

Hindcasting the dynamics of an Eastern Mediterranean marine ecosystem under the impacts of multiple stressors

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ABSTRACT: An important challenge for conserving and managing marine ecosystems is to advance our understanding of how multiple human stressors, environmental factors and marine resources interact and influence each other. The ecosystems of the Israeli Mediterranean coast have undergone significant ecological changes in recent decades, caused primarily by the introduction of alien species, fishing and the warming of the waters. Here we used a food-web model representing the continental shelf of the Israeli Mediterranean coast to explore the historical dynamics of the area considering the combined effect of alien species, fishing activities and changes in sea surface temperature and primary productivity. The food-web model was fitted to available time series of data from the early 1990s to 2010 using the temporal dynamic module of the Ecopath with Ecosim modeling approach. An important challenge was to model the numerous alien species inhabiting the Eastern Mediterranean Sea, one of the most invaded marine ecosystems of the world. Historical model simulations satisfactorily matched observed data, especially regarding alien groups. However, lack of data from the pelagic environment limited our ability to compare model output with historical observations. Trophic interactions, climate change and fishing were important factors explaining the historical dynamics of the ecosystem, which showed a degradation pattern over time. Results also highlighted an increasing proportion of alien species in biomass and catch over time, with important effects on the food web. This study represents an important step forward in understanding the changes that are occurring in the Israeli continental shelf ecosystem and the Levantine Sea.

KEY WORDS: Eastern Mediterranean Sea · Food-web model · Ecopath with Ecosim · Cumulative impacts · Alien species · Climate change · Fishing impact

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INTRODUCTION

During the last decades marine ecosystems have changed at surprising rates under the impacts of global, regional and local stressors, including climate change, biological invasions and direct human pres-

ures such as overexploitation, pollution and habitat modification (Costello et al. 2010, Halpern et al. 2015). Variations in the abundance of marine species and their distributions have been documented (Carlton & Ruiz 2005, Perry et al. 2005, Lotze et al. 2006), affecting the structure and functioning of marine

ecosystems (Byrnes et al. 2007, Doney et al. 2012, Christensen et al. 2014a) and the ecosystem services provided to humans (Worm et al. 2006, Katsanevakis et al. 2014b).

Given the range of human activities, stressors often co-occur in time and space. Thus most marine ecosystems are exposed to the impacts of multiple stressors (Breitburg & Riedel 2005, Halpern et al. 2015), in addition to the effects of environmental fluctuations (Ravier & Fromentin 2004, Cury et al. 2008). The ability to understand how human activities, environmental factors and marine organisms interact and influence each other is an issue of pressing importance.

A shift towards more comprehensive management of human activities following an ecosystem-based management (EBM) approach requires means to evaluate their interactive and cumulative impacts (Leslie & McLeod 2007, Giakoumi et al. 2015). Thus, studying cumulative impacts has become one of the most important challenges in ecology, conservation and management (Crain et al. 2009, Parsons et al. 2014).

Within this context, ecosystem modeling approaches have increasingly been adopted as useful tools to study marine ecosystems as a whole (Piroddi et al. 2015). They integrate available information to consider direct and indirect interactions among ecosystem compartments and stressors, e.g. trophic interactions and the impact of fishing activity (Plagányi 2007, Fulton 2010). One of the most used approaches is the Ecopath with Ecosim (EwE) modeling toolbox, which has been widely applied to model aquatic food webs (Heymans et al. 2014, Colléter et al. 2015).

The EwE approach has been mainly used to assess the impacts of fishing activities on marine ecosystems and investigate management options (Cury et al. 2005, Heymans et al. 2014). In addition, it is increasingly being used to assess the impact of cumulative stressors such as climate change, habitat modification and other stressors that are becoming more important in the marine environment (Coll et al. 2015, Colléter et al. 2015). One of these increasingly important stressors is the invasion of non-native species (e.g. Arias-González et al. 2011, Libralato et al. 2015).

Modeling species invasions using EwE models and evaluating their expansion and effects in the food web is a challenging task (Langseth et al. 2012, Corrales et al. 2014). For example, the time of arrival and important ecological traits of alien species need to be known in advance before their dynamics can be modeled. One solution has been to develop 2 food webs, 1 representing the ecosystem before the invasion and 1 after the invasion (e.g. Downing et al.

2012, Akoglu et al. 2014). However, this approach impedes the study of the expansion process and the impact of alien species on the food web during the intermediate period. Several alternative approaches have been used to simulate alien species and their temporal impacts (e.g. Arias-González et al. 2011, Langseth et al. 2012), which are briefly explained in 'Materials and methods: Incorporating the impact of alien species'.

The marine ecosystem of the Eastern Mediterranean Sea has undergone significant changes in recent decades, caused primarily by the introduction of alien species through the Suez Canal (known as Lessepsian migration), intense fishing activity and the effects of climate change (Lejeune et al. 2010, Katsanevakis et al. 2014a, Tsikliras et al. 2015).

In this study, a food-web model representing the Israeli Mediterranean continental shelf (ICS model) in the early 1990s (Corrales et al. 2017) was fitted to available time series of data from the early 1990s to 2010 using the temporal dynamic module Ecosim (Walters et al. 1997, Christensen & Walters 2004). The specific objectives of this study were to: (1) explore the historical dynamics of marine resources of the ICS model considering the effect of alien species, fishing activities and climate change (through historical changes in temperature) as the main ecosystem drivers, and (2) quantify ecological changes during this period using selected ecological indicators.

This study represents the first development of a temporal dynamic food-web model that quantifies the impact of multiple stressors in the Eastern Mediterranean Sea. We reviewed previous attempts to model species invasions in EwE, and we developed a strategy that satisfied the amount of available data and alien species in the study area. Given the large number of alien species inhabiting the Eastern Mediterranean Sea and the lack of temporal quantitative analysis on the impact of alien species in the region in addition to other human impacts, the present study represents an important step forward in modeling alien species, generally, and in the Mediterranean Sea in particular (Corrales et al. 2014).

MATERIALS AND METHODS

Study area

The study area comprises the Israeli Mediterranean continental shelf (hereafter referred to as ICS) (Fig. 1), in the Levantine Sea. The ecosystem modeled covers an area of 3725 km², including depths

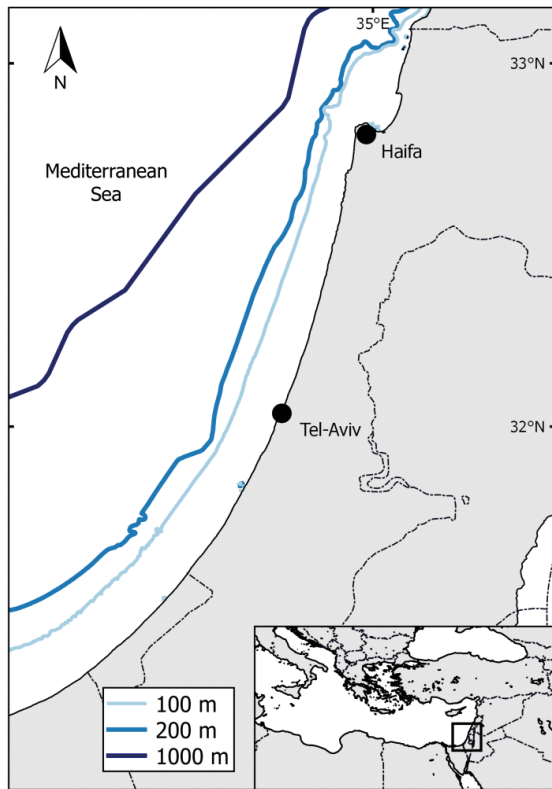


Fig. 1. The study area encompassing the Israeli Mediterranean continental shelf ecosystem and selected depth contours. Modeled area includes depths from 0 to 200 m

from 0 to 200 m. The Levantine Sea has the hottest, saltiest and most nutrient poor waters in the Mediterranean Sea (Azov 1991, Brasseur et al. 1996). Its circulation is characterized by a dominant northward current along with the general counterclockwise current gyre of the Eastern Mediterranean Sea (Hamad et al. 2006). The ecosystem along the Israeli Mediterranean coast has changed over recent decades due to direct anthropogenic impacts, in addition to the increasing water temperature (Edelist et al. 2013a, Goren et al. 2013, Sternberg et al. 2015). Currently, the Levantine Sea is the world's most invaded marine ecoregion (with a current ratio of alien to native species richness of 0.69) (Katsanevakis et al. 2014a) and the invasions have profoundly altered the ecosystem (Edelist et al. 2013a). The impact of fishing is also high, although overall commercial fishing effort has decreased in the past 20 yr (Fig. 2a) (Goren et al. 2013, Edelist et al. 2014). In addition, mean sea surface temperature has risen (1.26°C between 1994 and 2010) (Mediterranean Forecasting System COPERNICUS; <http://marine.copernicus.eu/>) (Fig. 2b), facilitating the establishment and spread of thermophilic species over time (Fig. 2c,d), which are mostly Lessepsian migrants. This has also negatively impacted native species (mainly cold-water species) by placing them at the edge of their thermal ranges (Ben Rais Lasram et al. 2010, Raitso et al. 2010).

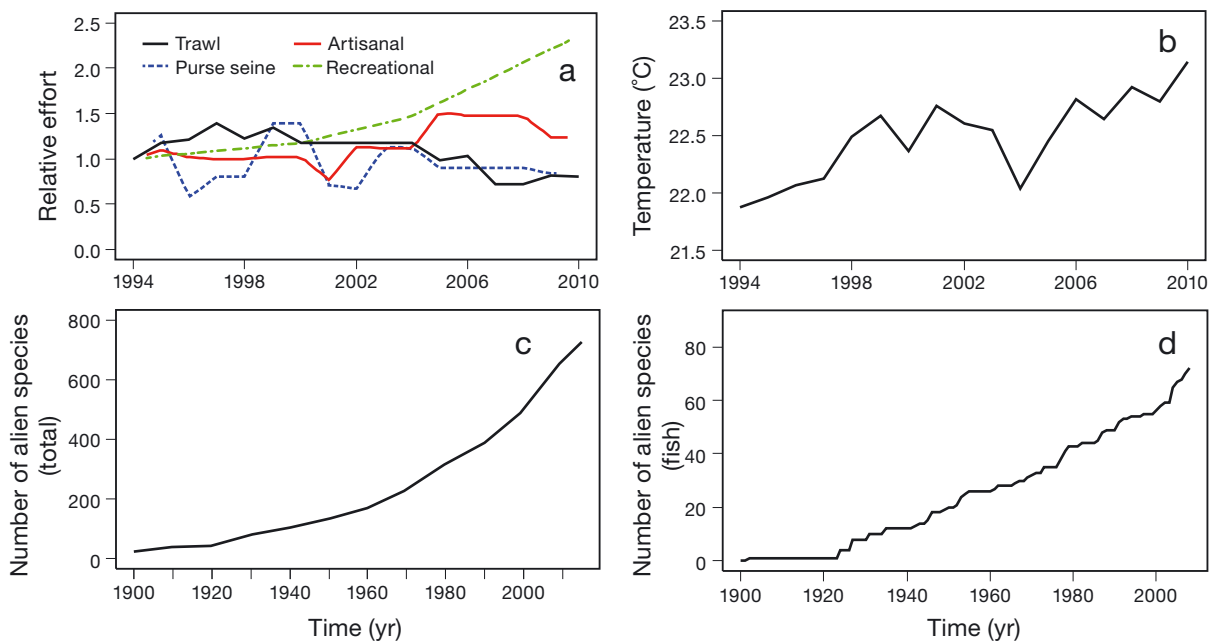


Fig. 2. Ecosystem drivers of the Israeli Mediterranean continental shelf ecosystem considered in this study: (a) relative fishing effort by fleet, (b) annual sea surface temperature, (c) number of alien species in the Mediterranean Sea (adapted from Galil et al. 2014) and (d) number of alien fish species in the Mediterranean Sea (adapted from Golani 2010)

Modeling approach

Ecopath with Ecosim framework

An Ecosim model representing the ICS ecosystem during the 1994–2010 period was fitted to time series of historical data. The Ecosim simulated the period between 2 Ecopath models representing the 1990–1994 and 2008–2010 time periods (Corrales et al. 2017). The original model representing the 1990–1994 period comprised 39 functional groups, including the main trophic components of the food web from primary producers to top predators (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m580p017_supp.pdf). The model included 6 alien groups encompassing several crustacean and fish species located at various trophic positions in the food web. The main fishing fleets acting in the ecosystem were also considered: bottom trawl fleet, artisanal gear consisting of longlines and gill-nets, purse seine and recreational fishers.

Two multispecies alien groups (new alien demersal fish and alien medium pelagic fish, new alien groups, hereafter), which incorporate alien species with different times of settlement, were absent in the previous version of the model (1990–1994) (Corrales et al. 2017). Thus they were added to the baseline Ecopath model (see ‘Incorporating the impact of alien species’). Input parameters of the baseline model have been fully described by Corrales et al. (2017) and the new input parameters are shown in Table S1 in the Supplement.

Ecosim is the time-dynamic module of the EwE framework and describes the temporal dynamics of species biomass and flows over time by accounting for changes in predation, consumption rate, fishing and the environment (Walters et al. 1997, Christensen & Walters 2004).

Ecosim uses a set of differential equations to describe biomass dynamics, expressed as:

$$\frac{dB_i}{dt} = \left(\frac{P}{Q}\right)_i \cdot \sum Q_{ji} - \sum Q_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i \quad (1)$$

where dB_i/dt is the growth rate of group i during time t in terms of its biomass B_i ; $(P/Q)_i$ is the net growth efficiency of group i ; M_i is the non-predation mortality rate; F_i is the fishing mortality rate; e_i is the emigration; and I_i is the immigration rate (Christensen & Walters 2004).

Consumption rates (Q_{ij}) are calculated based on the ‘foraging arena’ theory, which divides the biomass of a prey into a vulnerable and a non-vulnerable fraction and the transfer rate or vulnerability between

the 2 fractions determines the trophic flow between the predator and the prey. The vulnerability concept incorporates density-dependency and expresses how far a group is from its carrying capacity (Christensen & Walters 2004, Christensen et al. 2008). Default values of vulnerability ($v_{ij} = 2$) represents a mixed trophic flow, a low value ($v_{ij} < 2$) indicates a ‘bottom-up’ flow and a situation closer to carrying capacity, while a high value ($v_{ij} > 2$) indicates a ‘top-down’ flow and a situation further away from carrying capacity (Walters & Martell 2004, Ahrens et al. 2012). For each predator–prey interaction, consumption rates are calculated as:

$$Q_{ij} = \frac{a_{ij} \cdot v_{ij} \cdot B_i \cdot P_j \cdot T_i \cdot T_j \cdot M_{ij} / D_j}{v_{ij} + v_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot P_i \cdot T_j / D_j} \cdot f(\text{Env}_{\text{function}}, t) \quad (2)$$

where a_{ij} is the rate of effective search for prey i by predator j ; T_i represents prey relative feeding time; T_j is the predator relative feeding time; B_i is prey biomass; P_j is predator abundance; M_{ij} are the mediation forcing effects; and D_j represents effects of handling time as a limit to consumption rate (Christensen et al. 2008, Ahrens et al. 2012). Environmental response functions ($f(\text{Env}_{\text{function}}, t)$) can be used to account for external drivers that change over time, such as temperature (see ‘Incorporating the impact of climate change’). In particular, the intercept between the environmental response function and the environmental driver is used to calculate a multiplier factor (Eq. 2), which then modifies the consumption rates of the functional group with a maximum value of 1 and declining value as the environmental driver deviates from the optimum values (N. Serpetti pers. comm.).

A detailed explanation of the algorithms and equations of the EwE approach are given in Christensen & Walters (2004) and Heymans et al. (2016). A summary of the Ecosim fitting procedure followed in this study is provided in Fig. 3 and explained in detail below.

Incorporating the impact of alien species

We reviewed the main strategies that have been used to simulate species invasion and their impact using EwE and specially using Ecosim modeling and the fitting procedure (Table 1). These strategies ranged from using time series of data of alien species to force their biomass (e.g. Arias-González et al. 2011) to fit the models mainly based on 3 approaches: (1) initial biomass of alien species were set at low levels and their population increase was controlled by applying an artificial fishing mortality

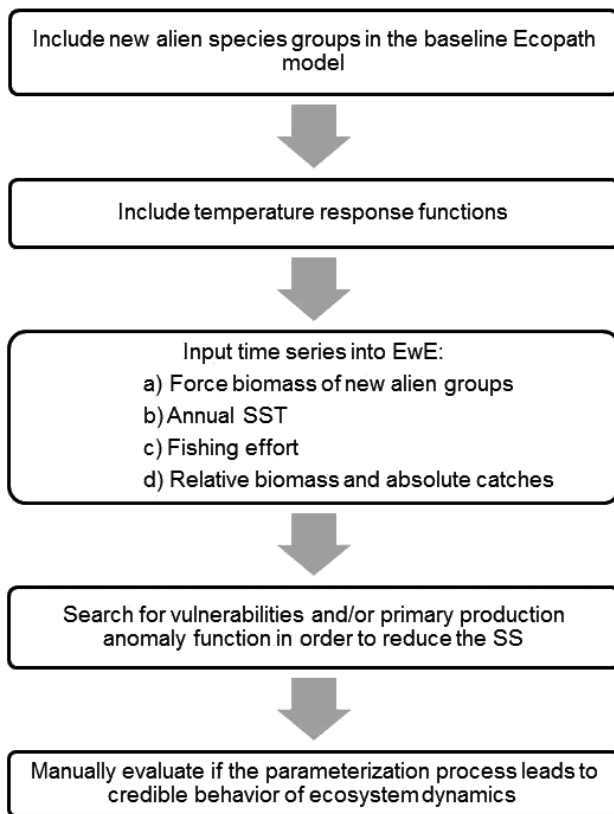


Fig. 3. Main steps followed to fit the Ecosim model to the time series

(e.g. Langseth et al. 2012); (2) alien species were set up with a high initial biomass and then were constrained by applying a high artificial fishing pressure (e.g. Kumar et al. 2016); and (3) using forcing functions to remove the effect of alien species on their preys and predators until the year of

invasion (e.g. Kao et al. 2016). In addition, other approaches to assess the impact of alien species without a fitting procedure were available and were also considered (e.g. Pinnegar et al. 2014, Libralato et al. 2015).

We adopted and modified one of the approaches proposed by Langseth et al. (2012). Under this strategy, we set the initial Ecopath biomass of new alien groups at the beginning of the temporal simulations with values equal to the 2008–2010 Ecopath model values (Corrales et al. 2017). This resulted in an unbalanced flow of biomass in the 1990–1994 Ecopath model due to the additional predation mortality of the new alien groups. To correct for this, we applied a negative biomass accumulation to their prey equal to the amount of prey consumed by these new alien groups in the 1990–1994 Ecopath model (see Table S1 in the Supplement). For predators that prey on these new alien groups, we used post-invasion contributions (as in the 2008–2010 period) of their diet to calculate appropriate levels of natural mortalities (M_0) of the new alien groups. Contributions of the other groups to the diet of these predators were proportionally reduced so the total standardized diet was maintained at the same level.

In Ecosim, biomasses of these 2 new alien groups were forced to zero until 4 yr before the invasion (2001 for new alien demersal fishes and 2000 for alien medium pelagic fishes) (Galil 2007b) (Table 2). This was done to account for the lag between the invasion and the discovery of the alien species, as there is a tendency to determine the presence of the alien species only after they have become established, especially in small and non-commercial species in poorly monitored areas (Azzurro et al. 2016).

Table 1. Summary of methods used to maintain 'low' levels and release 'high' levels of new alien species in Ecosim time dynamics food-web models. New alien groups represent groups that invaded the ecosystem after the period of the Ecopath baseline model. Only models fitted to time series are included

Method	Number of new alien groups	Time series of alien species	Ecopath biomass of alien species	Reference
Force time series	3	Forced	High	Langseth et al. (2012)
Artificial fishery	1	Forced	Low	Arias-González et al. (2011)
Force time series	2	Forced	Low	Rogers et al. (2014)
Artificial fishery	3	Fit	Low	Langseth et al. (2012)
Artificial fishery	3	Fit	High	Langseth et al. (2012)
Changes in vulnerabilities	3	Fit	High	Langseth et al. (2012)
Changes in vulnerabilities	2	Fit	Low	Kao et al. (2014)
Changes in vulnerabilities	3	Fit	Low	Kao et al. (2016)
Artificial fishery	3	Fit	High	Cox & Kitchell (2004)
Artificial fishery	1	Fit	High	Kumar et al. (2016)
Artificial fishery	2	Fit	Low	Zhang et al. (2016)
Force time series	2	Forced and fit	High	Present study

Table 2. Information on the time series used to fit the Israeli Mediterranean continental shelf ecosystem model to data. Data are organized by (see 3 rightmost columns) drivers, biomass forcing data and reference data for evaluating model fit. Dem: demersal

Functional group	Time series of data	Coverage	To drive the model	To force the biomass	To compare predicted results
1. Phytoplankton	Relative biomass	1998–2010			x
8. Native shrimp; 9. Alien shrimp; 11. Alien crabs; 13. Benthic cephalopods; 14. Benthopelagic cephalopods; 17. Hake; 18. Flatfishes; 25. Alien lizardfish; 26. Demersal fishes (upper slope)	Relative biomass Total catch	1994, 2000, 2010 1994–2010			x x
15. Mulletts; 16. Goatfishes	Relative biomass Total catch	1994, 2000, 2010 1994, 2000, 2008, 2009, 2010			x
19. Rocky fishes; 20. Small native dem. fishes; 21. Large native dem. fishes; 22. Alien herbivores; 23. Earlier alien dem. fishes; 27. Benthopelagic fishes; 29. Demersal sharks; 30. Rays and skates	Relative biomass Total catch	1994, 2000, 2010 1994–2010 (except 2008)			x x
24. New alien dem. fishes	Absolute biomass Relative biomass Total catch	1994–1997 1994, 2000, 2010 2002–2010		x	x x
31. Small pelagic fishes; 32. Horse mackerel; 33. Mackerel; 34. Native medium pelagic fishes; 36. Large pelagic fishes	Total catch	1994–2010 (except 2008)			x
35. Alien medium pelagic fishes	Absolute biomass Total catch Relative effort (all fleets) Environmental driver (temperature)	1994–1996 2005–2010 (except 2008) 1994–2010 1994–2010		x x	x

Incorporating the impact of climate change

The effect of climate change has been incorporated in Ecosim using forcing functions affecting the Q/B (consumption/biomass) ratio of selected functional groups, either by directly modifying their predation search rates (e.g. Ainsworth et al. 2011, Alva-Basurto & Arias-González 2014, Guénette et al. 2014) or modifying production, consumption and mortality values (Cornwall & Eddy 2015).

The most recent version of the EwE software (version 6.5) allows incorporating and linking environmental preferences of functional groups to any number of environmental drivers (e.g. temperature, salinity and oxygen) as has been previously described for Ecospace (Christensen et al. 2014b).

In our study, a time series of the annual sea surface temperature (SST, upper 30 m) from 1994 to 2010 (Fig. 2b, Table 2), obtained from the Mediterranean Forecasting System COPERNICUS (<http://marine.copernicus.eu/>), was used to drive the temporal dynamics of sensitive functional groups with available information (mostly crustaceans and fish groups) (see Table S2 in the Supplement).

The environmental response functions ($f(\text{Env}_{\text{function}}, t)$ in Eq. 2) that link the species or functional groups dynamics with the environmental drivers were first obtained from AQUAMAPS (www.aquamaps.org/) (Kaschner et al. 2006), which is a global database on species distribution. These environmental response functions are given as curves showing minimum and maximum tolerance levels and 10th and 90th preferable quintiles to the environmental parameters (in our case, temperature). As a second step, these functions were modified using expert opinion from scientists working in the Israeli Mediterranean ecosystem (mainly from Tel Aviv University) to incorporate local knowledge. The final environmental preferences for each functional group were obtained by weighting the values of the species included in a functional group to their relative biomass

contribution to that group (see Table S2 in the Supplement).

Although salinity also affects the marine resources in the Eastern Mediterranean Sea (Mavruk & Avsar 2008), this factor was not considered in this study as data on the environmental responses of many species was lacking.

Time series of fishing and the fitting to time series

In addition to alien species and SST changes, we compiled available time series of fishing activities to drive fisheries in the model (Table 2). These included data on nominal fishing effort, expressed in number of days at sea, obtained for trawls, purse seine and artisanal fleets (Fig. 2a). Data were obtained from the Fisheries Department of the Ministry of Agriculture and Rural Development of Israel. Fishing effort for the recreational fishers was estimated based on catch reconstruction efforts (Edelist et al. 2013b), as no data were available from official sources (Fig. 2a).

Available relative observed biomass and absolute observed catch data were used to compare model outputs (Table 2). Ecosim allows the incorporation of biomass and catch data as absolute or relative values (Christensen et al. 2008). When these data are introduced as relative values, Ecosim tries to fit the trends rather than absolute values. Relative observed biomass data for most of the demersal groups were ob-

tained from fishery dependent trawl surveys (swept-area method) conducted in the study area during 3 time periods (1990–1994, 2000 and 2008–2010) (Edelist et al. 2011, 2013a). In relation to the 1990–1994 and 2008–2010 biomass dataset, we used average values due to the large variability in the data and the uncertainty of the fishery-dependent survey. Absolute observed catch data were obtained from a reconstruction of Israeli catches, which included both commercial fleet and discards, the recreational fleet and the illegal, unregulated and unreported catch (Edelist et al. 2013b).

To fit the Ecosim model to these time series of observed data for the 1994–2010 period, we used the Stepwise Fitting Procedure (Scott et al. 2016), which automates the model-fitting procedure described by Mackinson et al. (2009) and Heymans et al. (2016). The fitting procedure tests alternative hypotheses related to the impact of fishing, changes in predator-prey dynamics (vulnerabilities), changes in primary production (production anomalies) or all of the above together (Table 3) (Mackinson et al. 2009, Heymans et al. 2016). A primary production anomaly is a forcing function applied to the primary production rate (in our study both phytoplankton and benthic primary producers) that may represent historical productivity changes impacting biomasses through the ecosystem. During the fitting procedure, vulnerabilities and production anomalies were estimated to improve model fits by comparing model predictions

Table 3. Fitting procedure applied to the Israeli Mediterranean continental shelf model. The procedure follows the methodology suggested by Mackinson et al. (2009) and Heymans et al. (2016)

Step	Description
1. Baseline	No environmental or fishery data are used to drive the model. All vulnerabilities with default values ($v_{ij} = 2$)
2. Baseline and trophic interactions	No environmental or fishery data are used to drive the model. Vulnerabilities are estimated using the 'fit to time series' module
3. Baseline and environment	No fishery data is used to drive the model. All vulnerabilities with default values ($v_{ij} = 2$). The 'PP anomaly' is estimated using the 'fit to time series' module
4. Baseline, trophic interactions and environment	No fishery data is used to drive the model. Vulnerabilities and the 'PP anomaly' are estimated using the 'fit to time series' module
5. Fishery	Fishing effort is included to drive the model. No environmental data is used to drive the model. All vulnerabilities with default values ($v_{ij} = 2$)
6. Fishery and trophic interactions	Fishing effort is included to drive the model. No environmental data is used to drive the model. Vulnerabilities are estimated using the 'fit to time series' module
7. Fishery and environment	Fishing effort is included to drive the model. All vulnerabilities with default values ($v_{ij} = 2$). The 'PP anomaly' is estimated using the 'fit to time series' module
8. Fishery, trophic interactions and environment	Fishing effort is included to drive the model. Vulnerabilities and the 'PP anomaly' are estimated using the 'fit to time series' module

to observed data using the sum of squares (SS) statistics. The fitting procedure finds the statistically 'best fit' model based on Akaike's information criterion (AIC), which penalizes for estimating too many parameters based on the number of time series available for estimating the SS (Mackinson et al. 2009, Heymans et al. 2016):

$$\text{AIC} = n \cdot \log(\text{minSS}/n) + 2k \quad (3)$$

where n is the number of observations, minSS is the minimum sum of squares calculated by the algorithm as a result of comparing predicted versus observed values, and k is the number of parameters. This number can include changes in vulnerabilities (Vs), changes on primary production anomaly (expressed as number of spline points [PPsp], which smooth the time series of the PP anomaly) or changes in both (Mackinson et al. 2009, Heymans et al. 2016). The maximum total number of parameters that can be estimated (Vs, PPsp or Vs + PPsp) is $k - 1$, where k is the number of observed time series (in this case biomass and catch time series) (Mackinson et al. 2009, Heymans et al. 2016). In this study, the maximum number of parameters that could be estimated was 47 (there were 48 time series of biomass and catch). We used the corrected Akaike's information criterion (AICc), calculated as follows:

$$\text{AICc} = \text{AIC} + 2k \cdot (k - 1)/(n - k - 1) \quad (4)$$

To choose the best final model, the last step is to manually evaluate whether the parameterization process leads to credible and sensible behavior (Heymans et al. 2016).

Importance of the drivers in historical biomass dynamics

To evaluate the importance of predator–prey interactions (vulnerabilities), climate change and fishing on the dynamics of functional groups, we ran the fitted Ecosim model 3 times, each time minimizing the effect of: (1) trophic interactions, which were set to the initial default value (vulnerability = 2); (2) temperature, which was kept constant over time; and (3) fishing effort for all the fleets, which was kept constant over time.

Ecological indicators and uncertainty

Once the fitting procedure was completed, we used the best fit model to examine biomass and catch

time series predicted by the model to explore the dynamics of functional groups, especially those related to alien species.

In addition, a selection of ecological indicators was used to describe ecological changes in the ecosystem over time. To calculate the ecological indicators we used the recently developed ECOIND plug-in (Coll & Steenbeek 2017) and the Ecological Network Analysis (ENA) module in EwE. The indicators selected for this analysis were:

(1) Total biomass (excluding detritus) (t km^{-2}), which includes biomass of all the functional groups excluding detritus (detritus and discards). This indicator was used to quantify changes at the whole ecosystem level (Heymans et al. 2014).

(2) Forage fish biomass (t km^{-2}), which includes the biomass of benthopelagic and small pelagic fishes, mackerel and horse mackerel. This indicator was analyzed to quantify changes in the pelagic compartment (Hilborn & Walters 1992).

(3) Predatory biomass (t km^{-2}), which includes biomass of all the groups with trophic level (TL) ≥ 4 and tends to decrease with increasing fishing impact in marine ecosystems (Rochet & Trenkel 2003).

(4) Invertebrate biomass (t km^{-2}), which includes biomass of benthic invertebrates groups. This indicator was used to assess the dynamics of benthic invertebrates in the ecosystem, which tend to benefit from reductions of fish and predator biomass (Pauly et al. 1998).

(5) Demersal fish biomass (t km^{-2}), which includes biomass of all the fish groups in the demersal compartment. This indicator was analyzed in order to quantify changes to the demersal compartment (Hilborn & Walters 1992).

(6) Kempton's index, which expresses biomass diversity by considering those organism with TL ≥ 3 and tends to decrease with ecosystem degradation (Kempton & Taylor 1976).

(7) Mean TL of the community (mTLco), which expresses the TL of the whole ecosystem, reflects the structure of the ecosystem and is used to quantify the impact of fishing (Rochet & Trenkel 2003).

(8) Mean TL of the catch (mTLc), which expresses the TL of the catch, reflects the fishing strategy of the fleet and is used to quantify the impact of fishing (Pauly et al. 1998).

(9) Total catch ($\text{t km}^{-2} \text{ yr}^{-1}$), which includes the annual catches of the different fleets and provides an idea of total fisheries removals (Hilborn & Walters 1992).

(10) Total system throughput ($\text{t km}^{-2} \text{ yr}^{-1}$) (TST), which estimates the total flows in the ecosystem and is a measure of ecosystem size (Ulanowicz 1986).

Table 4. Results of the fitting procedure of the Israeli Mediterranean continental shelf ecosystem fitted to time series of data from 1994 to 2010. The table shows the statistically 'best' model for each step. Vs is the number of vulnerabilities estimated, PPsp is the number of primary production spline points, k is the number of parameters (Vs + PPsp) and %IF is the improved fit compared to the baseline AICc. The 'best' model chosen in this study is highlighted in bold

Step	Vs	PPsp	k	SS	AICc	%IF
1. Baseline	0	0	0	229.8	-309.1	
2. Baseline and trophic interactions	12	0	12	151.9	-471.7	52.6
3. Baseline and environment	0	3	3	224.9	-312.7	1.2
4. Baseline, trophic interactions and environment	36	3	39	119.5	-513.2	66.0
5. Fishery	0	0	0	220.5	-327.8	6.1
6. Fishery and trophic interactions	22	0	22	133.6	-506.8	64.0
7. Fishery and environment	0	3	3	215.2	-332.9	7.7
8. Fishery, trophic interactions and environment	23	2	25	114.9	-568.0	83.8
8. Fishery, trophic interactions and environment	32	2	34	121.9	-517.9	67.6

(11) Finn's cycling index (FCI, %), which represents the proportion of the TST that is recycled in the system and is an indicator of stress and structural differences (Finn 1976).

(12) Path length (PL), defined as the average number of groups that flows through, which is an indicator of stress (Christensen 1995).

We addressed the uncertainty in Ecopath input parameters on Ecosim outputs (biomass and catch trends, and ecological indicators) by using the Monte Carlo (MC) uncertainty routine (Heymans et al. 2016, Coll & Steenbeek 2017). We ran 1000 MC simulations based on the coefficient of variation obtained from the pedigree routine, which assesses the quality of the input data (Corrales et al. 2017). Results from the MC simulations were used to plot the 5th and 95th percentile confidence intervals for the fitted biomass and catch trends and for ecological indicators. For ENA indicators (TST, FCI and PL), we used the recently developed ECOSAMPLER plug-in (J. Steenbeek pers. obs.), which creates a number of alternative balanced Ecopath models from MC runs, to assess uncertainty analyses in EwE results. Finally, we used Spearman's rank correlation to evaluate the correlation between model results (time series of biomass, catch and ecological indicators) with time.

RESULTS

Fitting of the model and final model configuration

The best fit model was obtained when trophic interactions, fishing and primary production anomaly were included in the model configuration (Step 8 in Table 4). The parameterization with 23 vulnerabili-

ties (trophic interactions between predators and their prey) and 2 spline points was identified as the best model based on the AICc test criteria (Step 8 in Table 4). However, this model was not able to reproduce the trends of alien shrimps and earlier alien demersal fishes satisfactorily, which are target groups of the study.

Therefore, we moved through the fitting procedure analysis to find the model that was able to reproduce the trends of most of the groups and still showed credible statistical behavior. We finally choose a model fit with 32 vulnerabilities and 2 spline points as the best fit model although the improvement of the model fits was reduced (Step 8 in Table 4).

Importance of ecosystem drivers

The best fit model improved the fit by 67.6% over the baseline model (Step 8 in Table 4). Our results showed that trophic interactions were the main factor explaining the historical dynamics (1994–2010) of marine resources (an average of 28.1% of the variability, $\pm 11.6\%$ SD), followed by climate change (12.1%), fishing ($8.1 \pm 7.7\%$) and changes in primary production ($4.7 \pm 4.1\%$) (Fig. 4).

Historical biomass and catch trends by species and group

Observed biomass and catch time series were satisfactorily reproduced by model predictions (Figs. 5 & 6) when using the best fit model (32 vulnerabilities and 2 spline points). Overall, alien shrimps (Figs. 5b & 6b), goatfishes (Figs. 5e & 6e) hake (Figs. 5f & 6f), small na-

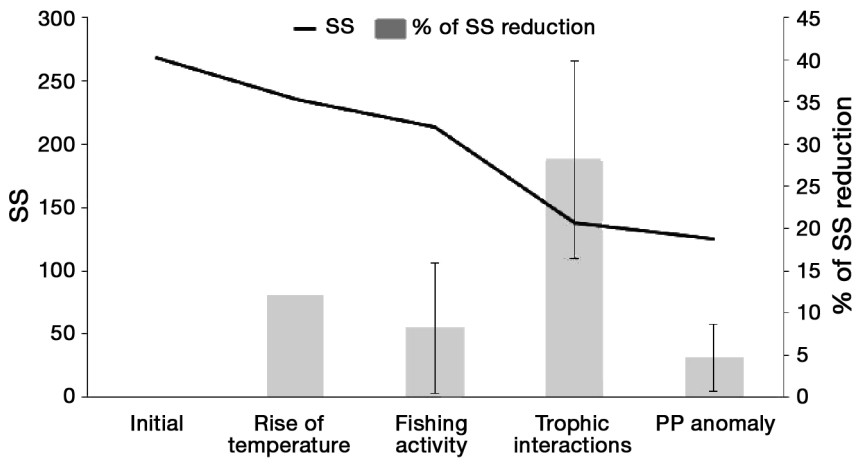


Fig. 4. Diagnostic of the model fitting process. Each step on the x-axis represents a step in the model fitting process (including the effects of the rise in temperature, Table 4) to minimize the sum of squares (SS, left y-axis) and their contribution (% SS reduction, right y-axis) and standard deviation. Standard deviation was calculated based on the different order according to which the drivers were included to reduce SS during the fitting process. Rise in temperature does not have a standard deviation because it was included before the fitting process. PP: primary production

tive demersal fishes (Figs. 5h & 6h), earlier alien demersal fishes (Figs. 5j & 6j), new alien demersal fishes (Figs. 5k & 6k) and alien lizardfish (Figs. 5l & 6l) showed the best fits, while benthic cephalopods, benthopelagic cephalopods, demersal fishes (upper slope), benthopelagic fishes, mackerel and horse mackerel were the least well fitted (see Figs. S1 & S2 in the Supplement).

The model also provided predicted biomass trends for 18 functional groups (Fig. 5o–r and see Fig. S1b–g,i,o–u in the Supplement) that lacked historical observations to be used in the fitting. However, we had catch data for 7 of these 18 functional groups (Fig. 6 and see Fig. S2 in the Supplement). In these cases, model predictions satisfactorily matched observed catch data except for large pelagic fishes, where the catches were underestimated (Fig. 6r), attesting to the migratory nature of these species and the ‘hit or miss’ nature of pelagic fisheries.

The model showed a decreasing historical pattern for the biomasses of several groups (Fig. 5). For example, mullets (Fig. 5d), hake (Fig. 5f) and large native demersal fishes (Fig. 5i) showed a large and significant decline. Small native demersal fishes did not show a significant decreasing trend, decreasing at the beginning of the simulation, followed by an increase from 1997 to 2001 and a decrease from 2002 to 2010 (Fig. 5h). On the contrary, alien shrimps (Fig. 5b), alien crabs (Fig. 5c), goatfishes (Fig. 5e), earlier alien demersal fishes (Fig. 5j), new alien demersal fishes

(Fig. 5k) and alien medium pelagic fishes (Fig. 5q) showed significant increasing biomass trends.

Catch time series estimated by Ecosim showed similar trends as those observed for biomass (Fig. 6 and see Fig. S2 in the Supplement). For example, we observed significant large declines for mullets (Fig. 6d), hake (Fig. 6f) and large native demersal fishes (Fig. 6i), while all alien demersal groups showed significant increasing trends (Fig. 6b,c,e,j,k,q) except alien lizardfish (Fig. 6l). For rocky fishes, although biomass trends showed a significant decrease (Fig. 5g), catches increased significantly (Fig. 6g) due to the growing impact of recreational fishers (Fig. 2a). Overall, catches predicted by the model satisfactorily matched observed data (Fig. 6). Despite this, the model at times overestimated (e.g. small pelagic fishes) (Fig. 6o) or underestimated (e.g. demersal sharks) (Fig. 6m) catches.

Trends in dynamics of alien groups were well reproduced (Figs. 5b,c,e,j,k,l,q & 6b,c,e,j,k,l,q). Remarkably, the model was able to simulate the invasion and population dynamics of the new alien groups, new alien demersal fishes and alien medium pelagic fishes, relatively well (Figs. 5k,q & 6k,q). The predicted biomass of new alien demersal fishes was slightly higher than the observed biomass although not enough data were available to establish a clear pattern (Fig. 5k). The predicted catch of this group satisfactorily matched observed data, although a clear overestimation occurred in 2006 (Fig. 6k). We were not able to compare predicted biomass of alien medium pelagic fishes to observed data as no data were available (Fig. 5q). The predicted catch of this group was reproduced relatively well although it was slightly underestimated (Fig. 6q). Moreover, although the catch time series started at 2005, the first species of this group that invaded the ecosystem was recorded in 2000.

In most cases, the main driver of population dynamics was trophic interactions (Fig. 7). In addition, results showed that the rise in temperature and fishing played an important role in the dynamics of small native demersal fishes, alien lizardfish and earlier alien demersal fishes. For mullets, the rise in temperature was the main driver and it also played an important role for hake. Fishing was an important driver for large native demersal fishes (Fig. 7).

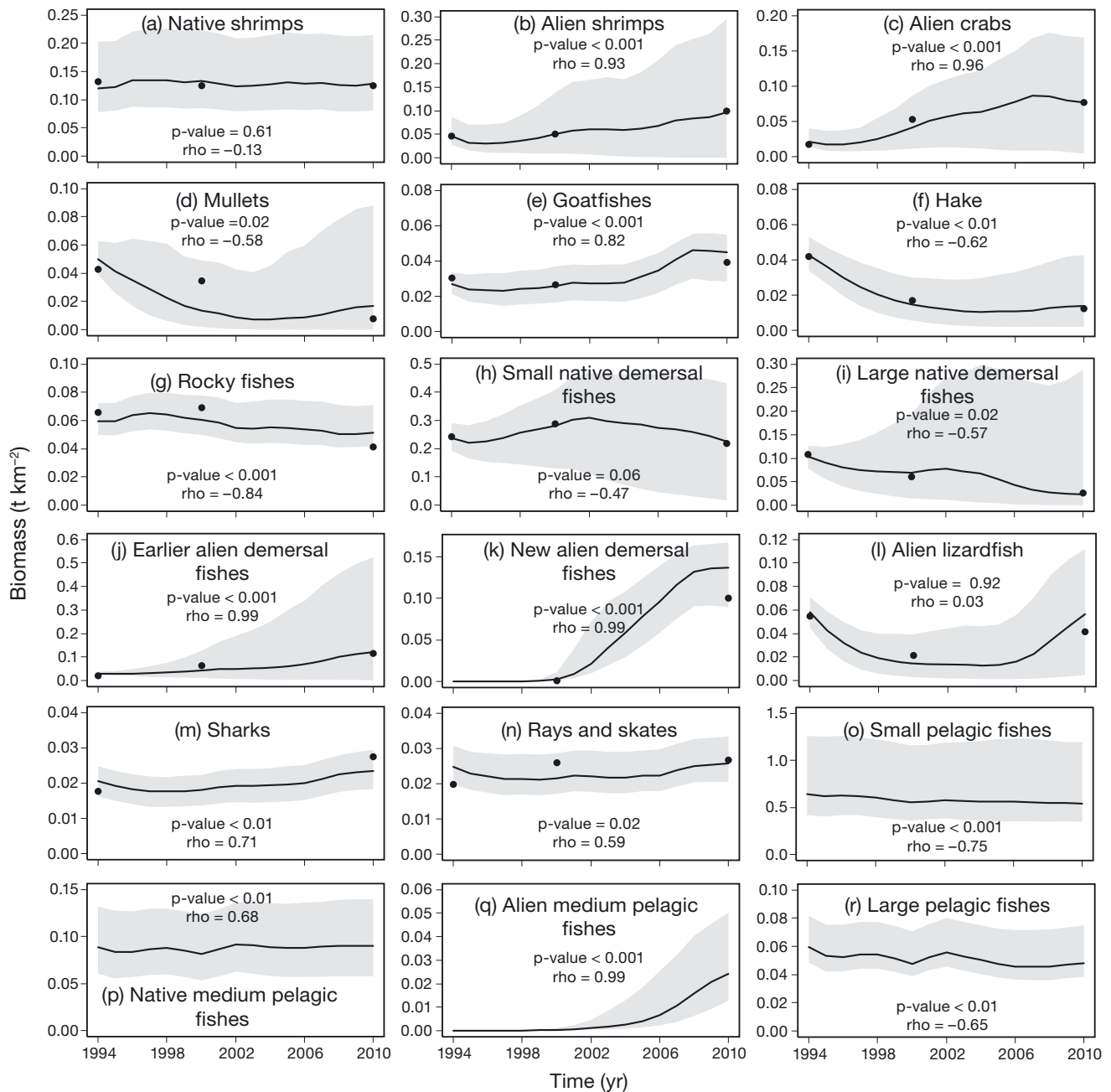


Fig. 5. Predicted (solid lines) versus observed (●) biomass (t km^{-2}) for the groups with available data for the Israeli Mediterranean continental shelf ecosystem model for the period 1994–2010. No data are available for the last 4 groups related to pelagic species. Grey shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine. Rho and p-value come from Spearman's rank correlation test

Ecological indicators

Indicators related to alien species showed the growing impact of these groups in the ecosystem. For example, total biomass of alien species increased from 0.19 to 0.59 t km^{-2} (Fig. 8a), representing 8.9% and 25.2% of the total biomass, respectively, if we include all the groups with sufficient information to split be-

tween native and alien species (shrimps, crabs, cephalopods and fishes). Biomass of alien invertebrates and demersal fish groups increased from 0.07 and 0.12 to 0.20 and 0.37 t km^{-2} , respectively (Fig. 8a), which represents an increase from 29.3% and 19.2% to 51.4% and 52.3% of the biomass of crustaceans (shrimps and crabs) and fishes, respectively. The analysis of the catch showed similar patterns to those observed in the

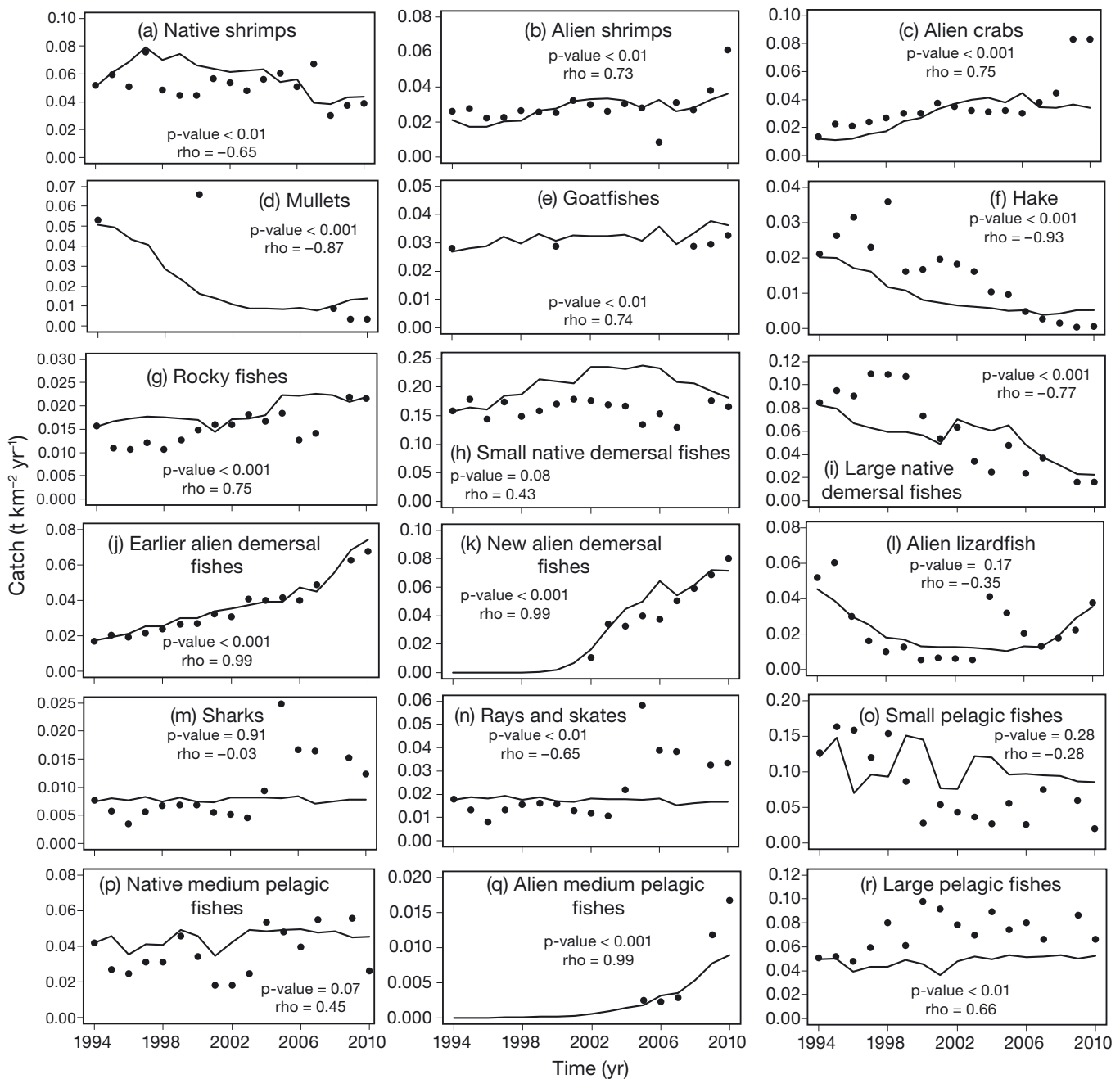


Fig. 6. Predicted (solid lines) versus observed (●) catches (t km⁻² yr⁻¹) for the groups with available data for the Israeli Mediterranean continental shelf ecosystem model for the period 1994–2010. Rho and p-value come from Spearman's rank correlation test

biomass (Fig. 8b). Total catch of alien groups increased from 0.12 to 0.31 t km⁻² yr⁻¹ (Fig. 8b), which represents an increase from 14.2% to 33.1%. By groups, this increase was from 0.03, 0.09 and 0 to 0.08, 0.22 and 0.01 t km⁻² yr⁻¹ for invertebrates, demersal fishes and pelagic fishes, respectively (Fig. 8b), that represents an increase from 39.5%, 21.1% and 0% to 62.7%, 47.3% and 3.5% for invertebrates, demersal fishes and pelagic fishes, respectively (Fig. 8b).

Other ecological indicators also showed that the ecosystem changed from 1994 to 2010 (Fig. 9). For example, we observed a significant increasing trend of total biomass (excluding detritus) (Fig. 9a) and a non-significant decreasing trend of forage fish biomass (Fig. 9b). Predatory biomass did not show a significant trend although it showed a decreasing trend at the beginning of the simulation followed by an increasing trend at the end (Fig. 9c). Invertebrate biomass and

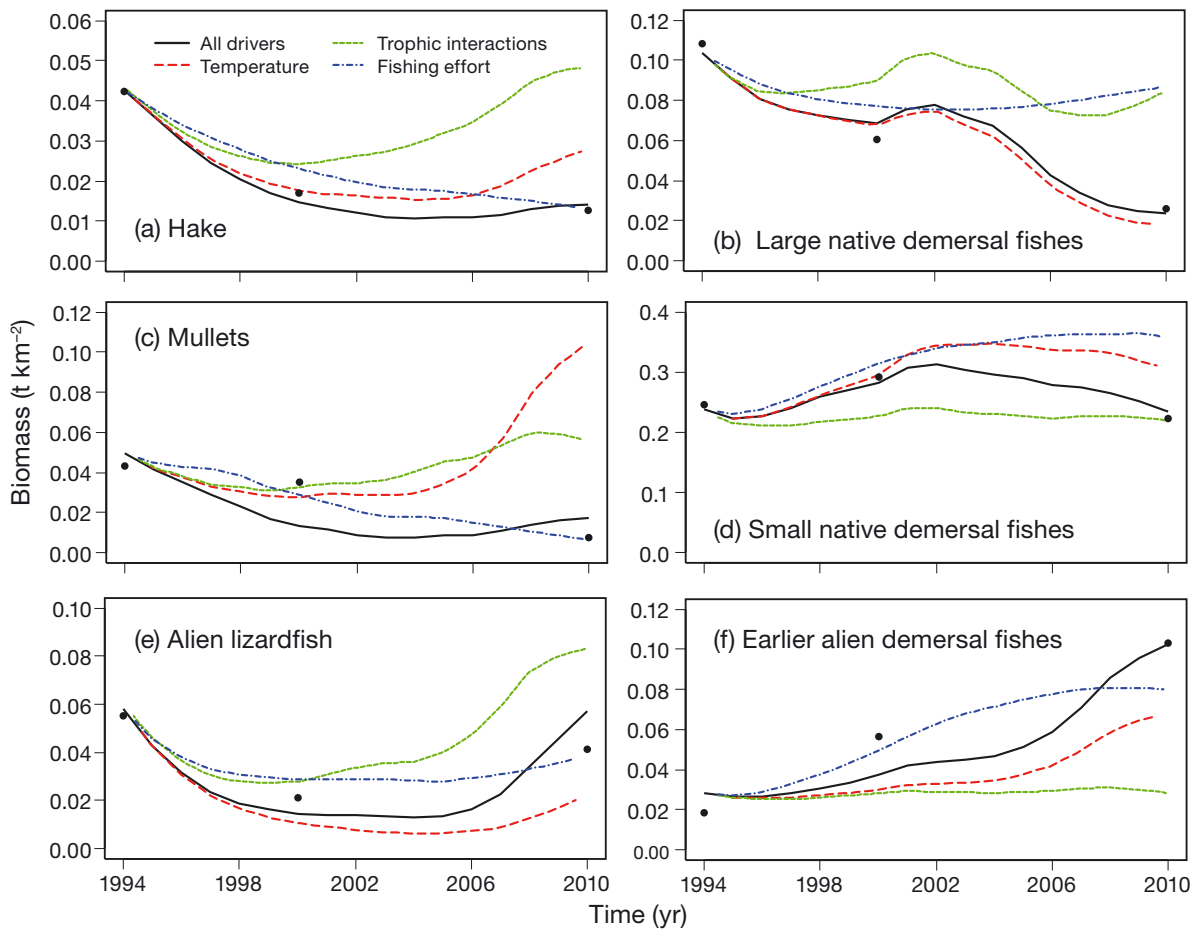


Fig. 7. Predicted (lines) versus observed (●) biomass (t km^{-2}) for (a) hake, (b) large native demersal fishes, (c) mullets, (d) small native demersal fishes, (e) alien lizardfish and (f) earlier alien demersal fishes, when 1 of the drivers (trophic interactions, temperature or fishing effort) were maintained constant in the Ecosim module, for the period 1994–2010

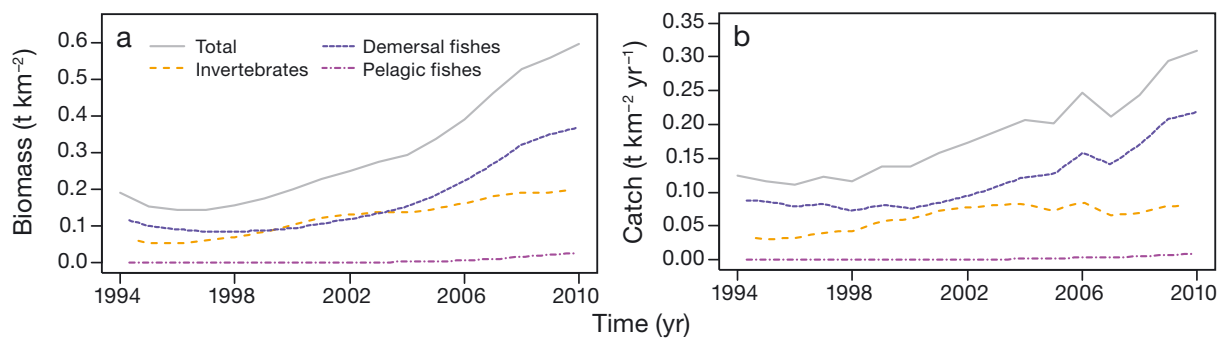


Fig. 8. Simulated (a) total biomass (t km^{-2}) and (b) catch ($\text{t km}^{-2} \text{yr}^{-1}$) of different groups of alien species for the period 1994–2010 for the Israel Mediterranean continental shelf ecosystem

demersal fish biomass showed a significant increasing trend (Fig. 9d,e). The Kempton's index fluctuated in time with a non-significant decreasing pattern (Fig. 9f). The mTLco showed a non-significant decreasing trend (Fig. 9g), while the mTLC showed an overall significant increasing pattern, firstly decreas-

ing and later increasing with time (Fig. 9h). Total catch presented several strong fluctuations in time with an overall significant increasing trend (Fig. 9i). TST showed a significant increasing trend (Fig. 9j), in line with total biomass (excluding detritus). FCI and PL presented a significant decreasing pattern (Fig. 9l).

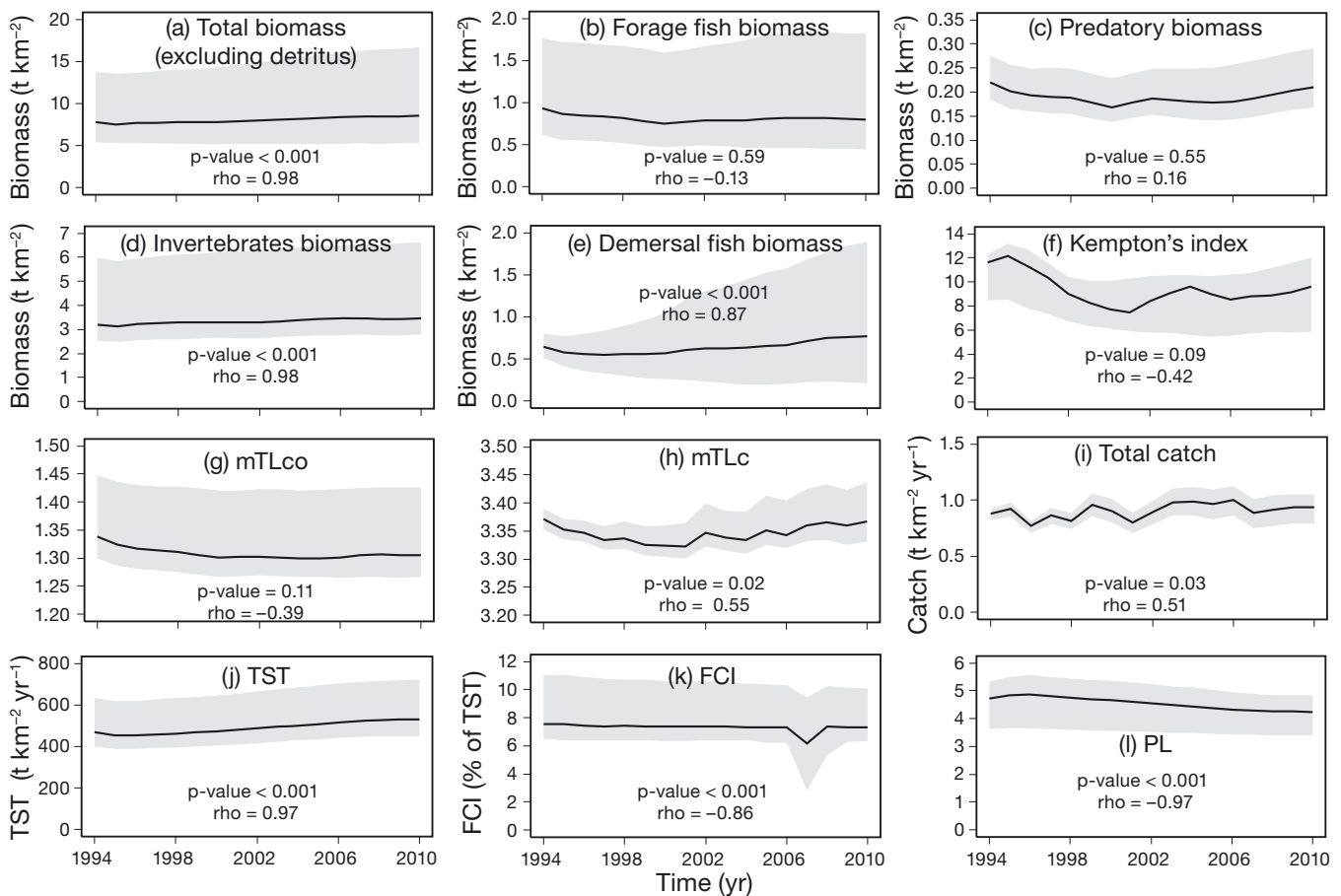


Fig. 9. Ecological indicators estimated for the period 1994–2010 from the Israeli Mediterranean continental shelf ecosystem. mTLco: mean trophic level of the community, mTLC: mean trophic level of the catch; TST: total system throughput; FCI: Finn's cycling index; PL: path length. Grey shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine

DISCUSSION

Ecosystem drivers of the Israeli Mediterranean continental shelf ecosystem

Our model explained a large proportion of the variability of available time series from 1994 to 2010 when trophic interactions, fishing and primary production anomaly were considered. Our results showed that trophic interactions explained the highest variability, highlighting the importance of trophic interactions in marine food web dynamics, as previously documented (Shannon et al. 2004, Coll et al. 2008, 2009).

In addition, climate change (included as an increase in sea surface temperature) explained a large proportion of the variability, indicating its impacts on the Israeli Mediterranean marine ecosystem. This is in line with the fact that climate change is strongly impacting marine ecosystems worldwide (Harley et

al. 2006, Hoegh-Guldberg & Bruno 2010) and particularly the Mediterranean Sea (Ben Rais Lasram et al. 2010, Lejeune et al. 2010, Moullec et al. 2016). Currently, the Mediterranean Sea is under a process of 'meridionalization' and 'tropicalization' of the northern and southern sectors, respectively, mainly due to the northward extension of native thermophilic species and the introduction of alien species through the Suez Canal and the Strait of Gibraltar (Bianchi 2007, Bianchi et al. 2013). Fish assemblages are expected to be significantly modified as a result of climate change (Ben Rais Lasram et al. 2010, Albouy et al. 2012), with potential effects on marine food webs and ecosystem structure (Albouy et al. 2014), especially in the Levantine Sea due to its 'naturally' extreme environmental conditions and the current rise in temperature.

Results also highlighted that fishing was an important historical driver of the ecosystem, especially for the exploited invertebrate and fish populations. It is

noteworthy, however, that the fishing effort of the Israeli fleet has declined over the past 2 decades (Edelist et al. 2013b).

Changes in primary production, captured in our model with the primary production anomaly (PP anomaly), represent the temporal variation of the primary productivity of the system and explained a smaller proportion of data variability. The PP anomaly predicted by the model showed an increasing trend (see Fig. S3 in the Supplement). This might be related to the nutrient enrichment from anthropogenic sources during the last decades in Egypt and Israel (Nixon 2003, Suari & Brenner 2015). This enrichment followed the drastic reduction in PP in the 1970s, when the flow of nutrient-rich Nile waters was substantially reduced by the construction of the Aswan High Dam (Nixon 2004). The southeastern Mediterranean is characterized by extreme oligotrophic conditions (Azov 1991), so local nutrient enrichment from land origins could play an important role as it may significantly enhance primary productivity at local scales (Barale et al. 2008, Macias et al. 2014, Suari & Brenner 2015). Yet, in our ecosystem and as shown in the results, changes in PP seemed to have only marginally explained the variation of observed biomass and catch data.

Biomass and catch trends

Our results showed changes in the temporal dynamics of marine resources from 1994 to 2010. Even though hundreds of species have invaded the Mediterranean Sea (Galil et al. 2014), causing the collapse of several native species (Edelist et al. 2013a) and rising concerns about dire consequences for Mediterranean marine ecosystems (Galil et al. 2015), quantitative studies that explain these changes and impacts of alien species are scarce (Rilov & Galil 2009, Golani 2010). For example, little is known about the dependency of population dynamics on environmental factors and the trophic interactions between alien and native species. Despite this, individual cases and general knowledge can be used to support and explain our results.

In general, our study revealed 3 main patterns: (1) native demersal predators, such as hake and large native demersal fishes decreased over time; (2) native medium trophic level fishes largely decreased (mulletts) or slightly decreased with time (rocky fishes and small native demersal fishes); and (3) an increase over time of alien species, mainly low and medium trophic levels (alien crabs and shrimps, alien herbi-

vores, earlier alien demersal fishes and new alien demersal fishes), but also high trophic levels (medium alien pelagic fishes). This was especially obvious at the end of the analyzed time period.

The first pattern (a decreasing trend for native demersal predators) is related to the impact of fishing activity, due to the high fishing mortalities, but could also be due to the negative impact of increasing temperatures and trophic interactions. In the current study, we have shown that an important driver for the decline in large native demersal fishes was fishing. The decline of predators due to overfishing has been observed worldwide (Pauly et al. 1998, Jackson et al. 2001) and also in the Mediterranean (Ferretti et al. 2008, Maynou et al. 2011). This is in line with studies at sub-regional levels, e.g. in the Catalan (Coll et al. 2008), Adriatic (Coll et al. 2009) and Ionian Seas (Piroddi et al. 2010); and at regional levels, e.g. in the whole Mediterranean Sea (Piroddi et al. 2017). For hake, we observed that the rise in temperature and trophic interactions were the main drivers. This is in line with studies showing that the decline in hake in the Levantine Sea can be attributed to oceanographic changes, overfishing, increase in temperature and the competition for resources with the alien lizardfish. These have led to its bathymetric displacement to deeper waters (Galil 2007a, Gucu & Bingel 2011, Halim & Rizkalla 2011, Edelist 2012).

The second pattern (a decreasing trend for native medium TL fishes) may be related to the cumulative impacts of fishing, climate change and competition for resources. For example, the large decrease in mulletts in Israel has been attributed to competition for resources with their alien competitor (goatfishes) and the warming of the waters. This could have caused a bathymetric separation of these groups (Golani 1994), as goatfishes currently dominate shallow strata (0 to 100 m) while mulletts occupy deeper waters, although it seems that goatfishes have recently extended their bathymetric distribution (Edelist et al. 2013a). In addition, mulletts have suffered high fishing mortality. Other native groups such as rocky fishes and small native demersal fishes decreased slightly over time. For these groups, we observed increasing fishing mortalities, mainly related to the increasing impact of recreational fishers, as in other Mediterranean areas (Pauly et al. 2014). Moreover, reductions in abundance and catches, and the displacement to deeper waters of native species that coincided with the explosion of alien species have been documented (Edelist et al. 2013a). For example, the native porgy *Pagellus erythinus* has been dis-

placed by the alien *Nemipterus randalli*. The reasons are poorly studied but a competitive exclusion between species related to the rise in temperature and trophic interactions have been suggested (Golani 1998, Galil 2008).

The third pattern (an increasing trend for invasive species) may be related to the combination of several factors such as the existence of underexploited niches in the ecosystem, overexploitation of native species, possible better adaptation and competitive properties of invaders and more favorable environmental conditions in the Eastern Mediterranean Sea as a result of climate change (Galil 2008, Rilov & Galil 2009, Edelist et al. 2011). In addition, the large increase in alien species (of low and medium trophic levels) could be attributed to the increase in primary production and the decrease in some top predators, which implies more food supply and could lead to increases in their prey species, respectively. In our study we observed an increase in invertebrate biomass (the main prey for these groups), a decrease in top predators and the importance of the rise in temperature for their dynamics.

Ecological indicators

Trends in ecological indicators documented ecological changes in the ICS ecosystem as a whole. For example, along the Israeli Mediterranean coast, alien species have become an important part of the ecosystem, as biomass and catches of alien species have increased with time, altering the structure of the food web.

We observed a large decrease in predators at the beginning of the period due to the decline in hake, large native demersal fishes and alien lizardfish. Since 2007, predatory biomass has increased due to the recovery of alien lizardfish and the explosion of medium alien pelagic fishes. This result is in line with the Kempton's index, which includes species or groups with TL ≥ 3 . In addition, demersal fish biomass increased due to the explosion of demersal alien species, mainly medium trophic level species.

The decline in mTLco and mTLc observed in our study coincides with more general trends observed in many marine ecosystems that are caused mainly by overfishing (Pauly et al. 1998). The depletion of top predators and biological invasions, predominantly by organisms with low TL, have caused a decrease in the TL of many marine ecosystems (Byrnes et al. 2007). Our results show that mTLco has decreased slightly over time with a stable trend at the end of the

period. However, in our study, we observed that mTLc has decreased and later increased. This is due to the depletion of top predators at the beginning of the period, the recovery of alien lizardfish afterwards and the increasing importance of alien species (medium and high trophic levels) in the catch. Indeed, alien medium trophic level species (earlier alien demersal fishes and new alien demersal fishes) have higher trophic levels than native medium trophic level species (rocky fishes and small native demersal fishes), as highlighted by Fanelli et al. (2015) and Goren et al. (2016).

Our results indicate a small but significant increase in TST with time. Finn (1976) suggested that an increase or decline in the TST could be a sensitive indicator of the state of the ecosystem, as it indicates if the ecosystem is in equilibrium. The increase in TST indicates that the ecosystem is not at equilibrium and may be a result of higher primary productivity with time that leads to an increase in the total production of the system, especially at low trophic levels, and of the increasing importance of alien species in the ecosystem. The FCI and PL showed a moderate decreasing trend. Odum (1969) found that cycling increases as systems mature (and thus FCI increases) and PL increases with maturity, with the opposite trends expected in stressed ecosystems (Odum 1985). Therefore, our results suggest a degradation trend of the food web during the simulated period.

Model assumptions and limitations

Modeling marine food webs is challenging due to their complexity, significant data requirements and high uncertainty, which requires the setting of different assumptions (Plagányi 2007, Fulton 2010, Rose et al. 2010). In addition, our understanding of the impact of individual stressors is limited and we have less understanding of the cumulative impact that different stressors would have on marine organisms and ecosystems. However, during the last decades, the data available for marine ecosystems has increased substantially and models have made considerable progress.

Several information gaps about the ecosystem of the Eastern Mediterranean Sea were identified by Corrales et al. (2017), which are mainly related to the pelagic compartment, benthic invertebrates and the reliability of catch data. In addition, the current study highlights a lack of historical biomass time series, as only a few data points were available through the analysis of 3 surveys conducted in the study area.

This limited our knowledge of historical trends in marine resources and therefore, the capability of the model to capture these patterns.

Temperature responses/preferences are key components for understanding the impact of climate change on marine ecosystems and therefore, marine organisms (Madeira et al. 2012). However, temperature responses of organisms are subject to uncertainty. In this study, the baseline information came from a general database (AQUAMAPS) (Kaschner et al. 2006). This is a very comprehensive database; however, it does not account for regional or sub-regional differences/preferences of species environmental responses, implying high uncertainty. To compensate for this somewhat, we incorporated expert local knowledge and corrected the general information. Although temperature is the most important environmental factor in driving population dynamics (Por 1978), salinity has been suggested to be an important factor to consider (Mavruk & Avsar 2008). However, this factor was not considered in the study due to the lack of data regarding the response of organisms to changes in salinity. This represents a limitation of the model which should be addressed in the future.

In addition, this study only included fish and crustacean (shrimps and crabs) alien species. At present, reliable information on ecological characteristics such as reproduction, habitat, trophic position and depth is available for most introduced fish species and some crustaceans species (Rilov & Galil 2009), but not for other groups, such as polychaetes, mollusks and jellyfish. Since biological invasions of other groups seems to be of the same magnitude or even larger (Rilov & Galil 2009, Galil et al. 2014), this limits our ability to assess the overall impact of alien species on this ecosystem and our estimation is likely conservative.

In order to assess the effect of uncertainty of the model parameters we applied a MC sampling routine. Our results show that uncertainty was generally high and varied among the functional groups. This is due to the high uncertainty of the initial Ecopath inputs and highlights the need of additional and accurate data. Recognizing this uncertainty is essential if this information is used for management advice.

Despite these limitations, this study included the best available data and thus is the best available representation of historical trends of the ICS ecosystem and a step forward in understanding its functioning. As new information is generated, the model should be updated and its quality improved.

CONCLUSION

This study represents the first example of a food-web model fitted to time series in the Eastern Mediterranean Sea to quantify the impact of multiple stressors. Our results show that trophic interactions, fishing activities and environmental factors (rise in temperature and primary production anomaly) played an important role in the historical dynamics of the Israeli Mediterranean continental shelf ecosystem from 1994 to 2010.

Our results highlight important changes in the biomass of several functional groups and species, such as a decrease in native top predators, a decrease in native medium trophic levels and an explosion of alien species, mainly medium trophic level organisms. Results from ecological indicators show a trend of ecosystem degradation over time.

Future work may include the development of forecasting scenarios in order to evaluate future cumulative impacts of multiple stressors to the Israeli Mediterranean continental shelf ecosystem. These scenarios can include different fishing management options, rise in temperature following Intergovernmental Panel on Climate Change (IPCC) projections and prognoses of increasing impact of alien species.

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