Modeling the role and impact of alien species and fisheries on the Israeli marine continental shelf ecosystem

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Abstract

The ecosystems of the Israeli Mediterranean coast have undergone significant changes in recent decades mainly due to species invasions and fishing activity. In order to characterize the structure and functioning of the marine continental shelf of the Israeli Mediterranean coast and assess temporal changes, we developed a food web model representing two time periods: 1990-1994 and 2008-2012.

Input data included local surveys and fishery statistics, published data on stomach content analyses, and the application of empirical equations to estimate consumption and production rates. The food web model was composed of 39 and 41 functional groups during both time periods, respectively, ranging from primary producers to top predator species, and included six and eight alien functional groups encompassing several crustacean and fish species.

Results highlighted the increasing impact of alien species on the ecosystem between 1990s and 2010s, emanated from competitive interactions between alien and native species and changes in trophic flows between food web components. Fishing activities had noticeable impacts in both time periods and played an important role in the ecosystem. Despite productivity rates and environmental differences, the Israeli marine ecosystem shared common features regarding structure and functional traits with other Mediterranean marine ecosystems. This is the first attempt to study the ecosystem of the Levant region using mass-balance models and to integrate such a large amount of alien species together into food web analyses.

Keywords: Eastern Mediterranean Sea; food web; Ecopath model; alien species; fishing.
1. Introduction

Biological invasions are currently considered one of the most important direct drivers of biodiversity change and pose a major threat on marine ecosystems, with both ecological and economic impacts (Bax et al., 2003; Molnar et al., 2008; Rilov and Crooks, 2009). These impacts can occur at varying biological levels, from changes in the genetic diversity of native species to species local extinctions and alterations of entire food webs (Grosholz, 2002; Levin and Crooks, 2011).

The Mediterranean Sea is one of the most severely affected marine ecosystem by alien species (Molnar et al., 2008; Costello et al., 2010), specially its eastern basin (Rilov and Galil, 2009; Edelist et al., 2013a; Katsanevakis et al., 2014). Currently, there are nearly 700 alien species described in the Mediterranean, of which more than half are considered to be established and spreading (Zenetos et al., 2010; Galil et al., 2014; Galil et al., 2016). Although no complete extinctions are recorded to have occurred in the Mediterranean Sea due to these alien species, sudden decline in abundance and local extirpations of native species concurrent with the proliferation of alien species have been documented (Galil, 2007a; Golani, 2010; Edelist et al., 2013a).

The Mediterranean Sea is currently classified among the most impacted ecoregions of the world (Costello et al., 2010; Halpern et al., 2015). The increasing impact of fishing activity in the Mediterranean Sea is evident. Many demersal and pelagic stocks are fully exploited or overexploited as a result of high fishing pressure, low fishing selectivity and the reduction of stocks (Vasilakopoulos et al., 2014; Tsikliras et al., 2015). In addition, the Mediterranean Sea is being altered by other anthropogenic activities posing notable impacts, such as habitat loss and degradation, pollution, eutrophication and climate change (Coll et al., 2010; Coll et al., 2012).

Within this context, the marine ecosystem of the Israeli Mediterranean coast, located within the Levantine Sea in the Eastern part of the Mediterranean basin, has undergone significant changes in recent decades caused primarily by species invasion, fishing activity, river damming and climate change (Edelist et al., 2013a; Goren et al., 2013; Edelist et al., 2014; Sternberg et al., 2015).

The Levantine Sea has the hottest, saltiest and most nutrient poor waters in the Mediterranean Sea (Azov, 1991; Brasseur et al., 1996), as a result of high evaporation
rates, very low riverine inputs and limited vertical mixing. These characteristics are perceived to be the main factors influencing several faunistic phenomena such as “Levantine nanism” (Sonin et al., 2007) and general faunal impoverishment compared to other Mediterranean regions (Coll et al., 2010).

It is discussed that multiple empty niches that can be used by alien species exist in the Levant ecosystem. This may be due to the low biodiversity in the region and the apparent existence of the native species in a habitat which is thought to be at the limits of their tolerance levels (Golani, 1998; Galil, 2008; Rilov and Galil, 2009). In addition, the opening of the Suez Canal in 1869, its continuous enlargement and the similarity between the Levantine Sea and the Red Sea in term of temperature and salinity allowed for the progressive introduction of many species of Indo-Pacific origin into the Eastern Mediterranean Sea (called Lessepsian immigrants) (Rilov and Galil, 2009). This phenomenon is almost entirely unidirectional, i.e. into the Mediterranean rather than out of it. These introductions accelerated during the second half of the 20th century and the first decade of the 21st century (Rilov and Galil, 2009; Golani, 2010).

The naturally extreme environment of the southeastern Mediterranean Sea has become more extreme to its native species due to climate change, favouring the establishment and spread of thermophilic species, such as most of the Lessepsian immigrants (Ben Rais Lasram et al., 2010; Lejeusne et al., 2010; Bianchi et al., 2013). Currently, the Levantine Sea is the world's most invaded marine ecoregion and the ecosystem has shifted considerably due to the collapses of several native species and the increasing dominance of alien species (Edelist et al., 2013a).

The study of biological invasions and their impacts on the marine environment has increased in the last few decades and it is providing new insights into their ecological consequences (Wonham and Lewis, 2009). Most studies of alien species on marine ecosystems have focused on population questions, such as population establishment, spread, impacts, invasion control and spatial distributions (e.g., Ruesink and Collado-Vides, 2006; Azzurro et al., 2013). In addition, several tools of varying levels of complexity have been employed to examine the impact of alien species (Wonham and Lewis, 2009). These applications range from analyses that include some groups within the pelagic compartment to modelling applications that include the entire food web.
Given the interconnectedness between species populations, environment and human activities, a shift towards a more comprehensive analysis and management of human activities is required, as it is emphasized by the ecosystem-based management (EBM) approach (Rosenberg and McLeod, 2005; Link, 2010a). Within this context, ecosystem modelling tools are particularly useful because they allow the study of marine ecosystems as a whole, integrating available information to study direct and indirect interactions among ecosystem compartments, i.e. trophic interactions and the impact of fishing activity on marine resources (Plagányi, 2007; Fulton, 2010). One popular modelling approach used to study marine food webs is the Ecopath with Ecosim (EwE) approach (Christensen and Walters, 2004), widely applied to describe the structure and functioning of aquatic food webs and to assess the impacts of human activities and environmental changes (Christensen and Walters, 2011; Heymans et al., 2014; Colléter et al., 2015; Heymans et al., 2016).

In the Mediterranean Sea, several Ecopath models have been built over the last decade (Coll and Libralato, 2012). However, all available ecosystem models (with the exception of the Gulf of Gabes (Hattab et al., 2013), in Tunis) were developed for the northern part of the Mediterranean, mostly in the western basin. However, no published models exist for the most eastern part of the Mediterranean Sea. In addition, the EwE approach has been used to study the impacts of alien species in several aquatic systems but typically, these studies have included only one or two alien functional groups, ranging from species located at the base of the food web to top predators (Corrales et al., 2014).

In order to characterize the structure and functioning and to assess the past and current impact of several alien species and fishing activity along the Israeli Mediterranean coast, we developed a food web Ecopath model of the Mediterranean continental shelf of Israel (ICS) for two time periods (1990-1994 and 2008-2012). Due to the large number of alien species in the region, this represents a major modeling challenge and an important step forward modeling alien species with EwE, generally, and the Mediterranean Sea in particular (Corrales et al., 2014).

2. Material and methods
2.1. Study area and time periods

The study area is the Israeli Mediterranean continental shelf ecosystem (thereafter referred to ICS) (Fig. 1), in the Levantine Sea. Each food web model developed covers the same area of 3725 km$^2$ with depths from 0 to 200 m, and represents two time periods, 1990-1994 (thereafter referred to 1990s) and 2008-2012 (thereafter referred to 2010s). The bathymetric extension of the model is constrained by biological and fishery considerations as the study area includes the entire continental shelf, where the alien species live and where the fishery mainly operates. The two time periods analyzed were chosen due to the availability of data and the difference in the extent of occurrence in the alien species, increasing from 1990 to present. At the same time, fishing activities decreased from 1990s to present (Edelist et al., 2013a; Goren et al., 2013).

Israeli Mediterranean fisheries are characterized by multi-species catches (Edelist et al., 2013b). Catches are made near the coast, mainly on the continental shelf (Edelist et al., 2011) and fisheries include a small semi-industrial trawl fleet, a small artisanal sector of gill and trammel-netters and longliners, a small purse seine fleet and a growing recreational sector (Edelist et al., 2013b; Goren et al., 2013).

2.2. Ecopath modeling approach

The Ecopath with Ecosim (EwE) software version 6.4.3 (Christensen and Walters, 2004; Christensen et al., 2008) was used to describe the Israeli Mediterranean continental shelf food web. In particular, we used the static Ecopath food web model, which provides a quantitative representation of the studied ecosystem or a “snapshot” in terms of flows and biomasses for a defined period of time. The ecosystem is modelled by using functional groups, which can consist of ontogenetic fractions of a species, single species or groups of species sharing common ecological traits, and these groups are linked through their trophic interactions.

The Ecopath model is based on two master equations for each functional group or "box" in the model: ones describes the production (Eq. 1) and the other one describes the consumption (Eq. 2) (Christensen and Walters, 2004; Christensen et al., 2008).

Production = predation mortality + fishing mortality + other mortality + biomass accumulation + net migration (Eq. 1)
Consumption = production + respiration + unassimilated food  \hspace{1cm} (Eq. 2)

The model is parameterized through a system of linear equations for all the functional
groups and the unknown parameters are estimated. For each functional group, three of
the four basic parameters (biomass (B), production (P/B) and consumption (Q/B) rates,
and Ecotrophic Efficiency (EE)) are required, in addition to the catch by fleet and
functional group and the diet composition of all groups. A detailed explanation of the
algorithms and equations of the approach and its main advantages and limitations are
described in Christensen and Walters (2004) and Heymans et al. (2016).

2.3. Functional groups and input data

To represent the ICS ecosystem, we defined the functional groups based on biological
and ecological features of species such as habitat, depth distribution and diets, and data
availability (especially biomass, diet and catch). We followed a similar food web
structure and parametrization of other Ecopath models developed for the Mediterranean
Sea (Coll et al., 2006; Tsagarakis et al., 2010; Corrales et al., 2015) (Table 1). The data
inputs of the two models are shown in Table 1 and a detailed description of these inputs
is provided in the Online supplement section 1.

As one of the objectives of this study was to assess the impact of alien species in the
ecosystem, we included specific alien functional groups. Due to the large number of
alien species and differences in time of settlement in the ecosystem, we included the
most abundant species (33 species in 1990s and 41 species in 2010s), that had sufficient
data, including crustaceans and fish species (see Online supplement section 2). At
present, sufficient information needed for other alien groups such as cephalopods,
molluscs, polychaetes and jellyfish is not available.

In addition to ecological traits (feeding habitats and habitat type), we combined alien
species into functional groups accounting for the period that they invaded the
ecosystem. For crustaceans we defined a group for alien shrimps and another for alien
crabs, and all the species of these two functional groups invaded the ecosystem before
1990. Alien fish species have invaded the ecosystem both before and after 1990. In the
demersal habitat, we defined the following groups for alien fish: goatfishes (Upeneus
sp.), alien herbivores (Siganus sp.), alien lizardfish (Saurida lessepsianus), earlier alien
demersal fishes (demersal fishes that invaded the ecosystem before 1990) and new alien
demersal fishes (demersal fishes that invaded the ecosystem after 1990). For the pelagic habitat, although the ecosystem hosts small, medium and large alien pelagic fishes, not enough information existed to allow separation in different size classes for these species. Therefore, for small pelagic fishes and large pelagic fishes, invasions occurred before 1990 and due to lack of information on these alien species, these groups were combined into two groups: small pelagic fishes and large pelagic fishes (both including native and alien species together). The native medium pelagic fishes group in the 1990s model combined native and alien species that arrived to the ecosystem before 1990, while a new group of alien medium pelagic fishes was created for the 2010s model.

In total, 39 functional groups were used in the ICS model for the 1990s period, including 2 primary producers, 12 groups of invertebrates, 20 groups of fishes, 1 group of sea turtles, 1 group of seabirds, 1 group of dolphins and 2 groups of detritus (natural detritus or "marine snow" and discards) (Table 1). Two alien fish groups were added to the 2010s model to account for the new arrivals (Table 1).

Input parameters for the species and functional groups were mainly obtained from published literature and unpublished information from the Israel Oceanographic and Limnological Research (IOLR) and the University of Tel-Aviv collected from the study area or surrounding areas (see Online supplement section 1 for details on parameterization of each functional group).

Biomass estimates to parameterise both models mainly came from fishery dependent bottom trawl survey (swept-area method), visual surveys conducted in the area, and additional information from the literature. For the pelagic habitat, biomass estimates were not available and therefore, we used realistic EE values to estimate the biomass of 10 functional groups (Heymans et al., 2016). Production and consumption rates were either estimated using empirical equations accounting for changes in water temperature between both time periods, or taken from literature or from other models and corrected for temperature changes following Opitz (1996). Diet information was compiled using published and unpublished data on stomach content analyses, giving preference to local or similar areas. To date, limited information on the diet of alien species is available. For alien crustaceans (shrimps and crabs), in the absence of information from the Mediterranean Sea, we assumed the same diet composition as for the native groups. For migratory species (large pelagic fishes, sea birds, turtles and dolphins), we set a fraction
of the diet composition as import based on the time that these species feed outside the system (Christensen et al., 2008; Heymans et al., 2016).

Fisheries data were obtained from a reconstruction of Israeli catches including both commercial and discards, the recreational fishery and unregulated and unreported catch (Edelist et al., 2013b). We considered three commercial fishing fleets: bottom trawl, purse seine and artisanal fisheries (including gillnets and longliners).

2.4. Pre-balancing and balancing analyses

An Ecopath model is considered ecologically and thermodynamically balanced under the following conditions: (1) estimated EE < 1 for all functional groups, (2) values of P/Q (production/consumption rate or gross efficiency of food conversion, GE) are between 0.1 and 0.35 with the exception of some fast growing groups, (3) R/A (respiration/food assimilation) < 1, (4) R/B (respiration/biomass) are between 1 and 10 for fishes and higher values for small organisms, (5) NE (net efficiency of food conversion) > GE and (6) P/R (production/respiration) < 1 (Christensen et al., 2008; Heymans et al., 2016) (Table 1 and Online supplement section 3).

Initial results of the ICS models showed that the EE > 1 for 16 (1990s) and 15 (2010s) demersal groups (fish, cephalopods and crustaceans). To achieve the mass balance, we applied a manual mass-balanced procedure following a top-down approach modifying some input parameters (starting from the groups with higher trophic levels) and following the best practice guidelines provided in the literature (Heymans et al., 2016). The pedigree information (see section 2.4.a) (Christensen and Walters, 2004) and pre-balancing analysis (PREBAL) (Link, 2010b) were used to validate the choice of parameters to modify.

In order to ensure that the model parameters obeyed general ecologic principles and to guide the balancing procedure we used the PREBAL analysis (Link, 2010b). This analysis highlighted that some P/B and Q/B values had to be adjusted since they were too low or too high in comparison with the rest of the groups. For additional information on the application of the PREBAL procedure see Online supplement section 4.

After the application of PREBAL, to achieve mass-balance we corrected the inputs mainly by readjusting biomass and diets as was done for several Mediterranean Sea...
Ecopath models (Coll et al., 2006; Tsagarakis et al., 2010; Corrales et al., 2015). For the biomass, we calculated the average and maximum value for each species and year from the bottom surveys and we first used the average values. In absence of catchability coefficients for the study area to correct the biomass estimates that were too low to ensure the mass-balance, we adjusted these values taking the maximum values of biomass estimates. We also adjusted the biomass inputs taking into account the fishing mortality patterns in other Mediterranean areas (demersal fish groups) and using a reasonable value of EE (EE values close but lower than 1) (Heymans et al., 2016), leaving the model to calculate the biomass (e.g. for crustacean and cephalopods groups). Finally, the diet matrix was slightly adjusted to take into account the abundances of species in the ecosystem (Online supplement section 5).

2.5. Pedigree index and quality of the model

The pedigree routine (Christensen and Walters, 2004) was used to quantify the uncertainty associated with the input parameters and the quality of the models. For each input datum, we selected the predefined values of the pedigree to record the degree of confidence associated with the data. With the information for each functional group, the pedigree index was calculated for the overall model. The pedigree index ranges between 0 (low quality) and 1 (high quality), allowing a description of the quality of the model that can be compared to other models. The confidence intervals for the pedigree analysis and index values used are described in Online supplementary section 6.

To evaluate the quality of the model we also compared some model outputs to the results of independent data. In our case, we compared the Trophic Level (TL) estimates from the Ecopath model for the 2010s period with the results from Stable Isotope Analysis (SIA) conducted on the Lebanese coast (Fanelli et al., 2015). The 2010s model was used for this comparison due to the proximity in time between the food web model and the SIA study (2011-2012). We compared the δ15N values (‰) of the species found in the SIA study that we included in our model. For those functional groups from the model with several δ15N values, we weighted these values using biomass proportions of these species in each functional group. TLs estimated by the Ecopath model were plotted against the δ15N values and the correlation was tested using the Spearman-rank non-parametric correlation coefficient test (Zar, 1984).

2.6. Model analyses and ecological indicators
In order to assess the changes between the two models and the possible role and impact of alien species and fisheries we analyzed a number of key food web indicators and we compared them between both time periods. In addition, we compare some of these results with those from several available Mediterranean Ecopath models: the South Catalan Sea (Coll et al., 2006), the Northern and Central Adriatic Sea (Coll et al., 2007) and the North Aegean Sea (Tsagarakis et al., 2010).

Although the topology (number of functional groups, distribution of the species, area modeled and depth range included) of the model affects many food web indicators as they are dependent to model construction (Heymans et al., 2014; Heymans et al., 2016), in here we assumed that the comparison was possible as: (1) both ICS models (1990s and 2010s) represent the same ecosystem with the same model structure with the exception of two new functional groups that invaded the ecosystem during the time (comparison between ICS models) and (2) the Mediterranean Ecopath models compared were developed following similar criteria (number of functional groups, distribution of the species and parameterization) and included similar depth ranges. In addition, for the Mediterranean model comparison, we only included robust indicators following previous studies (Heymans et al., 2014; Corrales et al., 2015).

a) Ecosystem structural and functioning traits

To represent the biomasses, trophic flows and Trophic Levels (TL), we used a flow diagram and a Lindeman spine representation (Lindeman, 1942). In the Lindeman spine, the flows and biomasses are aggregated for each discrete trophic level and the detritus box is separated from the primary producers to show the amount of energy that flows through it.

The Ecopath model outputs a variety of indicators related to the development and maturity of ecosystems according to Odum (1969). In this study, the following indicators were included: (1) Total System Throughput (TST, t·km\(^{-2}\)·year\(^{-1}\)), estimated as the total flows in the ecosystem (sum of all consumption exports, respiration and flow to detritus; (2) Total Biomass (TB, t·km\(^{-2}\)); (3) total Primary production/total Respiration (Pp/R); (4) total Primary production/ total Biomass (Pp/B, t·km\(^{-2}\)·year\(^{-1}\)); (5) the System Omnivory Index (SOI), (6) the Finn’s Cycling Index (FCI, %) and (7) the Finn’s mean Path Length (PL) (Odum, 1969; Finn, 1976; Christensen, 1995; Christensen et al., 2008; Heymans et al., 2014). We also included the Transfer
Efficiency (TE), the fraction of total flows of each discrete trophic level that are either exported out of the ecosystem (e.g., by the fishing activity) or transferred to higher trophic levels through consumption. Therefore, TE summarizes the inefficiency or energy dissipation between discrete trophic levels that is produced along the food web due to respiration, excretion, egestion, natural mortality and exports. We also calculate the mean Trophic Level of the community (mTLco), by weighting the TL of each functional group by its biomass.

b) Ecological roles of functional groups

We used the Trophic Level (TL) in order to analyze the ecological position of the functional groups of the ICS model (Lindeman, 1942; Stergiou and Karpouzi, 2001).

The Mixed Trophic Impact (MTI) analysis was used to quantify the direct and indirect impact in the food web that a hypothetical slight increase in the biomass of one functional group would have on the biomasses of all other functional group in the food web, including the fishing fleets (Ulanowicz and Puccia, 1990; Christensen et al., 2008).

The new keystoneness index developed by Valls et al. (2015) was used to identify the keystone species. A keystone species is defined as a predator species with a high and wide impact on the food web despite its low biomass (Paine, 1966, 1969; Valls et al., 2015). The index is calculated as:

\[ KS = IC \times BC \]  
(Eq. 3)

where IC is the impact component and BC is the biomass component. The IC component represents the overall effect of group (i) on all other groups in the food web excluding the impact on (i) itself and the impacts on dead groups and fleets (Libralato et al., 2006). The BC component is defined as the rank of the group according to their biomass values in descending order (Valls et al., 2015).

c) Impacts and role of alien species

To evaluate the impact of alien species on the ecosystem, we measured changes to the contribution of alien species to the biomass and the catch in the ecosystem, and changes to flows related to alien species between the two time periods analyzed: 1990s and 2010s. For the changes to flows related to alien species, we calculated the consumption.
by alien groups on their prey and the predation on alien groups by their predators for both time periods.

d) Ecosystem impacts of fishing

The impacts of fishing on the food web were assessed using the mean trophic level of the catch ($mTLc$) (Christensen, 1996) and the Primary Production Required to sustain the fisheries (% PPR) (Pauly and Christensen, 1995), taking into account both primary and detritus production. The MTI analysis was also used to quantify the direct and indirect impact of each fleet on the functional groups and the exploitation rate (fishing mortality/total mortality, $F/Z$) was calculated for the functional groups that are exploited.

3. Results

3.1. Ecosystem structural and functioning traits

Regarding the overall trophic flows among functional groups and TLs, results illustrate that most of the flows to detritus (93.3%), consumption (69%) and production (95.8%) were related to the pelagic compartment (Table 1 and 2) due to the contribution of planktonic groups during 1990s. Similar contributions (92.8%, 66.1% and 95.4%, respectively) were found in the 2010s period. The flow diagram evidenced an important bento-pelagic coupling (Fig. 2), with 23.4% (1990s) and 27% (2010s) of flows from the pelagic compartment transferred to the demersal habitat through consumption when predation of planktonic groups on their prey were excluded (results not shown). Results also emphasized the important role of small pelagic fishes (functional group or F.G. 31) in linking TL II from the pelagic compartment with higher trophic levels from the pelagic and demersal habitat. Of this group’s biomass, 74.6% and 83.5% was transferred to the pelagic higher trophic levels and 25.4% and 16.5% to the demersal higher trophic levels in 1990s and 2010s respectively (results not shown).

Most of the energy flows within the ICS ecosystem were between TL I, II and III (Fig. 3a and b). Exports, primarily represented by catches, were mainly focused on TL III and IV. An important link between detritus and TL II was found, as flows from the detritus and from the primary producers to TL II were similar in both time periods. The Transfer Efficiencies (TE), decreased with the increasing TL (Fig. 3). The mean TE was 18.9% and 19% for the two time periods, respectively (Table 3).
Analyses of flows in terms of the Lindeman spine for both time periods indicated similar patterns when studying the overall ecosystem (Fig. 3a and b). However, results from different habitats (pelagic versus demersal), highlighted a change in the food web over time (Fig. 4): biomass, production and consumption of groups located in TL III in the pelagic compartment decreased between the two time periods while values for TL IV remained constant. In contrast, the biomass, production and consumption of groups located in TL III in the demersal compartment increased between the two time periods while values at TL IV decreased (Fig. 4).

3.2. Ecological roles of functional groups

The functional groups ranged from TL = 1 for primary producers (F.G. 1 and 2) and detritus (F.G. 40-41) to TL = 4.33 for dolphins (F.G. 39) in 1990s (Table 2). The highest TLs (>4) corresponded to dolphins (F.G. 39), hake (F.G. 17), demersal sharks (F.G. 29), native and alien medium pelagic fishes (F.G. 34 and 35) and large pelagic fishes (F.G. 36). Invertebrates groups were classified with a TL between 2.05 and 2.97, with cephalopods (F.G. 13 and 14) showing higher TLs; and fish groups showed TLs between 3.02 and 4.25, with the exception of the alien herbivores (F.G. 22), with a lower TL. Similar TLs were found for the 2010s model. TLs estimated from the Ecopath model in 2010s were highly and positively correlated with the $\delta^{15}$N values from Lebanon (Fig. 5, Spearman-rank correlation coefficient, $R_s = 0.90$, n = 12, p < 0.0001). These results showed that an increase of $\delta^{15}$N values calculated from SIA matched with an increase of TLs estimated by the Ecopath model.

The MTI analysis showed that most of the groups had a negative impact on themselves as a result of competition for the resources within the group and had a direct negative impact on their main prey through predation (Fig. 6a and 6b). Results highlighted some indirect effects between groups through competition for resources. For example, between benthic invertebrates (F.G. 12) and alien herbivores (F.G. 22) and between small native dem. fishes (F.G. 20), earlier alien dem. fishes (F.G. 23) and new alien dem. fishes (F.G. 24). An important impact of small pelagic fishes (F.G. 31) and small native demersal fishes (F.G. 20) to higher and lower trophic levels was also observed. The comparison between both time periods highlighted the increasing impact of alien groups (e.g. earlier alien dem. fishes (F.G. 23), new alien dem. fishes (F.G. 24) and medium pelagic fishes (F.G. 35)), demersal sharks (F.G. 29) and rays and skates (F.G.
30) in the ecosystem, while we could observe the decreasing impact of mullets (F.G. 15), hake (F.G. 17), large native dem. fishes (F.G. 21), alien lizardfish (F.G. 25) and native medium pelagic fishes (F.G. 34) due to changes in biomass composition. Native medium pelagic fishes (F.G. 34), dolphins (F.G. 39), demersal sharks (F.G. 29), large pelagic fishes (F.G. 36), alien lizardfish (F.G. 25) and squids (F.G. 14) may have been potential keystone species of the ICS in both time periods (Fig. 7a and 7b). Hake (F.G. 17) was identified as potential keystone specie during the 1990s period but not during 2010s. This result indicates that the keystone role of hake (F.G. 17) in the ICS ecosystem disappeared in the latter period.

3.3. Impacts and role of alien species

The contribution of alien groups to the total biomass increased from 9.5% in 1990s to 23.3% in 2010s (Fig. 8a). For crustaceans (shrimps and crabs) and demersal fishes the alien species increased from 35.1% and 20.2% to 66.3% and 47.5%, respectively (Fig. 8a). For example, alien shrimps (F.G. 9) and earlier alien demersal fishes (F.G. 23) increased their biomass by 55.5% and 256.6%, respectively (Table 1). A remarkable result is the large biomass of the new alien demersal fishes (F.G. 24) within a decade of the invasion of the first specie of this group, with a rate of increase of 0.01 t·km$^{-2}$·year$^{-1}$. For pelagic fishes, results showed that biomass of alien species increased from 0% to 2.6% between both time periods (Fig. 8a).

The analysis of the catch showed similar patterns to those observed in the biomass. The contribution of alien groups to the total catch increased from 14.9% in 1990s to 34.1% during 2010s (Figure 8b). By groups, this increase was from 43.1%, 22.2% and 0% to 75.4%, 46.1% and 4.9% for crustaceans, demersal fishes and pelagic fishes, respectively (Figure 8b). For example, the catch of alien crabs (F.G. 11) and alien herbivores (F.G. 22) increased 399.1% and 224.3%, respectively (Table 1). The analysis of the percent contribution of alien species to the catch for each fleet showed that the largest increases corresponded to the trawl and the recreational fleet, with increases from 30.1% and 6.2% to 48% and 18.2% from 1990s to 2010s, respectively (Figure 8c).

The analysis of predation and consumption, as well as the MTI analysis, showed the increasing importance of alien groups on the ecosystem between the two time periods (Fig. 9a and 9b). Results also highlighted that the predation by alien species on their
prey increased slightly more than the consumption of alien species by their predators (Figure 9a and 9b). For example, the grazing of alien herbivores on primary producers increased 109.8% while the consumption on alien herbivores by their predators increased 90.6%.

The keystone index analysis applied to the alien species showed that alien lizardfish (F.G. 25) was identified as a potential keystone species in both time periods (Fig. 7a and 7b). It also showed the possibility of the alien medium pelagic fish (F.G. 35) to become a keystone species in the future, as this group presented a high keystone index despite its recent invasion (Fig. 7b).

### 3.4. Ecosystem impacts of fishing

Total catch in 1990s was 0.94 t·km$^{-2}$·year$^{-1}$, and did not differ considerably between both time periods, suggesting stable catch production (Table 3). Exploitation rates (F/Z) (Table 2) were high for many of the exploited demersal groups, including, for example, mullets (F.G. 15), goatfishes (F.G. 16), large native demersal fishes (F.G. 21), alien lizardfish (F.G. 25), demersal sharks (F.G. 29) and rays and skates (F.G. 30); and also for medium (F.G. 34 and 35) and large pelagic fishes groups (F.G. 36) (Table 2).

The percentage of Primary Production Required to sustain the fishery (%PPR) was 10.36% and 11.34% for the 1990s and 2010 time periods, respectively (Table 3).

The MTI analysis applied to the fishing fleets showed that the four fleets included in the ICS models had negative impacts on themselves and to a lesser extent on the other fleets, indicating direct and indirect competition for marine resources (Fig. 6a and 6b). The trawl fleet presented the highest impacts on many demersal and pelagic groups and also had a high impact on turtles (F.G. 37) via direct mortality and on dolphins (F.G. 39) via direct mortality and competition for resources. The other fleets had notable impacts on target species and the artisanal fleet had a high impact on turtles (F.G. 37) and seabirds (F.G. 38) via direct mortality.

### 4. Discussion

In this study we developed for the first time a food web model of the Israeli Mediterranean continental shelf ecosystem representing two time periods. After parameterization, data quality analysis and balancing the model, results showed that the
role of alien fish, shrimps and crabs on the southeastern Mediterranean Sea is important and their impact is high and have increased from 1990s to 2010s. We also showed that fishing activities had notable impacts on the ecosystem, already in the 1990s and in the 2010s. This study represents an important step forward in evaluating the past and current impacts of alien species and fishing activities in the Israeli Mediterranean continental shelf.

One of the main advantages of undertaking such a study is the identification of information gaps. The pedigree index values obtained for both ICS models indicated an acceptable quality of the models (Morissette, 2007; Lassalle et al., 2014) although they are among the lowest values in the Mediterranean Sea (Corrales et al., 2015). It is evident from the input data that there are many information gaps, especially regarding the pelagic habitat and benthic invertebrates. In particular, population assessments of small and medium pelagic fishes and plankton sampling in the study area are needed and would greatly improve the parameter estimates of these groups. Moreover, an annual scientific trawl survey (fishery independent) would improve the data available and would increase the ability to understand and quantify the changes that are occurring in the Levantine Sea. Detailed studies on stomach content analysis for several alien species are also needed to complement available information and our understanding of the impact of alien species in this area.

Obtaining good estimates of total catch (both official and IUU (Illegal, Unregulated and Unreported)) during this study (Edelist et al., 2013b) was challenging but the reconstruction used in this study eventually offered a better, more complete estimation than the official data available. However, as Edelist et al. (2013b) indicated, the catch data of the artisanal fleet and the purse seine were less reliable than the trawl catch due to the large number of vessels and landing sites. In addition, the recreational sector requires detailed examination due to its actual importance and its potential growth, as in other Mediterranean regions (Gaudin and De Young, 2007; Pauly et al., 2014).

Comparison and calibration of model outputs are important in order to validate results. Here we used information from Stable Isotope Analysis (SIA) from a neighboring area to compare outputs with trophic levels estimates from the model. In general, SIA estimates and our results showed a high correlation, highlighting that, in general, diet information used in the models represented the trophic relationships reasonably well.
Although the stomach content analysis and SIA were not performed in the same area, they are from the Levantine Sea and could be used here to parameterize and validate our models. Future work should include more independent analysis to validate the models (i.e. information on fishing mortalities from stock assessment) while the 1990s model should be calibrated to available time series of historical data using the temporal modeling approach Ecosim (Walters et al., 1997).

### 4.1. Ecosystem structural and functioning traits and ecological role of functional groups

In agreement with the oligotrophic nature of the Levantine Sea, TST and TB estimates, which can be used as a measure of ecosystem size, were much lower in the Israeli models than in other Mediterranean models set up in the western and central basin (Corrales et al., 2015). These features had been also observed on a broader scale including all the Mediterranean as a food web model (Piroddi et al., 2015). Remarkably, the TE's in both time periods were higher (almost double) than the average value of 10% reported worldwide (Pauly and Christensen, 1995), were also higher than in other Mediterranean areas (Corrales et al., 2015) and for the Mediterranean Sea as a whole (Piroddi et al., 2015). Such high values highlight the nutrient-poor waters of the Israeli Mediterranean coast.

Results related with the ecosystem development theory (Odum, 1969; Odum, 1971; Christensen, 1995), suggested that the Israeli ecosystem was at a developing stage in both time periods. For example, the Pp/R values were higher than 1, indicating that more energy was produced than respired within the system. The Pp/B values were high, indicating low levels of biomass accumulation within the system compared with productivity; and the FCI values, that represents the proportion of throughput cycled within the ecosystem, was low, indicating an immature system. Moreover, indices related to the food web complexity (SOI and PL) presented low values, suggesting that the ICS models look more chain-like than web-like. All of these indicators presented similar values in both time periods, suggesting that the functioning of the whole ecosystem did not suffer a large change. In addition, it could also show that the ecosystem was already highly impacted in the 1990s.

Results from the Lindeman spine suggested food web changes in different habitats. The increasing flows in the demersal habitat in TL III can be due to the increasing impact of
alien species on the ecosystem. This could be related to the empty niches left by the native species that the alien species occupied or as a result of a potential trophic cascade due to the overexploitation of top predators like hake (F.G. 17), large native dem. fishes (F.G. 21) and alien lizardfish (F.G. 25). However, the decreasing flows in TL III of the pelagic habitat were not clear and should be taken carefully since (1) there is a lack of data from the pelagic compartment and (2) rise of water temperature and river damming were postulated to play an important role in these declines (Edelist et al., 2013b).

The Israeli marine ecosystem was found to share some common features in structure and functioning with other Mediterranean ecosystems such as the important role of detritus via TL II, the dominance of the pelagic fraction in term of flows and the importance of the benthic-pelagic coupling. For example, the contribution of planktonic groups to the detritus and the relationship between detritus and organisms at TL II (mainly benthic invertebrate groups) was identified as a key process in the Mediterranean Sea (Coll et al., 2006; Tsagarakis et al., 2010; Corrales et al., 2015).

In both time periods the same keystone groups were identified with the exception of hake in 2010s. Most of these groups were also identified as keystone in other Mediterranean areas (Coll and Libralato, 2012; Corrales et al., 2015). Hake (F.G. 17) was not identified as a keystone species in the 2010s model, representing a native top predator that may have lost its ecological role. The decline of hake has been attributed to overfishing, oceanographic changes, increase of temperature and the competition for resources with the alien lizardfish (F.G. 25) (Galil, 2007a; Gucu and Bingel, 2011; Halim and Rizkalla, 2011; Edelist, 2012).

### 4.2. The role and impact of alien species

Our results show that along the Israeli Mediterranean continental shelf, alien species have become an important part of the ecosystem. Their increasing biomass, catch and flows within the ecosystem, have altered the structure of the food web. Higher percentages of alien species have been found in the catch than in the biomass, as most of the fishing effort has been redirected to the shallow waters (Edelist et al., 2013b), where most of the commercial demersal biomass is attributed to alien species nowadays (Edelist et al., 2013a).
A high proportion of alien species in the demersal habitat and in the catch has been found in other parts of the Eastern Mediterranean Sea as well ( Güncü and Bingel, 1994; Taşkavak et al., 1998; Harmelin-Vivien et al., 2005; Carpentieri et al., 2009; Güncü et al., 2010). The rapid expansion of the new alien demersal fishes (F.G. 24) is in line with studies that indicated that the most recent wave of invasion has established large populations along the Eastern Mediterranean Sea (Edelist et al., 2012; Nader et al., 2012; Edelist et al., 2013a; Stern et al., 2014). The fleets with the highest percentages of alien species in the catch were the trawls and recreational fishers. The high percentage in the former is because most of the trawl fishing effort are focused on shallow soft bottoms while the main species caught by the recreational fishers are the alien herbivores (F.G. 22), that constitute an important part of the total biomass on hard bottoms near the coast (Goren and Galil, 2001). Nevertheless, alien species do appear to be poorly established in the rocky littoral with the exception of the alien herbivores (Golani et al., 2007). However, it is important to note that we may have underestimated the importance of alien species in the catch of all the fleets, but especially in the artisanal and the purse seine, as an important part of the catch includes groups that we were not able to separate properly in our functional groups of the model (e.g. small pelagic fishes and native medium pelagic fishes).

Trophic flows related to alien species increased as a result of their biomass expansion and have impacted the ecosystem. For example, the explosion of the alien herbivores has altered the community structure of the rocky infralittoral ( Sala et al., 2011; Vergés et al., 2014) as prior to their arrival, the role of native herbivorous fishes were negligible, and therefore, they increased the rate of algal recycling and provided more food to potential predators (Galil, 2007b). Moreover, some competition for resources has been found in the demersal habitat. Our results highlighted that the consumption of prey by alien species increased more than the consumption on alien species by their predators. This may be due to the increasing importance of alien species on the catch, preventing energy transfer to higher trophic levels.

Several hypotheses have been proposed to explain the impact that alien species have on the marine ecosystem of the Eastern Mediterranean Sea and the decline of native species. Trophic interactions between native and alien species may cause native species to be outcompeted or partially displaced by the invaders (Galil, 2000; Galil, 2007a). Several authors indicated the success of some alien species could be related to the...
existence of underexploited niches in the ecosystem that could be exploited by the alien
species (Golani, 1998; Galil, 2008; Rilov and Galil, 2009). In addition, the impact of
fishing activity could facilitate the establishment and spread of alien species as a result
of the overexploitation of native species (Galil, 2008) and the possible better adaptation
and competition properties of alien species to proliferate in the highly impacted trawled
areas (Edelist et al., 2011). Moreover, environmental conditions (specially temperature
but also salinity) might have become more suitable for thermophilic species like most of
the Lessepsian migrants, providing various advantages when competing with temperate
native species (Golani, 1998; Galil, 2007a).

4.3. Ecosystem impacts of fishing

Results of this study showed that fishing activity played an important role over time on
the ecosystem and had noticeable impacts. For example, some groups presented higher
exploitation rates than the general reference point of 0.5 proposed by Rochet and
Trenkel (2003), suggesting the overexploitation of several marine resources.

However, the Primary Production Required to sustain the fisheries (%PPR) showed a
lower value than the 24.2% estimated for non-tropical shelves worldwide (Pauly and
Christensen, 1995) and it was lower than the he Northern and Central Adriatic Sea
model (Coll et al., 2007) and higher than the South Catalan Sea model (Coll et al.,
2006) and the North Aegean Sea model (Tsagarakis et al., 2010). Moreover, the results
showed a stable total catch between both periods. However, landings decreased around
20% from 1990s to 2010s while discards increased dramatically, corroborating the
unsustainability of the Israeli fisheries (Goren et al., 2013; Edelist et al., 2014). There
are many reasons for this (Edelist et al., 2013b). First, the trawl fleet refocused the effort
to the shallow waters, where many fish species are characterized by small size and
where many nursery habitats are found. Second, many of the new alien species found
mainly in shallow waters are discarded as they are small or are venomous/poisonous or
due to cultural reasons.

The mTLc values in the Israeli models, in line with the mTLco, were higher than
models developed in the western and central Mediterranean Sea and similar to those
developed for the eastern Mediterranean Sea (Coll and Libralato, 2012; Corrales et al.,
2015). This could be related to the lower proportion of low TL organisms such as small
pelagic fishes in the total catch and the ecosystem due to the oligotrophic nature of the
eastern Mediterranean Sea, as depicted also in the Aegean Sea (Tsagarakis et al., 2010). Moreover, the mTLc and mTLco in the Israeli model are similar during both time periods as the biomass and catch of top predators (i.e., hake (F.G. 17), large native demersal fishes (F.G. 21) alien lizardfish (F.G. 25)) and low trophic levels (like small pelagic fishes (F.G. 31)) decrease while the biomass and catch of medium trophic levels (i.e. earlier (F.G. 23) and new alien demersal fishes (F.G. 24)) increased. In fact, Edelist et al. (2013a) suggested that alien species have masked changes to the mTLco in the demersal fish community by replacing native by alien fishes with similar ecological position in the food web.

4.4. Concluding remarks

This study presents the first attempt to develop a food web model of the Israeli Mediterranean ecosystem and shows the large changes that have occurred in the ecosystem from 1990s to date. These changes are consequences of a significant impact of fishing activities and increasing the number and biomass of alien species.

The current state of the ICS ecosystem is a result of the cumulative impacts of alien species, overfishing and climate change superimposed on the geological history and environmental conditions of the Eastern Mediterranean Sea (Galil, 2008; Bianchi et al., 2014). It is difficult to quantify the contribution of each of these factors (Galil, 2007b) but they could be amplified by their cumulative effects. The nature of these effects (additive, synergistic or antagonist) is unknown, although some authors suggested synergistic effects between alien species, fishing and climate change (Galil, 2008; Goren et al., 2013).

Future work including the calibration and fitting of the 1990s to time series to historical data (Walters et al., 1997; Christensen and Walters, 2004) can be used to continue this analysis and evaluate both historical and potential future cumulative impacts of multiple stressors to the ecosystem dynamics of the southeastern Mediterranean Sea.

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Table legends

Table 1. Initial (in bold) and modified input data of the Israeli Mediterranean continental shelf model for 1990-1994 (1990s) and 2008-2012 (2010s) time periods. B = final biomass ($t \cdot km^{-2}$); P/B = production/biomass (year$^{-1}$); Q/B = consumption/biomass (year$^{-1}$); EE = ecotrophic efficiency; P/Q = production/consumption ratio; landings and discards ($t \cdot km^{-2} \cdot year^{-1}$). (*) indicates groups that were considered within pelagic compartment. Table 2. Output estimates of the Israeli Mediterranean continental shelf model for 1990-1994 (1990s) and 2008-2012 (2010s) time periods. TL = Trophic Level; F = fishing mortality (year$^{-1}$); M2 = predation mortality (year$^{-1}$); M0 = other natural mortality (year$^{-1}$); F/Z = exploitation rate (fishing mortality (F) / total mortality (Z)); FD = flow to detritus ($t \cdot km^{-2} \cdot year^{-1}$).

Table 3. Characteristics, statistics and ecological indicators for the Israeli Mediterranean continental shelf ecosystem (ICS).

Figure legends

Fig. 1. The study area encompassing the Israeli EEZ and depth contours.

Fig. 2. Flow diagram of the Israeli Mediterranean continental shelf model representing the 2008-2012 period. The size of each circle is proportional to the biomass of the functional group. The numbers identify the functional groups of the model (listed in Table 1). The thickness of the connecting lines is proportional to the magnitude of their trophic flows.

Fig. 3. Lindeman spine representation of the Israeli Mediterranean continental shelf ecosystem for the 1990-1994 (a) and the 2008-2012 (b) time periods. Trophic Level (TL) I is split into primary producers (P) and detritus (D). Flows are represented in $t \cdot km^{-2} \cdot year^{-1}$ and biomass in $t \cdot km^{-2}$.

Fig. 4. Biomass ($t \cdot km^{-2}$), production ($t \cdot km^{-2} \cdot year^{-1}$) and consumption ($t \cdot km^{-2} \cdot year^{-1}$) by discrete Trophic Levels (TL) and habitat in both time periods. Left hand panels are TL III and right panels are TL IV. Top row is biomass (a and b), middle row is production (c and d) and bottom row is consumption (e and f).
**Fig. 5.** Correlation between Trophic Level (TL) calculated with the Ecopath model (2008-2012 period) and the $\delta^{15}$N values calculated from stable isotope analysis conducted on the Lebanese coast (Fanelli et al., 2015). The numbers in the figure identify the functional groups of the model (listed in Table 1).

**Fig. 6.** Mixed Trophic Impact (MTI) analysis of the Israeli Mediterranean continental shelf ecosystem for 1990-1994 (a) and 2008-2012 (b) time periods. Negative (red) and positive (blue) impacts are represented.

**Fig. 7.** Functional groups plotted against keystone index and trophic level for 1990-1994 (a) and 2008-2012 (b) time periods. The numbers identify the functional groups of the model (listed in Table 1). The size of each circle is proportional to the biomass of the functional group.

**Fig. 8.** Contribution (%) of alien species to the total biomass (a), to the catch of different groups (b) and to the total catch of the various fleets (c). Total biomass includes all the groups with sufficient information to split between native and alien species (fish, cephalopods and crustaceans (shrimps and crabs)). Planktonic groups, suprabenthos, polychaetes and benthic invertebrates are excluded for the analysis. CRUS = Crustaceans (shrimps and crabs); DEMF = Demersal fishes; PELF = Pelagic fishes; PURSE = Purse seine; ARTIS = Artisanal; RECRE = Recreational.

**Fig. 9.** Predation (t·km$^{-2}$·year$^{-1}$) by alien species on their prey (a) and consumption (t·km$^{-2}$·year$^{-1}$) of alien species by their predators (b) for the two time periods (1990-1994 and 2008-2012). AH = Alien herbivores; AS = Alien shrimps; AC = Alien crabs; GF = Goatfishes; EADF = Earlier alien demersal fishes; NADF = New alien demersal fishes; ALIF = Alien lizardfish; AMPF = Alien medium pelagic fishes.
References


Table 1. Initial (in bold) and modified input data of the Israeli Mediterranean continental shelf model for 1990-1994 (1990s) and 2008-2012 (2010s) time periods. B = final biomass \((\text{t} \cdot \text{km}^{-2})\); \(P/B\) = production/biomass \((\text{year}^{-1})\); \(Q/B\) = consumption/biomass \((\text{year}^{-1})\); EE = ecotrophic efficiency; \(P/Q\) = production/consumption ratio; landings and discards \((\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1})\). (*) indicates groups that were considered within pelagic compartment.

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<th>Q/B</th>
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Table 2. Output estimates of the Israeli Mediterranean continental shelf model for 1990-1994 (1990s) and 2008-2012 (2010s) time periods. TL = Trophic Level; F = fishing mortality (year\(^{-1}\)); M2= predation mortality (year\(^{-1}\)); MO = other natural mortality (year\(^{-1}\)); F/Z = exploitation rate (fishing mortality (F) / total mortality (Z)); FD = flow to detritus (t·km\(^{-2}\)·year\(^{-1}\)).

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<th>M2 1990s</th>
<th>MO 2010s</th>
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<td>-</td>
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<td>1.00</td>
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Table 3. Characteristics, statistics and ecological indicators for the Israeli Mediterranean continental shelf ecosystem (ICS).

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<td>2008-2012</td>
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<tr>
<td>Number of alive functional groups</td>
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<td>Total System Throughput (TST)</td>
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<td>631.89 t·km⁻²·year⁻¹</td>
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<td>Total Primary Production/Total Respiration (Pp/R)</td>
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<td>Total Primary Production/Total Biomass (Pp/B)</td>
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<td>Finn's cycling index (of total throughput) (FCI)</td>
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<td>Total Biomass (excluding detritus) (TB)</td>
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<td>8.80 t·km⁻²</td>
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<td>mTLco (excluding TL=1)</td>
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<td>Total Catches (TC)</td>
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<td>0.93 t·km⁻²·year⁻¹</td>
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<td>Total Landings</td>
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<td>Mean Trophic Level of the Catch (mTLc)</td>
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<td>Primary Production Required to sustain the fishery (PPR, considering Pp + detritus)</td>
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<td>11.34 %</td>
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<tr>
<td>Mean Transfer efficiency (TE)</td>
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<td>Ecopath pedigree index</td>
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Fig. 1. The study area encompassing the Israeli EEZ and depth contours.
Fig. 2. Flow diagram of the Israeli Mediterranean continental shelf model representing the 2008-2012 period. The size of each circle is proportional to the biomass of the functional group. The numbers identify the functional groups of the model (listed in Table 1). The thickness of the connecting lines is proportional to the magnitude of their trophic flows.
**Fig. 3.** Lindeman spine representation of the Israeli Mediterranean continental shelf ecosystem for the 1990-1994 (a) and the 2008-2012 (b) time periods. Trophic Level (TL) I is split into primary producers (P) and detritus (D). Flows are represented in t·km$^2$·year$^{-1}$ and biomass in t·km$^2$. 
Fig. 4. Biomass (t·km$^{-2}$), production (t·km$^{-2}$·year$^{-1}$) and consumption (t·km$^{-2}$·year$^{-1}$) by discrete Trophic Levels (TL) and habitat in both time periods. Left hand panels are TL III and right panels are TL IV. Top row is biomass (a and b), middle row is production (c and d) and bottom row is consumption (e and f).
Fig. 5. Correlation between Trophic Level (TL) calculated with the Ecopath model (2008-2012 period) and the $\delta^{15}N$ values calculated from stable isotope analysis conducted on the Lebanese coast (Fanelli et al., 2015). The numbers in the figure identify the functional groups of the model (listed in Table 1).
Fig. 6. Mixed Trophic Impact (MTI) analysis of the Israeli Mediterranean continental shelf ecosystem for 1990-1994 (a) and 2008-2012 (b) time periods. Negative (red) and positive (blue) impacts are represented.
Fig. 7. Functional groups plotted against keystone index and trophic level for 1990-1994 (a) and 2008-2012 (b) time periods. The numbers identify the functional groups of the model (listed in Table 1). The size of each circle is proportional to the biomass of the functional group.
Fig. 8. Contribution (%) of alien species to the total biomass (a), to the catch of different groups (b) and to the total catch of the various fleets (c). Total biomass includes all the groups with sufficient information to split between native and alien species (fish, cephalopods and crustaceans (shrimps and crabs)). Planktonic groups, suprabenthos, polychaetes and benthic invertebrates are excluded for the analysis. CRUS = Crustaceans (shrimps and crabs); DEMF = Demersal fishes; PELF = Pelagic fishes; PURSE = Purse seine; ARTIS = Artisanal; RECRE = Recreational.
Fig. 9. Predation (t·km²·year⁻¹) by alien species on their prey (a) and consumption (t·km²·year⁻¹) of alien species by their predators (b) for the two time periods (1990-1994 and 2008-2012). AH = Alien herbivores; AS = Alien shrimps; AC = Alien crabs; GF = Goatfishes; EADF = Earlier alien demersal fishes; NADF = New alien demersal fishes; ALIF = Alien lizardfish; AMPF = Alien medium pelagic fishes.