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# An update on the feeding habits of fish in the Mediterranean Sea (2002-2015)

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## Abstract

In this study we updated a previous compilation of the feeding habits and trophic levels (TROPHs) of Mediterranean fish. In total, 178 publications were retrieved and analysed. Collected data refer to 148 species, with a TROPH value ranging from 2.00 to 4.54. The analysis of the TROPH distribution verified the previously proposed classification of species into functional trophic groups. Overall, information on diet composition exists for 204 fish species out of >700 fishes from the Mediterranean, suggesting that feeding habits are understudied despite their importance in ecological applications and fisheries management. More than half (60.3%) of these species are classified as omnivores with a preference for animal material, 36.7% are carnivores, 2.0% are omnivores with a preference for plants, and two (i.e. *Siganus luridus* and *S. rivulatus*) are pure herbivores. Finally, recommendations for future research are given in view of filling information gaps.

**Keywords**: Feeding, trophic levels, functional trophic groups, Mediterranean.

## Introduction

Feeding habits and trophic relations of fish have attracted attention for centuries, both in scientific essays [e.g. Aristotle (350 B.C.) Book 9, Chapter 2, 610b16: '*Ὁ δὲ πόλεμός ἐστι τοῖς κρείττοσι πρὸς τοὺς ἥττους κατεσθίει γὰρ ὁ κρείττων*' (*The stronger (fish) are hostile to the weaker, for the strong fish eat the others*)] and literature [e.g. Shakespeare (1607-1608) (Act II, Scene I): '*Master, I marvel how the fishes live in the sea' 'Why, as men do on land the great ones eat up the little ones'*]. Fish diets have been studied extensively, mainly by means of stomach content analysis, providing important information on the ecology, physiology and ethology of species, with wide ecological applications (see e.g. Stergiou & Karpouzi, 2002). Stergiou & Karpouzi (2002) reviewed all available relevant literature on feeding habits and estimated fractional trophic levels (TROPHs; see Pauly *et al*., 1998a,b, 2000a) for 148 fish species in the Mediterranean Sea. This work updates the compilation of Stergiou & Karpouzi (2002), reanalyses certain aspects using the combined data, and evaluates and further elaborates recommendations on future research on fish feeding habits.

## Materials and Methods

Publications on feeding habits were gathered using Google, Google-scholar and Web of Science. Grey literature, mainly referring to publications in the proceedings of conferences and/or symposia, was also collected. The following search-key was used: "fishes AND Mediterranean feeding OR diet", excluding the words "stable isotopes, reared, nutrition, lake, metabolic", in order to discount publications referring to aquaculture and freshwater species. The search was conducted for the years 2002-2015, but information published during 2000-2001 was also cross-checked for publications that were not included in Stergiou & Karpouzi (2002).

Collected information was tabulated, following the table format (Tables 1A and 1B) of Stergiou & Karpouzi (2002). Hence, for all species included therein, information on the study area and sampling period, as well as the sampling method and frequency was extracted from each publication. Length range and type, when reported, and sample size used were also recorded, along with the habitat type of each fish species (extracted from FishBase, www.fishbase.org; Froese & Pauly, 2016). Finally, the stomach content analysis method (including the vacuity coefficient when provided), main prey items and their contribution (by weight or/and number) were included in the table.

The fractional trophic level (TROPH) values were estimated using TrophLab and the Pauly *et al*. (2000b) equation:

$$TROPH_i=1+\Sigma^{G}_{j=1}DC_{ij}\times TROPH_j,$$

where $DC_{ij}$ is the weight contribution of prey item j to the diet of species i; $TROPH_j$ is the trophic level of prey item j and G is the number of prey species included in the stomach of i. In addition, TrophLab provides an estimate of omnivory, in the form of standard error (SE). Hence, the omnivory index (OI) is estimated as follows (Pauly *et al*., 2000b):

$$OI=\Sigma^{G}_{j=1}(TROPH_j-TROPH_i)^2\times DC_{ij},$$

and its square root is a standard error, i.e. SE=√OI (Christensen & Pauly, 1992).

Finally, the species were classified in functional trophic groups (FTGs), based on the scheme proposed by Stergiou & Kapouzi (2002): (a) herbivores (H; 2.0<TROPH<2.1), (b) omnivores with a preference for plants (OV; 2.1<TROPH<2.9), (c) omnivores with a preference for animal material (OA; 2.9<TROPH<3.7), (d) carnivores with a preference for decapods and fish (CD; 3.7<TROPH<4.0), and (e) carnivores with a preference for fish and cephalopods (CC; 4.0<TROPH).

## Results and Discussion

Overall, 178 publications were retrieved. The annual number of publications generally increased with time during the past 40 years (Fig. 1). The annual mean number of publications for the period 2002-2015 was 12.1 (Standard Deviation, SD = 5.01), which is two times higher than that for 1961- 2002 (mean±SD=5.67±2.90; based on data from Stergiou & Karpouzi, 2002). There was a slight decline in the number of publications on feeding after 2010 (Fig. 1). This could be attributed to the fact that basic research on biological traits, especially studies at local scale and/or studies on non-commercial species are of low priority for major publishers (Stergiou & Tsikliras, 2006; Dimarchopoulou *et al*., 2016), despite their importance for marine ecology, modelling and ecosystem management (see also e.g. Pauly *et al*., 1998a,b, 2000a; Stergiou & Karpouzi, 2002).

Out of the 178 publications, 290 datasets were extracted (Table 1; Table A online supplement), corresponding to 148 species (60 families, 21 Orders), 61 species of which are not included in Stergiou & Karpouzi (2002). Seventy three species were represented by only one dataset, whereas the largest number of datasets corresponded to *Arnoglossus laterna* and *Engraulis encrasicolus* (eight datasets each) (Table A online supplement). With respect to the spatial allocation of the datasets (Fig. 2), along the north-south Mediterranean axis, the vast majority of the datasets referred to the northern part of the Mediterranean Sea (230 datasets; 79.3%). Regarding the east-west axis, the number of datasets was higher in the Eastern Mediterranean (137 datasets; 47.2%), and decreased to 77 datasets (26.6%) in the Western Mediterranean, 40 datasets (13.8%) in the Central Mediterranean, 25 datasets (8.8%) in the Adriatic Sea and 12 datasets (4.2%) in the Marmara and Black Seas (Fig. 2).

The 290 datasets presented herein, include 320 subsets of feeding habits (Table 1; Table A online supplement). The sample size and length range of the studied specimens were reported by the original authors in 289 (90.6%) and 220 subsets (68.8%) out of the 320 subsets, respectively. The sampling gear used was reported in the vast majority

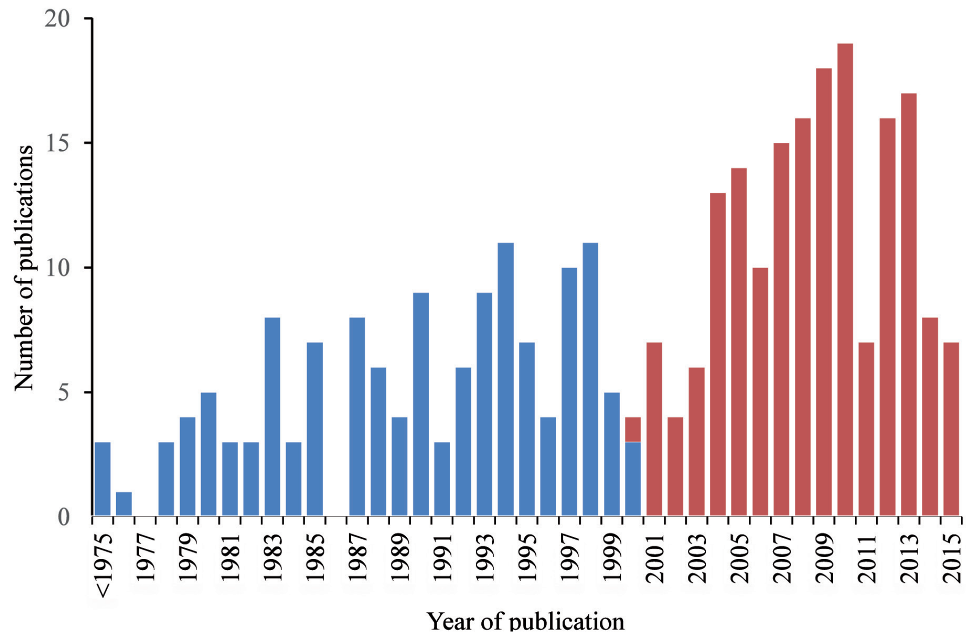



***Fig 1:*** Temporal distribution of publications referring to the feeding habits of fishes in the Mediterranean Sea. Blue bars refer to publications included in Stergiou & Karpouzi (2002), whereas red bars represent publications presented here.

**Table 1**. Number of datasets, subsets and cases extracted from 178 publications reviewed in this study.

| | Description | N |
|---|---|---|
| Datasets | information in a publication for a species, study area and year | 290 |
| Subsets | when feeding habits within a dataset are presented separately, by sampling gear and/or season | 320 |
| Cases | within the datasets (for 52 species) diet composition was given for different length classes. Thus, “cases” correspond to individual trophic level values estimates | 610 |

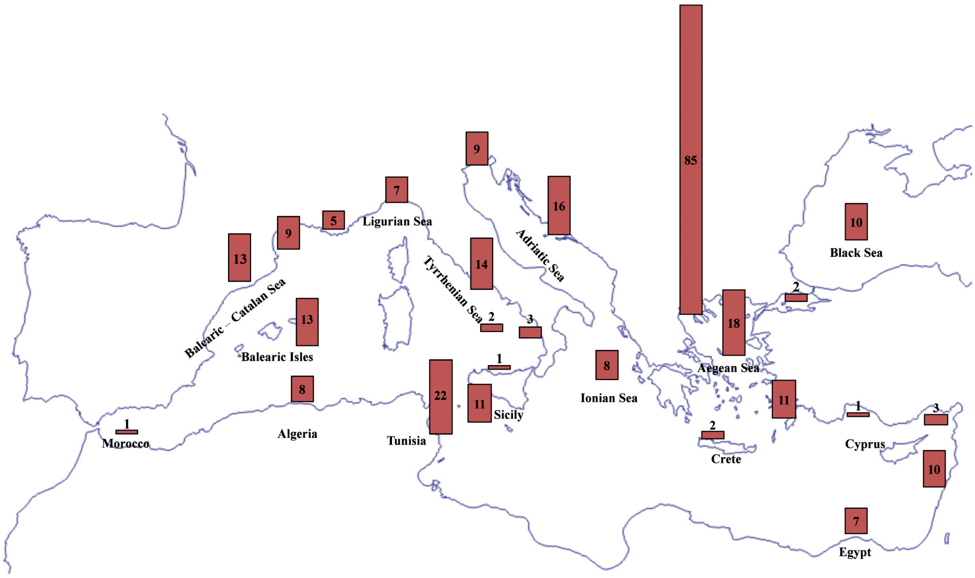
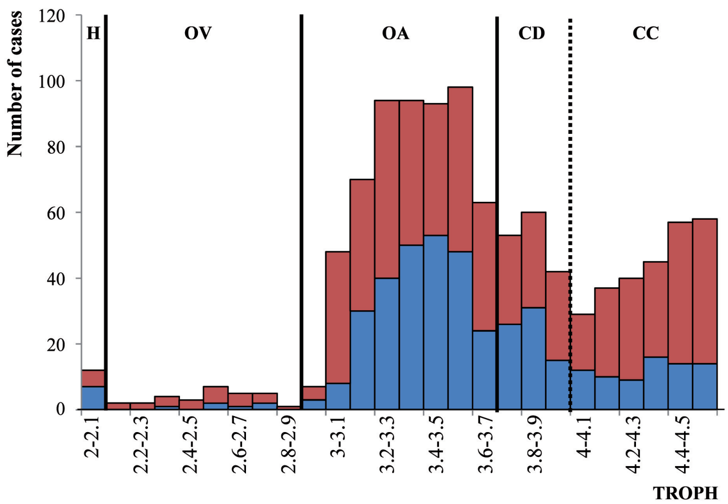



***Fig 2:*** Spatial distribution of datasets included in this study.

of subsets (287 subsets; 98.7%), whereas information on sampling frequency was provided in 162 subsets (50.6%). The method used for stomach content analysis (Table A online supplement) was almost always reported (310 subsets; 96.9%). Feeding habits were qualitatively studied in 217 subsets (67.8%) and quantitatively in 259 subsets (80.9%) (Table A online supplement). The stomach vacuity coefficient was estimated by the original authors in 242 subsets (75.6%) (Table A online supplement).

Fractional trophic levels (TROPHs) were estimated for 610 cases (Table 1; Table A online supplement). They ranged from 2.00±0.00 (for *Sarpa salpa*, *Siganus luridus* and *Siganus rivulatus*) to 4.54±0.60 (for *Lophius budegassa*) (Table A online supplement; Fig. 3). The dif-



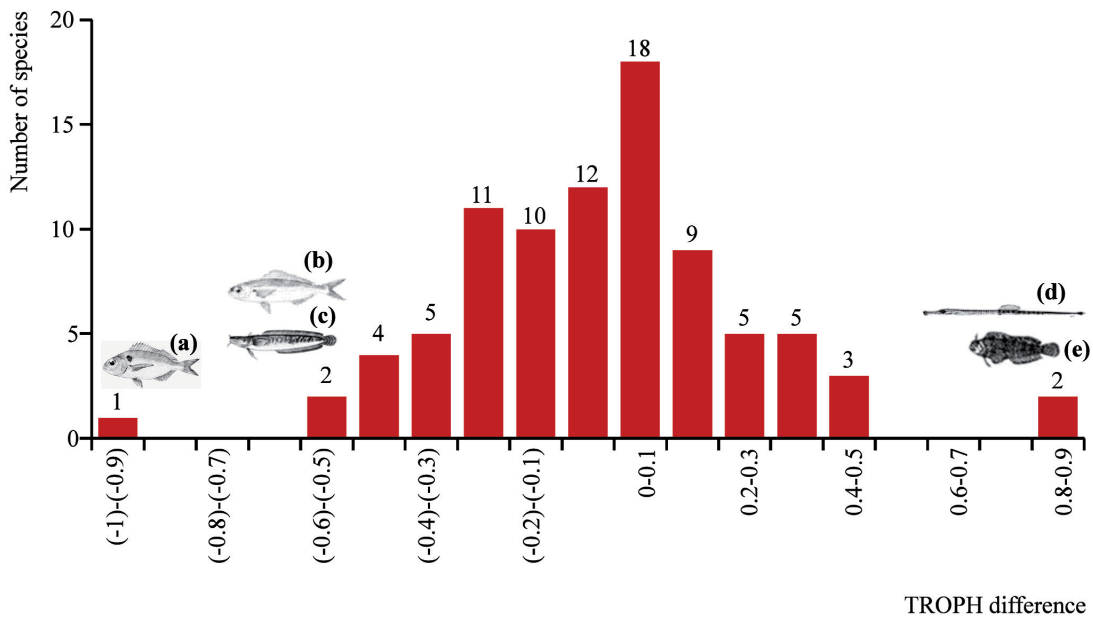

| FTG | Stergiou & Karpouzi (2002) | | This study | | Combined | |
|---|---|---|---|---|---|---|
| | N | $TROPH_m$±SD | N | $TROPH_m$±SD | N | $TROPH_m$±SD |
| H | 7 | 2.02±0.03 | 6 | 2.02±0.04 | 13 | 2.02±0.03 |
| OV | 6 | 2.59±0.18 | 25 | 2.56±0.22 | 31 | 2.56±0.21 |
| OA | 265 | 3.37±0.18 | 321 | 3.35±0.21 | 586 | 3.36±0.19 |
| CD | 67 | 3.84±0.08 | 73 | 3.86±0.08 | 140 | 3.85±0.08 |
| CC | 71 | 4.32±0.16 | 188 | 4.33±0.15 | 259 | 4.33±0.15 |

***Fig 3:*** Distribution of trophic level (TROPH) estimates based on feeding habit studies in the Mediterranean Sea. Blue bars refer to estimates included in Stergiou & Karpouzi (2002), whereas red bars represent studies presented here. FTG=functional trophic group; H=pure herbivore 2.0<TROPH<2.1); OV= omnivore with preference to plants (2.1<TROPH<2.9); OA=omnivore with a preference for animal material (2.9<TROPH<3.7); CD=carnivore with a preference for decapods and fish (3.7<TROPH<4.0); and CC=carnivore with a preference for fish and cephalopods (4.0<TROPH<4.5); N=number of TROPH estimates; $TROPH_m$=mean TROPH; SD=standard deviation.

ference in TROPH estimates of the 87 species that are common in both studies, ranged from 0 (for four species, namely: *Eutrigla gurnardus*, *Siganus luridus*, *Siganus rivulatus* and *Raja radula*) to 0.96 (for *Pagellus bogaraveo*) (Table B online supplement). For the vast majority of the common species (82 out of 87 species; 94.3%) the difference in TROPH was less than 0.5 TROPH units, whereas only in five species this difference was >0.50 TROPH units (Fig. 4). Such differences could be attributed mainly to the different methodological approaches used for stomach content analyses, variations in the sample size and length range of the studied sample, as well as spatio-temporal differences in prey availability and use (e.g. Karachle & Stergiou, 2006, 2008). Thus, using similar protocols in diet studies, including the largest possible size range of adequate sample sizes, could result in minimizing differences in TROPH estimates. Nevertheless, the fact that the identified differences are relatively small further indicates that, when TROPH estimates are required for model development and are not available at local scale, then available values for similar ecosystems or generic estimates (such as those provided in FishBase) could be considered as good proxies.

The distribution of TROPH values in this study largely verified the functional trophic groups (FTGs) identified in Stergiou & Karpouzi (2002), given that similar distributional modes were identified in the two studies (Fig. 3). Overall, of the 148 species presented herein three were classified as herbivores (H), three as omnivores with a preference for plants (OV), 78 as omnivores with a preference for animal material (OA; 2.9<TROPH<3.7), 25 as carnivores with a preference for decapods and fish (CD), and 39 as carnivores with a preference for fish and cephalopods (CC). For 26 (29.9%) of the 87 common species in the two studies, there was a difference in FTG (Table B online supplement). For three species (i.e. *Syngnathus typhle*, *Conger conger* and *Pagellus bogaraveo*), this difference amounted to two FTGs, whereas for the remaining 23 species to one FTG (Table B online supplement).

Based on Stergiou & Karpouzi (2002) and this study, data on feeding habits in the Mediterranean exists for 204 fish species (Table 2).



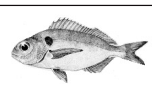

| | | Species | TROPH difference | Potential explanation |
|---|---|---|---|---|
| (a) |  | *Pagellus bogaraveo* | -0.96 | length range |
| (b) |  | *Boops boops* | -0.61 | sample size, method used for estimating diet composition |
| (c) |  | *Gaidropsarus mediterraneus* | -0.54 | method used for estimating diet composition |
| (d) |  | *Syngnathus typhle* | 0.80 | length range, sample size |
| (e) |  | *Parablennius gattorugine* | 0.89 | length range, method used for estimating diet composition |

***Fig 4:*** Frequency distribution of the difference between the trophic level (TROPH) values for the 87 species that are common in Stergiou & Karpouzi (2002) and this study. All species with a TROPH difference >0.5 are given, along with the most probable explanation. Pictures of fishes are from FishBase (www.fishbase.org; Froese & Pauly, 2016).

**Table 2.** Minimum, maximum and mean trophic level estimated for 204 fishes, in alphabetic order, aggregated (included both in Stergiou & Karpouzi (2002) and this study). An asterisk (*) denotes species that are included only in this study, whereas a cross (+) indicates species that appear only in Stergiou & Karpouzi (2002). N=number of trophic level values estimates; min, max and mean=minimum, maximum and mean trophic level estimates; SD=standard deviation; SE=standard error; FTG=functional trophic group; H=pure herbivore 2.0<TROPH<2.1); OV= omnivore with a preference for plants (2.1<TROPH<2.9); OA=omnivore with a preference for animal material (2.9<TROPH<3.7); CD=carnivore with a preference for decapods and fish (3.7<TROPH<4.0); and CC=carnivore with a preference for fish and cephalopods (4.0<TROPH<4.5).

| Species | N | min | max | mean | SD | SE | FTG |
|---|---|---|---|---|---|---|---|
| *Alepocephalus rostratus+* | 4 | 3.39 | 3.91 | 3.56 | 0.2439 | 0.122 | OA |
| *Alosa fallax** | 2 | 4.32 | 4.5 | 4.41 | 0.1273 | 0.09 | CC |
| *Anthias anthias** | 1 | | | 3.54 | | | OA |
| *Aphanius fasciatus** | 2 | 3.25 | 3.27 | 3.26 | 0.0141 | 0.01 | OA |
| *Aphia minuta** | 1 | | | 3.09 | | | OA |
| *Apletodon dentatus+* | 1 | | | 3.19 | | | OA |
| *Apogon imberbis* | 2 | 3.54 | 3.98 | 3.76 | 0.3111 | 0.22 | CD |
| *Arnoglossus laterna* | 12 | 3.21 | 4.35 | 3.71 | 0.4356 | 0.1258 | CD |
| *Arnoglossus thori* | 2 | 3.29 | 3.61 | 3.45 | 0.2263 | 0.16 | OA |
| *Atherina boyeri+* | 1 | | | 3.3 | | | OA |
| *Bathypterois mediterraneus+* | 1 | | | 3.2 | | | OA |
| *Belone belone** | 3 | 3.16 | 3.5 | 3.38 | 0.1908 | 0.1102 | OA |
| *Boops boops* | 3 | 2.53 | 3.52 | 3.12 | 0.5198 | 0.3001 | OA |
| *Bothus podas* | 7 | 3.37 | 3.47 | 3.41 | 0.0358 | 0.0135 | OA |
| *Buenia jeffreysii+* | 1 | | | 3.6 | | | OA |
| *Buglossidium luteum* | 7 | 3.13 | 3.31 | 3.21 | 0.0631 | 0.0238 | OA |
| *Callionymus risso+* | 1 | | | 3.09 | | | OA |
| *Capros aper+* | 2 | 3.16 | 3.21 | 3.19 | 0.0354 | 0.025 | OA |
| *Caranx crysos** | 4 | 4.28 | 4.48 | 4.4 | 0.0835 | 0.0417 | CC |
| *Caranx rhonchus** | 6 | 3.68 | 4.5 | 4.15 | 0.2901 | 0.1184 | CC |
| *Cataetyx alleni+* | 1 | | | 3.1 | | | OA |
| *Centrophorus granulosus** | 1 | | | 4.5 | | | CC |
| *Centroscymnus coelolepis+* | 2 | 4.16 | 4.35 | 4.26 | 0.1344 | 0.095 | CC |
| *Cepola macrophthalma* | 6 | 3 | 3.15 | 3.09 | 0.0554 | 0.0226 | OA |
| *Chelidonichthys cuculus+* | 2 | 3.6 | 3.82 | 3.71 | 0.1556 | 0.11 | CD |
| *Chelidonichthys lucerna* | 7 | 3.4 | 3.91 | 3.69 | 0.1771 | 0.0669 | OA |
| *Chelidonichthys obscurus* | 6 | 3.2 | 3.73 | 3.41 | 0.1998 | 0.0816 | OA |
| *Chimaera monstrosa+* | 5 | 3.38 | 3.59 | 3.46 | 0.0898 | 0.0402 | OA |
| *Chromis chromis* | 3 | 3.18 | 4.21 | 3.55 | 0.5755 | 0.3323 | OA |
| *Citharus linguatula* | 12 | 3.47 | 4.49 | 4.15 | 0.3002 | 0.0866 | CC |
| *Clinitrachus argentatus** | 3 | 3.32 | 3.34 | 3.33 | 0.0115 | 0.0067 | OA |
| *Coelorinchus caelorhincus* | 6 | 3.17 | 3.6 | 3.3 | 0.1785 | 0.0729 | OA |
| *Coelorinchus labiatus** | 1 | | | 3.12 | | | OA |
| *Conger conger* | 21 | 3.2 | 4.49 | 4.08 | 0.3949 | 0.114 | CC |
| *Coris julis* | 6 | 3.27 | 3.63 | 3.39 | 0.1338 | 0.0546 | OA |
| *Coryphaena hippurus** | 8 | 3.81 | 4.5 | 4.27 | 0.2525 | 0.0893 | CC |
| *Coryphaenoides guentheri** | 3 | 3.25 | 3.28 | 3.26 | 0.0173 | 0.01 | OA |
| *Coryphaenoides mediterraneus** | 2 | 3.36 | 3.44 | 3.4 | 0.0566 | 0.04 | OA |
| *Ctenolabrus rupestris+* | 1 | | | 3.19 | | | OA |
| *Dalatias licha* | 3 | 4.35 | 4.5 | 4.45 | 0.0866 | 0.05 | CC |
| *Dasyatis marmorata+* | 1 | | | 3.7 | | | OA |
| *Dasyatis pastinaca** | 10 | 3.46 | 3.8 | 3.67 | 0.1033 | 0.0327 | OA |
| *Deltentosteus quadrimaculatus+* | 3 | 3.11 | 3.3 | 3.24 | 0.1097 | 0.0633 | OA |
| *Dentex dentex* | 3 | 4.49 | 4.5 | 4.5 | 0.0058 | 0.0033 | CC |
| *Diaphus metopoclampus** | 3 | 3.44 | 3.66 | 3.56 | 0.1124 | 0.0649 | OA |
| *Diplodus annularis* | 8 | 2.59 | 3.41 | 3.19 | 0.2689 | 0.0951 | OA |
| *Diplodus puntazzo* | 5 | 2.69 | 3.3 | 3.08 | 0.2386 | 0.1067 | OA |

*(continued)*

**Table 2** *(continued)*

| Species | N | min | max | mean | SD | SE | FTG |
|---|---|---|---|---|---|---|---|
| *Diplodus sargus sargus* | 11 | 3.04 | 3.5 | 3.25 | 0.1429 | 0.0431 | OA |
| *Diplodus vulgaris* | 7 | 3 | 3.7 | 3.26 | 0.2501 | 0.0945 | OA |
| *Dipturus nidarosiensis** | 1 | | | 3.8 | | | CD |
| *Dipturus oxyrinchus** | 15 | 3.41 | 4.28 | 3.75 | 0.2304 | 0.0595 | CD |
| *Engraulis encrasicolus* | 24 | 3 | 3.5 | 3.1 | 0.1603 | 0.0327 | OA |
| *Epigonus telescopus+* | 1 | | | 3.4 | | | OA |
| *Epinephelus aeneus+* | 1 | | | 4.1 | | | CC |
| *Epinephelus caninus+* | 1 | | | 3.8 | | | CD |
| *Epinephelus costae** | 1 | | | 3.39 | | | OA |
| *Epinephelus fasciatus+* | 1 | | | 4.5 | | | CC |
| *Epinephelus marginatus* | 6 | 3.73 | 4.38 | 4.06 | 0.2292 | 0.0936 | CC |
| *Etmopterus spinax* | 6 | 3.69 | 4.39 | 3.98 | 0.303 | 0.1237 | CD |
| *Etrumeus golanii** | 4 | 3.6 | 3.67 | 3.64 | 0.0299 | 0.0149 | OA |
| *Euthynnus alletteratus* | 8 | 4.3 | 4.5 | 4.45 | 0.0759 | 0.0268 | CC |
| *Eutrigla gurnardus* | 2 | 3.58 | 3.58 | 3.58 | 0 | 0 | OA |
| *Fistularia commersonii** | 9 | 4.5 | 4.5 | 4.5 | 0 | 0 | CC |
| *Gadiculus argenteus+* | 2 | 3.55 | 3.9 | 3.73 | 0.2475 | 0.175 | CD |
| *Gaidropsarus biscayensis* | 4 | 3.4 | 3.93 | 3.67 | 0.2195 | 0.1098 | OA |
| *Gaidropsarus granti** | 1 | | | 3.6 | | | OA |
| *Gaidropsarus mediterraneus* | 3 | 3.41 | 3.95 | 3.59 | 0.3089 | 0.1784 | OA |
| *Gaidropsarus vulgaris+* | 2 | 3.42 | 3.49 | 3.46 | 0.0495 | 0.035 | OA |
| *Galeus melastomus* | 9 | 3.34 | 4.5 | 3.97 | 0.3467 | 0.1156 | CD |
| *Gnathophis mystax* | 5 | 3.51 | 3.85 | 3.63 | 0.1324 | 0.0592 | OA |
| *Gobius auratus+* | 2 | 3.1 | 3.3 | 3.2 | 0.1414 | 0.1 | OA |
| *Gobius bucchichi+* | 1 | | | 2.74 | | | OV |
| *Gobius cruentatus+* | 1 | | | 3.25 | | | OA |
| *Gobius fallax+* | 1 | | | 3.37 | | | OA |
| *Gobius geniporus+* | 1 | | | 3.5 | | | OA |
| *Gobius niger* | 7 | 3.2 | 3.57 | 3.46 | 0.1471 | 0.0556 | OA |
| *Gobius vittatus** | 8 | 3.25 | 3.46 | 3.32 | 0.0697 | 0.0246 | OA |
| *Helicolenus dactylopterus+* | 4 | 3.63 | 4.01 | 3.84 | 0.166 | 0.083 | CD |
| *Hexanchus griseus ** | 2 | 4.2 | 4.5 | 4.35 | 0.2121 | 0.15 | CC |
| *Hippocampus guttulatus** | 1 | | | 3.1 | | | OA |
| *Hippocampus hippocampus* | 2 | 3.15 | 3.2 | 3.18 | 0.0354 | 0.025 | OA |
| *Hoplostethus mediterraneus+* | 1 | | | 3.5 | | | OA |
| *Hymenocephalus italicus* | 3 | 3.2 | 3.4 | 3.27 | 0.1102 | 0.0636 | OA |
| *Labrus bergylta** | 1 | | | 3.24 | | | OA |
| *Labrus merula+* | 1 | | | 3.47 | | | OA |
| *Labrus viridis* | 3 | 3.29 | 3.84 | 3.65 | 0.3119 | 0.1801 | OA |
| *Lagocephalus sceleratus** | 2 | 3.73 | 3.86 | 3.8 | 0.0919 | 0.065 | CD |
| *Lampanyctus pusillus** | 2 | 3.05 | 3.1 | 3.08 | 0.0354 | 0.025 | OA |
| *Lepidion lepidion+* | 2 | 3.3 | 3.67 | 3.49 | 0.2616 | 0.185 | OA |
| *Lepidopus caudatus+* | 5 | 3.2 | 3.84 | 3.66 | 0.263 | 0.1176 | OA |
| *Lepidorhombus boscii+* | 11 | 3.22 | 3.85 | 3.64 | 0.1829 | 0.0551 | OA |
| *Lepidorhombus whiffiagonis+* | 3 | 4.01 | 4.24 | 4.11 | 0.1193 | 0.0689 | CC |
| *Lepidotrigla cavillone* | 8 | 3.1 | 3.5 | 3.31 | 0.1304 | 0.0461 | OA |
| *Lesueurigobius suerii** | 1 | | | 3.35 | | | OA |
| *Leucoraja naevus** | 1 | | | 3.93 | | | CD |
| *Lithognathus mormyrus* | 8 | 2.78 | 3.5 | 3.21 | 0.2183 | 0.0772 | OA |
| *Lophius budegassa* | 11 | 3.9 | 4.54 | 4.38 | 0.1657 | 0.05 | CC |
| *Lophius piscatorius* | 2 | 4.3 | 4.48 | 4.39 | 0.1273 | 0.09 | CC |
| *Merlangius merlangus** | 3 | 3.75 | 4.38 | 3.97 | 0.3528 | 0.2037 | CD |

*(continued)*

**Table 2** *(continued)*

| Species | N | min | max | mean | SD | SE | FTG |
|---|---|---|---|---|---|---|---|
| *Merluccius merluccius* | 45 | 3.2 | 4.5 | 4.09 | 0.3793 | 0.0565 | CC |
| *Microchirus variegatus** | 1 | | | 3.06 | | | OA |
| *Micromesistius poutassou* | 9 | 3.34 | 4.39 | 3.92 | 0.2926 | 0.0975 | CD |
| *Molva macrophthalma+* | 1 | | | 4.5 | | | CC |
| *Monochirus hispidus** | 1 | | | 3.19 | | | OA |
| *Mullus barbatus* | 21 | 2.79 | 3.57 | 3.29 | 0.204 | 0.0445 | OA |
| *Mullus surmuletus* | 24 | 3.03 | 3.58 | 3.34 | 0.1436 | 0.0293 | OA |
| *Muraena helena** | 4 | 4.11 | 4.27 | 4.2 | 0.0661 | 0.033 | CC |
| *Mustelus mustelus** | 8 | 3.5 | 4.41 | 4.05 | 0.3553 | 0.1256 | CC |
| *Mustelus punctulatus** | 6 | 3.59 | 4.29 | 3.91 | 0.3255 | 0.1329 | CD |
| *Myliobatis aquila** | 2 | 3.37 | 3.84 | 3.61 | 0.3323 | 0.235 | OA |
| *Naucrates ductor** | 2 | 3.19 | 3.37 | 3.28 | 0.1273 | 0.09 | OA |
| *Nemipterus randalli** | 1 | | | 3.7 | | | OA |
| *Neogobius melanostomus** | 1 | | | 3.44 | | | OA |
| *Nezumia aequalis* | 5 | 3.09 | 3.49 | 3.25 | 0.1518 | 0.0679 | OA |
| *Notacanthus bonaparte+* | 1 | | | 3.4 | | | OA |
| *Oblada melanura* | 6 | 3.1 | 3.53 | 3.28 | 0.1727 | 0.0705 | OA |
| *Ophichthus rufus+* | 1 | | | 4.25 | | | CC |
| *Ophidion barbatum+* | 2 | 3.47 | 3.56 | 3.52 | 0.0636 | 0.045 | OA |
| *Pagellus acarne* | 5 | 3.47 | 3.84 | 3.61 | 0.1427 | 0.0638 | OA |
| *Pagellus bogaraveo* | 4 | 3.4 | 4.43 | 3.71 | 0.484 | 0.242 | CD |
| *Pagellus erythrinus* | 21 | 3.08 | 3.83 | 3.37 | 0.1847 | 0.0403 | OA |
| *Pagrus auriga+* | 1 | | | 3.31 | | | OA |
| *Pagrus caeruleostictus+* | 1 | | | 3.51 | | | OA |
| *Pagrus pagrus* | 9 | 3.36 | 3.9 | 3.71 | 0.1646 | 0.0549 | CD |
| *Parablennius gattorugine* | 2 | 2.11 | 3 | 2.56 | 0.6293 | 0.445 | OV |
| *Parablennius rouxi+* | 1 | | | 3.2 | | | OA |
| *Parablennius tentacularis+* | 1 | | | 3.11 | | | OA |
| *Parophidion vassali+* | 1 | | | 3.43 | | | OA |
| *Pegusa impar** | 1 | | | 3.2 | | | OA |
| *Pegusa lascaris** | 2 | 3.12 | 3.15 | 3.14 | 0.0212 | 0.015 | OA |
| *Phycis blennoides* | 7 | 3.55 | 3.89 | 3.72 | 0.1167 | 0.0441 | CD |
| *Phycis phycis+* | 1 | | | 4.09 | | | CC |
| *Pomatomus saltatrix** | 2 | 4.46 | 4.5 | 4.48 | 0.0283 | 0.02 | CC |
| *Pomatoschistus bathi+* | 2 | 3.2 | 3.3 | 3.25 | 0.0707 | 0.05 | OA |
| *Pomatoschistus quagga+* | 1 | | | 3.29 | | | OA |
| *Ponticola platyrostris** | 1 | | | 3.88 | | | CD |
| *Pteroplatytrygon violacea** | 2 | 4.5 | 4.5 | 4.5 | 0 | 0 | CC |
| *Raja asterias** | 10 | 3.6 | 3.97 | 3.76 | 0.1107 | 0.035 | CD |
| *Raja brachyura** | 9 | 3.4 | 4.5 | 4.27 | 0.4168 | 0.1389 | CC |
| *Raja clavata** | 13 | 3.35 | 4.27 | 3.83 | 0.2812 | 0.078 | CD |
| *Raja miraletus* | 13 | 3.29 | 3.9 | 3.59 | 0.194 | 0.0538 | OA |
| *Raja polystigma** | 1 | | | 3.68 | | | OA |
| *Raja radula* | 6 | 3.5 | 4.22 | 3.9 | 0.2682 | 0.1095 | CD |
| *Rhinobatos rhinobatos* | 13 | 3.5 | 4.28 | 3.93 | 0.2087 | 0.0579 | CD |
| *Ruvettus pretiosus** | 1 | | | 4.5 | | | CC |
| *Sarda sarda* | 5 | 4.46 | 4.5 | 4.48 | 0.0148 | 0.0066 | CC |
| *Sardina pilchardus* | 10 | 2.1 | 3.2 | 2.76 | 0.432 | 0.1366 | OV |
| *Sardinella aurita** | 22 | 2.4 | 3.54 | 2.97 | 0.3231 | 0.0689 | OA |
| *Sargocentron rubrum* | 2 | 3.36 | 3.5 | 3.43 | 0.099 | 0.07 | OA |
| *Sarpa salpa* | 6 | 2 | 2.5 | 2.11 | 0.1946 | 0.0794 | OV |
| *Saurida undosquamis* | 3 | 3.8 | 4.5 | 4.26 | 0.4013 | 0.2317 | CC |

*(continued)*

**Table 2** *(continued)*

| Species | N | min | max | mean | SD | SE | FTG |
|---|---|---|---|---|---|---|---|
| *Sciaena umbra* | 3 | 3.5 | 3.8 | 3.61 | 0.1652 | 0.0954 | OA |
| *Scomber colias** | 1 | | | 3.99 | | | CD |
| *Scomber scombrus* | 2 | 3.9 | 4.37 | 4.14 | 0.3323 | 0.235 | CC |
| *Scorpaena notata* | 7 | 3.43 | 3.6 | 3.51 | 0.0648 | 0.0245 | OA |
| *Scorpaena porcus* | 17 | 3.4 | 4.2 | 3.82 | 0.272 | 0.066 | CD |
| *Scorpaena scrofa* | 9 | 3.9 | 4.4 | 4.18 | 0.1706 | 0.0569 | CC |
| *Scyliorhinus canicula* | 12 | 3.37 | 4.5 | 4.04 | 0.3961 | 0.1143 | CC |
| *Seriola dumerili+* | 10 | 3.4 | 4.5 | 4.1 | 0.4388 | 0.1388 | CC |
| *Serranus cabrilla* | 6 | 3.3 | 4.37 | 3.76 | 0.3907 | 0.1595 | CD |
| *Serranus hepatus* | 7 | 3.47 | 3.77 | 3.63 | 0.118 | 0.0446 | OA |
| *Serranus scriba* | 3 | 3.7 | 3.94 | 3.84 | 0.1234 | 0.0713 | CD |
| *Siganus luridus* | 4 | 2 | 2 | 2 | 0 | 0 | H |
| *Siganus rivulatus* | 3 | 2 | 2 | 2 | 0 | 0 | H |
| *Solea solea* | 26 | 2.26 | 3.34 | 2.95 | 0.3452 | 0.0677 | OA |
| *Sparus aurata+* | 1 | | | 3.42 | | | OA |
| *Spicara maena* | 13 | 3 | 4.1 | 3.25 | 0.2966 | 0.0823 | OA |
| *Spicara smaris* | 3 | 3 | 3.49 | 3.2 | 0.2589 | 0.1495 | OA |
| *Spondyliosoma cantharus* | 5 | 3.29 | 3.62 | 3.44 | 0.1214 | 0.0543 | OA |
| *Squalus acanthias** | 3 | 3.61 | 4.4 | 4.08 | 0.4158 | 0.2401 | CC |
| *Squalus blainville** | 1 | | | 4.42 | | | CC |
| *Symphodus cinereus+* | 3 | 3.1 | 3.3 | 3.23 | 0.1102 | 0.0636 | OA |
| *Symphodus mediterraneus+* | 2 | 3.1 | 3.22 | 3.16 | 0.0849 | 0.06 | OA |
| *Symphodus ocellatus* | 6 | 2.55 | 3.57 | 3.18 | 0.3617 | 0.1477 | OA |
| *Symphodus rostratus+* | 3 | 3.3 | 3.41 | 3.37 | 0.0608 | 0.0351 | OA |
| *Symphodus tinca* | 7 | 2.95 | 3.71 | 3.33 | 0.2643 | 0.0999 | OA |
| *Symphurus nigrescens* | 4 | 3.2 | 3.42 | 3.32 | 0.0918 | 0.0459 | OA |
| *Synaptura lusitanica** | 1 | | | 3.1 | | | OA |
| *Syngnathus abaster** | 1 | | | 3.28 | | | OA |
| *Syngnathus acus+* | 2 | 3.44 | 3.47 | 3.46 | 0.0212 | 0.015 | OA |
| *Syngnathus typhle* | 2 | 3.51 | 4.31 | 3.91 | 0.5657 | 0.4 | CD |
| *Synodus saurus* | 2 | 4.2 | 4.5 | 4.35 | 0.2121 | 0.15 | CC |
| *Tetrapturus belone** | 1 | | | 4.5 | | | CC |
| *Thalassoma pavo** | 1 | | | 3.42 | | | OA |
| *Thunnus thynnus+* | 4 | 4 | 4.5 | 4.3 | 0.2259 | 0.113 | CC |
| *Torpedo marmorata* | 5 | 4.39 | 4.5 | 4.47 | 0.0487 | 0.0218 | CC |
| *Torpedo torpedo* | 7 | 4.02 | 4.5 | 4.26 | 0.212 | 0.0801 | CC |
| *Trachinus draco** | 1 | | | 4.19 | | | CC |
| *Trachurus mediterraneus* | 22 | 3.15 | 4.01 | 3.52 | 0.2842 | 0.0606 | OA |
| *Trachurus trachurus* | 26 | 3.2 | 4.18 | 3.8 | 0.3356 | 0.0658 | CD |
| *Trachyrincus scabrus* | 6 | 3.14 | 3.83 | 3.47 | 0.2579 | 0.1053 | OA |
| *Trigla lyra+* | 9 | 3.28 | 3.7 | 3.45 | 0.1301 | 0.0434 | OA |
| *Trigloporus lastoviza* | 7 | 3.32 | 3.58 | 3.46 | 0.092 | 0.0348 | OA |
| *Tripterygion delaisi+* | 2 | 3.5 | 3.5 | 3.5 | 0 | 0 | OA |
| *Trisopterus capelanus* | 10 | 3.39 | 4.13 | 3.7 | 0.2132 | 0.0674 | OA |
| *Umbrina cirrosa+* | 1 | | | 3.51 | | | OA |
| *Upeneus asymmetricus+* | 1 | | | 3.6 | | | OA |
| *Upeneus moluccensis+* | 2 | 3.4 | 3.89 | 3.65 | 0.3465 | 0.245 | OA |
| *Upeneus pori+* | 1 | | | 3.51 | | | OA |
| *Uranoscopus scaber* | 8 | 3.8 | 4.43 | 4.26 | 0.2319 | 0.082 | CC |
| *Xiphias gladius* | 4 | 4.33 | 4.5 | 4.46 | 0.0835 | 0.0417 | CC |
| *Xyrichtys novacula** | 3 | 3.24 | 3.49 | 3.37 | 0.125 | 0.0722 | OA |
| *Zeus faber* | 9 | 4.36 | 4.5 | 4.47 | 0.0539 | 0.018 | CC |
| *Zosterisessor ophiocephalus+* | 1 | | | 3.16 | | | OA |

**Table 3.** Issues raised by Stergiou & Karpouzi (2002) regarding future efforts in studying the diet of fishes, and how or whether these have been addressed based on the findings of this study. Recommendations in addressing those issues are also provided.

| Issue | Stergiou & Karpouzi (2002) | This study | Recommendation |
|---|---|---|---|
| *Feeding habits of new species and habitats* | Report on a total of 146 species. Main effort so far on demersal, benthopelagic and pelagic species. Should expand to other habitats with emphasis on bathypelagic and bathydemersal fishes | Report on 148 species, 61 not included in Stergiou & Karpouzi (2002). There was an increase towards pelagic and reef-associated species, but information on bathypelagic and bathydemersal ones is still lacking. | Effort should continue, as out of >700 fishes in the Mediterranean (Froese & Pauly, 2016), diet information exists only for 204. As the vast majority of samples of the studied species originate from trawling (i.e. mainly depths >50m), sampling with other gear, and/or in shallower waters will increase our knowledge. In addition, future efforts should focus on filling the information gap as regards bathypelagic and bathydemersal species |
| *Feeding habits of certain species*: (a) commercially important fish and/or essential for Ecopath with Ecosim models | Effort on studying the feeding habits of e.g. *Scomber colias*, *Sardinella aurita, Sprattus sprattus, Merlangius merlangus*, *Auxis* spp., *Pomatomus saltatrix*, *Mustelus* spp., *Psetta maxima*, *Sphyraena* spp, *Belone belone*, *Dentex macrophthalmus*, *Squalus acanthias*, *Caranx* spp., *Squatina squatina*, *Platichthys flesus*, *Katsuwonus pelamis*, *Lamna nasus*, *Thunnus obesus*, *Istiophorus albicans*, *Pleuronectes platessa* | Of the 20 species/genera proposed, information now exists for nine (*Scomber colias*, *Sardinella aurita, Merlangius merlangus*, *Pomatomus saltatrix*, *Mustelus* spp., *Sphyraena* spp, *Belone belone*, *Squalus acanthias*, *Caranx* spp.) | Effort should continue in that direction, especially regarding top/apex predators, to gain knowledge valuable for ecosystem modelling and management of aquatic resources |
| *Feeding habits of certain species*: (b) Elasmobranchs | Diet of 11 Elasmobranch species presented | Diet of 25 Elasmobranch species. Nine were also included in Stergiou & Karpouzi (2002), with the exception of *Centroscymnus coelolepis* and *Dasyatis marmorata* | As they are top/apex predators and, as such, of high importance for Marine Strategy Framework Directive Descriptor 4 (EU, 2008), additional efforts should be made, taking into consideration the IUCN status of the species (most of them are protected) regarding sample size. Moreover, samples should be exhaustively treated for all aspects of biology |
| *Reported length range of specimens* | Reported at a rate of 58.7% | Reported at a rate of 68.8% | Length range should always be reported, and is in the vast majority of cases. This information is also essential for identifying/explaining intraspecific differences in trophic level estimates (see figure 4 also). Yet, many studies provide the entire length range of the sample without further indicating the actual range of the subsample used for stomach content analyses. The actual length range of the sample should be reported |
| *Estimates of TROPH* | Should always be estimated and reported | Reported rarely | Authors of diet-reporting papers must apply TrophLab, a user friendly and free downloadable (from www.fishbase.us/download/TrophLab2K.zip) MicroSoft Access-routine |

For nine out of the 204 species (i.e. *Merluccius merluccius*, *Solea solea*, *Trachurus trachurus*, *E. encrasicolus*, *Mullus surmuletus*, *Sardinella aurita*, *Trachurus mediterraneus*, *Mullus barbatus*, and *Pagellus erythrinus*; Table 2), all highly commercial, there are more than 20 TROPH estimates. Yet, given that there are more than 700 fishes in the Mediterranean Sea (Froese & Pauly, 2016), the number of fish for which information on their feeding habits in the Mediterranean Sea is currently unavailable is still extremely high. Those approximately 500 species that have not been studied in the Mediterranean include some key species in terms of habitat (e.g. bathypelagic and bathydemersal species), abundance/value (e.g. *Auxis* spp., *Psetta maxima*, *Dentex macrophthalmus*, *Platichthys flesus*, *Katsuwonus pelamis*, *Thunnus obesus*, *Pleuronectes platessa*) and ecological importance (e.g. Elasmobranchs) (Table 3).

Out of the total 204 species for which information currently exists for the Mediterranean Sea, 75 (36.8%) are carnivores (29 CD and 46 CC species). The latter are of high importance for monitoring the status of aquatic food webs (e.g. Pauly *et al.*, 1998a, 2000a; Stergiou & Karpouzi, 2002), and this is also depicted in the first indicator of the Marine Strategy Framework Directive (EU, 2008), namely Descriptor 4 (D4: food webs) '*Performance of key predator species using their production per unit biomass (productivity)*'.

Stergiou & Karpouzi (2002) provided guidelines for future research on feeding studies, many of which have been addressed to some extent (Table 3). These guidelines are hitherto updated and refined, in order to set needs/priorities for studies on feeding habits (Table 3). It should be noted that there is still a need to accumulate knowledge on all aspects of Mediterranean fish biology (e.g. age and growth, mortality, fecundity, reproduction) and for as many species as possible (Tsikliras *et al.*, 2010; Tsikliras & Stergiou, 2014, 2015; Apostolidis & Stergiou, 2014; Dimarchopoulou *et al.,* 2016). Thus, collected samples intended for study, should be treated exhaustively in order to extract the maximum possible information from them.

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