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Balancing complexity and feasibility in Mediterranean coastal food-web models: uncertainty and constraints

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ABSTRACT: Mass-balance trophic models (Ecopath and EcoTroph) are valuable tools that can be used to describe ecosystem structure and functioning, identify target species to be monitored, and allow comparisons of ecosystem states under different management options. Nevertheless, the Ecopath modelling approach is constrained by 2 major sources of uncertainty: model complexity and input data quality. We developed an approach for identifying the optimum model structure that considers trade-offs between feasibility, complexity, and uncertainty, using a Mediterranean coastal ecosystem as a case study. We began with an existing well-documented and good-quality food-web model comprising 41 functional groups at Port-Cros National Park, France. Based on this model, we assessed the effects of different aggregation choices, driven by a simplification of sampling effort, on the Ecopath and EcoTroph model outputs. We identified the functional groups in which imprecise biomass input significantly influenced the food-web model, and measured the relative effects on the ecosystem trophic structure and ecosystem maturity and complexity indices. A simplified model comprising 32 functional groups was identified as the best compromise between model complexity and reliability. High trophic level predators, abundant primary producers, and groups with a high biomass and/or diversified diet significantly influenced the model structure. We concluded that the collection of local and accurate biomass data, especially for the most influential functional groups we identified, should be a priority when developing food-web models for similar ecosystems. Our method enables simplified and standardized models, while considering both the feasibility and reliability of the Ecopath and EcoTroph applications for Mediterranean coastal ecosystems.

KEY WORDS: Aggregation · Uncertainty · Complexity · Trophic spectrum · Ecosystem indices · Biomass · Ecopath · EcoTroph · Mediterranean Sea

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INTRODUCTION

With the oceans facing increasing impacts by humans, unravelling the complexity of marine ecosystem functioning and species interactions has gradually become a pressing necessity. Single species approaches are not sufficient to ensure a sustainable exploitation of marine resources (Botsford et al.

1997, Hofmann & Powell 1998). Instead, ecosystem-based approaches enable a deeper understanding of the consequences of human exploitation by considering the whole ecosystem, and assist managers in implementing the sustainable use of natural resources (Coll et al. 2013a).

The development of the ecosystem approach to fisheries has triggered an exponential growth of

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modelling tools worldwide (Plagányi 2007, Espinoza-Tenorio et al. 2012). Originally developed by Polovina (1984), Ecopath with Ecosim (EwE) (Christensen & Pauly 1992, Walters et al. 1997, Christensen & Walters 2004) is the most widely used approach to represent marine food webs. About 400 EwE models with different objectives and representing a wide variety of ecosystems worldwide have been published (Colléter et al. 2013), ranging from exploring food-web interactions to computing ecosystem indicators useful for cross-system comparisons, as well as for assessing the impact of fishing or marine protected areas (MPAs) on the ecosystem (Pauly et al. 2000, Christensen & Walters 2005, Guénette et al. 2014). Ecopath is a mass-balanced and species-based model in which species with similar life cycles and diets are aggregated into functional groups. The descriptive Ecopath model is the key initialization step in the EwE modelling process, from which further dynamic and spatial predictions can be simulated with Ecosim and Ecospace for policy scenario testing (Walters et al. 1997, 1999). EcoTroph, a trophodynamic model recently integrated as a plug-in in the EwE software (Gascuel 2005, Gascuel & Pauly 2009, Gascuel et al. 2009, 2011), is based on the idea that an ecosystem can be represented by the distribution of its biomass across trophic levels (TLs), called the biomass trophic spectrum. The simplified picture of ecosystem functioning provided by EcoTroph has proven to be very useful for exploring theoretical aspects of ecosystems, as well as for analysing the impacts of fishing or protection (Colléter et al. 2012, Gasche & Gascuel 2013).

The use of ecosystem models such as the EwE model is generally constrained by 2 major sources of uncertainty: (1) structural complexity (Abarca-Arenas & Ulanowicz 2002, Fulton et al. 2003, Pinnegar et al. 2005, Johnson et al. 2009), and (2) the amount and quality of the input data (Essington 2007, Link 2010, Fulton 2010, Kearney et al. 2013, Lassalle et al. 2014). Structural complexity in Ecopath models is measured as the number of compartments in the model, the way species are aggregated in these compartments, and the inclusion of stanzas, i.e. groups representing different life history stages for species that have a complex trophic ontogeny. In fact, it is unrealistic to include all interactions at the species level in a food web model. Moreover, adding complexity does not necessarily improve a model's performance, but generally increases uncertainty (Fulton et al. 2003). Species aggregation is thus necessary, but can strongly influence the model outputs. The over-aggregation of certain components of the food web, at either the

upper or lower trophic levels, produces models with very different behaviours (Pinnegar et al. 2005) and has sometimes led to dissimilar and conflicting recommendations for management action (Punt & Butterworth 1995, Yodzis 2001). In addition, Ecopath models require a large amount of input data, the quality of which can vary significantly. An in-depth evaluation of the sensitivity of Ecopath models to imprecise input data showed that the Ecopath modelling process is most sensitive to biomass and production rate parameters, and only occasionally sensitive to consumption rate and diet (Essington 2007). In our analysis, we decided to focus on the biomass input parameter. Biomass is of direct relevance to marine resource management, yet it is not easy to estimate accurately for the totality of the food web components due to the costs and constraints of sampling in the marine environment.

In the Mediterranean Sea, several Ecopath models have been built with various levels of detail, depending on the research questions and data availability (Table 1). For some exploited ecosystems (e.g. Northern Adriatic Sea, South Catalan Sea, Northern Aegean Sea, and Greek Ionian Sea), rather comprehensive models have been developed that include more than 30 functional groups based on the high availability of biomass data from industrial fishing monitoring (experimental trawling) (Table 1). In contrast, few models (e.g. Libralato et al. 2006, Albouy et al. 2010, Valls et al. 2012) representing coastal zones in the Mediterranean Sea have been developed and used to analyse MPAs (Table 1). The scarcity of food-web models for the Mediterranean coastal MPAs is likely due to the high diversity and complexity of their food webs (Sala 2004), and the many challenges in terms of data collection. A protected area is a zone in which fishing and other human impacts are restricted to achieve conservation objectives. Thus, destructive sampling methods such as experimental fishing (i.e. trawl surveys), which could provide extensive data on the studied ecosystem, are generally prohibited or limited. However, less destructive methods also have limitations. Underwater monitoring techniques, such as visual censusing to assess fish and mega-invertebrate biomass or suction pumps to sample macrofauna, are time consuming and require a considerable workload for collecting the samples in the field and analysing them at the laboratory. Thus, field-based estimates of biomass are generally available only for a subset of species of recognized ecological importance in coastal zones and/or of particular management relevance in protected areas. For instance, in the Mediterranean,

Table 1. Origin of biomass input data for 22 models of the Mediterranean. The 4th column lists the number of groups included in the related model (excluding non-living groups, i.e. detritus, bycatch/discard and dissolved organic matter). The next columns express the percentages of functional groups for which biomass data were derived from the method specified in column header. Sampling-based data are derived from either experimental fishing, monitoring or field-based local studies. Estimates from the indirect method include data obtained from empirical models, personal communications, and extrapolation from visual surveys for marine mammals, sea turtles and birds. The list of models was derived from Coll & Libralato (2012) and Collefer et al. (2013). Art.: artisanal; Ind.: industrial

ID	Location	Fishing	Functional groups (n)	Sampling	Experimental fishing/monitoring	Local field studies	Indirect method	Non-local literature/other model	Model estimate	Source
1	Miramare Natural Marine Reserve 2000–2003	None/Art.	23	78.3	65.2	13.0	21.7	0	0	Libralato et al. (2006, 2010)
2	Bonifacio Straits Natural Reserve, Corsica 2000–2001	None/Art.	31	48.4	48.4	0	0	9.7	32.3	Albouy et al. (2010)
3	Port-Cros National Park 1998–2008	None/Art.	40	57.5	0	57.5	15.0	0	27.5	Valls et al. (2012)
4	Bay of Calvi, Corsica 1998	None/Art.	26	61.5	0	61.5	7.7	30.8	0	Pinnegar (2000)
5	Arancy Bay, Sardinia 2006	Ind.	12	25.0	25.0	0	25.0	0	50.0	Diaz Lopez et al. (2008)
6	Santa Pola Bay, Spain 2001–2007	Ind.	39	100	0	100	0	0	0	Bayle-Sempere (2013)
7	Southern Catalan Sea 1994	Ind.	36	86.1	66.7	19.4	2.8	0	11.1	Coll et al. (2006)
8	N Adriatic Sea 1997–2000	Ind.	17	100	0	100	0	0	0	Zucchetto et al. (2003)
9	NC Adriatic Sea 1975–1980	Ind.	37	100	81.1	18.9	0	0	0	Coll et al. (2008)
10	N Adriatic Sea 1990	Ind.	32	84.4	53.1	31.3	6.3	0	9.4	Barousse et al. (2009)
11	N Adriatic Sea 1997–2000	Ind.	17	100	0	100	0	0	0	Pranovi & Link (2009)
12	NE Ionian Sea 1964	Ind.	17	23.5	5.9	17.6	76.5	0	0	Piroddi et al. (2010)
13	N Aegean Sea 2003–2006	Ind.	38	76.3	68.4	7.9	18.4	2.6	2.6	Tsagarakis et al. (2010)
14	Greek Ionian Sea 1998–2006	Ind.	37	70.3	70.3	0	10.8	13.5	5.4	Moutopoulos (2013)
15	Black Sea 1960	Ind.	13	100	0	100	0	0	0	Daskalov (2002)
16	Black Sea 1960	Ind.	6	66.7	0	66.7	0	0	33.3	Gucu (2002)
17	Black Sea 1980, 1990	Ind.	6	50.0	0	50.0	0	0	50.0	Gucu (2002)
18	Etang de Thau Lagoon 1980s	Ind.	10	30.0	0	30.0	0	0	70.0	Palomares et al. (1993)
19	Venice Lagoon – Palude della Rosa 1990s	None/Art.	15	73.3	66.7	6.7	26.7	0	0	Carrer & Opitz (1999)
20	Venice Lagoon 1990s	Ind.	19	26.3	0	26.3	0	73.7	0	Libralato et al. (2002)
21	Venice Lagoon 1998	Ind.	25	72.0	36.0	36.0	20.0	8.0	0	Pranovi et al. (2003)
22	Orbetello Lagoon 1995, 1996	Ind.	11	0	0	0	18.2	0	81.8	Brando et al. (2004)

there is extensive knowledge on the trophic interactions between sea bream, sea urchins, and macroalgae and their role in controlling coastal ecosystem states (Sala et al. 1998, Guidetti 2007). These groups are thus common monitoring targets in Mediterranean MPAs, while we face a lack of data and knowledge for many other functional groups (Sala 2004). Consequently, the application of food-web modelling has remained relatively limited in coastal Mediterranean ecosystems.

The objective of this work was to determine an optimum and standardized model structure to represent a northwestern Mediterranean coastal food web that accounts for the trade-offs between feasibility, complexity, and uncertainty. To do so, we selected the Ecopath model representing the MPA of Port-Cros, a French marine national park in the northwestern Mediterranean Sea (Valls et al. 2012). This model was originally built to synthesize all available data and identify knowledge gaps regarding the described ecosystem. Thus, the study presents detailed information on species aggregation into the 41 defined functional groups (Table 2), which makes it the most detailed model available representing a Mediterranean coastal food web (Table 1). Such a comprehensive synthesis was made possible by the many years of research and monitoring that produced a significant amount of data for this old MPA, created in 1963 (e.g. Khoury 1987, Francour 1990). Hence, the biomass parameters were estimated from local field-based studies for 57.5% of the functional groups, which is a relatively high score compared to similar modelled ecosystems (Table 1). We used the original Port-Cros model as our control state, and we simplified its trophic structure by applying different levels of species aggregation, the choice of which was driven by sampling feasibility con-

Table 2. The 41 functional groups of the Port-Cros control model. Details in Valls et al. (2012). Only the least destructive methods were considered: visual survey (VS), visual census (VC), acoustics (Ac), suction sampler (SS), scraping (SC), plankton nets/bottles (PNB), chlorophyll remote sensing (CRS), corer (Co), and net fishing (NF). The groups in **bold** are those considered for aggregation

Sampling method	Functional group
VS	Seabirds
VC	Amberjack+
VC	Dusky grouper – medium
VC	Dusky grouper – large
VC	Dusky grouper – small
VC, NF	Rays
VC, NF	Large-scaled scorpionfish+
VC, NF	Scorpionfishes+
VC, NF	Striped red mullet+
VC, NF	<i>Pagellus</i>
VC, Ac, NF	Horse mackerels+
VC, NF	<i>Diplodus</i> +
VC, NF	Wrasses
VC, NF	Mullets
VC, C	Cephalopods
VC, SS	Blennies
VC, SS	Pipefishes+
VC, SS	Gobies
SS, SC	Gastropods
SS	Small crustaceans
SS	Amphipods
SS	Brittle stars+
SS, SC	Suspensivores
SS, VC	Crabs
SS, VC	Decapods
SS, Co, SC	Polychaetes
SS, VC, SC	Bivalves
VC	Sea stars
VC	Sea cucumbers
VC	Sea urchins
PNB	Large zooplankton
PNB	Small zooplankton
VC	Gorgonians
VC, NF	Salema – adults
VC	Salema – juveniles
Co, SC	Foraminifera
A, SC	<i>Posidonia</i>
SC	Shallow seaweeds
SC	Deep seaweeds
PNB, CRS	Phytoplankton
Co, SS	Detritus

siderations. We then identified the functional groups for which local and accurate biomass data should be collected as a priority, as they have the most significant influence on the model outputs. Specifically, we focused on 3 main questions: (1) how do sampling-driven aggregation choices alter the model description of ecosystem functioning; (2) to what level of aggregation can the model be simplified without sig-

nificantly altering its accuracy; and (3) what are the functional groups in the simplified model for which imprecise biomass input significantly influences the biomass calculations of other groups, and thus the overall description of the ecosystem functioning.

By addressing these issues, we intended to propose some priority guidelines, in terms of model structure and data collection, that could enable the development of standardized models of complex Mediterranean coastal ecosystems.

METHODS

Two food-web modelling approaches were used in our analysis: the species-based Ecopath model and the TL-based EcoTroph model. Ecopath was used to build several versions based on the control model, with different levels of aggregation and different input biomass values, while EcoTroph was used to compute the trophic spectra for each new model. Sensitivity analyses were performed on selected ecosystem maturity and complexity indices computed by Ecopath, and on the trophic description of the ecosystem provided by EcoTroph.

Ecopath

Ecopath uses a mass-balanced food-web model, assuming that the production of one functional group is equal to the sum of all predation, non-predatory losses, exports, biomass accumulations, and catches, as expressed by the following equation:

$$P/B_i \times B_i = P/B_i \times B_i \times (1 - EE_i) + \sum_j (Q/B)_{ji} \times B_j \times DC_{ji} + Y_i + NM_i + BA_i \quad (1)$$

where B is the biomass, P/B_i is the production rate, Q/B is the consumption rate, DC_{ji} is the diet composition representing the fraction of prey i in the diet of predator j , NM_i is the net migration of prey i , BA_i is the biomass accumulation of prey i , Y_i is the catch of prey i , and EE_i is the ecotrophic efficiency of prey i (the proportion of production that is used in the system, e.g. through predation and harvest). Assuming there is no export and no biomass accumulation, and the catches are known, only 3 of the 4 remaining parameters (B , P/B_i , Q/B , and EE_i) have to be set initially for each group. The parameterization routine solves the equations for each missing parameter iteratively (Christensen et al. 2008).

A comprehensive Ecopath model was built by Valls et al. (2012) for the Port-Cros MPA (Table 2), which

covers a surface area of 13 km² and reaches a maximum depth of 50 m. Biotopes are typical of the north-western Mediterranean, with nearshore rocky reefs, large *Posidonia oceanica* meadows, and a coralligenous habitat, hosting a high biodiversity of commercially important fish and decapod crustaceans; only 5% of the reserve is a no-take area, outside of which fishing is permitted with severe restrictions (Francour et al. 2001). The Ecopath model represents an average situation for the period from 1998 to 2008, defined by the data used in the model. Large amounts of data were available for this old and well-studied MPA, which allowed for the development of a relatively detailed model, including 40 living functional groups (plus one detrital group). More precisely, the model comprises 18 groups of fish, 17 groups of invertebrates, 4 groups of primary producers, and 1 group of seabirds. In addition, the model is well documented in terms of both species aggregation choices and species-level information for each functional group. Moreover, all fish biomass data are of good quality as they were derived from visual censusing and scientific trawling in the area. Local field-based biomass data were also available for some invertebrate and primary producer groups. Details on the species composition of each functional group in the control Port-Cros model, as well as the input parameters for each group, can be found in Valls et al. (2012). Finally, the model respected Link's recommendations of data quality (Link 2010), and its representation of the Port-Cros ecosystem was in accordance with the current available knowledge (Valls et al. 2012).

EcoTroph

The trophic level-based EcoTroph model assumes that biomass has a continuous distribution in an ecosystem as a function of continuous TLs. The biomass is represented as entering the system at TL = 1, generated by the photosynthetic activity of primary producers or recycled from the detritus by the microbial loop. Then, at TLs >2, the biomass is distributed along a continuum of TL values and all fractional TLs are filled due to the diet variability of the various consumers. The resulting biomass distribution constitutes the biomass trophic spectrum (Gascuel et al. 2005). The functioning of the ecosystem is then modelled as a continuous flow of biomass, surging up the food web from lower to higher TLs, through predation and ontogenic processes.

Based on the usual equations of fluid dynamics, the flow of the biomass present in the ecosystem at TL τ under steady-state conditions is expressed as:

$$\varphi(\tau) = D(\tau) \times K(\tau) \quad (2)$$

where $\varphi(\tau)$ refers to the amount of biomass that moves up the food web through TL τ (metric t per year), $D(\tau)$ is the density of biomass at TL τ (metric t per trophic level), and $K(\tau)$ is the speed of flow, which quantifies the velocity of biomass transfers in the food web (number of TLs crossed per year).

The continuous distribution of the biomass across a TL is calculated using a discrete approximation based on small trophic classes. EcoTroph conventionally considers trophic classes of width $\Delta\tau$ equal to 0.1 TL, from TL 2 (corresponding to first-order consumers) to TL 5 (a value considered sufficient to cover all top predators likely to occur in marine ecosystems). Thus, the mean biomass B_τ (in metric t), which is present in the $[\tau, \tau + \Delta\tau]$ trophic class under steady-state conditions, can be estimated as $\int D(\tau) \times d\tau$ or $D(\tau) \times \Delta\tau$ for a small interval $\Delta\tau$. Therefore,

$$B_\tau = \varphi_\tau \times \Delta\tau / K_\tau \quad (3)$$

where φ_τ and K_τ are the mean biomass flow and mean speed of flow within the $[\tau, \tau + \Delta\tau]$ trophic class, respectively; see the supplementary material in Valls et al. (2012) for further explanation.

In this study, we used the ET-Transpose routine described in Gascuel et al. (2009) to translate the outputs of the original Ecopath model into an EcoTroph model and to build the biomass trophic spectrum. The biomass of each functional Ecopath group was distributed over a range of trophic classes around the mean TL of the group (estimated by Ecopath), assuming a log-normal distribution. The trophic spectrum is the curve obtained by summing the biomass parameter over all functional groups and provides a synthetic view of the trophic structure of the ecosystem.

We then used the ET-Diagnosis routine to conduct sensitivity testing. We simulated how the baseline ecosystem would be impacted by increasing or decreasing the fishing effort. Fishing effort can be modified per fleet by applying various effort multipliers, and the structure of the trophic spectrum will vary under different efforts (Gascuel et al. 2011, Gasche & Gascuel 2013).

Aggregated models and comparisons

The original version of the Ecopath model for the Port-Cros National Park's MPA, described by Valls et

al. (2012), was selected as the control model in our simplification procedure, and 6 models were derived from this, using successive aggregation steps. Purely taxonomical aggregations were avoided. Aggregation choices were driven by sampling efficiency considerations; for each functional group, the most adequate and least destructive sampling methods were assigned, and groups that shared at least one common sampling method were considered for aggregation. Thus, aggregation choices were also consistent with the habitat use among groups, so that species in the same group occupied the same habitat. Aggregation choices were also constrained by diet composition overlap and similarities in production and consumption (P/B and Q/B rates), which should differ by less than 3-fold between groups (Fulton et al. 2003). Small cryptobenthic fish (blennies, pipefishes, and gobies) were grouped based on the difficulty in sampling them and because they share similar life-history parameters. The other fish functional groups were not further aggregated relative to the original model, in which they were grouped according to their TL, maximum length, and feeding type (Valls et al. 2012).

Starting from the first aggregated model (the one with the broadest aggregation of the invertebrate groups), a biomass trophic spectrum was computed, and the trophic spectra ratios between this first model and the control were compared. The TLs corresponding to the widest changes in the trophic spectrum were identified, and the corresponding functional groups were isolated in the subsequent model, in which different levels of aggregation were tested. For each new model, static ecosystem indices were computed and the percentage difference between each aggregated model and the control were compared. This procedure was repeated stepwise until the aggregation with the fewest differences from the control in the trophic spectra and ecosystem indices was identified. P/B and Q/B ratios were computed for the newly aggregated groups; they were weighted with the biomass and summed over all of the groups to be aggregated. Similarly, the new diet compositions were obtained by weighting the food intake of each group with the consumption of the group, and then summing the food intakes over all of the groups to be aggregated.

To evaluate the successive species aggregations, we compared the ecosystem indices that are most widely accepted as indicators of ecosystem maturity and complexity in the literature: Finn's cycling index (FCI), system omnivory index (SOI), relative ascendancy (%A), and TL of the community (TL_{co}) (Chris-

tensen 1995, Libralato et al. 2010). Because the total amount of matter flowing in each model was maintained constant and equal to the original, the maturity indices related to the flows and biomasses were not considered. FCI measures the fraction of the ecosystem's throughput that is recycled. The degree of energy and nutrient recycling in an ecosystem is assumed to increase as ecosystems mature and develop routes for nutrient conservation (Odum 1969). SOI is defined as the average omnivory index of all consumers, weighted by the logarithm of the food intakes (Christensen & Pauly 1992). It expresses the variance in the TLs of the consumers' prey groups (Pauly et al. 1993) and is considered a measure of food-web complexity. Ascendancy is a measure of the average mutual information in a system, scaled by system throughput, and is derived from information theory (Ulanowicz & Norden 1990). If one knows the location of a unit of energy, the uncertainty about where it will flow to next is reduced by an amount known as the 'average mutual information'. The amount of the average mutual information multiplied by the total system throughput (TST) gives the ascendancy (A). There is an upper limit for the development of the ascendancy, which is called the 'development capacity'. Here, we are considering %A, defined as the ratio between A and the development capacity that was demonstrated to be clearly correlated with maturity *sensu* Odum (Christensen 1994). The average TL_{co} is estimated as the biomass-weighted average TL for all functional groups of the web, excluding those at $TL = 1$. Libralato et al. (2010) showed that TL_{co} was consistently lower in a fished food web compared to an adjacent unexploited one. Given the similarity of fishing patterns in coastal Mediterranean waters, we retained TL_{co} as a good indicator of the fishing effects.

The model that showed the smallest differences from the control in the trophic spectra and ecosystem indices was considered to offer the best species aggregation scheme, and was therefore selected for further analysis. The ET-Diagnosis function was applied to test whether the selected model would behave differently from the control in terms of assessing the fishing impact on the ecosystem. For both the control and the selected model, we built 2 different fishing scenarios by applying 2 effort multipliers (mF) to the current fishing mortality of each trophic class. Specifically, we applied an $mF = 0$ to simulate a closure of the fishery and an $mF = 12$ to simulate an increase in fishing effort. The latter value of mF was shown to be of the same order of magnitude as those observed in surrounding and similar

unprotected areas (Valls et al. 2012). We then compared the simulation outputs to the unexploited state and identified the differences between the patterns of the 2 models.

Sensitivity to error in input biomass and identification of the most influential species

The model selected after aggregation was set as the new reference (ref. model) to test the effects of variation in each group's input biomass on the biomass estimates of the other groups, and to evaluate the impact of these errors on the overall model outputs; 31 new models were built by increasing the biomass of each group by 10% and obtaining the biomass of the other groups (except primary producers) from the Ecopath equation solutions (with ecotrophic efficiencies fixed). During this process, the biomass of the primary producers was not obtained from the Ecopath equation solutions, but instead was kept at its original value, because it was input data in the original model and therefore avoided a potential modelling artefact: i.e. strong increases in primary producer biomass to sustain increased consumer abundance due to the Ecopath routine estimation of the primary production required to sustain consumption. Thus, we were conservative by evaluating the minimum impact that imprecise input biomass for consumers would have on the model outputs. Subsequently, the biomass of each primary producer was also varied by 10%, and the biomasses of all other groups were obtained from the Ecopath equation solutions to test the influence of an error in the primary producer input biomass.

A variation of 10% was assumed to be small enough to keep the models mass-balanced and large enough to create differences between the models. To test the model sensitivity to the biomass increments, the biomass trophic spectra and maturity indices were compared between each new model and the ref. model. The trophic spectra of the ratios between the new model and the ref. model were plotted, and 3 indices were derived: the number of trophic levels affected by a variation in the biomass of >1% (i.e. the width of the trophic spectra, *Width_TS*); the maximum level of biomass increase (i.e. the peak of the trophic spectra, *Peak_TS*), and the total biomass increase (i.e. the area of the trophic spectra, *B_TS*); the latter was expressed as the percentage difference from the ref. model biomass and was increased for several functional groups simultaneously to test for any amplifying effect on the trophic spectra. The percentage

differences from the ref. model were compared for %A, SOI, FCI, TL_{co} , and 2 additional flow indices: the ratio of total primary production to total respiration (TPP/R) and the ratio of total biomass to total system throughput (B/TST). The latter 2 flow-related maturity indices were included at this step of the analysis because variations in the functional groups' biomass inputs induced variations in the amount of matter flowing in the model.

A principal component analysis (PCA) was conducted to visualize the impact of each functional group on the ecosystem attributes. The previously mentioned indices of maturity, complexity, and trophic structure were the explicative variables of the PCA, while the different models obtained by 10% increases in the biomass of each functional group were the samples. All variables were standardized to a zero mean and unit variance to compensate for differences in the value ranges. TL and biomass were included in the PCA as supplementary continuous variables and trophic class was included as a supplementary categorical variable, so that they would not be considered in the computation of the principal components. The groups were then ranked according to their contribution to each of the first 3 principal components, and their mean ranking was computed. Thus, summarized information was obtained for the functional groups with the most impact on the variables overall. The functional groups were then plotted in decreasing order of their mean rank (a rank of 1 was attributed to the group having the greatest impact). The groups with the highest rankings were identified and selected as those having the most impact on the model's output, and thus requiring local and accurate biomass input data.

RESULTS

Model aggregations and comparisons

Model A included 33 living groups (Table 3) and was characterized by the largest aggregation of invertebrate groups that can be sampled with suction devices (gastropods, small crustaceans, amphipods, brittle stars, suspensivores, crabs, decapods, and polychaetes comprised a new Epifauna+ group). Sea stars and sea cucumbers were not included, because their constant production and consumption rates differ significantly from the other invertebrates, and estimates of their biomass are more commonly obtained from a visual census. Model B (34 living groups) differed from Model A by the separation of a

Table 3. Aggregation schemes. The groups that were not modified from the control model are not listed. Number of functional groups (excluding detritus) given at bottom. Grey boxes indicate functional groups that have been mapped to an aggregate group listed higher in the table. Co: corer; SC: scraping; SS: suction sampler; VC: visual census

Sampling	Control	Model A	Model B	Model C	Model D	Model E	Model F	
VC, SS	Blennies	Blennies	Blennies	Blennies+ (blennies, pipefishes)	Blennies+ (blennies, pipefishes)	Blennies+ (blennies, pipefishes)	Gobies+ (blennies, pipefishes, gobies)	
VC, SS	Pipefishes+	Pipefishes+	Pipefishes+					
VC, SS	Gobies	Gobies	Gobies	Gobies	Gobies	Gobies		
SS, SC	Gastropods	Epifauna (gastropods, small crustaceans, amphipods, brittle stars, suspensivore, crabs, decapods, polychaetes)	Epifauna (gastropods, small crustaceans, amphipods, brittle stars, suspensivore, polychaetes)	Epifauna (gastropods, small crustaceans, amphipods, brittle stars, polychaetes)	Epifauna (gastropods, small crustaceans, amphipods, brittle stars)	Epifauna (gastropods, small crustaceans, amphipods, brittle stars, suspensivore, bivalves)	Epifauna (gastropods, small crustaceans, amphipods, brittle stars)	
SS	Small crustaceans							
SS	Amphipods							
SS	Brittle stars+							
SS, SC	Suspensivores		Suspensivores+ (bivalves, suspensivores)	Suspensivores+ (bivalves, suspensivores)				
SS, VC	Crabs		Decapods+ (crabs, decapods)	Decapods+ (crabs, decapods)	Decapods+ (crabs, decapods)	Decapods+ (crabs, decapods)		Decapods+ (crabs, decapods)
SS, VC	Decapods							
SS, Co, SC	Polychaetes				Polychaetes	Polychaetes		Polychaetes
SS, VC, SC	Bivalves	Bivalves	Bivalves					
VC	Sea stars	Sea stars	Sea stars	Echinoderms+ (sea stars, sea cucumbers)	Echinoderms+ (sea stars, sea cucumbers)	Echinoderm+ (sea stars, sea cucumbers)	Echinoderms+ (sea stars, sea cucumbers)	
VC	Sea cucumbers	Sea cucumbers	Sea cucumbers					
SC	Shallow seaweeds	Shallow seaweeds	Shallow seaweeds	Seaweeds+ (shallow seaweeds, deep seaweeds)	Seaweeds+ (shallow seaweeds, deep seaweeds)	Seaweeds+ (shallow seaweeds, deep seaweeds)	Seaweeds+ (shallow seaweeds, deep seaweeds)	
SC	Deep seaweeds	Deep seaweeds	Deep seaweeds					
No. of groups	40	33	34	31	32	31	31	

pooled crab and decapod group (Decapods+) from the Epifauna+ group. In Model C, suspensivores were excluded from the Epifauna+ group as well, and aggregated with bivalves (Suspensivores+). Moreover, sea stars were grouped with sea cucumbers (Echinoderms+), blennies with pipefishes (Blennies+), and shallow seaweeds with deep seaweeds (Seaweeds+), resulting in an overall aggregation into 31 living groups. Model D (32 living groups) was equal to Model C, except for the polychaetes, which were excluded from the Epifauna+ group and defined as a separate group. In Model E (31 living groups), the suspensivores and bivalves were added to the Epifauna+ group, while the polychaetes were kept separated. Finally, Model F (31 living groups) was characterized by an Epifauna+ group that included gastropods, small crustaceans, amphipods,

and brittle stars. The previously defined groups of Decapods+, Suspensivores+, Echinoderms+, and Seaweeds+ remained as separate groups, while a Gobies+ group was created to aggregate gobies, blennies, and pipefishes.

For every aggregated model, FCI and %A were higher than in the control model, while the SOI was systematically lower. The differences in TL_{CO} were either negative or null. The aggregation that caused the largest variations in ecosystem indices (Fig. 1) and trophic spectra (Fig. 2) was that of crabs and decapods with Epifauna+ (Model A), causing a 30% increase in FCI (Fig. 1) and negative biomass differences for $TL > 3.5$ (Fig. 2a). Suspensivores+ and polychaetes also significantly affected ecosystem indices and trophic spectra when aggregated with the Epifauna+ group; Mod-

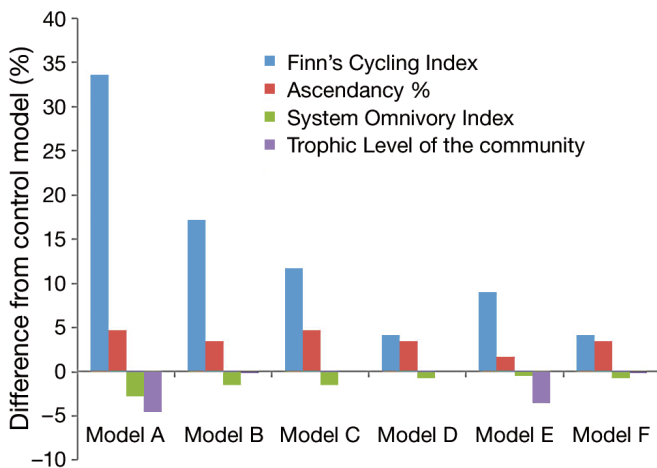


Fig. 1. Percentage differences in the system indices between the aggregated models and the control model

els D and F showed the least differences from the control (Figs. 1 & 2b). The aggregations of Echinoderms, Seaweeds+ and Gobies+ caused no major modifications in model properties. Model F, with 31 living functional groups, had the most simplified species aggregation scheme, i.e. the smallest variations in the ecosystem indices and trophic structure relative to the control for the highest level of species aggregation possible.

The simulation test confirmed that the behaviour of Model F was similar to that of the control, when both closure ($mF = 0$) and increased fishing effort ($mF = 12$) were simulated. The exploitation effect was significant only at $TL > 3.5$, and in neither the original nor the aggregated model did the exploitation cause major biomass variations at the lower TLs (Fig. 3). Model F was thus selected for successive analysis.

Sensitivity to error in the input biomass

A sensitivity analysis was applied to Model F. The analyses of the trophic spectra (Fig. 4) and the differences in the ecosystem indices due to biomass variations (see Appendix 1) showed that the high TL predator groups, Amberjack+ and Dusky grouper – large, had the largest impacts on the biomass of the other groups, and thus most influenced the trophic spectra and ecosystem indices. Increments of 10% in the biomass of these 2 large fish

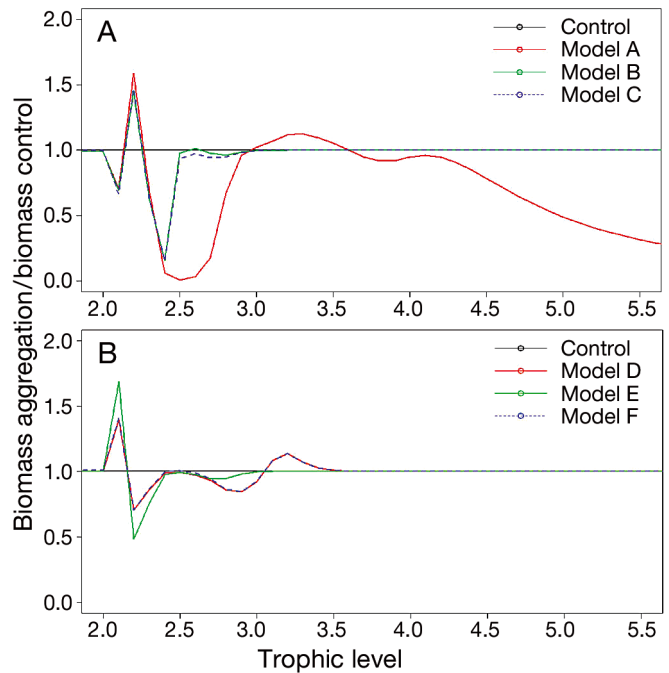


Fig. 2. Trophic spectra of the ratios of the biomass between the control model and (A) aggregated Models A, B, and C or (B) aggregated Models D, E, and F, in relative values

groups affected the biomass of all other trophic groups by more than 1%, with most TLs affected by more than 5% (Fig. 4A). The trophic spectra sensitivity to Dusky grouper – large increased when $TL \geq 4$, since this was the only group occupying the highest TLs. The trophic spectra for both Amberjack+ and Dusky grouper – large reached peaks with an approximately 9% increase in biomass, and overall biomass increased (B_TS) by 0.25 and 0.28%, respectively, relative to Model F. With regard to the other fish groups, the highest impact in terms of number of TLs affected and shifts in biomass was caused by

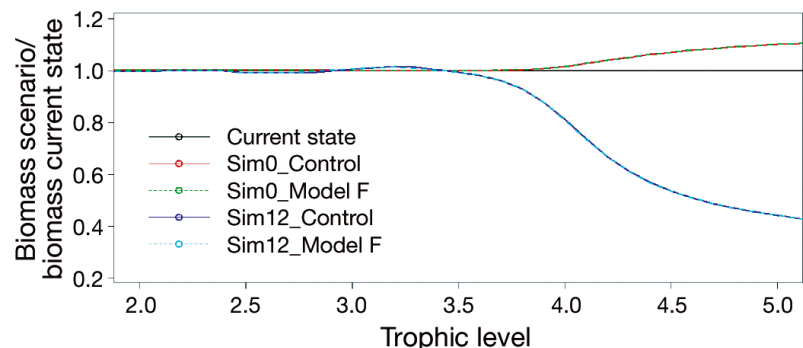


Fig. 3. Simulation scenarios for Model F and the control model. Relative biomass values were obtained from the trophic spectra ratios, with effort multipliers $mF = 12$ (Sim12) and $mF = 0$ (Sim0) applied to both models

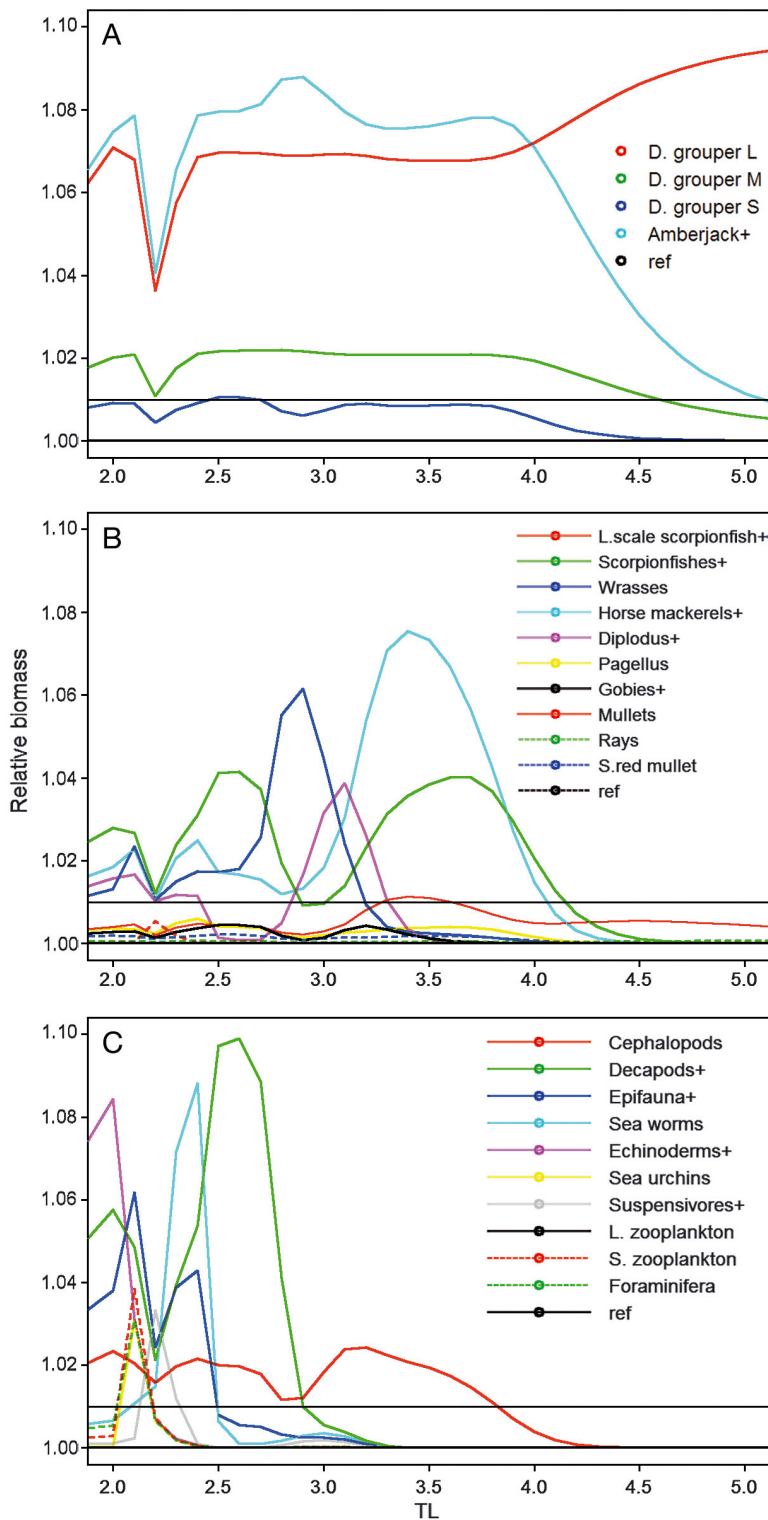


Fig. 4. Biomass ratios between the trophic spectra of each model obtained after an increase of 10% to the biomass of one functional group and the trophic spectra of the reference model (represented by the solid line at relative biomass = 1). The dotted line corresponds to the threshold value of a 1% variation in biomass. (A) Higher trophic level predators; (B) other fish groups; (C) invertebrates

Horse mackerels+ (Width_TS = 21, Peak_TS = 7.5%, B_TS = 0.09%), followed by Scorpionfishes+ and Wrasses (Fig. 4B).

Among the invertebrates (Fig. 4C), Cephalopods+ affected the largest number of trophic levels (Width_TS = 19), followed by Decapods (Width_TS = 9). Decapods was the group with the most impact on the Peak_TS index; under their influence, the trophic spectrum reached the maximum peak resulting from a 10% increment in the biomass. An increase of 10% in the biomass of Sea worms and Echinoderms+ led to high biomass peaks in the trophic spectra (Peak_TS = 8.8, Peak_TS = 8.4%, respectively), but their impacts were limited to a very narrow range of TLs corresponding to their own range (Width_TS = 4, Width_TS = 2, respectively). A simultaneous biomass increase of several functional groups resulted in a simple additive effect on the trophic spectra and thus was not considered further.

Similar to the trophic spectra analysis, a 10% increment in the biomass of the Dusky grouper – large and Amberjack+ groups caused the largest variations in absolute terms in all ecosystem indices, especially impacting FCI (7.2 and 8.1%, respectively), TPP/R (6.4 and 7.2%, respectively), and %A (2.1% for both). As for the Epifauna+, Decapods+, Cephalopods, and Horse mackerels+ groups, the biomass increments caused large variations in FCI (max. value = 7.0% for Epifauna+) and SOI (max. value = 1.6% for Horse mackerels+). Increments in the biomass of Foraminifera and Small zooplankton had a strong influence on FCI (6.3 and 6.6%, respectively). *Posidonia oceanica* had a high overall impact and principally caused large variations in the flow indices TPP/R (4.7%) and B/TST (6.1%), and in %A (2.1%).

Principal component analysis

A PCA on all indices was performed (Fig. 5). The first PC accounted for almost 50% of the variability of the data, and the second PC accounted for 25% (Fig. 5A). The first PC summarized the variability explained by 2 sets of variables: recycling

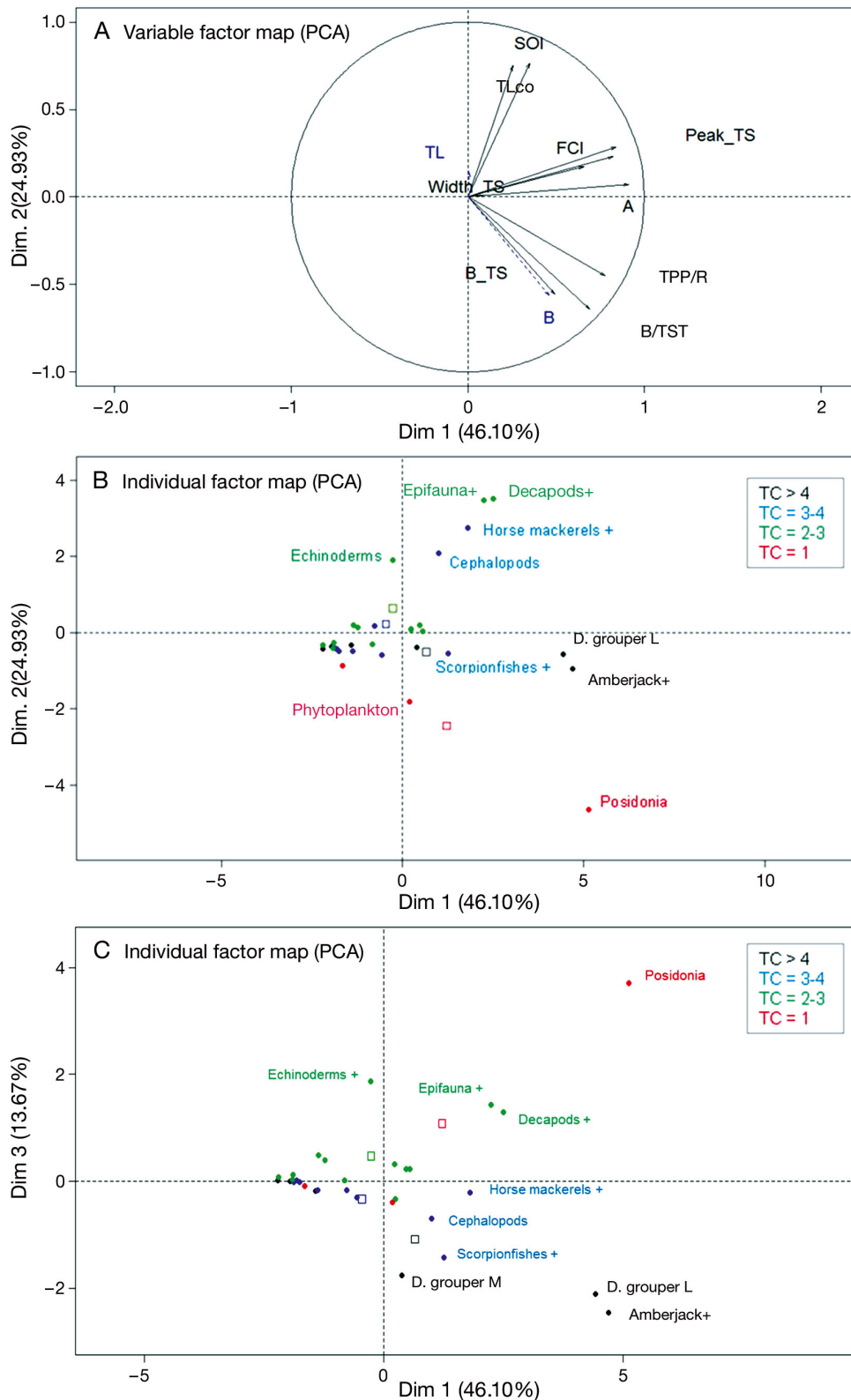


Fig. 5. Principal component analysis (PCA) plots. (A) Variables and (B) individual factors for the first 2 principal components. (C) Individual factors for principal components 1 and 3. In the variables plot (A), B and TL are the supplementary variables (blue). In the individual factor plots (B,C), only the non-overlapping points were labelled to improve visualization. B: biomass; B_TS: biomass of the trophic spectra; B/TST: biomass/total system throughput; FCI: Finn's cycling index; Peak_TS: peak of the trophic spectra; SOI: system omnivory index; TC: trophic class; TL_{co}: mean trophic level of the community; TL: trophic level; TPP/R: total primary production/total respiration; TS: trophic spectra; Width_TS: width of the trophic spectra

(FCI), %A, and trophic spectra structure (Width_TS and Peak_TS) on the one hand, and the energy flux indices (TPP/R and B/TST) and trophic spectra-derived biomass index (B_TS) on the other. Within each set, the variables appeared to be highly correlated to one another. The influence of the functional groups on the variables (i.e. their effect on the indices) was related to their biomass. Several species which cover the whole range of trophic levels, but with low biomass, influenced the variables less than average (Fig. 5b). In contrast, the top predators Dusky grouper – large and Amberjack+ (TL >4), having higher biomasses, strongly affected many ecosystem indices, particularly the trophic spectra indices (Width_TS, Peak_TS), ecosystem maturity (FCI, %A), and flow indices (TPP/R, B/TST) summarized by PC1. Groups feeding on a wide range of trophic levels and with consistent biomass (Decapods, Epifauna+, Horse mackerels+ and Cephalopods) affected the ecosystem complexity indices (SOI and TL_{co}), while the Posidonia group affected the flow and biomass related indices (TPP/R, B/TST, and B_TS).

When the third PC was visualized (Fig. 5C), the functional groups were ordered by TL. Following the high TL predator groups, the Scorpionfishes+, Cephalopods, and Horse mackerels+ were arranged in decreasing order of TL and contributed equally to PC1. On the positive side of PC3, the TL of the groups decreased, and biomass became the dominant supplementary variable. Thus, Decapods+ and Epifauna+ contributed equally to both PC1 and PC3 in terms of the ecosystem complexity indices (SOI

and TL_{co}), while *Posidonia*, having the highest biomass, showed the highest contribution to PC1 and PC3 in terms of overall biomass increase (B_TS), and to PC1 for %A.

The first 3 PCs summarized approximately 80% of the variability explained by the indices, so the functional groups were ranked according to their contributions to these axes. By plotting the species in decreasing order of their mean rank (rank of 1 for the species having the highest impact) (Fig. 6), we highlighted 2 major gaps among the ranking scores. The first and most evident gap separated *Posidonia*, Amberjack+, Epifauna+, Decapods+ and Dusky grouper – large, which had the highest ranking on all 3 PCs, from Cephalopods. The second gap separated the Cephalopods and Horse mackerels+ from the other groups. The rankings gradually decreased after these groups, so no further groups were selected.

DISCUSSION

We have addressed 2 issues in this paper related to model uncertainty: functional group aggregation and sensitivity to biomass data input. Our intent was to improve the feasibility of Ecopath applications for complex Mediterranean coastal ecosystems by accounting for the constraints that field sampling and monitoring impose on the collection of reliable data. We evaluated how these constraints might lead to an altered description of ecosystem functioning and proposed a model structure that allows for a compromise between reliability and feasibility.

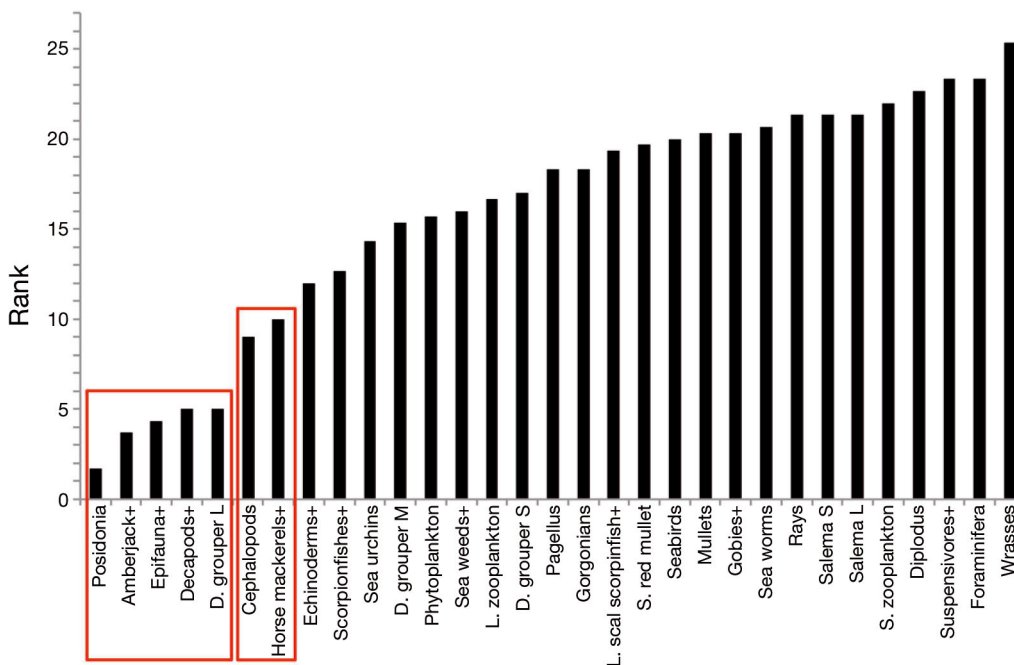


Fig. 6. Ranking of the functional groups based on their contributions to the first three principal components. Red boxes separate the first and second groups with the highest rankings

Aggregating trophic groups

Initially, we dealt with the effects of aggregation on food-web properties. The issue of the ecosystem indices' dependence upon the model structure has been largely discussed in the literature. Many studies have concluded that food-web properties are affected not only by the reduction in the number of compartments, but also and primarily by the way the functional groups are aggregated in such compartments (Christensen 1995, Abarca-Arenas & Ulanowicz 2002, Fulton et al. 2003, Pinnegar et al. 2005). Until further knowledge is obtained, models built in a standardized way, at least for similar ecosystems, could increase the reliability of model comparisons over time and/or space (Dame & Christian 2006, Fulton 2010).

Focusing on a northwestern Mediterranean coastal ecosystem, we identified which species aggregation choices, defined on the basis of sampling efficiency considerations, caused major modifications in the model description of the ecosystem state and should therefore be avoided. We mainly focused on lower TL groups that are often less studied and overly aggregated in ecosystem models.

From our analysis, it appeared that some indices (SOI and %A) vary significantly less than others (FCI) among the different model configurations (Fig. 1). These configurations primarily differed for the invertebrate functional groups. Pinnegar et al. (2005) tested aggregation schemes emphasizing different parts of the food web (fish, marine mammals, and invertebrates) and reported greater variation for the same 2 indices compared to our results. Nevertheless, in a recent meta-analysis on 105 food-web models from different areas of the world, %A proved to be robust to the model construction in terms of the number of functional groups (Heymans et al. 2014). FCI showed the strongest variations among all our model configurations.

Decapods, crabs, suspensivores, and polychaetes were responsible for the main differences between the ecosystem structures described by the models. These groups show different degrees of connection within the food web in comparison to the other macrofaunal invertebrates (amphipods, small crustaceans, gastropods, and brittle stars) and have different predators (low predator overlap index). Consequently, aggregating them together increased the connections between the primary producers and the upper levels of the food web, and it introduced cannibalism within the group. By altering the feedback cycles in the model, it is likely that this pooling affects the overall stability of the system (Dambacher

et al. 2003). This aggregation thus led to an erroneous and increased quantification of FCI, which might affect interpretation of the ecosystem's resilience and maturity. This result agrees with the analysis in Pinnegar et al. (2005), in which the fish-centred model, including a compartment equivalent to our epifaunal group, showed the greatest increase in FCI. In addition, SOI largely decreased, because the variety of the TLs upon which the upper consumers feed is reduced. Species interactions in the food web might thus appear less complex than they are in reality. More particularly, given the important biomass of decapods and their connections with higher TLs, their inclusion in the Epifauna group significantly altered the biomass trophic spectrum, impacting the distribution of biomass up to higher TLs and causing a general decrease in the mean TL of the community. Trophic spectra are now recognized as a useful tool with which to analyse the impacts of fisheries and/or protection on the whole trophic network (Gascuel et al. 2009, Libralato et al. 2010, Coll  ter et al. 2012, Lassalle et al. 2012), but if they are initially altered by a biased model structure, inaccurate conclusions could be derived from their observation. The inclusion of polychaetes and suspensivores in the Epifauna group should be avoided, although it would simplify sampling. This confirms the existing knowledge that groups accessing primarily different food sources within the system should not be over-aggregated (Fulton et al. 2003, Pinnegar et al. 2005).

The groupings that did not significantly affect the model behaviour were the amphipods with small crustaceans, gastropods, and brittle stars; decapods with crabs; suspensivores with bivalves; sea stars with sea cucumbers; and grouping all small cryptobenthic fishes together (i.e. gobies, blennies, and pipefishes). Some of these results may be explained by the similar functional role of the groups (amphipods, small crustaceans, and gastropods), while others are possibly due to the very low biomass of one of the 2 groups in the control model (i.e. bivalves and sea stars). It would be interesting to compare such results with other aggregation approaches used in ecosystem modelling. The regular coloration algorithms applied in Johnson et al. (2001), for example, formalize the aggregation procedure by collapsing groups that have ties to equivalent prey and predators, with equivalent groups being those that pertain to the same TL.

The simplified trophic structure implied a substantial reduction in complexity and a simplification of the data collection process due to greater aggregation than in the control model (31 living groups instead of 40). Nevertheless, even after applying a

simulated increase in the fishing effort, the level of aggregation did not noticeably affect the distribution of biomass across the TLs. The simplified model is still rather detailed in comparison to other models of the Mediterranean, such as the Miramare Natural Marine Reserve model (Libralato et al. 2006), which has 23 functional groups, or the Bonifacio Strait Natural Reserve model (Albouy et al. 2010), which has 31 groups.

Prioritizing groups for biomass estimates

Next, we assessed the model uncertainty related to the quality of the biomass input data. Based on Essington's conclusions on biomass input data being the parameter that most affects the model output estimations, we wanted to identify which groups our model was most sensitive to after a variation in their biomass. The most influential species we identified were all characterized by a high biomass, a high TL and a diversified diet, or a combination of the two. Abundant high TL predators, such as the large dusky grouper *Epinephelus marginatus* and species in the Amberjack group (including *Seriola dumerili*, *Sphyrna viridensis*, *Dicentrarchus labrax*, *Conger conger*, and *Muraena helena*; see Appendix 1), comprised the groups with the most impact on the trophic spectra and ecosystem maturity indices (%A, FCI, TPP/R, and TB/TST). Thus, inaccurate input biomass data for these groups would alter the biomass estimates of all other groups. As demonstrated by the biomass trophic spectra, higher prey biomass would be required to sustain a higher biomass for these predators, consequently affecting the trophic structure of the ecosystem. Our results were similar to Christensen & Pauly's (1998) simulations, where the top predators' biomass was increased to assess the carrying capacity of an ecosystem. A 10-fold increase in the top predators' biomass, given a fixed primary production, increased FCI and TPP/R approached 1, meaning less sedimentation, better utilization of the detritus, and nutrient recycling within the food web, which corresponds to an image of a more mature system *sensu* Odum (1969). Our results on the influence of high TL predators on food-web properties are in accordance with the general knowledge that these predators are good indicators of ecosystem health and maturity (Ray et al. 2005, Prato et al. 2013), and their recovery in a protected zone is the first sign of improved ecosystem health (Sandin & Sala 2012). As we demonstrated, models built with inaccurate biomass data for high TL predators and fixed primary

producer values would depict a significantly altered food web.

Epifauna, Decapods+, Horse mackerels+, and Cephalopods were the groups that most influenced the ecosystem complexity by modifying the SOI and the mean TL of the community. Epifauna and decapods are abundant in the ecosystem and are the main prey items of many other groups (high ecotrophic efficiencies), and therefore act as connectors between the primary producers and the upper TLs. The planktivorous fish group (including horse mackerels, *Chromis chromis*, *Spicara* spp., *Boops boops*, and *Oblada melanura*) and cephalopods significantly affected the biomass trophic spectra, causing biased biomass estimates for a wide range of functional groups. Indeed, planktivorous fish represent up to 32% of fish biomass and are responsible for up to 40% of all fish throughput in some Mediterranean ecosystems (Pinnegar & Polunin 2004). These fishes are important prey for coastal predators, as well as important detritus producers (Pinnegar 2000, Pinnegar & Polunin 2004). They may also be involved in wasp-waist control mechanisms, similar to those in the South Catalan Sea (Coll et al. 2006). Cephalopods have high consumption rates (the highest among all upper TLs), a widely diversified diet, and are a preferred prey for many predatory fish. Thus, this group is very likely playing a significant role in the energy and material flow of marine ecosystems (Coll et al. 2013b). However, it is often difficult to assess their abundance and role in marine ecosystems, primarily due to logistical problems (Piatkowski et al. 2001).

The strong influence of *Posidonia oceanica* on the maturity indices related to flow measures was probably due to its high biomass, which was an order of magnitude greater than any other functional group. Moreover, given the low consumption rate of *P. oceanica* by other functional groups (low ecotrophic efficiency), an increase in its biomass might cause an increased flow to detritus, thereby affecting FCI.

Our study was based on the single example of the Port-Cros ecosystem, for which a large amount of information was available. Nonetheless, useful insights can be derived from an in-depth analysis of a well-known complex food web and applied to comparable ecosystems (i.e. northwestern Mediterranean) (Sala 2004).

The identification of high TL predators and *P. oceanica* as the most influential groups in our study is in agreement with Mediterranean monitoring programs (Moreno et al. 2001, Levin & Grimes 2002, Coll et al. 2008, Montefalcone 2009, Di Franco et al. 2009, Prato et al. 2013). Nevertheless, accurate methods to

assess their biomass are still a challenging issue, especially for high TL predators. In addition to these groups, our results highlighted the important role in the food web of groups that are usually poorly detailed, such as epifauna, decapods, planktivorous fish, and cephalopods. Although the importance of these groups has been demonstrated in Mediterranean coastal ecosystems (Sala 1997, Pinnegar 2000, Piatkowski et al. 2001, Goñi et al. 2006), they are rarely included in monitoring programs for many reasons, e.g. the challenges in obtaining good quality data, the absence of commercial value or of a protection status, and the lack of public awareness for non-charismatic species.

CONCLUSIONS

Food-web modelling enables setting reference levels for indicators of ecosystem structure and functioning (Dame & Christian 2006, Heymans et al. 2014), which is very useful in the context of the ecosystem approach to marine resource management. In this study, we showed that ecosystem indicators largely depend on model structure and that the reliability of the reference levels for the ecosystem indicators may be improved by developing standardized models that account for input data quality.

We identified a level of trophic aggregation that simplifies the model structure and data collection, without significantly altering the model results. The priority functional groups requiring accurate biomass estimates were also identified (Dusky grouper – large, Amberjack+, *Posidonia oceanica*, Decapods+, Epifauna+, Horse mackerels+, and Cephalopods). Link et al. (2012) stated that if the component of model uncertainty linked to observation error needs to be overcome, sampling designs should be improved in a cost-effective way; priority should be given to increasing the data accuracy for poorly known components of the food web, rather than adding further precision to already well-known groups. However, we should acknowledge that obtaining accurate biomass data for all functional groups is not always feasible in complex and highly diverse Mediterranean coastal ecosystems. Thus, we suggest focusing on better documenting the biomass of the poorly known but important groups (such as those we identified), which could help to increase the reliability of the Ecopath-standardized applications in such complex ecosystems.

The methodological approach proposed here to address the issue of model simplification is of interest

for 2 reasons: (1) it increases the feasibility of model building in terms of data collection; and (2) it adds to our knowledge of the modelled system by analysing the effects of simplification and imprecise biomass data on the ecosystem indices, trophic structure, and the capacity of the model to assess fishery impacts. This approach is easily applicable, and it could help foster the development of standardized Ecopath models to represent complex Mediterranean food webs.

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APPENDIX

Table A1. The sensitivity of the model indices to 10% increments in functional group biomass. The values of the system indices are given as the percentage difference from the control model. TL: trophic level; TS: trophic spectra

Functional groups	Trophic level	Biomass	Width_TS	Peak_TS	Biomass_TS	Relative ascendancy	Finn's cycling index	System omnivory index	TL community	Biomass/total system throughput	Total primary production/respiration
Rays	4.37	0.03	0	0.073	0.002	0.412	0.154	0.094	0.000	0.015	0.050
Groupers large	4.37	4.32	31	9.333	0.256	2.058	7.220	0.003	0.052	1.953	6.379
Groupers medium	4.25	0.43	26	2.201	0.076	0.823	2.304	0.026	0.003	0.610	2.043
Large-scale scorpionfish+	4.20	0.49	4	1.126	0.018	0.412	0.768	0.024	0.024	0.190	0.589
Seabirds	4.09	0.29	0	0.230	0.002	0.000	0.154	0.050	0.006	0.059	0.136
Amberjack+	4.08	5.55	31	8.796	0.283	2.058	8.141	0.071	0.002	2.212	7.162
Groupers small	3.99	0.25	2	1.061	0.033	0.412	1.075	0.020	0.011	0.266	0.905
Scorpionfishes+	3.78	4.29	20	4.140	0.101	1.235	3.533	0.008	0.014	0.980	3.186
Pagellus	3.66	0.65	0	0.596	0.014	0.412	0.461	0.000	0.005	0.116	0.397
Striped mullet+	3.62	0.24	0	0.211	0.007	0.412	0.307	0.049	0.004	0.056	0.190
Cephalopods	3.59	3.00	19	2.434	0.079	0.823	6.670	1.565	0.058	0.227	0.550
Horse mackerels+	3.52	20.00	21	7.538	0.089	0.823	6.750	1.550	0.137	0.228	0.548
Gobies+	3.34	0.58	0	0.445	0.010	0.412	0.307	0.015	0.010	0.087	0.304
Diplodus+	3.10	3.63	10	3.879	0.053	0.412	0.768	0.033	0.081	0.183	0.727
Large zooplankton	3.04	2.19	3	2.311	0.009	0.412	3.072	0.070	0.005	0.810	1.693
Wrasses+	2.95	5.04	12	6.158	0.066	0.823	1.690	0.031	0.069	0.430	1.558
Decapods+	2.66	17.21	9	9.907	0.168	1.646	6.880	1.518	0.280	0.227	0.545
Sea worms	2.33	27.83	4	8.822	0.058	0.823	2.458	0.011	0.072	0.633	1.982
Mulletts+	2.27	4.50	0	0.537	0.005	0.412	0.154	0.002	0.006	0.021	0.066
Suspensivores	2.26	27.89	2	3.330	0.032	0.412	1.690	0.021	0.042	0.445	1.347
Gorgonians	2.23	40.56	2	4.834	0.044	0.412	0.154	0.014	0.064	0.003	0.092
Epifauna+	2.18	72.45	5	6.177	0.150	2.058	6.950	1.513	0.305	0.227	0.545
Sea urchins	2.15	38.27	1	3.087	0.045	0.412	0.307	0.017	0.099	0.029	0.274
Small zooplankton	2.10	9.70	1	3.850	0.058	0.000	6.605	0.061	0.136	1.350	2.230
Echinoderms+	2.06	77.79	2	8.436	0.129	0.412	0.461	0.045	0.364	0.040	0.294
Foraminifera	2.00	4.84	1	3.088	0.050	0.823	6.298	0.057	0.118	0.990	1.823
Salema large	2.00	0.00	0	0.583	0.006	0.412	0.000	0.057	0.022	0.003	0.028
Salema small	2.00	0.00	0	0.442	0.004	0.000	0.154	0.057	0.017	0.000	0.040
Posidonia	1.00	8666.85	1	9.677	9.281	2.058	4.455	0.000	0.000	6.068	4.673
Phytoplankton	1.00	20.16	0	0.023	0.022	0.412	3.994	0.000	0.000	2.625	4.082
Seaweeds+	1.00	182.98	0	0.204	0.196	0.000	1.229	0.000	0.000	0.626	1.245