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Stock dynamics and predator–prey effects of Atlantic bonito and bluefish as top predators in the Black Sea

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This study uses surplus production model-based methods to assess data-poor stocks and estimate key reference points for Atlantic bonito (*Sarda sarda*) and bluefish (*Pomatomus saltatrix*) in the Black Sea. Our results demonstrate that the catch maximum sustainable yield (CMSY) method, using catch data only, yields similar results to the more accurate Bayesian Schaefer model (BSM) method, fitted with commercial catch-per-unit-of-effort data, and therefore is suitable in assessing data-poor stocks. We explore the ecological impacts of the two stocks on other commercial species and compare impacts of predation and fishing. Prior to 1995, the consumption of bonito and bluefish on anchovy, horse mackerel, and sprat exceeded the removal of those prey species by the fisheries. Later on, the trends reversed, with catches of prey species becoming more than three times higher than their predation by bonito and bluefish. Horse mackerel, the main prey of bluefish, has declined to critical levels since 1995, which is likely contributing to the general decline in bluefish, along with overfishing. Heavy fishing of bonito and bluefish has caused their current depleted states and combined with their significant impact on prey fish contributed to the ecosystem regime shift in the Black Sea. Due to the present steady positioning of low stock regimes, the recovery of the two stocks need decisive and possibly prolonged rebuilding measures, including a reduction in fishing pressure, efficient control of under-sized catch, and ensuring sufficient prey biomass availability.

Keywords: data-poor stocks, fisheries management, MSY, *Pomatomus saltatrix*, reference points, *Sarda sarda*, stock assessment methods

Introduction

Fisheries science theory teaches that when a virgin fish stock is first fished, the production or yield initially increases (Beverton and Holt, 1957), and the highest level of catches that can be sustained at an optimal level of fishing pressure is called the "Maximum Sustainable Yield" (MSY; Schaefer, 1954; Murawski, 2010). If fishing pressure increases beyond that optimal level, the biomass and catches begin to decline. The level of fishing mortality associated with *MSY* is an important reference point that needs to be accurately determined as scientific advice to fisheries managers. In addition, changes in fishing tactics and fisheries regulations (McGarvey *et al.*, 2016), environmental factors (Alheit *et al.*, 2014), and predator–prey interactions (Christensen *et al.*, 2008) contribute to dynamics of fish stocks and catches.

The Black Sea is a nearly enclosed basin only connected to the Mediterranean Sea via the narrow Bosphorus Strait, Marmara Sea, and Dardanelle Straits. The Black Sea is subject to pronounced anthropogenic driven land-based influences due to its extensive catchment area. The continental shelf is much wider in the northern and western parts of the Black Sea, and narrow in the south and east. Due to its enclosed nature and subsequent lack of strong vertical currents, water deeper than ∼200 m is very poorly ventilated and anoxic, thus incapable of supporting aerobic life (Sorokin, 1982). This deeper water is saturated with hydrogen sulphide, which has been accumulating from decaying organic matter and anoxic bacterial processes in the Black Sea for thousands of years. Over its recent history, the Black Sea ecosystem has undergone several basin-wide transformations, such as the removal of large predatory fish, intense eutrophication resulting in bottom hypoxia, devastation of the benthic ecosystem, and harmful non-indigenous species invasions, which together drove the ecosystem to violent regime shifts and fisheries collapses (Daskalov, 2011; Friedrich *et al.*, 2014; Oğuz, 2017). By 1970, large pelagics were heavily overfished and nearly extinct in the Black Sea (Daskalov *et al.*, 2008; Ulman *et al.*, 2020). Bluefin tuna (*Thunnus thynnus*), disappeared from Black Sea catches, followed by large bonito, swordfish (*Xiphias gladius*), and Atlantic mackerel (*Scomber scombrus*, Daskalov *et al.*, 2008; Ulman and Pauly, 2016). In addition to the decrease in biodiversity, the average size of the enduring species is also decreasing (Ulman *et al.*, 2020); for example Mediterranean horse mackerel (*Trachurus mediterraneus*, called horse mackerel hereafter) used to be considered a medium-sized pelagic fish but, from the 1970s onwards, is considered a small pelagic due to its considerably smaller mean size (Daskalov *et al.*, 2008). Similarly, since the early 1990s, the bluefish stock is largely dominated by juvenile individuals resulting in considerably reduced mean size and growth rate (Georgieva and Daskalov, 2019). At present, only two medium-sized pelagic fish: Atlantic bonito (*Sarda sarda*), called bonito hereafter, and bluefish (*Pomatomus saltatrix*) remain as top pelagic fish predators in the Black Sea and, thus, it is imperative that these stocks endure to maintain their essential role in exerting top-down control over the food web (Daskalov *et al.*, 2008).

The scarcity of biological data and lack of analytical stock assessments for some commercial stocks has led to regard the Black Seas as a "data-poor" region (Pilling *et al.*, 2008). Data-poor situations require a different approach to fisheries management that diverge from classical age-structured stock assessment methods. To overcome this issue, we use novel stock assessment techniques designed to produce fisheries reference points when biological data are deficient and biomass time series are either short or incomplete (Froese *et al.*, 2017). We perform the first comprehensive assessment of stock status, fisheries, and predatory effects of bonito and bluefish stocks in the Black Sea for the 1950–2016 period by applying the new catch maximum sustainable yield (CMSY) method (Froese *et al.*, 2017). Bonito and bluefish were selected since they are the last remaining medium-sized pelagic predatory fishes in the Black Sea ecosystem, lacking both age-structured data and analytical stock assessments. Data from recent feeding studies are used to assess consumption and dietary requirements of bonito and bluefish and to evaluate their predatory impacts on other commercially important fish stocks. Since stock assessments are limited in the Black Sea, this study uses new methods to assess stock status, exploitation rates, and predation effects of bonito and bluefish to improve the knowledge necessary for the formulation of scientific advice to be able to transition towards ecosystem-based fisheries management.

Material and methods

Data

Bonito and bluefish are known to migrate from the Marmara Sea to the Black Sea for feeding and reproduction during the warm season (May–November) and return back to Marmara Sea in the cold season (December–April) to overwinter (Tkacheva *et al.*, 1960; Ivanov and Beverton, 1985; Zengin and Dinçer, 2006; Atılgan *et al.*, 2016). Their migratory makes the separation of stocks from different seas difficult. Earlier research confined their stock areas to mainly the Black and Marmara Seas, and to a lesser extent, the Aegean Sea. Studies from their life history and migration also confirm that the Black and Marmara Seas are their main areas of distribution (Tkacheva *et al.*, 1960; Ivanov and Beverton, 1985; Zengin and Dinçer, 2006; Atılgan *et al.*, 2016; Georgieva and Daskalov, 2019). Molecular genetic studies (Turan *et al.*, 2015) successfully differentiated the bonito population in the Black and Marmara Seas from populations in the Aegean Sea and Mediterranean Sea. Turan *et al.* (2006) found differences between morphometric and meristic traits of bluefish from the Eastern Black Sea and Western Black Sea/Sea of Marmara/Aegean Sea. However, genetic analyses of bluefish would bring more clarity on differences between sub-populations of bluefish in the region, and research on this topic would be useful.

Bonito and bluefish landings data from FAO (FAO, 2017), national fisheries statistics from Turkey [Turkish Statistical Institute (TUIK), 2017], and other Black Sea countries (Scientific, Technical and Economic Committee for Fisheries (STECF), 2017) were analysed to determine which catch data best capture the distribution range of these two stocks. The comparative analyses of landings data for both species show that the majority of catches is taken from the Black Sea and Marmara Sea, with adjacent seas only having minor contributions: for bonito 71% Black Sea, 17% Marmara Sea, and 11% Aegean Sea; for bluefish 67% Black Sea, 27% Marmara Sea, and 6% in the Aegean Sea, averaged from 1950 to 2016. Cluster analyses of landings data also confirmed that the Black Sea time series data are primarily related to Marmara Sea data (Figure 1), while the Aegean and Mediterranean catches are attributed to different clusters. Therefore, under the informed assumption that the Black and Marmara Seas are the main areas inhabited by bonito and bluefish stocks from which the majority of the catches in these seas is taken (see Discussion section for additional arguments and references), a pragmatic *ad hoc* approach was adopted using combined catch data from the Black and Marmara Seas as the input catch data for stock assessment. The estimated biomass belongs to the Black Sea stocks of bonito and bluefish, which inhabit the Black Sea during the warm season and migrate to the Marmara Sea during winter. Only the predatory impacts of bonito and bluefish on their Black Sea prey species are assessed here, as the data necessary for performing such analyses were not available from Marmara Sea.

Commercial catch-per-unit-of-effort (*CPUE*) time series data (1984–2016) were used to fit the assessment models. Data from purse-seine fisheries in the Black Sea were derived from previous work (Zengin and Dinçer, 2006). To calculate the time series of *CPUE* (kg h^{-1}) of bonito and bluefish, the total number of purse-seiners in operation in the Black Sea from 1984 to 2016 was used along with the average number of active fishing days (55 for bonito, 80 for bluefish), average number of daily operations (2 for bonito, 3 for bluefish) and their average duration in hours (1.75

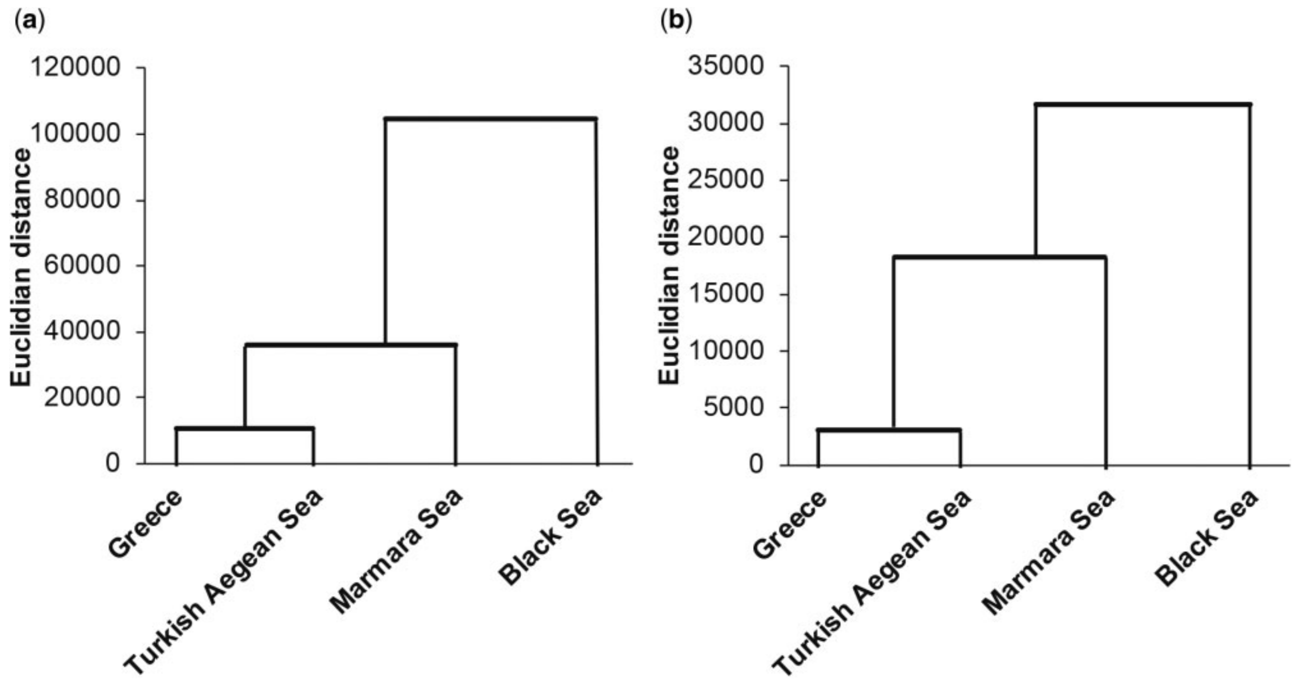

Figure 1. Cluster analyses of time series data of landings (1950–2016) of bonito (a) and bluefish (b).

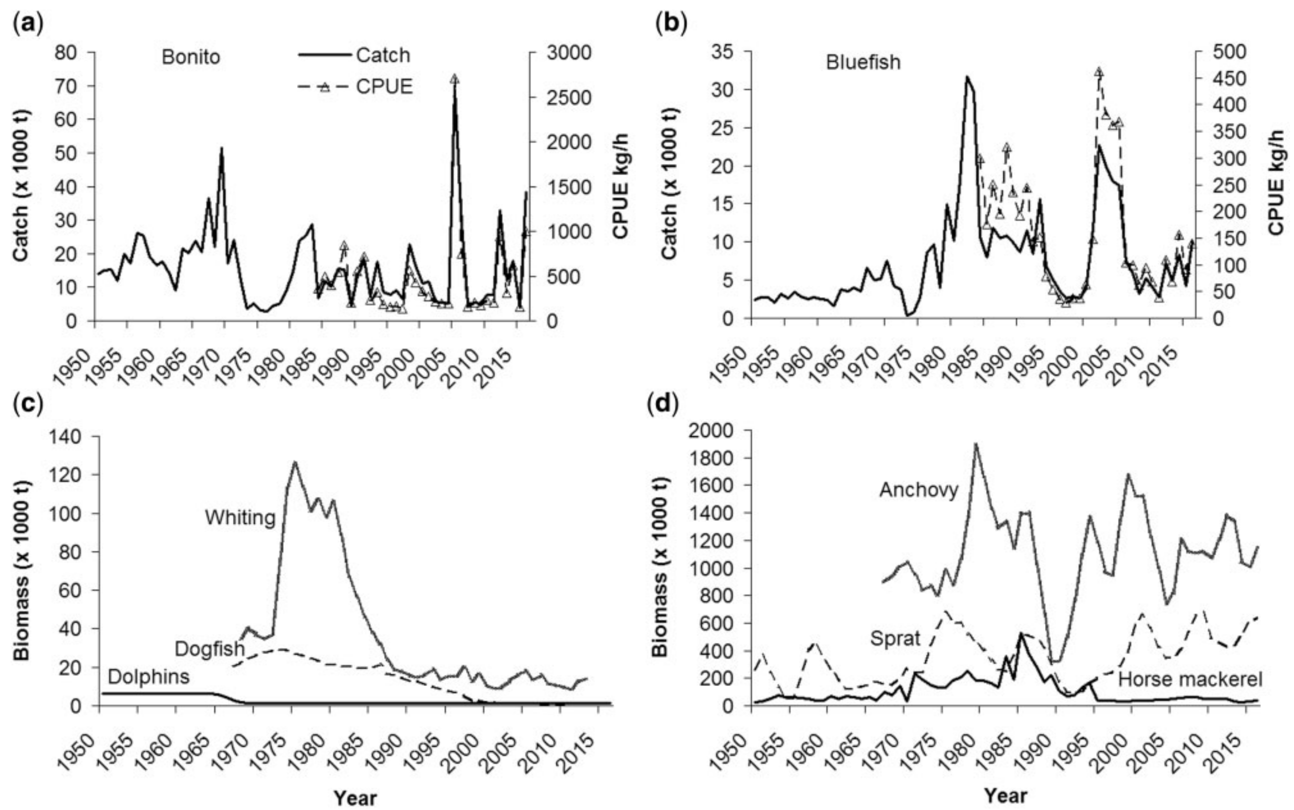

Figure 2. Catches and CPUE times series of bonito (a), bluefish (b), biomass of (c) other predators: whiting, dogfish, and dolphins and (d) small pelagic fish: anchovy, horse mackerel, and sprat.

for bonito, 1.5 for bluefish, Figure 2). The *CPUE* data solely from the Black Sea were used for fitting of Bayesian Schaefer model (BSM), assuming that it is a representative index of relative biomass of the two stocks. Indeed, for the period covered by the *CPUE* data (1984–2016), the dominant majority of the catches were from the Black Sea: 86% for bonito and 69% for bluefish, compared to 14% for bonito and 31% for bluefish from Marmara Sea. Fishing effort in the number of boats and daily effort was not available from Marmara Sea; since Marmara is often fished by boats registered to the larger Black and Aegean Seas, we excluded the effort analyses here to avoid double-counting of boats. Therefore, only the *CPUE* data from the Black Sea were used as a reliable index of relative biomass of both stocks.

Stock assessment

Bonito and bluefish stocks were assessed using the CMSY and BSM methods (Froese *et al.*, 2017). CMSY is a method for data-limited stock assessment using catches and informative priors to estimate stock biomass and *MSY*-based reference points for fisheries management. CMSY is coupled with a Bayesian production model (BSM, Froese *et al.*, 2017) that uses research survey indices of biomass, or commercial *CPUE* to fine tune the estimated biomass. Both CMSY and BSM are based on the Schaefer surplus production model (Schaefer, 1954):

$$B_{t+1} = B_t + r\left(1 - \frac{B_t}{k}\right)B_t - C_t, \quad (1)$$

where B_t and B_{t+1} are the biomass of the stock at time t and $t+1$, respectively; r is the maximum intrinsic rate of population growth; and k is the population-carrying capacity (size of unexploited stock and C_t is the catch in year t). Surplus production or yield is represented by $r\left(1 - \frac{B_t}{k}\right)B_t$ in the above equation.

To account for reduced recruitment in severely depleted stocks (also called depensation, Barrowman and Myers, 2000), a linear decline in surplus production is incorporated if biomass falls below 0.25 k. This is done by multiplying the yield term $r\left(1 - \frac{B_t}{k}\right)B_t$ by 4 B_t/k that assumes a linear decline in recruitment below half the biomass capable of producing MSY (Froese *et al.*, 2017):

$$B_{t+1} = B_t + 4\frac{B_t}{k}r\left(1 - \frac{B_t}{k}\right)B_t - C_t \Big| \frac{B_t}{k} < 0.25. \quad (2)$$

CMSY is very useful in data-poor situations because the necessary input data can be limited only to catch time series. Adding possible ranges of the parameters r and k improves the input information and makes it possible to fit the production model.

Key assumptions are based on the relationship between maximum population growth r and population resilience to stock collapse due to fishing. Musick (1999) related resilience categories to population growth r, individual growth, maturity, fecundity, and lifespan parameters. Resilience categories of several species of fishes are assigned based on life history parameters and published in FishBase (Froese and Pauly, 2018). Prior ranges of the parameter r of bonito and bluefish are assigned based on the following resilience categories: high 0.6–1.5; medium 0.2–0.8; low 0.05–0.5; and very low 0.15–0.1 (Froese *et al.*, 2017).

Prior range of carrying capacity k is derived from the information of maximum catch and assumed range of the population growth r. The method is using the assumption that k is always larger than the maximum realized catch, so the maximum catch in the time series is used to inform about the lower range of k. As MSY and therefore F_{MSY} depend on the productivity of the stock, the range of possible k values can be expressed as ratios of maximum catch and upper and lower bounds of r (the empirical relationships as obtained by Froese *et al.*, 2017):

$$k_{low} = \frac{C_{max}}{r_{high}}; \quad k_{high} = \frac{4C_{max}}{r_{low}}. \quad (3)$$

As the maximum catch would constitute a larger fraction of k in a substantially depleted rather than a lightly depleted stock, the above empirical equations (3) are to be used in cases where the prior biomass is low (highly depleted). Similar empirical equations are built to be used in cases where the prior biomass is relatively high [(4), lightly depleted]. Suitable ranges of C_{max}/r have been produced empirically using simulated data where the true values of k have been known (the empirical relationships as obtained by Froese *et al.*, 2017):

$$k_{low} = \frac{2C_{max}}{r_{high}}; \quad k_{high} = \frac{12C_{max}}{r_{low}}, \quad (4)$$

where k_{low} and k_{high} are the lower and upper bounds of the prior range of k, C_{max} is the recorded maximum catch in the time series, and r_{low} and r_{high} are the lower and upper bounds of the range of r values.

The CMSY method also needs prior range of relative biomass (B/k) at the beginning, the end, and optionally in an intermediate year of the time series. Possible broad ranges of relative biomass that can be assigned depending on the level of stock depletion are: very strong depletion 0.01–0.2; strong depletion 0.1–0.4; medium depletion 0.2–0.6; low depletion 0.4–0.8; and nearly unexploited stock 0.75–1 (Froese *et al.*, 2017). The ranges are derived based on patterns in the catch time series, e.g. the timing and ratio of minimum catch and maximum catch (Froese and Kesner-Reyes, 2002).

The CMSY runs by applying a Monte Carlo approach to generate an area of random "viable" r–k pairs that are able to produce estimates of the biomass compatible with prior ranges of relative biomass (Froese *et al.*, 2017). From there, the most probable r–k pair and respective confidence intervals are estimated in the area of a triangular-shaped cloud in right hand side of "viable" r–k area (Froese *et al.*, 2017; Supplementary Figures S2 and S7).

BSM uses Markov Chain Monte Carlo (MCMC) simulation and tuning indices (biomass, or commercial *CPUE*) to fit a state-space production model. Initially, the ranges of r and k are transformed into prior densities by assuming log-normal distributions. To use *CPUE* indices, a prior range of the catchability coefficient q is needed (as $CPUE = qB$). The suitable range of q is derived from the following empirical equations (Froese *et al.*, 2017):

$$q_{low} = \frac{0.25 r_{pgm} CPUE_{mean}}{C_{mean}}, \quad (5)$$

$$q_{high} = \frac{0.5 r_{high} CPUE_{mean}}{C_{mean}}, \quad (6)$$

where q_{low} and q_{high} are the lower and higher bounds of q, respectively; r_{pgm} is the geometric mean of the prior range for r; $CPUE_{mean}$ is the mean *CPUE* of the last 5 or 10 years, and C_{mean} is the mean catch over the same period. In stocks with a low recent biomass, the multipliers are doubled from 0.25 to 0.5 for q_{low} (Eqn. 5) and from 0.5 to 1 for q_{high} (Eqn. 6). The uniform q

range is then transformed into a prior density function assuming log-normal distribution (Froese *et al.*, 2017). In stocks with medium and high resilience, catch and *CPUE* are averaged over the last 5 years, whereas in stocks with low or very low resilience, catch and *CPUE* are averaged over the last 10 years.

The state-space model implementation of the BSM follows Millar and Meyer (1999) and is included in the CMSY software (Froese *et al.*, 2019; http://oceanrep.geomar.de/33076). The JAGS software (Plummer, 2003) is used for sampling the probability distributions of the parameters with the MCMC.

Finally, both CMSY and BSM can be used to estimate reference points such as MSY $= rk/4$; $F_{\mathrm{MSY}} = 0.5r$; and $B_{\mathrm{MSY}} = 0.5k$ (Schaefer, 1954; Ricker, 1975). The reference points and their confidence intervals estimated with the BSM are preferred over reference points from CMSY, to be used for advice to management, and are presented as standard output from the software (Supplementary Material).

Predator–prey assessment method

Predator–prey relationships are explored using the same methods as in trophic modelling (Ecopath with Ecosim, Christensen *et al.*, 2008), where the predator stock biomass is multiplied by their individual annual consumption rate (consumption/biomass, *Q*/*B*) to derive the total prey amounts consumed by the predators. To calculate the consumption of specific prey items, total consumption of predators is multiplied by the percentage of each prey item from the predators' diet. Input data used to estimate consumption are the biomass estimates, consumption rates, and diets of bonito, bluefish, and other important predators (Table 1). Biomass of bonito and bluefish is produced in this study (using the BSM method), and biomass of other important predators is taken from Scientific, Technical and Economic Committee for Fisheries (STECF) (2017, Figure 3a). The biomass of dolphins is taken from Daskalov (2002), under the assumption (due to a lack of contemporary population estimates) that it has not changed since 1970. Consumption rates of bonito and bluefish are from FishBase (Froese and Pauly, 2018), and their diets are from recent studies (M. Zengin, unpublished data; Başçınar *et al.*, 2017; Georgieva and Daskalov, 2019; Table 1). Consumption rates and diets of the other predators (Table 1) are from Daskalov (2015).

Predatory impacts are assessed using ratios of their prey species' biomasses and the standing stock biomasses of their prey species for a particular year (a proxy of predation mortality, Christensen *et al.*, 2008). The biomass estimates of sprat (*Sprattus sprattus*), anchovy (*Engraulis encrasicolus*), and horse mackerel were taken from the most recent stock assessment report (Scientific, Technical and Economic Committee for Fisheries (STECF) 2017; Figure 3b). The predation impacts on important prey species, such as anchovy, sprat, and horse mackerel, are then compared to the amounts of the prey biomass removed by the fisheries, expressed as the annual exploitation rate (catch-to-biomass ratio), as a proxy of the annual fishing mortality.

Results

Stock assessment

Both CMSY and BSM assessment models were applied to bonito and bluefish. Input ranges for the priors are presented in Table 2. In both species, prior ranges of the intrinsic population growth (*r*) were set to correspond to medium resilience in agreement with the life history parameters published in FishBase (Froese and Pauly, 2018). The ranges for relative biomass (*B*/*k*) in the initial year were set to correspond to both stocks being lightly depleted, since in the early years, some fisheries targeted these highly valuable species. The (*B*/*k*) for the intermediate and final years of both stocks was set assuming heavy exploitation (Table 2 and Supplementary Figures S1 and S6). The intermediate year in which a prior for the *B*/*k* was set is the middle of the time series (1990) where the two stocks were already heavily depleted. All the priors were estimated according to the rules presented in the Material and Methods section. It can be seen that posterior distributions differ from prior distributions in both CMSY and BSM analyses, accentuating the ability of the methods to produce estimates taking into account information from input data (catches and biomass indices). We tried different settings while evaluating the results using model diagnostics (Supplementary Material). The final model settings were selected based on the least mean squared errors (MSE) between observed and estimated logarithmically transformed *CPUE* (plot of residuals is presented in Supplementary Material). In the BSM model for bluefish, the data points 1996–1999 from the *CPUE* time series were not used to fit the model because there were many influencing outliers producing a high level of uncertainty.

The assessments using the CMSY and BMS methods show comparable results in terms of biomass and fishing mortality (*F*) trajectories and estimated confidence bands (Figure 3). In both stocks, the CMSY method estimates a slightly higher biomass and lower *F* and differences between the two models were not significant. We can see, however, a more clear influence of using the *CPUE* data for the fitting of the BSM model in the period 1984–2016, especially in bonito (Figure 3a). From observing the residuals (Supplementary Figures S3 and S8), an autocorrelative pattern is seen, as well as some extra-large residuals (in fact data points for 1996–1999 in bluefish from the *CPUE* series were not used in the BSM model adjustment because of their extreme

Table 1. Consumption to biomass (*Q*/*B*) ratio, average consumption (for 1950–2016), and diet of main predators.

Species	*Q*/*B*	Consumption (× 1 000 tonnes)	% prey in diet: % anchovy	% horse mackerel	% sprat	% other fish	% total fish	% small pelagics
Bonito	1.6	144	63	27	3	7	100	93
Bluefish	1.9	148	29	22	24	13	93	86
Whiting	2.5	91	28	0	30	8	65	89
Dogfish	3	43	15	6	20	59	100	41
Horse mackerel	4.5	372	15	2	10	0	27	100
Dolphins	19	47	35	10	35	20	100	80

The last column shows the relative amount of small pelagic fish (sprat, anchovy, and horse mackerel) as a % of the fish portion in the diet of the predators.

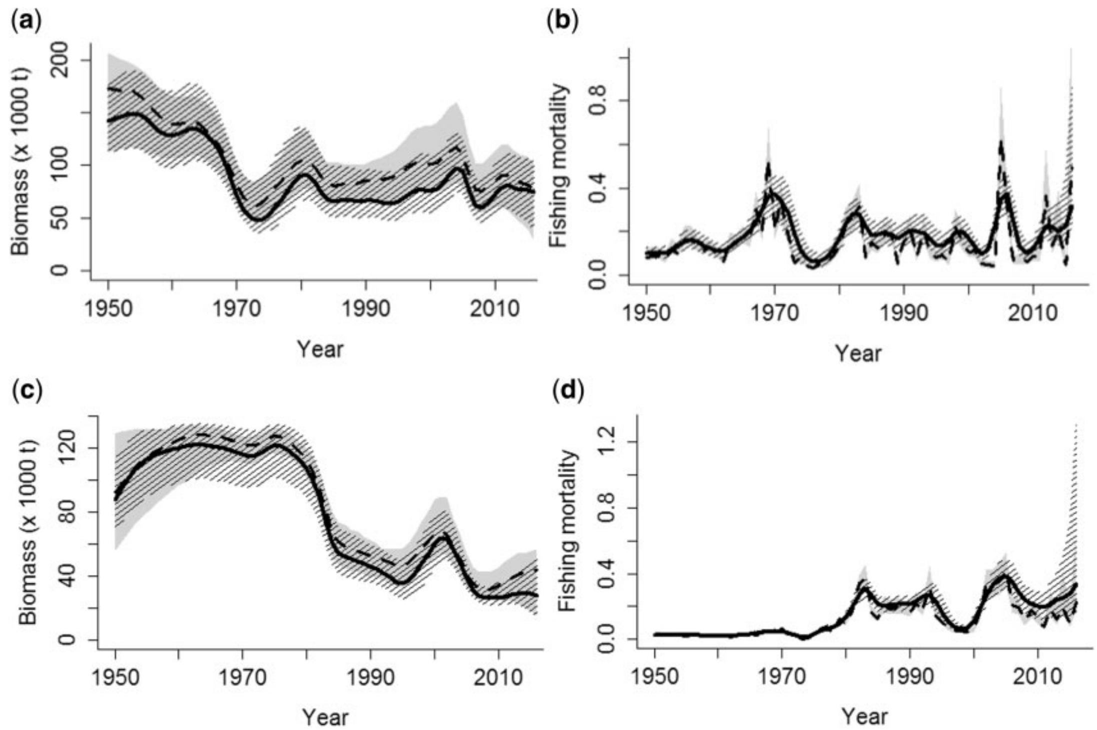

Figure 3. Stock dynamics of bonito biomass (a), fishing mortality (b), and bluefish biomass (c) and fishing mortality (d), estimated by CMSY (dashed line, grey confidence area) and BSM (solid line, shaded confidence area).

Table 2. Input prior ranges for the parameters in the CMSY and BSM assessment models.

Prior	Meaning	Bonito	Bluefish
Resilience	Medium resilient	0.2–0.6	0.2–0.6
Start *B*/*k*	Light depletion	0.4-0.9	0.4-0.8
Intermediate *B*/*k* (in 1990)	Strong depletion	0.1–0.4	0.1–0.4
End *B*/*k*	Strong depletion	0.1–0.4	0.1–0.4

influence on model stability). The results from the BSM analyses must be interpreted with caution as the accuracy of the *CPUE* data is limited: they are derived from the total landings divided by the number of vessels fishing for bonito and bluefish (standardized by average haul duration), and not from vessels' *CPUE* targeting bonito or bluefish, and therefore one can expect the data to be quite noisy. The BMS assessment was chosen for the interpretation of historical stock trajectories and the estimation of reference points because it is based on richer data sets (including *CPUE* series). The retrospective analyses (Supplementary Figures S4 and S9) show small but consistent patterns of decreasing biomass estimates and increasing *F* in the last years of the analyses over 2013–2016, with the assessment of bonito producing slightly better retrospective patterns. These results combined with the relatively low quality of the tuning data and the large uncertainty in the terminal year *Fs* (Figure 3b and d) warns against using assessment results in short-term catch forecasting.

The bonito stock was in a healthier state between 1950 and 1965, with a relatively high biomass and low fishing mortality (Figure 3a and b). After 1970 and until 2016, the stock size decreased and *F* increased to unhealthy levels ($F/F_{MSY} > 1$, Supplementary Figure S5). In 1985–1995 and 2008–2010, the biomass levels were at about half the size required to produce MSY (Supplementary Figure S5). The level of fishing mortality has been exceedingly high in 1966–1971 and for most years after 1980 (Figure 4b). After 2000, a pulse of relatively higher stock biomass was evidenced that provided the grounds for the record catch in 2005 (Figure 2a) but provided that the fishing pressure had remained quite high; a marked recovery did not ensue. The bluefish catches considerably increased after 1975 and have been exceeding the estimated MSY (Supplementary Figure S10) since 1980. The estimated stock biomass dropped drastically after 1980, and although a slight increase has been marked around 2000, the stock size remained steadily below B_{MSY} (Figure 3c and Supplementary Figure S10). The biomass and *F* trajectories indicated that bluefish has been fished unsustainably for most years since 1980, apart from a short period between 1995 and 2000 where signs of improving state could be seen, but a stable recovery failed most probably due to sustained heavy fishing (Figure 3c and d and Supplementary Figure S10).

Estimated parameters and reference points are presented in Table 3. For most of the analysed period, the reference ratios (B/B_{MSY} and F/F_{MSY}) demonstrate unsustainable exploitation of both bonito and bluefish (Figure 3 and Supplementary Figures S5 and S10).

Evaluation of predatory impacts

About 90% of the fish consumed by the main predators in the Black Sea are small pelagic fish such as anchovy, horse mackerel, and sprat (Table 1 and Figure 4). The total consumption of prey of both bonito and bluefish was at its highest (~300,000 tonnes) during the 1950–1960s, when the two predator species were abundant (Figure 4). In the 1980s, their combined consumption

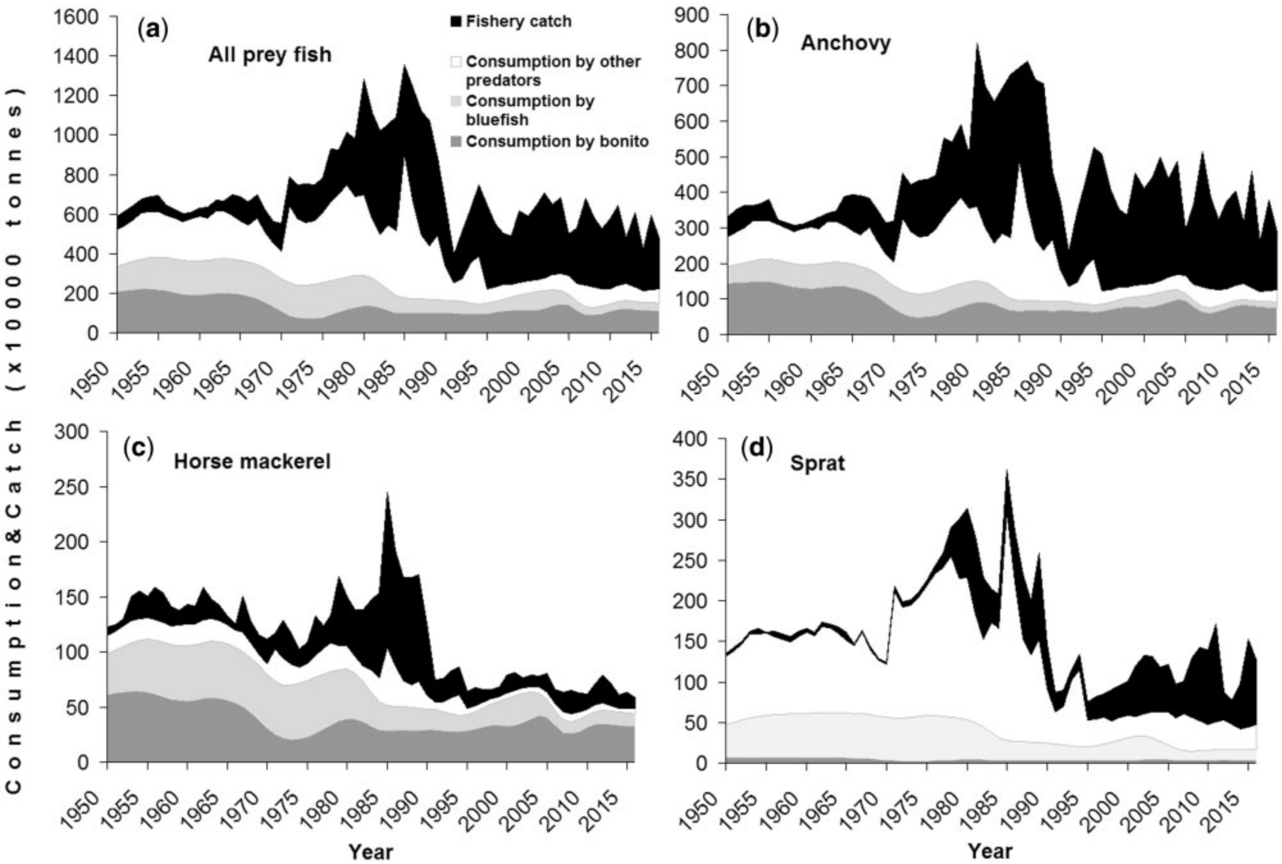

Figure 4. Consumption of bonito, bluefish and other major predators compared to fishery catch of (a) all prey fish, (b) anchovy, (c) horse mackerel, and (d) sprat.

Table 3. Estimated parameters, goodness of the fit (MSE), and reference points (from BSM) and their 95% confidence levels (in brackets).

Estimated parameters and reference points	Bonito	Bluefish
r	0.296 (0.201–0.435)	0.302 (0.2–0.455)
k ($\times$ 1 000 tonnes)	231 (163–328)	137 (101–187)
q	0.0052 (0.0034–0.0078)	0.0038 (0.0026–0.0056)
MSE	0.46	0.263
MSY ($\times$ 1 000 tonnes)	17 (14.7–19.8)	10.4 (8.63–12.4)
B_{MSY} ($\times$ 1 000 tonnes)	115 (81.3–164)	68.6 (50.4–93.5)
F_{MSY}	0.148 (0.1–0.218)	0.123 (0.082–0.186)
B/B_{MSY} (2016)	0.646	0.408
F/F_{MSY} (2016)	2.15	2.21

decreased about threefold corresponding to the biomass decline in their stocks. There was some increased predation in the 2000s, corresponding to a partial recovery of bonito and to lesser extent for bluefish (the latter between 2000 and 2005 only). Consumption of prey fish (by all predators) clearly dominates over their catches prior to 1980, but since 1992, the fishery catch tends to prevail (Figure 4a and b). It should be noted that consumption rates and diet composition used are time-invariant values (Table 1), and therefore, the consumption estimates strictly follow the trends in predator biomass (Supplementary Figure S11).

Bonito consumes mostly anchovy, both bonito and bluefish prey on horse mackerel, while sprat is mostly a prey of whiting, dolphins, bluefish, and dogfish (Table 1 and Figure 4). Anchovy catches increased to about three to four times greater than their consumption by major predators after 1995 (Figure 4b), which is reflected in the mortality estimates: the fishing mortality is two to three times higher than predation mortality of anchovy since 1995 (Figure 5a). Contrarily, the amount of horse mackerel (consumed predominantly by bonito and bluefish) is about two to four times higher than its catches (Figure 4c). Horse mackerel catches steadily increased during the 1980s, when they exceeded predation by about two times (Figure 4c). Post-1995, the horse mackerel stock and catches dropped substantially (Figure 2d) and predation mortality increased due to the low prey biomass (Figure 5b). Consequently, the predation mortality of horse mackerel is higher than its fishing mortality, except for the 1980s, when fishing intensity was higher. Bluefish predation on sprat is much higher than bonito predation on sprat (Figure 4d and Supplementary Figure S11) due to the bluefish higher dietary preference of sprat (Table 1). After 1995, sprat catches first equated to and then exceeded predation by bonito, bluefish, and other predators, and fishing mortality of sprat exceeded their predation during the last decade (Figures 4d and 5c).

Evaluation of the impact of fishing

The shifts in the stocks in relation to the fishing mortality are presented on phase space plots (Figure 6), where different panels

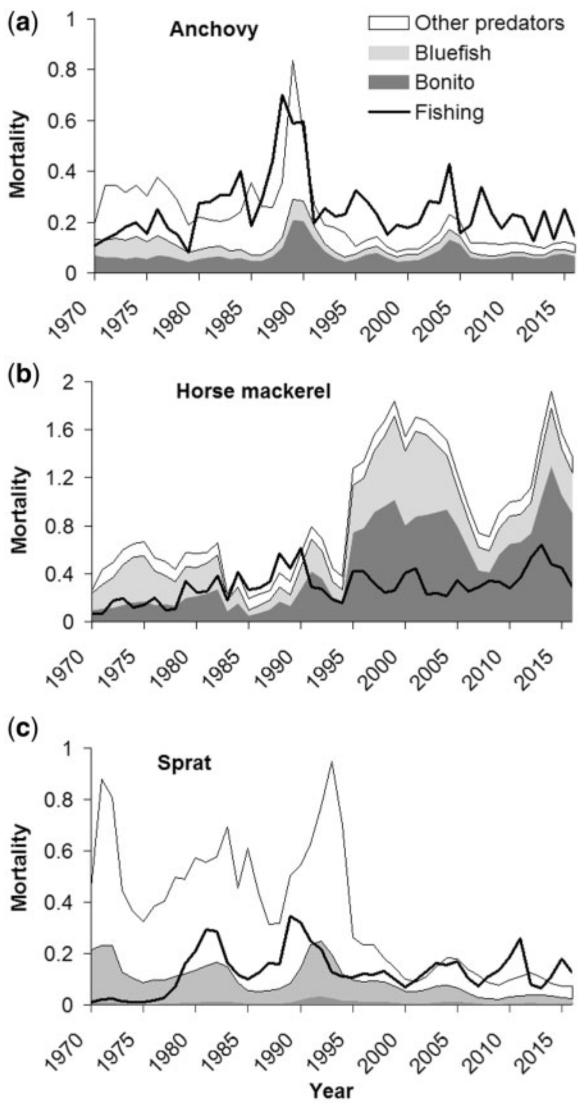

Figure 5. Predation mortality by bonito, bluefish, and other major predators, compared to fishing mortality on (a) anchovy; (b) horse mackerel, and (c) sprat.

represent various states of the stock trajectory with reference to the healthy states represented by B_{MSY} and F_{MSY}. The panels are depicted with traffic light colours: green (lower right areas on Figure 6) indicates a healthy stock and no ongoing overfishing, orange (upper right areas) is a shift to depletion due to overexploitation, red (upper left areas) indicates where stock is overexploited and depleted, and yellow (lower left areas) is a still depleted stock, but fishing pressure being reduced (Park 2009; Froese *et al.*, 2019). In bonito, for the initial 10–15 years, the stock was in a healthy state, then quickly shifting towards a depleted state where it remained regardless of some brief periods of reduced fishing mortality, driving the trajectory into the yellow (lower left) area (Figure 6a). These periods were due to either strong reduction in the fishery, the lack of fish in the mid-1970s (the catches positioned below MSY are due to low stock sizes and not to reduced fishing effort), or contrarily, a relative increase in biomass providing a basis for the peak catch in 2006. These occasional good fishing years, however, do not lead to a lasting recovery of the stock. The uncertainty around the last assessment year (2016) indicates with a high probability (99.8%), that the stock remains in the depleted state (Figure 6a). Similarly, the bluefish trajectory starts in the healthy green (lower right) area and stays there until the mid-1970s, when driven by the strong fishing pressure (intensified by the introduction of nylon nets in the early 1970s, Ulman *et al.*, 2020), it rapidly moves into a depleted state of low biomass and high fishing mortality (Figure 6b), where it still remains. The evolution of these two stocks and their fisheries over the years proves that, although they are quite productive ($r \sim 0.2$–0.45, Table 3), the lack of operational management results in exhausted parental biomass and highly fluctuating catches that reduce the effectiveness of the fisheries.

Discussion

In this study, a combination of stock assessments and evaluation of predatory impacts is presented to better understand the long-term dynamics and ecological effects of the last two major pelagic predatory fish species: bonito and bluefish, in relation to the other main predatory and prey fishes in the Black Sea. Bonito and bluefish are key predators predominantly preying on the most abundant small pelagic fishes (sprat, anchovy, and horse mackerel), therefore having the potential (if abundant) to greatly influence the entire ecosystem. After having been in a relatively healthy state until the 1970s, bonito and bluefish stocks were decimated by overfishing and have remained depleted for about half a century and until now. In fact, the estimated biomass trajectories of the two species display typical regime shift-like dynamics, in this case caused by a long period of unsustainable exploitation. The substantial predatory impacts of bonito and bluefish on prey fish, established in this study, further support the hypothesis that extinguishing major pelagic predators by the fisheries has been a primary driver of the trophic cascade and ecosystem regime shift during the 1980s reported in the Black Sea (Daskalov *et al.*, 2007).

As production models do not resolve for size and age structure, they fail to account for potential growth overfishing (consistent overfishing of small individuals), which is occurring in both bonito and bluefish (Ulman *et al.*, 2020) and is partly responsible for the high fluctuations of the catches (General Fisheries Commission of the Mediterranean (GFCM), 2014; Scientific, Technical and Economic Committee for Fisheries (STECF), 2015). In recent years, juveniles dominate the catch, especially in bluefish (Atılgan *et al.*, 2016; Georgieva and Daskalov, 2019), and recruitment overfishing (consistent overfishing of immature fish) is likely to put the stability of the stocks at risk, as the juveniles are deprived the chance to mature. The current minimum legal landing size (MLLS) of bluefish being 18 cm in Turkey (no size limitation is applied in Bulgaria) is well below the length of first maturity for this species (26 cm, Atılgan *et al.*, 2016; Ilkyaz, 2018). The same is valid for bonito where MLLS is set to 25 cm in Turkey and 28 cm in Bulgaria, whereas it does not reach maturity until 42.5 cm (Froese and Pauly, 2018). Although it was recommended to increase the MLLS to 45 cm for bonito and 26 cm for bluefish in Turkish regulations (Yildiz and Ulman, 2020), these changes were not applied for the new Turkish regulations for 2020–2024. The discard ratio of the bluefish fishery by purse-seine has been 83.3%, mainly consisting of juveniles (Scientific, Technical and Economic Committee for Fisheries (STECF), 2017), and a similar high discard rate was reported for the

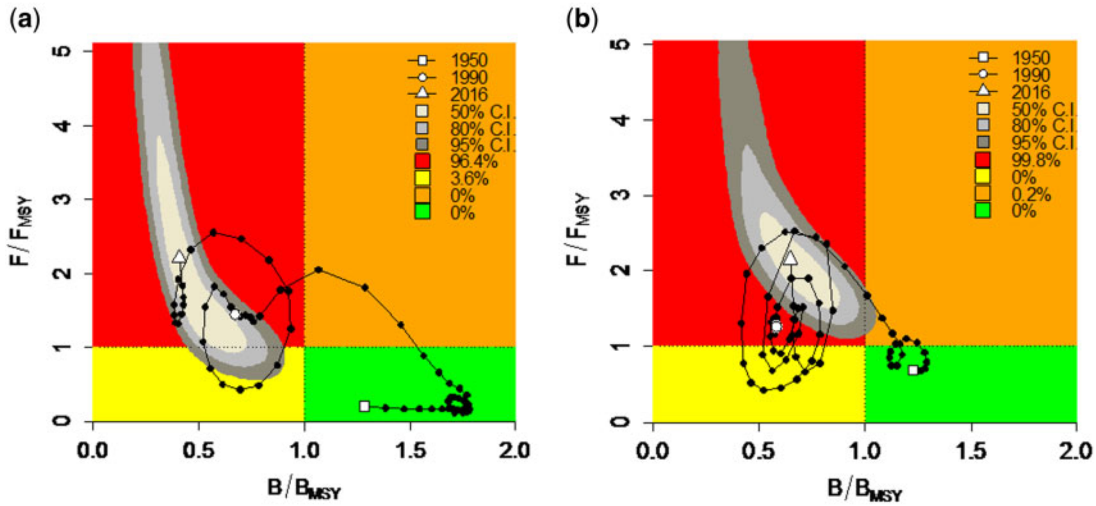

Figure 6. Phase space plot of stock state indicated by B/B_{MSY} vs. fishing pressure, F/F_{MSY}, based on BSM model for bonito (a) and bluefish (b). Green (lower right), orange (upper right), red (upper left), and yellow (lower left) areas indicate healthy stock, shift to depletion, depleted stock, and depleted stock/ceasing of overfishing, respectively. The "banana" shape around the assessment of the final year triangle indicates uncertainty with yellow for 50%, grey for 80%, and dark grey for 95% confidence levels. The legend in the upper right graph also indicates the probability of the last year falling into one of the coloured areas (see text for further explanation, colour figure available online).

bluefish fishery in the migration period from the Black Sea to Marmara Sea (Atılgan *et al.*, 2016). The occurrence of both growth and recruitment overfishing seems to be the root of the apparent volatility and depressed state of many stocks (Froese *et al.*, 2016). Due to the present steady positioning of low stock regimes, the recovery of the two stocks should not be expected, unless decisive and possibly prolonged restoration measures, including fishing effort and/or catch limitations, as well as efficient control over catching of under-sized immature individuals, are undertaken. To help the rebuilding of the stocks, the MLLS of both species needs to be increased at least to the minimum length at sexual maturity, in addition to having effective control and enforcement at landing sites, along with mandated observers placed on industrial vessels to prohibit the discarding of juveniles.

Major declines in the biomasses of large-sized predators (tuna, large bonito, dolphins) occurred up until the early 1970s due to overexploitation (Daskalov *et al.*, 2008). The stocks of demersal predators (whiting, turbot, dogfish) substantially decreased during the 1980s and 1990s, in parallel with the declines in small pelagic fish, again from overfishing and with a secondary effect of the introduction and explosion of invasive comb-jelly *Mmeniopsis leidyi* (Shlyakhov and Daskalov, 2008; Demirel *et al.*, 2020). Furthermore, bonito and bluefish may considerably affect other commercial stocks and have previously contributed to the disappearance of the Black Sea mackerel (*S. scombrus*, Ivanov and Beverton, 1985; Prodanov *et al.*, 1991). The highest consumption of anchovy and sprat occurred in the 1970s and 1980s, due to higher abundances and consumption from bluefish, whiting, and horse mackerel. This resulted in high overall predation mortality, coinciding with *M. leidyi* invasion during the 1980s and early 1990s, when both anchovy and sprat stocks collapsed (Daskalov *et al.*, 2008). Contrarily, the highest predation impact (mortality) on horse mackerel occurred after 2000, coinciding with the continuous decrease in horse mackerel stock biomass. Overall, the predation effects of bonito and bluefish are lower than that of other predators for sprat, at broadly comparable level for anchovy and dominant for horse mackerel, where it also exceeds the amount of the fishery catch. Therefore, the lack of recovery of horse mackerel after 1995 (unlike anchovy and sprat) can be partly attributed to strong predation by bonito and bluefish, although environmental conditions may also have played a role (Daskalov *et al.*, 2017). While anchovy and sprat are planktivores, horse mackerel is an omnivore, sporting a larger body, richer in energy (Georgieva and Daskalov, 2019); hence, horse mackerel is a more preferred prey species for the fast and voracious bonito and bluefish (Georgieva and Daskalov, 2019).

Our experience with CMSY and BSM demonstrated that stock assessments can be performed in data-poor situations, bringing useful results such as trajectories of biomass and fishing mortality and estimates of population rates, reference points, and underlying uncertainty. The CMSY method, using solely catch data, was validated, as it yielded similar results to the more accurate BSM method (fitted with additional *CPUE* data), proving that it could be applied for the assessment of other data-poor stocks.

The recovery of fish populations from low biomass levels, aside from the reduction of fishing effort and catches, is also dependent on their life history traits, food availability, and trophic interactions amongst species (Hutchings and Reynolds, 2004; Audzijonyte and Kuparinen, 2016). In the Mediterranean and the Black Sea, large predatory fishes were the first group subject to overfishing, followed by medium-pelagics, demersals, and finally small pelagics (Daskalov *et al.*, 2008; Froese *et al.*, 2018; Demirel *et al.*, 2020). Our results illustrate the classic scenario of "Fishing down marine food webs" (Pauly *et al.*, 1998), clearly demonstrating the depletion of valuable predatory fish and the reduction of their trophic impact on prey fish in the Black Sea. It should be stressed that the healthy state of small pelagic stocks is of vital importance for the recovery of their predators, as the voracious migratory bonito and bluefish need large food supplies to ensure population growth. To ensure the future survival of the last pelagic predatory fishes in the Black Sea, sufficient prey biomass must remain in the system, along with strong and lasting reduction in fishing pressure.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

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