting conditions

The previous simulations keep the top predator fishing mortality rate uniform at the value of 0.7 after 1970. An interesting and notably different stocks organisation develops if the top predator fishing pressure reduces after the depletion of its stock. The simulation described here reports the case when f_3 decreases from 0.7 at 1976 to 0.2 at 1981 and retaining this value afterwards (see the broken lines in Fig. 6). The top predator stock then recovers partially around 80 ktons (Fig. 7c) at the expense of diminishing small and medium pelagic stocks (Fig. 7a, b). The system, therefore, changes drastically by reverting back to the pristine conditions. The increase in the top predator stock size under low f_3 was made possible by simultaneous decrease in f_1 from its high to moderate values and the low stock size of small pelagics. As described before, the equilibrium solution shown by the curve 1 in Fig. 5c is consistent with this case and suggest that a linear increase in F_3 up to ~ 4 (80 ktons) is possible when $f_3 = 0.2$, $f_2 \sim 0.2 – 0.3$ and f_1 decreases to ~ 0.5 from its higher values.

Interpretation of stock variations in terms of regime shifts

The time-dependent simulations performed by using two alternative settings of the top predator harvesting rate reveal considerably different stock progression events and associated regime shift dynamics. For the simulations of observed stock variations, the small pelagic stock (F_1) and the top predator stock (F_3) versus f_1 and f_3 plots (Fig. 10a, b) display a rapid rise of the small pelagic stock from its low to high stock regime (TR1) at constant $f_1 \sim 0.3$ and increasing f_3 from 0.4 to 0.7 and vice versa for the top predator stock. The second transition (TR2) occurs along constant $f_3 \sim 0.7$ and for increasing f_1 as evident by the gradual decrease of F_1 and low values of F_3. The stocks are always characterized by single equilibrium state on both sides of these threshold harvesting rates and thus the TR1 and TR2 represent the smooth regime shifts. On the other hand, the simulation with the alternative top pelagic harvesting rate reveals multiple equilibria and alternative stable states for $0.2 < f_3 < 0.7$ and $0.3 < f_1 < 0.6$ for the small pelagic stock and $0.3 < f_1 < 0.9$ for the top pelagic stock (Fig. 11a, b). The low and high stock states thus alternate through the discontinuous regime shifts.

Future stock assessment scenarios

Motivated by the performance of the model for reproducing the long-term observed stock and catch variations, model simulations are further used to assess possible stock distributions under different harvesting conditions during the next two decades (1999 - 2019). The parameter values are retained as in the hindcasting mode implying that the internal conditions of the system will remain unchanged. Admittedly, this assumption may not be entirely realistic. Te changes in the life history traits, habitat alteration, changes in species assemblages, genetic changes (e.g., reduction in growth of overfished populations) as well as the environmental conditions (e.g., resource availability, food competition with gelatinous species, climate) may alter the community dynamics and influence the recovery process (Conover & Munch 2002, Hutchings & Reynolds 2004). Nevertheless, the assessment of future stock variations under different harvesting scenarios alone may still be instructive for fishery management strategies that can mitigate or reverse stock depletion.

The first scenario of likely stock variations during 1999 - 2019 involves keeping the harvesting rates of small pelagics steady at three different values: $f_1 = 0.3$, 0.5 and 0.7, and taking the others same as in the 1990s (i.e., $f_2 = 0.3$, $f_3 = 0.7$). The model integration starts at 1960 and continues up to 2019. For $f_1 = 0.3$, the small pelagic stock will tend to increase up to 1500 ktons within the first five years and remains steady afterwards (Fig. 12a) implying its stabilisation in the HSR. The medium pelagic stock also recovers up to 150 ktons within the next 20 years (Fig. 12b). Reduction in the harvesting rate of medium pelagics to 0.2, on the other hand, helps building up their stock gradually up to about 500 ktons (Fig. 12b) with a compensatory reduction in the small pelagic stock to 1000 ktons (Fig. 12a). Then, both small and medium pelagics will be in their HSRs. Under this scenario, the top predator stocks will remain depleted and small pelagics will continue to play the main predator role in the food web. Higher choice of f_1 (e.g. 0.5) will cause a continuous depletion of small pelagic stock from 1000 to 200 ktons within 20 years (Fig. 12a), while the medium pelagic stock increase linearly up to 500 ktons (Fig. 12b). The choices of $f_1 \sim 0.3$ and $f_2 \sim 0.25$ appears to be the most appropriate for keeping both groups in their high stock regime towards the end of next decade. The top predator stock may gradually build up if their harvesting rate reduces to 0.1. This recovery will, however, take place at the expense of small pelagic stock and is not a desirable stock development; the preferred one is to have balanced stocks of small and medium pelagics whereas keeping the top predator stock at relatively low level.

CONCLUSIONS

Using a three trophic level predator-prey model, this study puts the long-term (1960-1999) pelagic fish catch observations into a dynamical framework and simulates temporal variations of small, medium and large predatory pelagic fish stocks. The other issues addressed are to explore dynamical response of the system to simultaneous changes in the harvesting rates and to assess their optimum conditions for sustainable yield of stocks. Understanding likely response of the pelagic fish stocks to over-exploitation constitutes an integral part of the efforts for elucidating the mechanisms that govern the long-term organisation of Black Sea ecosystem under different environmental factors.

The equilibrium analyses suggest different stock arrangements for different combinations of the consumption and harvesting rates. The parameter values which best describe the observed characteristics of stocks before and after 1970 are determined among these possible alternatives. The appropriate parameter values are then implemented to the time-dependent simulations to predict the stock changes compatible with the available catch data. In essence, the modelling approach combines both steady-state and time dependent dynamics to arrive at a unified understanding of the mechanisms controlling the long-term fish stocks in the Black Sea. A through analysis of the equilibrium characteristics of the system under different parameter settings are useful to understand many structural details of the stocks progression described by the time-dependent dynamics and offers more realistic specification of the harvesting rate variations in the time-dependent simulations.

The model analysis supports marked changes of the stocks after 1970 conjectured by the catch data. These changes were controlled primarily by simultaneous variations of the esting rates. The harvesting rate of small pelagics regulates the entire stocks through the changes in resource availability (bottom-up control). Similarly, the harvesting rate of top pelagics changes the top predator stock size that then alters the trophic cascade (top-down control). Their simultaneous changes introduce even more complex simultaneously operating top-down and bottom-up controls within the higher trophic level and thus more complex dynamics of stock changes.

The pristine system prior to excessive harvesting of the stocks is dominated by large predatory group whose sufficiently strong predation pressure maintained smaller species at their low population densities. This state of the system then shifted to an opposite one once the harvesting rate of top predator group exceeded its critical threshold (~ 0.5) and the harvesting rates of other groups were low (~ 0.3). The new state was populated by small and medium pelagics whereas the top predator stock remained depleted. The system was disturbed subsequently by the changes in harvesting conditions of small and medium pelagics. The small and medium pelagic stocks shifted simultaneously from their high to the low stock states when their harvesting rates exceeded the critical value of 0.6. The small pelagic stock then shifted back again to the high stock state at the same threshold during the decreasing mode of its harvesting rate. The medium pelagic stock however stayed in the low stock regime for its harvesting rate around 0.4. The low stock regime of top predators remained unaltered after 1970 since their harvesting rates persisted above the threshold. All these stock arrangements represent different forms of single equilibrium state of the system and occur through smooth regime shifts. It is also shown that the top predator stock could shift back to the high stock state under a different threshold combination of the harvesting rates (e.g., $f_1 > 0.5$, and f_2 , $f_3 \leq 0.3$) and the system would then possess multiple equilibria and discontinuous regime shifts.

In addition to the changes in harvesting rates, the changes in the consumption rate parameters (r_2 and r_3) of the medium and top predator groups may also alternate the states. Their values, however, are not likely subject to large temporal variations and therefore they are kept constant throughout the simulation period. The appropriate choice of their values is critical for the simulation of observed stock and catch variations. Their slightly different choices give rise to different stock arrangements which are inconsistent with the observations.

The Black Sea highest trophic level is characterized by a relatively simple structure (controlled by small pelagics) after the early 1970s and represents a marked example of fishing down effect. The present level of small pelagic stock is likely maintained if their harvesting rate is retained around 0.5 during the next decade. The medium pelagic stock may, however, build up slowly if their harvesting rate is kept steady around 0.2 - 0.3. Building up of the top predator stock is even more challenge and requires maintaining their harvesting rate as low as 0.1. But, in this case, the small pelagic stock must reduce considerably because the small pelagic and top predator groups can not co-exist at the same stable state under the present parameter setting. Considering a great economical value of anchovy for the region, the best management option seems to sustain balanced stocks of small and medium pelagics by harvesting them below their critical rates and leave the top predator stock depleted.

An important implication of the stock assessment simulations is the significance of a multi-species dynamical approach for fisheries management due to the nonlinear response of different stocks to the harvesting rates of different groups as well as other environmental conditions. The classical single-species approach that ignores species and/or community interactions and maximizes the catch of a single target species / group would not be entirely adequate for managing sustainable utilization of future stocks. This assertion was tested by simplifying the model to the form of a prey-consumer system and a prey system alone and by prescribing the predator stocks from one of the simulations shown in Fig. 7. The reduced models were able to reproduce stock variations of the fully-coupled model only partially when the harvesting rate variations are adopted directly. The reconstruction of stock variations consistent with those provided by the full model was only possible when the harvesting rate variations were modified to some extent. The discrepancy between the harvesting rates of reduced and full models may be considered to reflect the difference between single and multi-species approach.

The present study highlights how a simple model, when carefully tuned, may provide detailed information on the dynamics of fish stocks and realistically reproduce the observations. In essence, the model dynamically reconstructs unobserved properties of the system by making use of limited data set. It forms a basis for studying more complex systems involving anchovy and sprat populations as two independent resource groups, impacts of climate-induced fluctuations, and more proper representation of the enrichment effect (increasing carrying capacity) associated with intense eutrophication.

Acknowledgements. B. McKenzie and M. R. d'Alcala are thanked for their helpful comments on the manuscript. This study is a contribution to EU 6th Framework

Programme Sesame Project, Turkish Scientific and Technological Research Council Project 104Y289, and NATO-CLG Project 982453.

LITERATURE CITED

Abrams PA, Roth JD (1994) The effects of enrichment of three-species food chains with nonlinear functional responses. Ecology 75: 1118-1130

Bilio M, Niermann U (2004) Is the comb jelly really to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the Caspian Sea. Mar. Ecol. Prog. Ser 269: 173-183

Caswell H, Neubert MG (1998) Chaos and closure terms in plankton food chain models. J. Plank. Res 20: 1837-1845

Collie JS, Richardson K, Steele JH (2004) Regime shifts: can ecological theory illuminate the mechanisms? Progr. Oceanogr 60: 281-302

Conover DO, Munch SB (2002) Sustaining fisheries yields over evolutionary time scales. Science 297: 94-96

Daskalov GM (2002) Overfishing drives a trophic cascade in the Black Sea. Mar. Ecol. Prog. Ser 225: 53-63

Daskalov GM (2003) Long-term changes in fish abundance and environmental indices in the Black Sea. Mar. Ecol. Prog. Ser 255:259-270

Daskalov G, Prodanov K, Zengin M (2006) The Black Sea fisheries and ecosystem change: discriminating between natural variability and human-related effects. Proc. of Fourth World Fishery Congress, AFS Book. In press.

deYoung, B, Harris R, Alheit J, Beaugrand G, Mantua N, Shannon L (2004) Detecting regime shifts in the ocean: data considerations. Progr. Oceanogr 60:143-164

Edwards MA, Yool A (2000) The role of higher predation in plankton population models. J. Plank. Res 22:1085-1112

Gibson GA, Musgrave DL, Hinckley S (2005) Non-linear dynamics of a pelagic ecosystem model with multiple predator and prey types. J. Plank. Res 27: 427-447

Gucu AC (2002) Can overfishing be responsible for the successful establishment of *Mnemiopsis leidyi* in the Black Sea? Estuarine, Coastal and Shelf Science 54:439-451

Hastings A, Powell T (1991) Chaos in a three-species food chain. Ecology 72: 896-903

Hutchings JA (2000) Collapse and recovery of marine fishes. Nature 406:882-885

Hutchings JA, Reynolds JD (2004) Marine fish population collapses: Consequences for recovery and extinction risk. BioScience 54:297-309

Ivanov L, Panayotova M (2001) Determination of the Black Sea anchovy stocks during the period 1968 - 1993 by Ivanov's combined method, Proceedings of the Institute of Oceanology, Bulgarian Academy of Sciences 3:128-154

Jackson JB, et al (2001) Historical overfishing and the recent collapse of ecosystems. Science 293:629-638

Kemp WM, Brooks MT, Hood RR (2001) Nutrient enrichment, habitat variability and trophic transfer efficiency in simple models of pelagic ecosystems. Mar. Ecol. Prog. Ser 223:73-87

Kideys AE (2002) Fall and rise of the Black Sea ecosystem. Science 297: 1482-1484

Lima ID, Olson DB, Doney SC (2002) Intrinsic dynamics and stability properties of size-structured pelagic ecosystem models. J. Plank. Res 24:533-556

May RM (1977) Thresholds and breakpoints in ecosystems with multiplicity of stable states. Nature 269:471-477

May RM, Beddington JR, Clark JW, Sidney JH, Laws RM (1979) Management of multispecies fisheries. Science 205:267-277

Morozov AY, Nezlin NP, Petrovskii SV (2005) Invasion of a top predator into an epipelagic ecosystem can bring a paradoxical top-down trophic control. Biological invasions 7:845-861

Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280-283

Oguz T (2005a) Long term impacts of anthropogenic forcing on the reorganisation of the Black Sea ecosystem. Oceanography 18(2):112-121

Oguz T (2005b) Black Sea ecosystem response to climatic variations. Oceanography 18(2):122-133

Oguz T, Gilbert D (2007) Abrupt transitions of the top-down controlled Black Sea pelagic ecosystem during 1960-2000: evidence for regime shifts under strong fishery exploitation and nutrient enrichment modulated by climate-induced variations. Deep-Sea Res I doi:10.1016/j.dsr.2006.09.010

Oguz T, Dippner JW, Kaymaz Z (2006) Climat,c regulation of the Black Sea hydro-meteorological and ecological properties at interannual-to-decadal time scales. J. Mar. Syst 60: 235-254

Pauly D, Christensen V, Dallsgaard J, Froese R, Torres F (1998) Fishing down marine food webs. Science 279: 860-863

Petraitis PS, Dudgeon RD (2004) Detection of alternative stable states in marine communities. J. Exp. Mar. Biol. Ecol 300:343-371

Scheffer M, Rinaldi S, Kuznetsov YA (2000) Effects of fish on plankton dynamics: a theoretical analysis. Can. J. Fish. Aquat. Sci 57:1208-1219

Scheffer M, Carpenter S, Folley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591-596

Spencer PD, Collie JS (1995) A simple predator-prey model of exploited marine fish populations incorporating alternative prey. ICES J. Mar. Sci 53:615-628

Steele JH, Henderson EW (1984) Modeling long-term fluctuations in fish stocks. Science 224:985-986

Yel M, Ozdamar E, Amaha A, Miyazaki N (1996) Dolphin fishery on the Turkish coast of the Black Sea. In: Proceeding of the First International Symposium on the marine mammals of the Black Sea, Istanbul, Turkey (Ed. B. Ozturk):31-40

Zaitsev Y,. Mamaev V (1997) Marine Biological Diversity in the Black Sea: A Study of Change and Decline. GEF Blac k Sea Environmental Programme, United Nations Publications, 208pp

Zemsky VA (1996) History of Russian fishery of dolphins in the Black Sea. In: Proceeding of the First International Symposium on the marine mammals of the Black Sea, Istanbul, Turkey (Ed. B. Ozturk):46-48

Figure Captions

Figure 1. Long-term catch variations of dolphins (DOL), demersals (DEM), large pelagics (LP), medium pelagics (MP), and small pelagics (SP) during 1950-2003. The original data are smoothed using 5 point Gaussian filter. The abscissa on the left shows catch values for the small pelagic group, and on the right for the other groups.

Figure 2. The sum of top predator (dolphins and large pelagics) and demersal catches versus the total catch of small and medium pelagics showing two distinct modes of the Black Sea fish populations before and after 1970.

Figure 3. Relative stock biomass versus top predator consumption rate variations obtained from the equilibrium solution of the model for (a) small pelagic, (b) medium pelagic and (c) top predator groups for both increasing (continuous lines) and decreasing (broken lines) values of r_3 and different choices of the medium pelagic consumption rate r_2=0.5 (circles), r_2=0.7 (squares), r_2= 0.9 (stars). The stock curves for $r_2 > 0.9$ are the same with those of r_2=0.9 and therefore are not shown. The peaks shown in (c) correspond to limit cycle solutions of the model. For the sake of clarity, the symbols are not shown for the solutions for decreasing r_3 values.

Figure 4. Relative stock biomass versus top predator fishing mortality rate variations obtained from the equilibrium solution of the model for (a) small pelagic, (b) medium pelagic and (c) top predator groups for both increasing (continuous lines) and decreasing (broken lines) values of f_3 and for different values of the medium pelagic consumption rates; r_2=0.5 (circles), r_2=0.7 (triangles), and r_2= 1.0 (squares). For the sake of clarity, the symbols are not shown for the solutions for decreasing f_3 values.

Figure 5. Relative stock biomass versus small pelagics fishing mortality rate variations obtained from the equilibrium solution of the model for (a) small pelagic, (b) medium pelagic, and (c) top predator groups for different choices of the medium pelagic and top predator fishing mortality rates; f_2=0.3 and f_3=0.3 (curve 1), f_2=0.3 and f_3=0.5 (curve 2), f_2=0.3 and f_3=0.7 (curve 3), and f_2=0.5 and f_3=0.7 (curve 4). The continuous (broken) lines represent stock variations for increasing (decreasing) f_1.

Figure 6. Temporal variations of the fishing mortality rates for the small pelagic group (f_1, circles), medium pelagic group (f_2, squares), and top predator group (f_3, stars) used in the simulations of observed stock variations. The broken line represents the alternative fishing mortality rate variation for the top predator group used to show possible recovery of the top predator stock.

Figure 7. Temporal variations of relative stock biomass for the (a) small pelagic group, (b) medium pelagic group, (c) top predator group using the parameter values given in Table 2; those with squares correspond to the simulation number 1, triangles to number 2, and stars to number 3. The dash lines represent the results of the fourth simulation using the alternative fishing mortality rate variations for the top predator group. The curve with circles in (a) represent the small pelagic stock variation estimated by Daskalov et al. (2006).

Figure 8. Temporal variations of catches for the (a) small pelagic group (SP), (b) medium pelagic group (MP), (c) top predator group (TP) using the parameter values given in Table 2; the curves with squares correspond to the simulation number 1, triangles to number 2, and stars to number 3. The continuous curves represent the observed catch variations.

Fig. 9. Relative stock biomass versus small pelagics fishing mortality rate variations obtained from the equilibrium solution of the model for (a) small pelagic, (b) medium pelagic groups and the parameter values of first simulation in Table 2. The solutions are presented for $f_3 = 0.7$ and four different choices of the medium pelagic fishing mortality rate; $f_2 = 0.25$ (curve 1), $f_2 = 0.28$ (curve 2), $f_2 = 0.3$ (curve 3), and $f_2 = 0.4$ (curve 4). The continuous (broken) lines represent stock variations for increasing (decreasing) f_1.

Figure 10. Relative small pelagic stock biomass (circles) and top predator stock biomass (squares) versus the fishing mortality rate variations of (a) small pelagic group, (b) top predator group for the simulation number 1 in Table 2. Broken lines represent the threshold values of stocks.

Figure 11. Relative small pelagic stock biomass (circles) and top predator stock biomass (squares) versus the fishing mortality rate variations of (a) small pelagic group, (b) top predator group for the simulation with the alternative top predator fishing mortality rate variations shown in Fig. 6 by broken lines. Broken lines represent the threshold values of stocks.

Figure 12. Prediction of (a) small pelagic, (b) medium pelagic stock biomass during 1999-2019 under three different settings: $f_1 = 0.3$ and $f_2 = 0.3$ (circles), $f_1 = 0.3$ and $f_2 = 0.2$ (squares), and $f_1 = 0.5$ and $f_2 = 0.2$ (triangles).

Table 1. Nondimensional parameters and their values used in the simulations.

Nondimensional parameters	Dimensional Parameters	Range of nondimensional parameter values used in the simulations
K	K_1/K_2	40-50 (time dependent)
r_2	R_2/R_1	0.5-0.7
r_3	R_3/R_1	0.7
d_2	D_2K_3/R_1	0.0-0.01
d_3	D_3K_3/R_1	0.01-0.04
f_i	f_i^*/R_1	0.25-0.90 (time dependent)
γ	K_2/K_3	2.5
F_1	S_1/K_2	Predicted
F_2	S_2/K_3	Predicted
F_3	S_3/K_3	Predicted

Table 2. Nondimensional parameter values of the consumption and natural mortality rates used in three long-term simulations of observed stock and catch variations.

Simulation number	r_2	r_3	D_2	d_3
1	0.62	0.7	0.005	0.04
2	0.65	0.6	0.007	0.04
3	0.65	0.68	0.01	0.03

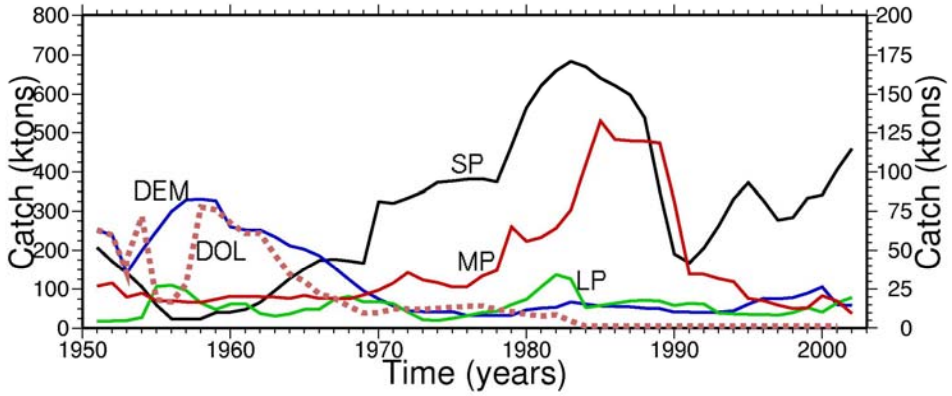

Fig. 1. Long-term catch variations of dolphins (DOL), demersals (DEM), large pelagics (LP), medium pelagics (MP), and small pelagics (SP) during 1950-2003. The original data are smoothed using 5 point Gaussian filter. The abscissa on the left shows catch values for the small pelagic group, and on the right for the other groups.

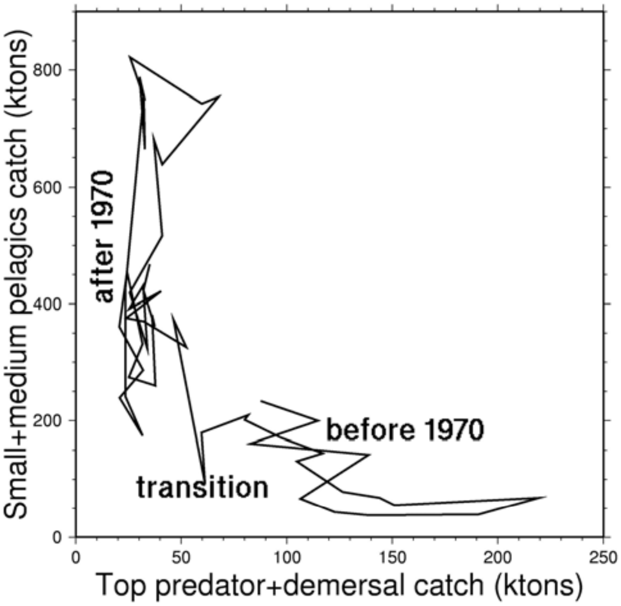

Fig. 2. Total catch of top predators (dolphins and large pelagics) and demersals versus total catch of small and medium pelagics showing two distinct modes of the Black Sea fish populations before and after 1970.

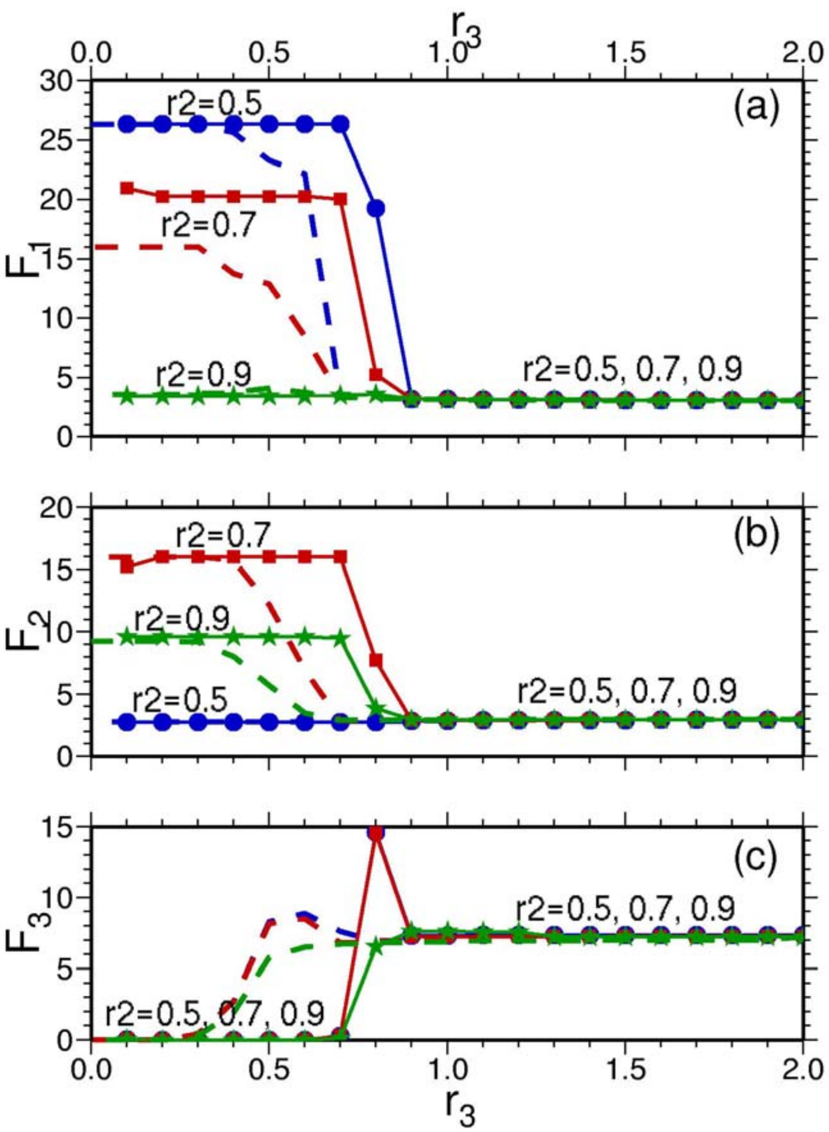

Fig. 3. Relative stock biomass versus top predator consumption rate variations obtained from the equilibrium solution of the model for (a) small pelagic, (b) medium pelagic and (c) top predator groups for both increasing (continuous lines) and decreasing (broken lines) values of r_3 and different choices of the medium pelagic consumption rate r_2=0.5 (circles), r_2=0.7 (squares), r_2= 0.9 (stars). The stock curves for $r_2 > 0.9$ are the same with those of r_2=0.9 and therefore are not shown. The peaks shown in (c) correspond to limit cycle solutions of the model. For the sake of clarity, the symbols are not shown for the solutions for decreasing r_3 values.

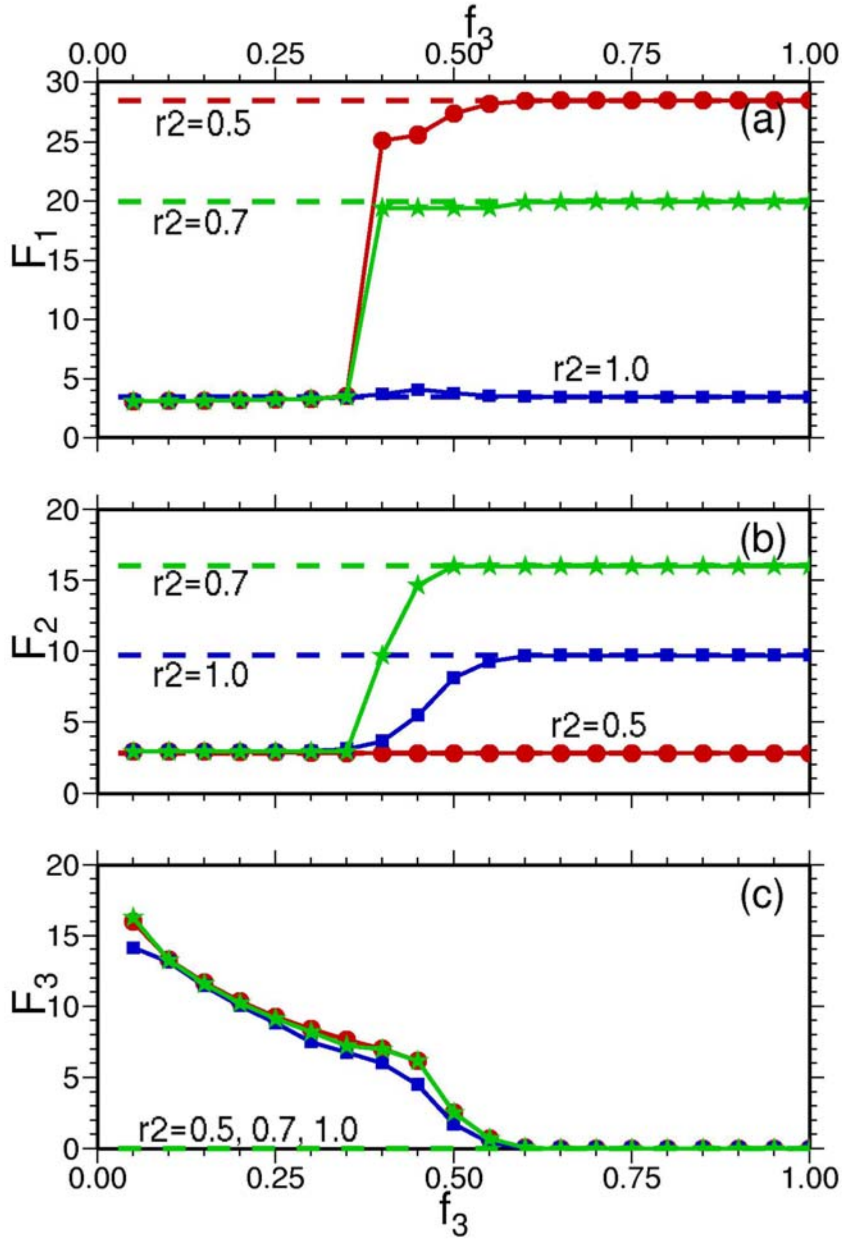

Fig. 4. Relative stock biomass versus top predator fishing mortality rate variations obtained from the equilibrium solution of the model for (a) small pelagic, (b) medium pelagic and (c) top predator groups for both increasing (continuous lines) and decreasing (broken lines) values of f_3 and for different values of the medium pelagic consumption rates; r_2=0.5 (circles), r_2=0.7 (triangles), and r_2= 1.0 (squares). For the sake of clarity, the symbols are not shown for the solutions for decreasing f_3 values.

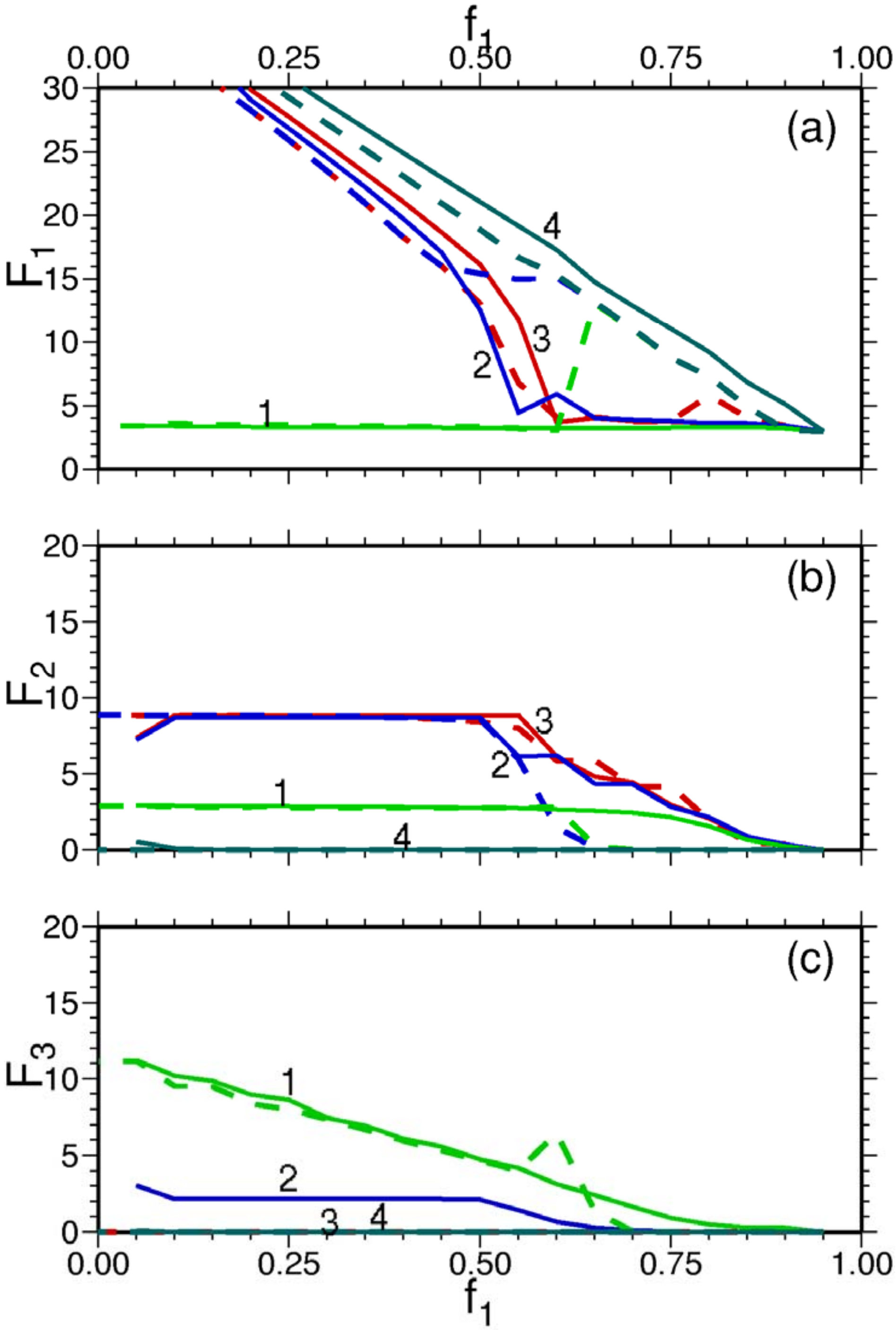

Fig. 5. Relative stock biomass versus small pelagics fishing mortality rate variations obtained from the equilibrium solution of the model for (a) small pelagic, (b) medium pelagic groups and for different choices of the medium pelagic and top predator fishing mortality rates; f_2=0.3 and f_3=0.3 (curve 1), f_2=0.3 and f_3=0.5 (curve 2), f_2=0.3 and f_3=0.7 (curve 3), and f_2=0.5 and f_3=0.7 (curve 4). The continuous (broken) lines represent stock variations for increasing (decreasing) f_1.

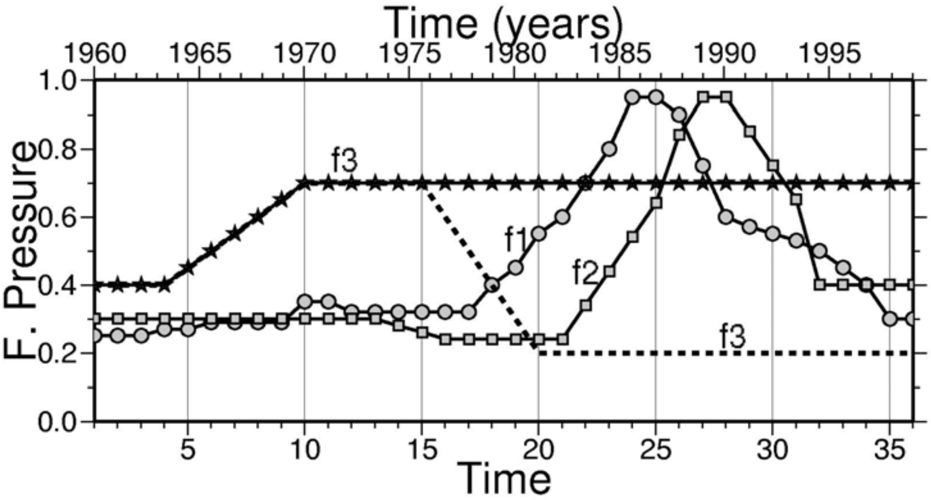

Fig. 6. Temporal variations of the fishing mortality rates for the small pelagic group (f_1, circles), medium pelagic group (f_2, squares), and top predator group (f_3, stars) used in the simulations. The broken lines represent the alternative fishing mortality rate variation for the top predator group used to show possible recovery of the top predator stock.

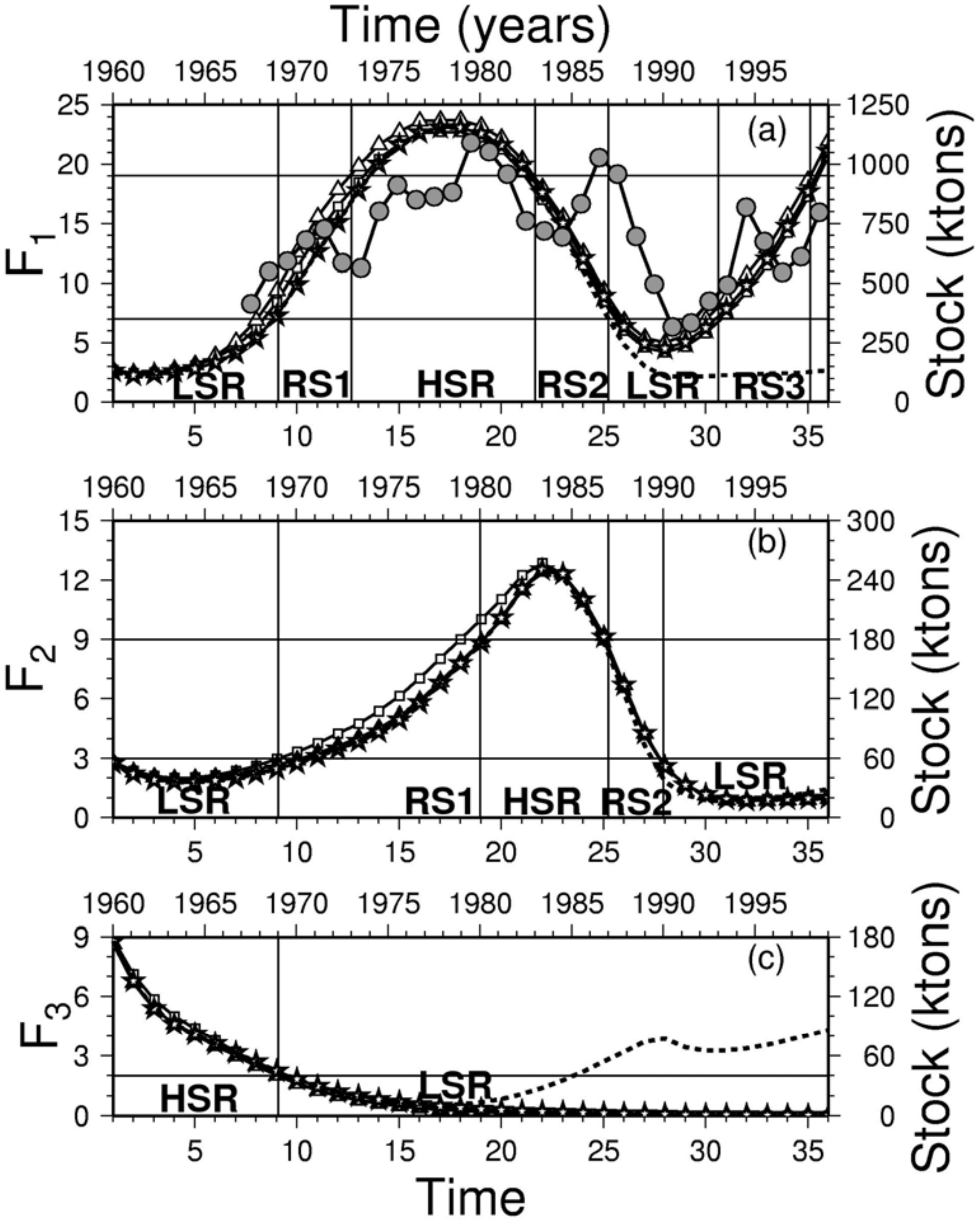

Fig. 7. Temporal variations of stocks for the (a) small pelagic group, (b) medium pelagic group, (c) top predator group using the parameter values given in Table 2; those with squares correspond to the simulation number 1, triangles to number 2, and stars to number 3. The dash lines represent the results of the fourth simulation using the alternative fishing mortality rate variations for medium and top predator groups used to test possible recovery of these two groups within the 1990s. The curve with circles in (a) represent the small pelagic stock variation estimated by Daskalov et al. (2005).

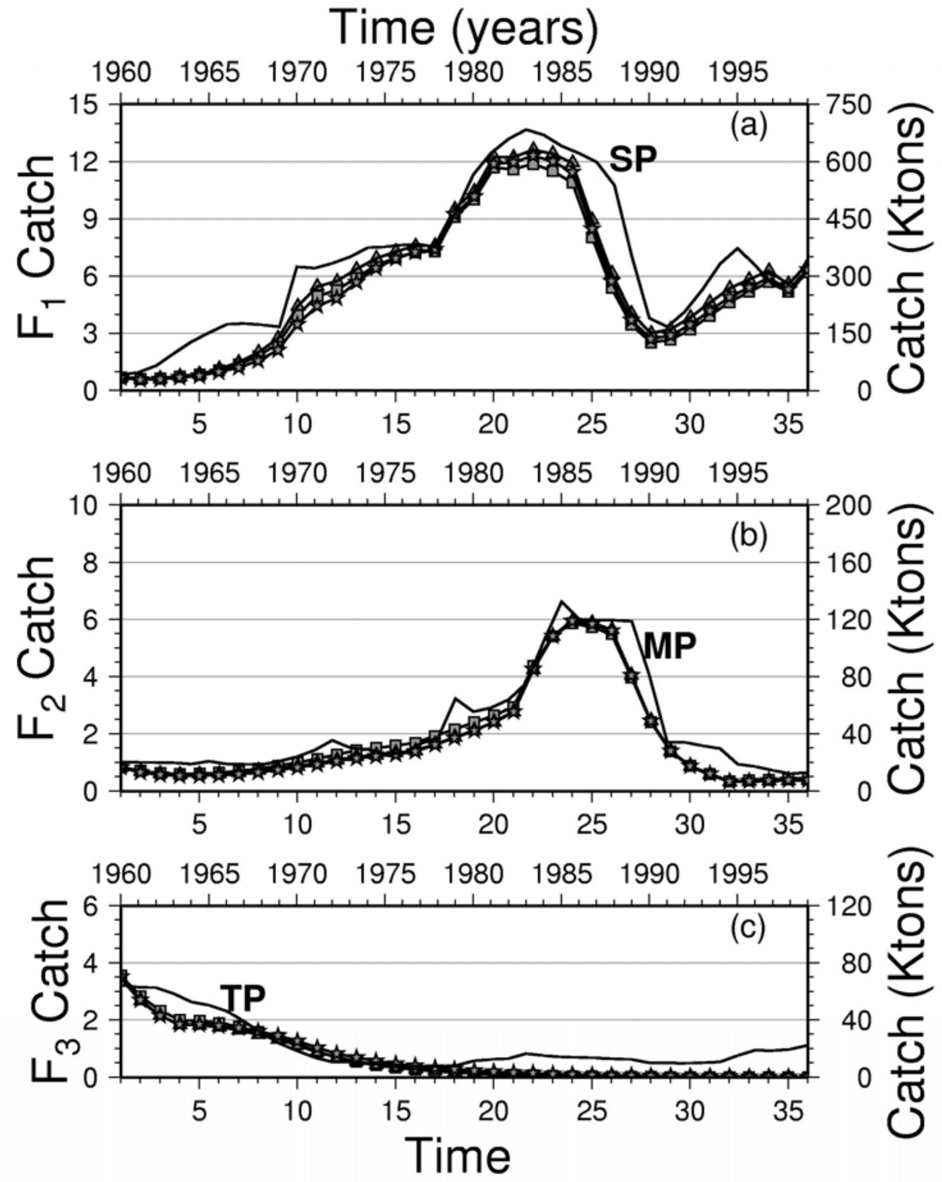

Fig. 8. Temporal variations of catches for the (a) small pelagic group (SP), (b) medium pelagic group (MP), (c) top predator group (TP) using the parameter values given in Table 2; the curves with squares correspond to the simulation number 1, triangles to number 2, and stars to number 3. The continuous curves represent the observed catch variations.

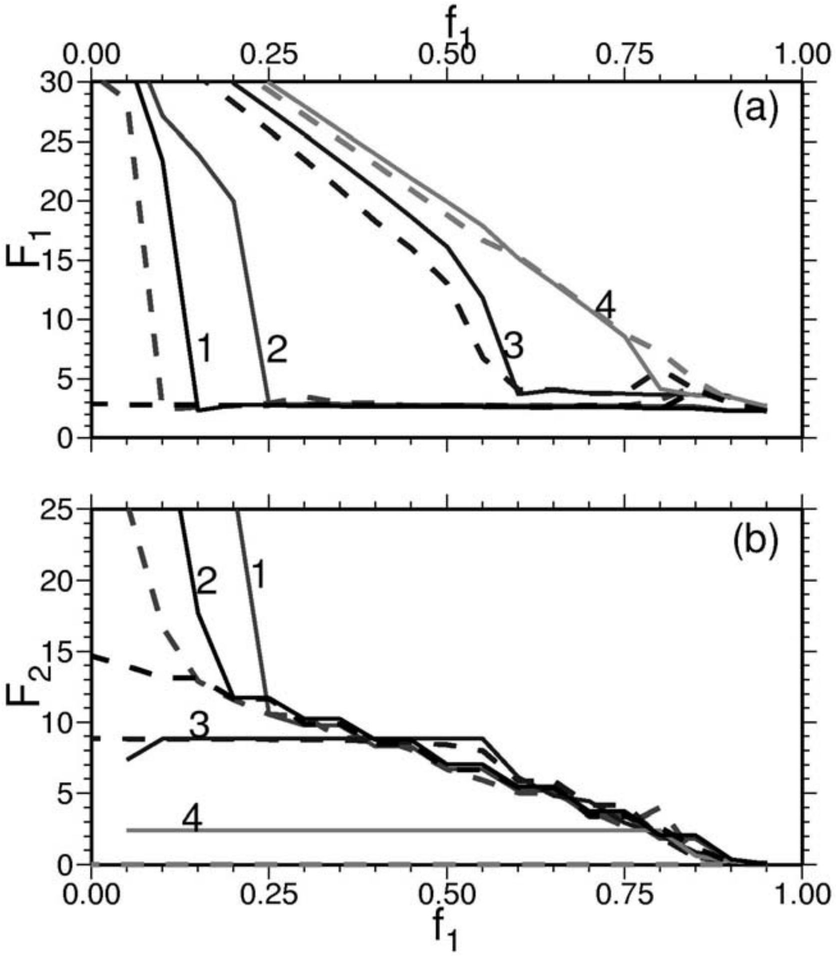

Fig. 9. Relative stock biomass versus small pelagics fishing mortality rate variations obtained from the equilibrium solution of the model using the top predator mortality rate variations shown in Fig. 6 for (a) small pelagic, (b) medium pelagic groups and for different choices of the medium pelagic fishing mortality rate; f_2=0.25 (curve 1), f_2=0.28 (curve 2), f_2=0.3 (curve 3), and f_2=0.4 (curve 4). The continuous (broken) lines represent stock variations for increasing (decreasing) f_1.

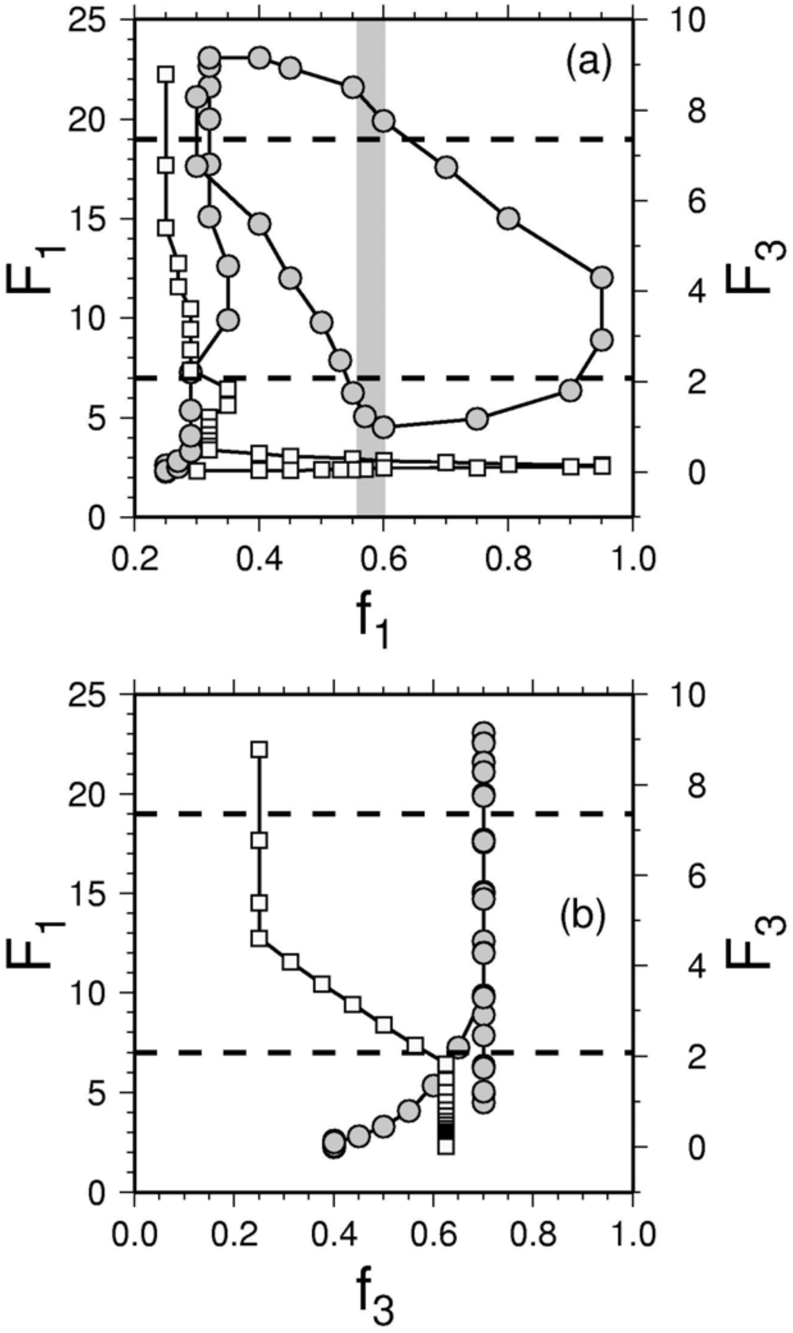

Fig. 10. Changes in the small pelagic stock (circles) and top predator stock (squares) with respect to the fishing mortality rate of (a) small pelagic group, (b) top predator group for the simulation number 1 in Table 2. The broken lines represent the threshold values of stocks.

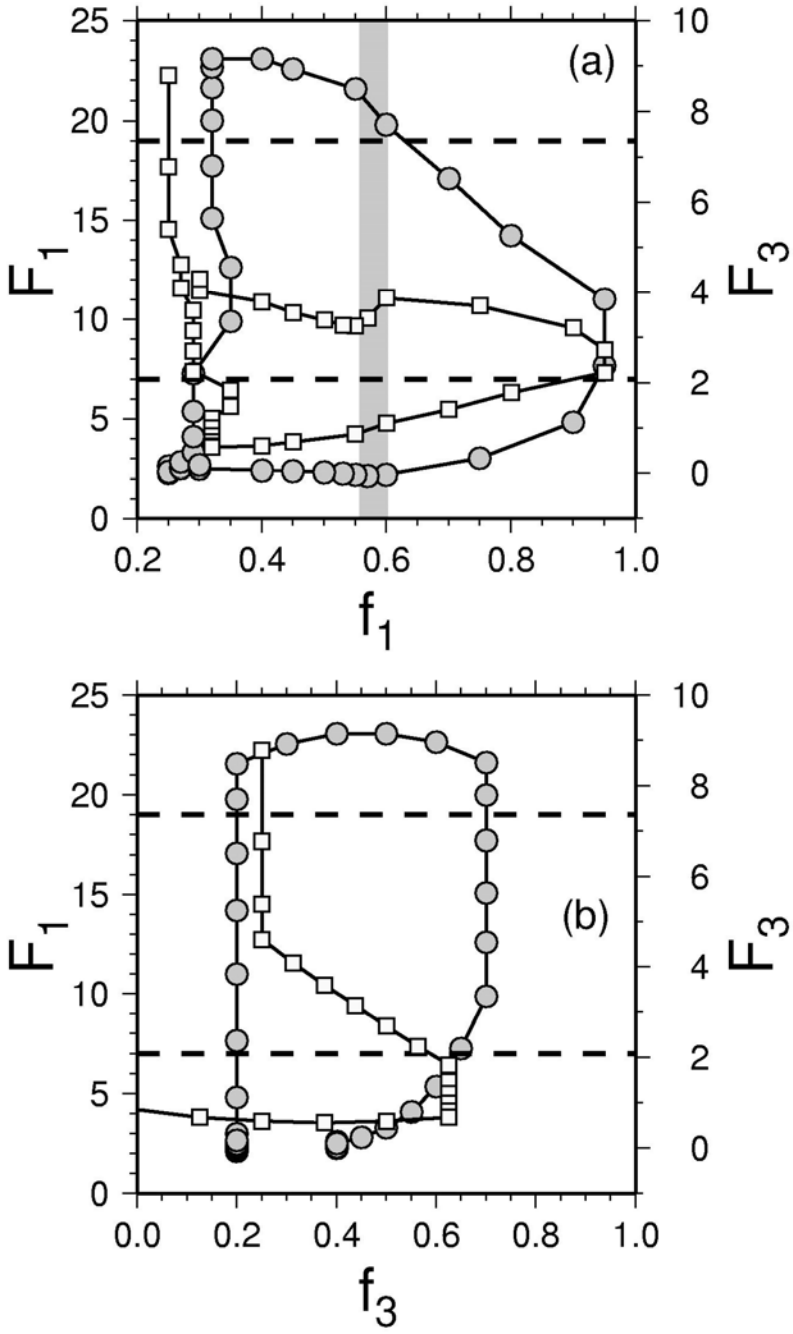

Fig. 11. Changes in the small pelagic stock (circles) and top predator stock (squares) with respect to the fishing mortality rate of (a) small pelagic group, (b) top predator group for the simulation with the alternative top predator fishing mortality rate variations shown in Fig. 6 by broken lines. The broken lines represent the threshold values of stocks.

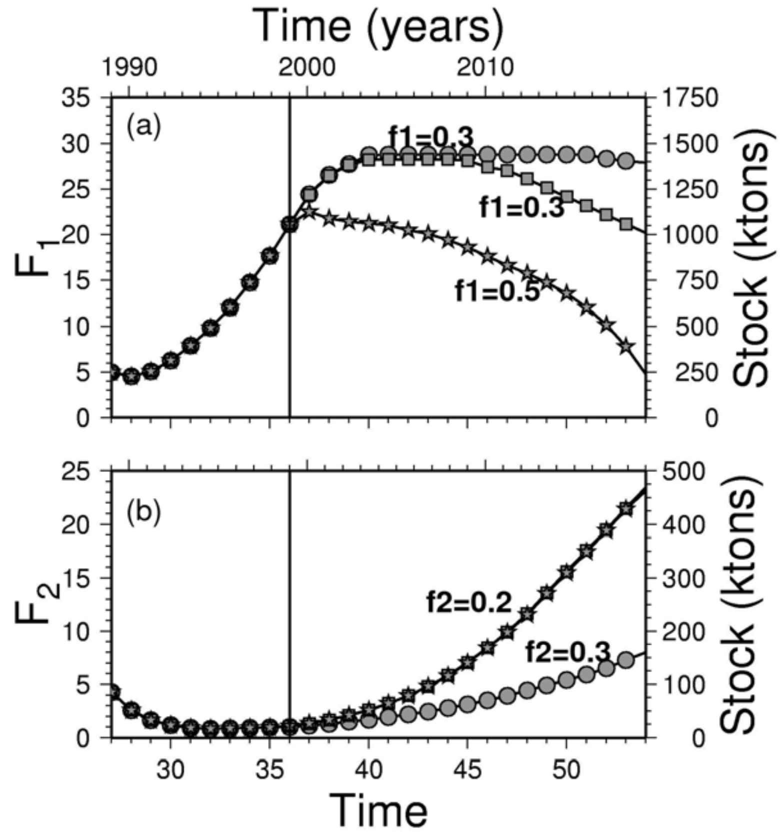

Fig. 12. Prediction of (a) small pelagic, (b) medium pelagic stocks during 1999-2019 under three different settings: f_1=0.3 and f_2=0.3 (circles), f_1=0.3 and f_2=0.2 (squares), and f_1=0.5 and f_2=0.2 (triangles).