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Comparison of ecosystem modelling and isotopic approach as ecological tools to investigate food webs in the NW Mediterranean Sea

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ABSTRACT

Understanding how marine ecosystems are structured and how they function is a scientific challenge. Nowadays, to learn about ecosystem trophic dynamics ecologists use two complementary methodological approximations, mass-balance ecosystem models and isotopic tools. However, despite the wide applications of these methodologies, the comparison and combination of both are still scarce. The aim of this study was to examine the trophic dynamics of representative species of the South Catalan marine ecosystem (North-western Mediterranean) using the Ecopath ecosystem modelling tool and the stable isotope approach. By using the two methodologies we depicted the trophic position (trophic level and $\delta^{15}\text{N}$ values) and trophic width (omnivory index and total isotopic area) of several species of fish, cephalopods, cetaceans, seabirds and one sea turtle. Our results show a clear correlation between the trophic levels estimated by the Ecopath model and the $\delta^{15}\text{N}$ values, which validate the trophic position of several species in the study area and indicate that both methodologies are useful to determine the trophic position of marine species in Mediterranean marine food webs. In contrast, the two estimators of trophic width (the omnivore index and the total isotopic area) were not strongly related, since the relationship between modelling and stable isotope results was evident only for some species. Further comparisons of trophic width calculated in other marine food webs may provide a better understanding of our results and validate the accuracy of both methodological approaches to calculate trophic width.

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1. Introduction

Marine food webs are subjected to anthropogenic and environmental disturbances that can impact ecosystem structure and functioning, and thus affect natural resource availability (e.g. Jackson et al., 2001; Lotze et al., 2006). To progress towards an understanding on how marine ecosystems are structured is a fundamental but also a challenging scientific task. In this context, ecologists are now focused on novel ecosystem models or biogeochemical approximations that complement classical approaches representing marine food webs and are very useful not only to study the structure of ecosystems, but also to detect, prevent and mitigate environmental and human changes (e.g. Christensen et al., 2005; Peterson and Fry, 1987).

Ecosystem models are particularly useful because they allow the study of marine ecosystems as a whole (Plagányi, 2007; Fulton, 2010). For example, the Ecopath modelling approach, a mass-balance model integrated in the Ecopath with Ecosim software (Christensen and

Walters, 2004) that provides a representation of the food web, can be used to depict the structure and functioning of marine ecosystem and calculate different ecological indicators (Pauly et al., 2000; Christensen and Walters, 2004). Based on this methodology, we can estimate the trophic levels of species or functional groups included in the model. We can also measure how specialist or generalist these species or groups are through the calculation of the omnivory index (Christensen and Walters, 2004; Libralato, 2008).

The use of intrinsic markers such as the stable isotopes (SIA) of nitrogen ($^{15}\text{N}/^{14}\text{N}$, denoted as $\delta^{15}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$, denoted as $\delta^{13}\text{C}$) are widely used as dietary tracers and can depict trophic position and trophic habits of species (Peterson and Fry, 1987; Kelly, 2000; Layman et al., 2007; Newsome et al., 2007). This approach is based on the fact that $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values are transformed from dietary sources to consumers in a predictable manner (Peterson and Fry, 1987; Kelly, 2000). Nitrogen isotopic values show a predictable increase in the isotopic ratio throughout the trophic levels, i.e., typically from 2.5‰ to 5‰ (Post, 2002; Kelly, 2000). Carbon isotopic values show little change with trophic transfers, but are useful indicator of the dietary source of carbon (De Niro and Epstein, 1981).

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Despite the extensive use of both mass-balance models and SIA approaches, the comparison and combination of both approaches in ecological studies are still scarce (but see Kline and Pauly, 1998 and Dame and Christian, 2008). The application of both methodologies simultaneously could provide more accurate information of the structure and functioning of marine food webs and be a useful tool to validate results. One of the most common comparative studies is the calculation of trophic levels from both methodologies; however, to our knowledge, comparison of trophic width or omnivory index calculated from these two methodologies has not yet been pursued. Moreover, although comparative studies have been done including different functional groups from marine systems, top predators such as cetaceans or seabirds have not been included (e.g. Nilssen et al., 2008).

The Mediterranean Sea has been subjected to several quantitative studies on trophic ecology and ecosystem modelling (e.g. Polunin et al., 2001; Coll and Libralato, 2009; Forero and Hobson, 2003). A highly studied Mediterranean marine area is the South Catalan Sea, in the NW Mediterranean (Fig. 1), where various Ecopath models have recently been developed (Coll et al., 2006, 2008). These models revealed that the Southern Catalan Sea supports a complex food web with a strong link between the pelagic and the benthic compartments (Fig. 2; Coll et al., 2006, 2008). In addition, several isotopic studies have investigated the trophic ecology of different organisms in this area including fish, seabirds, cetaceans or marine turtles (e.g. Cardona et al., 2007; Ramos et al., 2009; Navarro et al., 2009, 2010). Due to the large amount of information available about the structure and functioning of the food web in this marine ecosystem, the South Catalan Sea provides an excellent case study to analyse similarities and discrepancies between ecosystem modelling and stable isotope methodologies.

Therefore, the aim of the present study was to analyse the trophic structure of several representative species present in the food web of the South Catalan marine ecosystem by using the two complementary

approaches: Ecopath modelling and stable isotope analysis. Specifically, we compared the results for trophic position (trophic level and $\delta^{15}\text{N}$ values, from Ecopath and SIA, respectively) and of the trophic width (omnivore index and total isotopic area, from Ecopath and SIA, respectively). We focussed on predatory species of this marine ecosystem including several fish, cephalopods, cetaceans, marine turtles and seabirds (Table 1).

2. Materials and methods

2.1. Study area and species

The South Catalan Sea comprises the continental shelf and upper slope associated with the Ebro River Delta (Fig. 1). The area used for the modelling exercises has a depth range between 50 m and 400 m and covers a total area of soft bottom sediments of 4500 km². Generally this region is oligotrophic, where nutrient enrichment occurs due to regional environmental events related to wind episodes, the conditions of a temporal thermocline, and a shelf slope current and river discharges (Salat, 1996).

We focused our study in 24 representative species on this ecosystem, including 16 fish (anchovy *Engraulis encrasicolus*, black-belly rosefish *Helicolenus dactylopterus*, blotched picarel *Spicara flexuosa*, blue whiting *Micromesistius poutassou*, bluefin tuna *Thunnus thynnus*, boarfish *Capros aper*, European hake *Merluccius merluccius*, glasshead grenadier *Hymenocephalus italicus*, greater forkbeard *Phycis blennoides*, jewel lanternfish *Lampanyctus crocodilus*, sardine *Sardina pilchardus*, poor cod *Trisopterus minutus*, red bandfish *Cepola macrophthalma*, shortnose greeneye *Chlorophthalmus agassizi*, silvery cod *Gadiculus argenteus*, and tonguesole *Symphurus nigrescens*) and 2 cephalopods (common bobtail *Sepietta oweniana* and common squid *Allotheuthis subulata*), 2 cetaceans (bottlenose dolphin *Tursiops truncatus* and striped dolphin *Stenella coeruleoalba*), 3 seabird species (Audouin's gull *Larus audouinii*, Balearic shearwater *Puffinus*

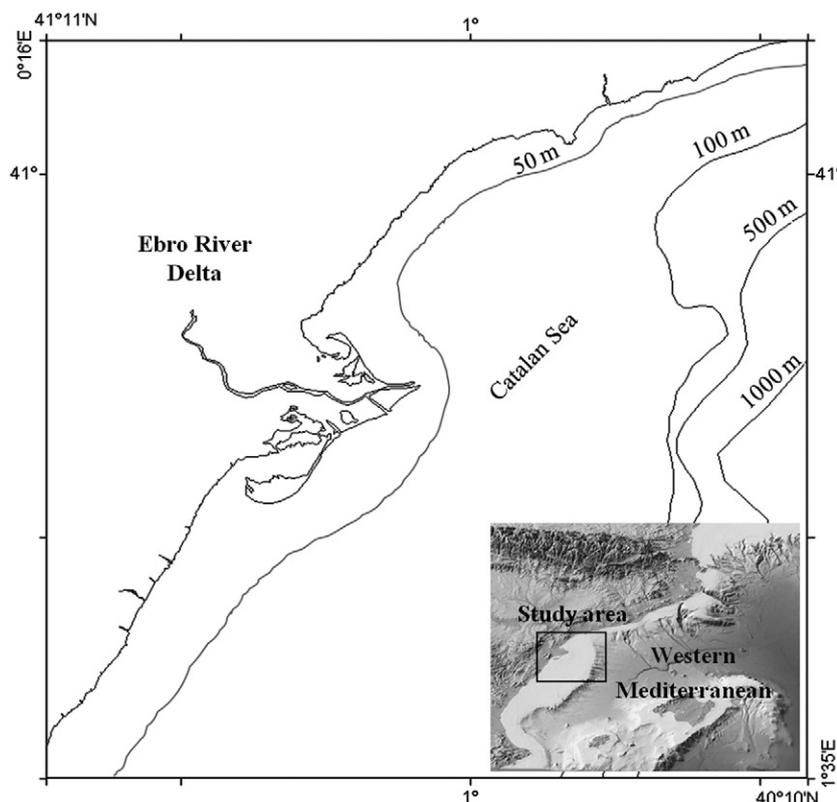


Fig. 1. Map of the South Catalan Sea study area. Modified from Catalano–Balearic Sea–Bathymetric chart 2005; www.icm.csic.es/geo/gma/MCB.

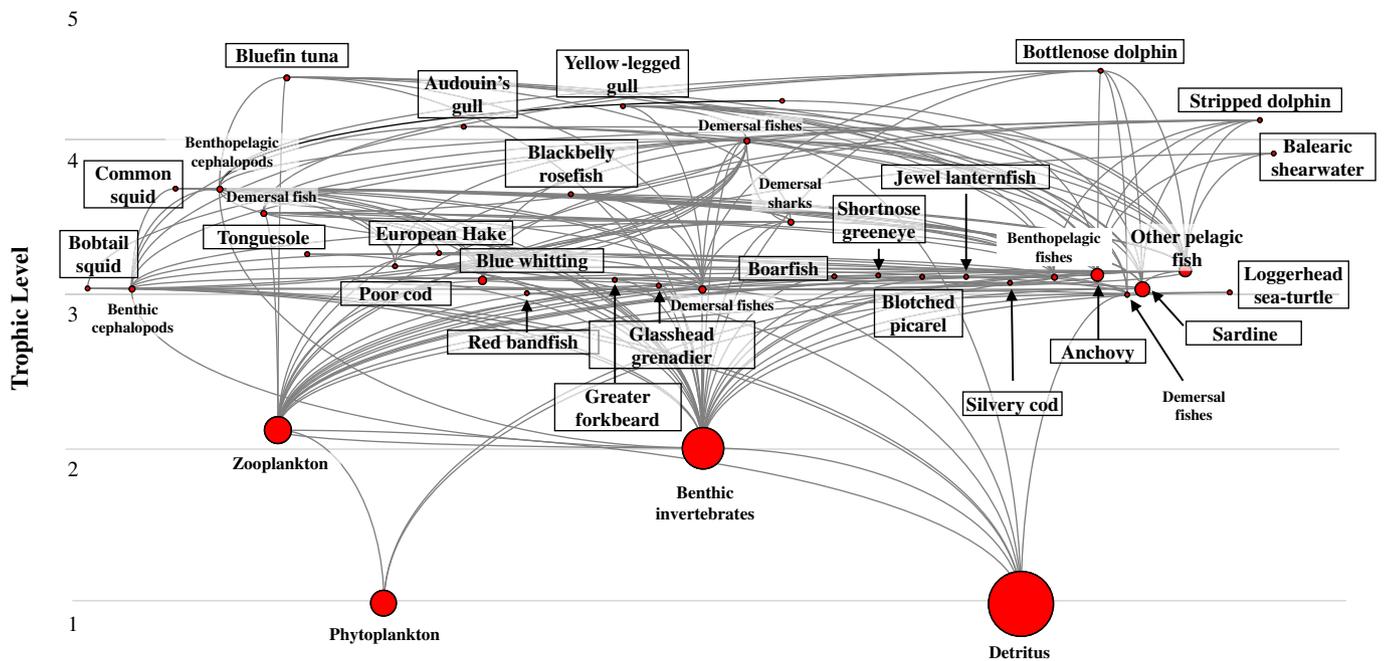


Fig. 2. Overview of the flow diagram of the modified mass-balance model of the South Catalan Sea (NW Mediterranean, Coll et al., 2006, 2008) to specifically visualise the species with stable isotope data. The components of the ecosystem are structured along the vertical axis according to their trophic level (estimated with Ecopath). All species used in the isotopic approach are indicated in larger letters and are within a box. The area of each red circle is proportional to the biomass of each functional group during the mid–late 1990s.

mauretanicus, and yellow-legged gull *Larus michahellis*), and 1 marine turtle (loggerhead sea-turtle *Caretta caretta*) (Table 1).

2.2. Mass-balance ecosystem model

Ecopath is the mass-balance routine of Ecosim with Ecosim software that allows building averaged trophic models of food webs (e.g. Polovina, 1984; Pauly et al., 2000; Christensen and Walters, 2004; Christensen et al., 2005). This modelling tool describes the ecosystem considering functional groups, each representing a species, a subgroup of a species or a group of several species that have functional and ecological similarities. The basic routine of Ecosim describes the balance between production of the functional groups and consumption flows, including fishing activities. A detail description of the main equations of the Ecosim model is described in Appendix 1.

In the present study, we modified a recently developed mass-balance model that originally represented the Southern Catalan ecosystem during the mid–late 1990s (details are fully described in Coll et al., 2006). This model had 40 functional groups and was calibrated with time series data using independent fishing effort and fishing mortality, biomass and catch data from 1978 to 2003 to assess the capability of the model to hindcast ecosystem dynamics (Coll et al., 2008). Detailed information on the model development and data limitations is provided in Coll et al. (2006, 2008).

Here we modified the 1990s model to explicitly separate those species with detailed information from stable isotopes (see following section) that were included as individual functional groups in the model. To do so we used the information available regarding diet composition, biomass, catch, production/biomass, and consumption/biomass ratios for those species (see full references in Coll et al., 2006, and specifically Macpherson, 1981; Würtz and Marrale, 1993; Bosch et al., 1994; Orsi Relini et al., 1995; Oro et al., 1997; Granadeiro et al., 1998; Arcos, 2001; Blanco et al., 2001). The modified version of the model was initially balanced so no further modifications were performed.

Once the South Catalan Sea model was modified, we analysed the trophic levels (TL_i) by functional group. The trophic level (TL_i) was first defined as an integer identifying the position of organisms within

food webs (Lindeman, 1942) and it was later modified to be fractional (Odum and Heald, 1975). Following an established convention, a TL of 1 is given to primary producers and detritus and the TL can be formulated as follows:

$$TL_j = 1 + \sum_{i=1}^n DC_{ji} \cdot TL_i \quad (1)$$

where j is the predator of prey i , DC_{ji} is the fraction of prey i in the diet of predator j and TL_i is the trophic level of prey i .

Ecosim models also allow calculating the Omnivory Index (OI_i), a measure of the distribution of feeding interactions among trophic levels by a species or functional group (Christensen and Walters, 2004; Libralato, 2008). The OI_i is calculated as the variance of TL of the preys j :

$$OI_i = \sum_{j=1}^n [TL_j - 1]^2 \cdot DC_{ij} \quad (2)$$

where the contribution of each prey j to the variance of the consumer i is a proportion of the fraction of prey j in the diet of consumer i (DC_{ij}). When the OI_i is zero, the consumer is specialised, i.e. it feeds on a single trophic level. A high value of OI_i indicates that the consumer feeds on many trophic levels and thus shows a more generalist strategy. The OI is dimensionless and the square root of the OI represents the standard error of the TL (i.e. a measure of the TL 's uncertainty about the TL due to omnivory and sampling variability, Christensen and Walters, 2004; Libralato, 2008).

2.3. Stable isotope data

We used published isotopic data ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values) from 15 species (Table 1; Borell et al., 2006; Cardona et al., 2007; Revelles et al., 2007; Ramos et al., 2009; Navarro et al., 2009, 2010). In addition to these data, we performed stable isotopic analysis on 7 fish species and 2 species of cephalopods (Table 1). Samples for these species were collected on May 2003 from an experimental oceanographic trawling

Table 1
Trophic level (TL, mean±sd) and trophic width estimators, total area (TA) and omnivory index (OI), for fish, cephalopods, seabirds, cetaceans and marine turtles from the South Catalan Sea (NW Mediterranean). The source of the stable isotope and the sample sizes for each species (n) are also indicated. ND = No data available.

| Species | TL | OI | TA | n | Source |
|--|-------------|------|------|-----|-------------------------|
| Fish | | | | | |
| Anchovy <i>Engraulis encrasicolus</i> (ENG) | 3.05 ± 0.01 | 0 | 0.18 | 9 | (Navarro et al., 2009) |
| Blackbelly rosefish <i>Helicolenus dactylopterus</i> (HEL) | 4.14 ± 0.26 | 0.19 | 0.12 | 10 | Present study |
| Blotched picarel <i>Spicara flexuosa</i> (SPI) | 3.49 ± 0.35 | 0.35 | 0.08 | 9 | (Navarro et al., 2009) |
| Blue whiting <i>Micromesistius poutassou</i> (MIC) | 3.40 ± 0.41 | 0.46 | 0.14 | 9 | (Navarro et al., 2009) |
| Bluefin tuna <i>Thunnus thynnus</i> (THU) | 4.42 ± 0.32 | 0.11 | ND | 2 | (Cardona et al., 2007) |
| Boarfish <i>Capros aper</i> (CAP) | 3.65 ± 0.28 | 0.22 | 0.12 | 10 | Present study |
| European hake <i>Merluccius merluccius</i> (MER) | 3.39 ± 0.61 | 1 | 0.07 | 9 | Present study |
| Glasshead grenadier <i>Hymenocephalus italicus</i> (HYM) | 3.61 ± 0.24 | 0.32 | 0.05 | 6 | Present study |
| Greater forkbeard <i>Phycis blennoides</i> (PHY) | 3.89 ± 0.05 | 0.01 | 0.03 | 9 | (Navarro et al., 2009) |
| Jewel lanternfish <i>Lampanyctus crocodilus</i> (LAM) | 3.49 ± 0.35 | 0.35 | 0.18 | 8 | Present study |
| Sardine <i>Sardina pilchardus</i> (SAR) | 2.97 ± 0.27 | 0.21 | 1.01 | 9 | (Navarro et al., 2009) |
| Poor cod <i>Trisopterus minutus</i> (TRI) | 3.25 ± 0.51 | 0.71 | 0.21 | 10 | Present study |
| Red bandfish <i>Cepola macrophthalmia</i> (CEP) | 3.25 ± 0.30 | 0.25 | 0.53 | 9 | Present study |
| Shortnose greeneye <i>Chlorophthalmus agassizi</i> (CHL) | 3.05 ± 0.01 | 0 | 0.01 | 5 | Present study |
| Silvery cod <i>Gadiculus argenteus</i> (GAD) | 3.18 ± 0.37 | 0.38 | 1.01 | 9 | (Navarro et al., 2009) |
| Tonguesole <i>Symphurus nigrescens</i> (SYM) | 3.31 ± 0.45 | 0.56 | 0.08 | 8 | (Navarro et al., 2009) |
| Cephalopods | | | | | |
| Common bobtail <i>Sepietta oweniana</i> (SEP) | 3.08 ± 0.29 | 0.24 | 0.06 | 9 | Present study |
| Common squid <i>Allotheuthis subulata</i> (ALL) | 3.66 ± 0.53 | 0.77 | 0.45 | 6 | (Navarro et al., 2009) |
| Cetaceans | | | | | |
| Bottlenose dolphin <i>Tursiops truncatus</i> (TUR) | 4.51 ± 0.50 | 0.25 | ND | 7 | (Borell et al., 2006) |
| Striped dolphin <i>Stenella coeruleoalba</i> (STE) | 4.22 ± 0.26 | 0.07 | ND | 5 | (Cardona et al., 2007) |
| Seabirds | | | | | |
| Audouin's gull <i>Larus audouinii</i> (AUD) | 4.01 ± 0.95 | 0.91 | 2.44 | 107 | (Navarro et al., 2010) |
| Balearic shearwater <i>Puffinus mauretanicus</i> (PUF) | 3.96 ± 1.02 | 1.05 | 1.35 | 145 | (Navarro et al., 2009) |
| Yellow-legged gull <i>Larus michahellis</i> (MIC) | 4.27 ± 0.93 | 0.87 | ND | 23 | (Ramos et al., 2009) |
| Marine turtle | | | | | |
| Loggerhead sea-turtle <i>Caretta caretta</i> (CAR) | 3.06 ± 0.79 | 0.63 | ND | 27 | (Revelles et al., 2007) |

cruise along the continental shelf of the Ebro Delta (MEDITS—Mediterranean International Trawl Survey; Bertrand et al., 2002). From each individual, we sampled a small portion of muscle that was stored frozen at $-21\text{ }^{\circ}\text{C}$ until stable isotope analyses. Each sample was lyophilized and one aliquot was immediately prepared for $\delta^{15}\text{N}$ analysis. The other underwent lipid extraction prior to $\delta^{13}\text{C}$ analysis (Sholto-Douglas et al., 1991; Schlechtriem et al., 2003). Lipids were extracted using the methods described by Smedes (1999). All samples (about 0.5–1 mg) were combusted at $1020\text{ }^{\circ}\text{C}$ using continuous-flow isotope-ratio mass spectrometry (CFIRMS) system by means of a Carlo Erba 1500NC elemental analyser interfaced with a Delta Plus CL mass spectrometer. All isotope abundances were expressed in δ -notation as parts per thousands (‰) deviation from IAEA standards AIR (^{15}N) and VPDB (^{13}C). Based on within-run replicate measurements of laboratory standards, we estimated the measurement error to be ± 0.2 and $\pm 0.1\%$ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively. The average of the $\delta^{15}\text{N}$ values was used as a proxy of the trophic level of each species (Peterson and Fry, 1987; Kelly, 2000).

To explore the functional relationship between the predators and their potential prey, we predicted the range of expected $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic values to be found in a potential predator that consumes the species located at lower trophic levels (fish and cephalopods). For this prediction, the range was calculated by two times the standard deviation of the mean isotopic values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of all fish (excluding the bluefin tuna and the tonguesole) and cephalopods species after consumer–prey correction by an isotopic fractionation of $+3$ and $+1$ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, respectively (Kelly, 2000).

As trophic width isotopic estimators, we used the total isotopic area (TA) represented by the convex hull polygon for all individuals of each species (Layman et al., 2007). Convex hull polygon is the total area encompassed by the smallest convex polygon containing these individuals in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ niche dimensions (Layman et al., 2007). To calculate TA we needed the isotopic data of all individuals from each species. We had these information for those species of fish and cephalopods sampled in the present study (Table 1) and also for some

fish, cephalopods and seabirds, which individual stable isotope values were provided from authors of these studies (Navarro et al., 2009, 2010). As the number of values for individuals of the two seabirds' species was higher than for the fish species, the convex hull area was calculated for 100 subsets of 10 individuals randomly selected from the total seabird individuals. The convex hull areas were calculated using the Animal Movement Extension in the ArcView GIS 3.3 (ESRI, Redlands, CA, USA). Additional information on the application of convex hulls in ecological studies can be found in Cornwell et al. (2006) and Layman et al. (2007).

2.4. Comparison between Ecopath and isotopic results

Comparisons between trophic level and trophic width measurements calculated from ecosystem modelling and SIA were made at the level of species. The trophic level TL estimated by the Ecopath model was plotted against the corresponding average $\delta^{15}\text{N}$ values and their correlation was calculated by means of the Spearman–rank correlation coefficient (Zar, 1984). Similarly, we analysed the correlation between the OI estimated from the Ecopath model and the TA estimated with the isotopic values.

3. Results

3.1. Ecopath model: trophic level and omnivory index

Trophic levels calculated with the Ecopath model revealed that the studied species (see Table 1) were located between a trophic level of 2.97 (European sardine) and a trophic level of 4.51 (bottlenose dolphin). Seabirds, cetaceans and two species of fish (bluefin tuna and blackbelly rosefish) showed the higher trophic levels (Fig. 2). In contrast, the remaining fish and cephalopods, and the loggerhead sea-turtle showed lower trophic levels (Fig. 2).

The OI estimated with the Ecopath model indicated that species ranged from highly specialised consumers (thus with an OI = 0 for

anchovy and shortnose greeneye) to generalist predators ($OI = 1.05$ for Balearic shearwater). Higher OI values were found for three species of seabirds and for the European hake and poor cod (Table 1) indicating that these organisms feed in a diverse range of trophic levels. Conversely, lower OI values were found for some fish, including anchovy and bluefin tuna, and striped dolphin (Table 1).

3.2. Isotopic results

$\delta^{15}\text{N}$ values varied between 6.81‰ (silvery cod) and 12.68‰ (bottlenose dolphin) (Fig. 3A). Higher $\delta^{15}\text{N}$ values (indicating higher trophic positions in the food web) were found for the two cetaceans, seabirds and two fish (bluefin tuna and tonguesole). In contrast, the loggerhead sea-turtle, the remaining fish, and cephalopods showed lower $\delta^{15}\text{N}$ values (Fig. 3A). In the case of $\delta^{13}\text{C}$, the values varied between -19.93% (anchovy) and -17.37% (tonguesole) (Fig. 3A).

The predicted range of expected isotopic values to be found in a potential predator that consume the different species is located at a

lower trophic level (Fig. 3B, see Materials and methods) matched with the trophic position of the dolphins, bluefin tuna, two seabirds (Balearic shearwater and yellow-legged gull) and the fish tonguesole (Fig. 3B). In contrast, the Audouin's gull, although showed $\delta^{15}\text{N}$ values similar to the predicted range, showed $\delta^{13}\text{C}$ values lower than the $\delta^{13}\text{C}$ values of the predicted range (Fig. 3B). Similarly, the loggerhead sea-turtle mismatched with the predicted range (Fig. 3B), indicating that these species fed different preys than the ones studied here.

3.3. Comparison between Ecopath and isotopic results

The trophic levels estimated by the Ecopath model were highly and positively correlated with the $\delta^{15}\text{N}$ values for the different species (Fig. 4A). Spearman-rank correlation coefficient, $R_s = 0.69$, $p < 0.0001$. These results show that higher trophic levels from the food-web model also showed higher $\delta^{15}\text{N}$ values, thus evidencing a good agreement between both methodologies. In addition, the OI estimated by the Ecopath model was marginally correlated with the TA estimated by the

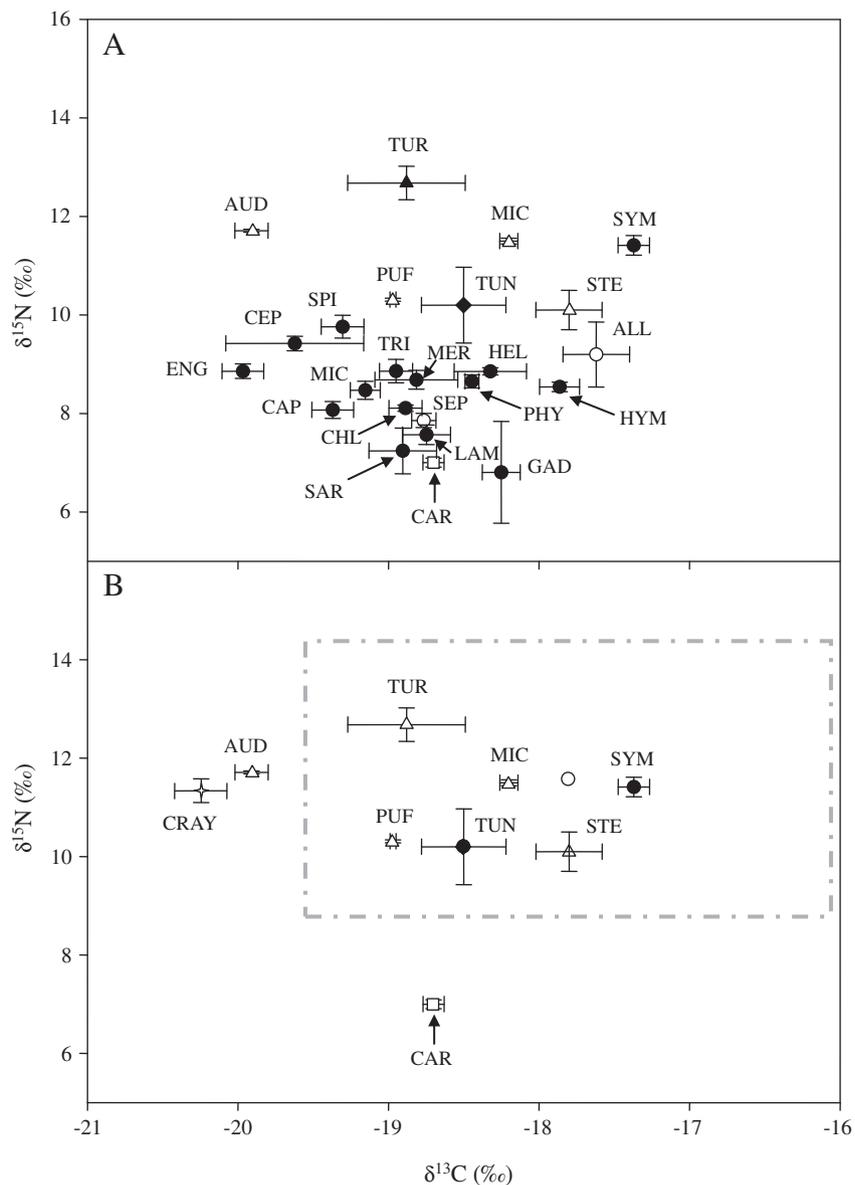


Fig. 3. Mean \pm standard error of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for: (A) fish (black circles), cephalopods (white circles), seabirds (white triangles), cetaceans (black triangles) and marine turtles (white square) from the NW Mediterranean Sea, and (B) apical predators (seabirds, cetaceans and a marine turtle, the Tonguesole fish and a pool of fish and cephalopods (black and white circles)). The grey box represents the range of expected isotopic values from the predators, considering two times the standard deviation of the mean for the pool of fish and cephalopods, accounting for prey–predator isotopic fractionation of 3‰ and 1‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, respectively. Abbreviations of the different species and the source of the isotopic values are given in Table 1. Values of freshwater American crayfish *Procambarus clarkii* (CRAY) are also reported in panel (B) (from Navarro et al., 2010).

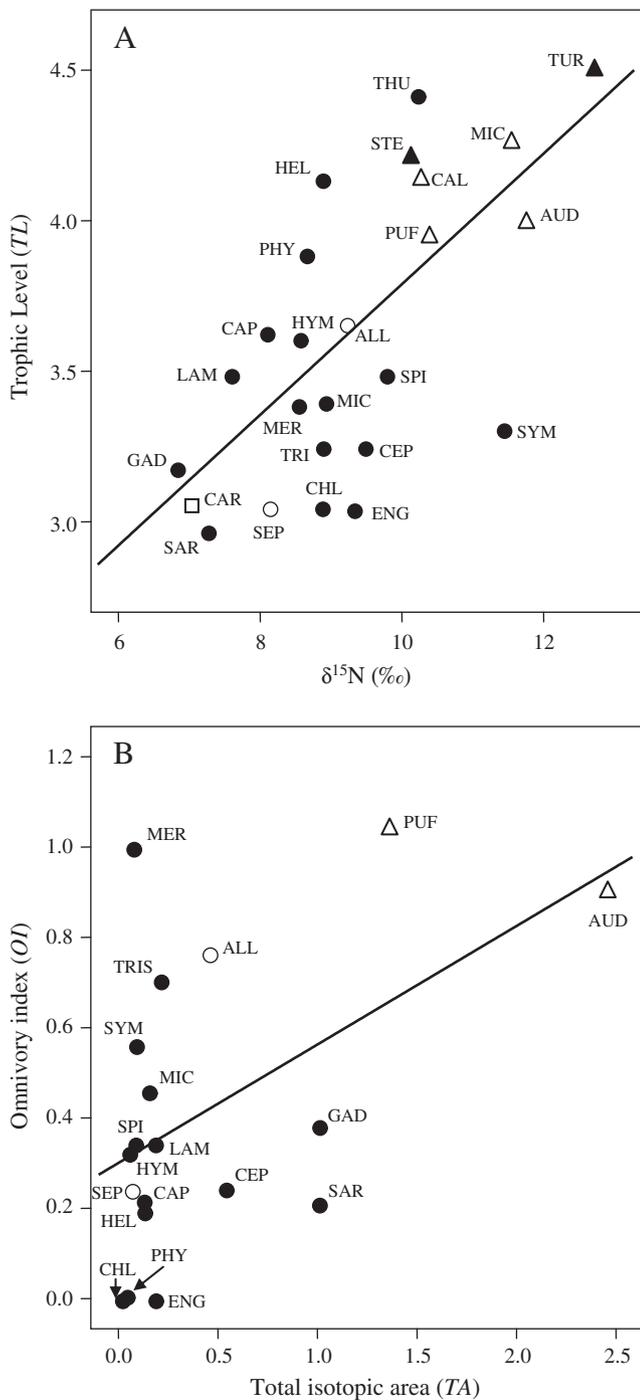


Fig. 4. Relationships between: (A) the trophic level (mean) calculated with the Ecopath model and the $\delta^{15}\text{N}$ values (mean), and (B) the omnivory index (OI) calculated with Ecopath model with the total area (TA) calculated with the isotopic values for fish (black circles), cephalopods (white circles), seabirds (white triangles), cetaceans (black triangles), and marine turtles (white squares) from the NW Mediterranean Sea. Abbreviations of the different species and the source of the isotopic values are given in Table 1.

isotopic values (Fig. 4B, $R_s = 0.44$, $p = 0.06$). However, these results showed higher variability between both methods and only some species such as the Audouin's gull showed a good correspondence between both measures of trophic width (Fig. 4B).

4. Discussion

By using two different methodologies we were able to depict and confirm the trophic position and trophic width of several species of

fish, cephalopods, cetaceans, seabirds and one marine turtle present in the food web of the South Catalan Sea, in the North-Western Mediterranean. Our results revealed a clear correlation between the trophic levels estimated by the food-web model and the $\delta^{15}\text{N}$ values. This indicates that both methodologies are useful to determine the trophic position of marine organisms in the Mediterranean marine food webs. In addition, although the two estimators of trophic width (the omnivore index and the total isotopic area) were also marginally correlated, this relationship was only clear for some species.

The good relationship between the trophic models estimated by the Ecopath model and the $\delta^{15}\text{N}$ values highlights that the diet information that was used for the species in the Ecopath models was accurate (Coll et al., 2006). This result is similar to other comparative studies between the two methodologies (Kline and Pauly, 1998; Dame and Christian, 2008) and extends previous results to the top end of the food web.

As expected, the high trophic level and high $\delta^{15}\text{N}$ values of cetaceans, seabirds and the bluefin tuna confirm their position as the main top predators in the NW Mediterranean food web, and indicate that the major part of the fish and cephalopod species present in the lower and intermediate trophic levels can be part of their diet (i.e. Würtz and Marrale, 1993; Estrada et al., 2005; Ramos et al., 2009; Navarro et al., 2009, 2010; Orsi Relini et al., 1995). Reinforcing this result, the isotopic position regarding $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of dolphins, bluefin tuna and two seabirds (Balearic shearwater and yellow-legged gull) matched with the predicted range of expected isotopic values to be found in a potential predator that consumes the different species located at a lower trophic level, suggesting that these predators consume these preys. Among apical predators, only the Audouin's gull did not match with this predicted range. This is probably a consequence of the consumption by Audouin's gull of freshwater resources such as the American crayfish *Procambarus clarkii* that shows low $\delta^{13}\text{C}$ values (Fig. 3B, $\delta^{13}\text{C} = -27.73 \pm 1.56\text{‰}$, Navarro et al., 2010). This would impact the C isotopic results of Audouin's gull towards depleted values (Navarro et al., 2010).

In contrast, the lower trophic levels and lower $\delta^{15}\text{N}$ values of fish species and cephalopods confirmed their intermediate positions in this marine food web and the fact that they are mainly exploiting the benthos, phytoplankton and zooplankton resources (Tudela and Palomera, 1997; Stergiou and Karpouzi, 2001; Coll et al., 2006). In the particular case of the loggerhead sea-turtle, both methodologies indicated its low trophic position in the food web, close to the fish and cephalopods. Moreover, this marine turtle was completely segregated from the isotopic range predicted for a potential predator consuming fish and cephalopods. All these results confirmed that the loggerhead sea-turtle exploits resources located at a lower trophic level of the food-web such as the planktonic preys or the benthic invertebrates (Revelles et al., 2007).

The largest discrepancy in the estimation of trophic level was found for the demersal tonguesole. Although the Ecopath model estimated a low trophic level, the isotopic analysis showed high $\delta^{15}\text{N}$ values, close to the main top predators. Moreover, the isotopic values of the tonguesole matched with the isotopic range of a predator consuming fish and cephalopods. This discrepancy was probably a consequence of assigning trophic level 1 to detritus in the Ecopath model (Burns, 1989; Nilsen et al., 2008). The scavenger benthic community consumes the dead fish and invertebrates provided by the fisheries' discards (Bozzano and Sardà, 2002; Kaiser and Hiddink, 2007), and thus they integrate the isotopic values of these preys that in turn enrich the $\delta^{15}\text{N}$ values of their predators (in our case the tonguesole; Stergiou and Karpouzi, 2001). Due to this reason, $\delta^{15}\text{N}$ is a better estimator than the Ecopath model of the high trophic position of scavenger species in the studied food web if this is not directly taken into account in the trophic model and highlights the importance of assigning in specific occasions a higher trophic level to detritus in the food-web calculations.

Regarding trophic width estimations, the omnivore index and the total isotopic area were not strongly correlated. Based on our previous knowledge on the ecosystem, we expected to find different dietary preferences among the studied species, from highly specialist large predatory fish such as the bluefin tuna to generalist seabirds (i.e. Macpherson, 1981; Stergiou and Karpouzi, 2001; Estrada et al., 2005; Ramos et al., 2009). However, the omnivory index was the only indicator that captured the different degrees of trophic width among the different species. The omnivory index was very low (close to 0) for specialist top predators, such as the striped dolphin and the bluefin tuna or fish specialist species such as the shortnose greeneye, and was higher for opportunistic species such as the seabirds, bottlenose dolphin or few fish such as the European hake or poor cod. In contrast, despite the isotopic methodology indicated a high isotopic area for the seabird species (Audouin's gull and Balearic shearwater), the other species had similar and small trophic width, thus showing a lower correlation between both trophic width indicators. These results may highlight that the trophic width measured using the total isotopic area is most useful for generalist predators (Hoeinghaus and Zeug, 2008). In fact, for the Audouin's gull, a well-known opportunist species that exploit resources with very different isotopic values, from demersal fish or pelagic fish to freshwater invertebrates (Navarro et al., 2010), the relationship between both food-web and isotopic methodologies was similar. Moreover, we have to take into account that we could not estimate the total trophic area for all the species included in this study (see **Materials and methods**), therefore we could not compare trophic width estimations of other species with contrasting trophic ecology, such as the bluefin tuna (high specialist, Stergiou and Karpouzi, 2001) or yellow-legged gulls (high generalist, Ramos et al., 2009).

In conclusion, this study highlights that the trophic position of Mediterranean marine organisms can be correctly estimated by using the Ecomod (trophic level) and the isotopic approach ($\delta^{15}\text{N}$ values). Since both methodologies are being widely applied in the Mediterranean Sea, these results highlight that they could be used together to depict the structure of Mediterranean marine food webs. In contrast, the trophic width estimated with the Ecomod model (omnivory index) and with the isotopic approach (total isotopic area) did not show such a clear correlation. Further studies should include additional data on the trophic width calculated with the isotopic approach to contrast our results from Mediterranean marine food webs.

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