Trophic signatures of marine organisms in the Mediterranean as compared with other ecosystems

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ABSTRACT. We compared several large marine ecosystems in terms of species numbers of fishes, sea birds, marine mammals, and cephalopods. We examined how these numbers were distributed by trophic level, from herbivores to top predators. We created group-specific trophic signatures as plots of number of species by trophic level, and used these to identify similarities and discrepancies between taxonomic groups and ecosystems. Preliminary results suggested that trophic signatures are similar for ecosystems previously known to share major features, and different for dissimilar ecosystems. In the Mediterranean, as well as in the other large marine ecosystems, fish clearly dominate the predatory trophic levels above 3.0. Preliminary signatures for cephalopods, marine mammals, and sea birds in the Mediterranean and in the North Sea indicate that these groups are restricted to trophic levels above 3.0, and are represented by many fewer species than are predatory fish. Notably, cephalopods are the only invertebrates present at higher trophic levels (>= 4). Invertebrates other than cephalopods are restricted to trophic levels below 3, with very few exceptions. Trophic signatures appear to be useful tools for better understanding of the roles that different groups of organisms play in different ecosystems. We also applied free-scale network theory to analyse the food web created by trophic links of fishes. Our preliminary results indicated that Mediterranean fishes are, on average, only two trophic links away from each other.

KEY WORDS : trophic level ; food web ; Mediterranean ; North Sea ; Baltic ; Black Sea ; Caribbean ; South China Sea

INTRODUCTION

There is wide agreement that modern fisheries management has to take into account not only prey and predators of a target species, but also their role in an overall ecosystem context (CHRISTENSEN, 1996). There also are increasing calls for ecosystem-based management as an alternative, or at least a complement, to the single-species approaches so far used exclusively, and with little success, to manage commercial fisheries (NRC, 1999). Large Marine Ecosystems (LMEs) have been identified as suitable units for management (see SHERMAN & DUDA, 1999 and http ://www.edc.uri.edu/lme/), yet our understanding of LMEs is still limited. In this study we compared the Mediterranean with five other LMEs based on the respective trophic structures of important species groups. We used signatures created by plots of number and average size of species by trophic level as conservative, long-term characteristics of LMEs. We compared these signatures between groups of organisms and between LMEs. Our first hypothesis was that a given group of organisms will show similar signatures in similar LMEs, and vice-versa. Our second hypothesis stated that different groups of organisms will have typical and different signatures. We expected that the subtropical Mediterranean would show an intermediate position between temperate LMEs (North Sea, Baltic and Black Sea) and tropical LMEs (Caribbean and South China Sea).

Another type of trophic signature is generated by a plot of species frequency in relation to their number of trophic links (WILLIAMS et al., 2000). Such plots can be interpreted by applying 'small world' or 'free-scale network' theories (JEONG et al., 2000 ; ALBERT & BARABASI, 2002). Within such framework species are nodes that are interconnected through trophic relationships (links). The distance or path length between two species is the number of links (k) between them. For example, a species A is one link away from species B if A is prey or predator of B ; it is two links away if A and B do not interact directly but A shares with B at least one prey or predator, etc. Analysis of non-biological free-scale networks suggested that path length will increase considerably if a certain quantity of the most connected nodes is removed, compared with a random removal of nodes, which will have little effect on path length. Here we test this prediction for the Mediterranean.

MATERIAL AND METHODS

For the purpose of this study, we used fish, cephalopods, marine mammals and sea birds as groups of organisms. We followed the LME definitions of SHERMAN & DUDA (1999). We used the Baltic and the Black Sea as analogue brackish, temperate, and species-poor ecosystems. We used the North Sea as a marine, temperate ecosystem, and we used the Caribbean and the South China Sea as examples of tropical, species-rich ecosystems.

For fishes, we used the trophic levels, maximum lengths, and LME assignments given in FishBase (FROESE & PAULY, 2000 ; www.fishbase.org). For cephalopods, we used data on distribution and food in NORMAN (2000) and in CephBase (www.cephbase.org). For marine mammals, we used trophic levels from PAULY et al. (1998). For marine birds, we used information on food and distribution from DEL HOYO et al. (1992 ; 1996), BEZZEL (1985), MELTOFTE et al. (1994), and SKOV et al. (1995). Trophic levels (trophs) were calculated from diet composition data as Troph = 1 + weighted mean troph of the food items (see CHRISTENSEN & PAULY (1992) for details, including estimation of standard errors). If no diet composition, but individual food items were known, trophic levels and their standard errors were estimated using a Monte Carlo routine described in PAULY & SA-A (2000). Both routines are implemented in the TrophLab software, which can be downloaded at www.fishbase.org/download/. If no food information was available for a given species, it was assigned the mean troph of congeners or of the respective family. For invertebrates, we relied on an estimate of Mediterranean 'macroscopic fauna' (8500 species) by the European Environment Agency (www/eea/ei/int.). We subtracted from this estimate the 691 Mediterranean species of fish, birds, cephalopods and marine mammals, and assumed that, for the purpose of this study, the remainder could be assigned to trophic levels between 2 and 3.49 (see below).

For the free-scale network analysis we used data on prey items as recorded in FishBase (FROESE & PAULY, 2000). In FishBase food items of fishes are classified into 59 categories such as diatoms, polychaetes, euphausiids, or squids/cuttlefish (SA-A et al., 2000). These categories are similar to the 'trophic species', which have been used in other food web studies and which are defined as "functional groups of taxa that share the same consumers and resources within a food web" (WILLIAMS et al., 2000). For the purpose of this study we considered 385 Mediterranean fish species as nodes and their reported food categories as links.

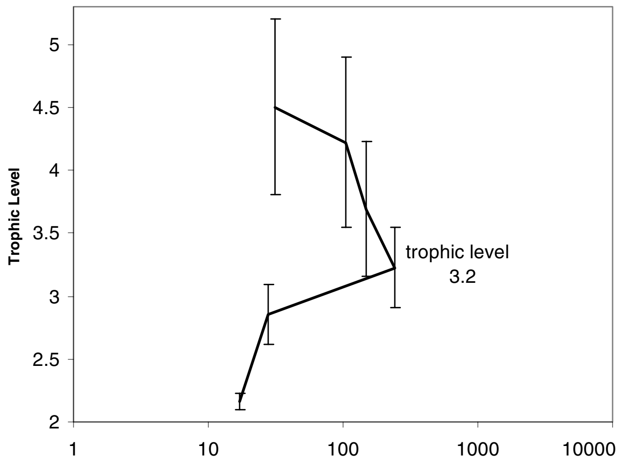

Fig. 1. – Number of fish species of the Mediterranean by trophic level. Error bars show the mean standard error of individual trophic level estimates.

RESULTS AND DISCUSSION

Fig. 1 shows the trophic signatures of 567 species of fish in the Mediterranean, plotted as number of species per 0.5 trophic level. The standard errors increase with trophic levels because second and third-level predators typically exploit a wide range of prey, from herbivores to other second or third-level predators.

Fig. 2 shows the trophic signatures of fishes in the Baltic, the Black Sea, the North Sea, the Mediterranean, the Caribbean and the South China Sea, with total number of species increasing in the same sequence. Despite the considerable differences between these ecosystems in terms of salinity, size, temperature, and species numbers, the signatures are strikingly similar : in all ecosystems fishes cover the whole range of trophic levels, from herbivores near 2.0 to top predators at above 4.5. Both herbivores and top predators contribute about or less than 5% of total species numbers. Highest species numbers always occur around troph 3.2, i.e., with first-level predators feeding mainly on herbivorous organisms. The signatures of the brackish, species-poor Baltic and Black Seas are more similar to each other than to the marine, more speciose North Sea, which has more top-predators and fewer lower-level species, resulting in a signature that cuts across that of the brackish systems. As expected, the subtropical Mediterranean takes an intermediate position between the temperate and the tropical systems. The Caribbean signature is the only one where the lower leg is bent to the right, indicating a relatively higher number of herbivorous fishes than in the other systems.

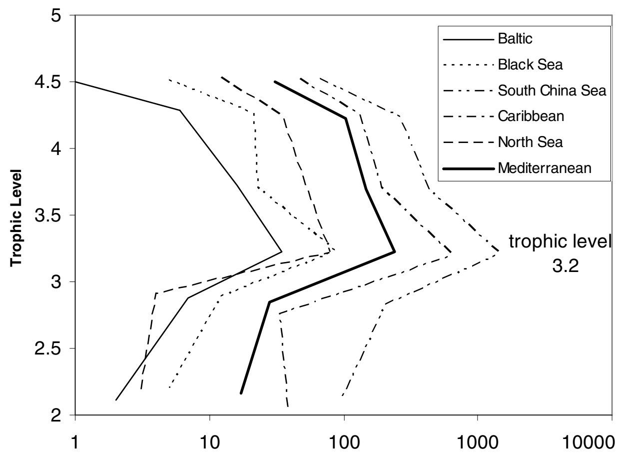

Fig. 2. – A comparison of trophic signatures of fishes in six large marine ecosystems.

Fig. 3 shows the geometric mean maximum lengths of Mediterranean fishes per half trophic level class. Most first-level predators at trophs of about 3.0 are small fishes of about 20 cm maximum length, generally feeding on zooplankton and/or small benthic invertebrates. As expected the mean maximum length increases with trophic level to 1.5 m for top-predators, but it also increases to about 27 cm for herbivores. Variation in 95% confidence limits follows the same pattern.

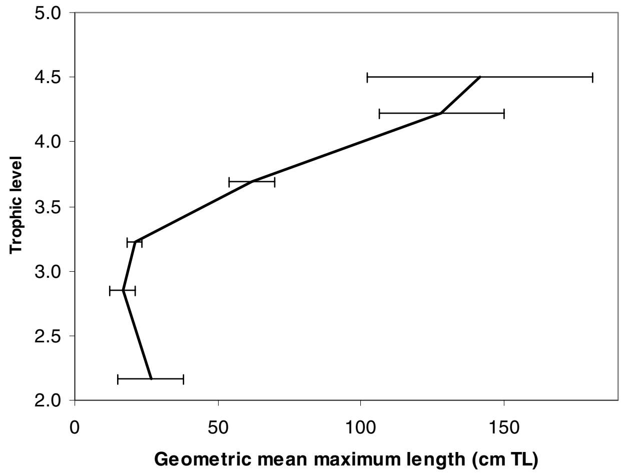

Fig. 3. – Geometric mean maximum length of Mediterranean fishes at different trophic levels, with error bars showing 95% confidence limits.

Fig. 4 shows the length signatures of all six LMEs, all with a signature roughly similar to that of the Mediterranean, with minimum mean size around trophic level 3 and an increase towards higher and lower trophic levels. Tropical systems are typically dominated by smaller species, which is shown here by the signatures of the South China Sea and the Caribbean being mostly left of the temperate systems. The subtropical Mediterranean shows again an intermediate position between temperate and tropical systems, except for the lower trophic levels where it overlaps with the tropical systems.

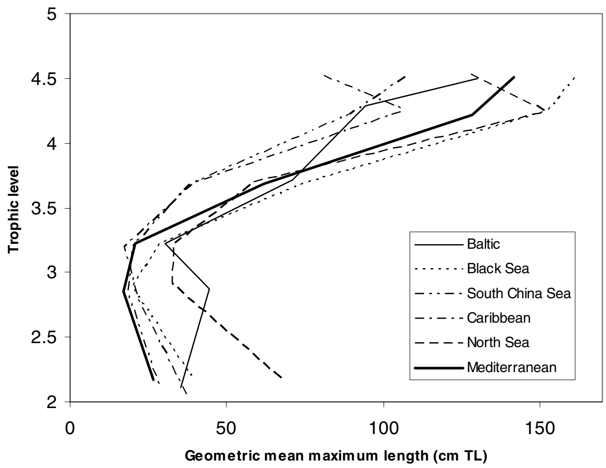

Fig. 4. – Geometric mean maximum length of Mediterranean fishes at different trophic levels, with error bars showing 95% confidence limits.

Fig. 5 shows the trophic signatures of fish, cephalopods, sea birds, and marine mammals in the Mediterranean. Total species numbers of fish are an order of magnitude higher than those of the other groups. Only fish species occupy all trophic levels, whereas birds, cephalopods and mammals are restricted to levels above 3.0. Most cephalopods feed at about trophic level 3.7 (0.5 above fish), and most birds and mammals feed above 4.0, one level above fish. Because of the low number of marine mammals (17), their signature must be viewed with some caution, as improved understanding of the diet of just a few species may alter the signature. Nevertheless, the maximum at 4.2 for marine mammals shows their position as top predators in the Mediterranean, also confirmed by a plot (not shown here) of all marine mammals in the world showing a similar signature and the same maximum. Fig. 6 shows a similar graph for the North Sea, with similar signatures for the respective groups. Species numbers for fish and cephalopods in the North Sea are only about 1/3 of that in the Mediterranean, whereas numbers for sea birds and marine mammals are increased by 50% and 20%, respectively. This reflects the greater role of homoeothermic groups (i.e., marine mammals and sea birds) in colder waters.

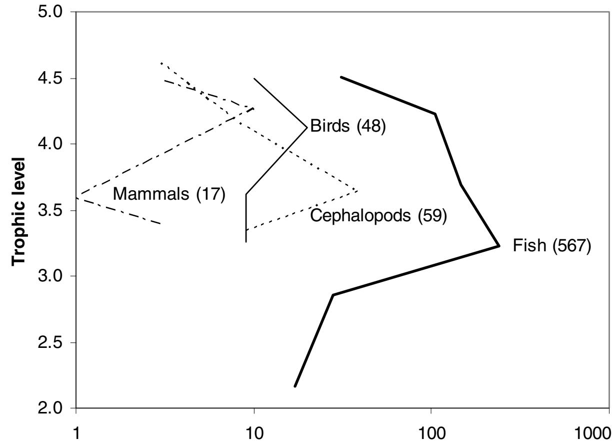

Fig. 5. – Number of species per trophic level for four groups of organisms in the Mediterranean.

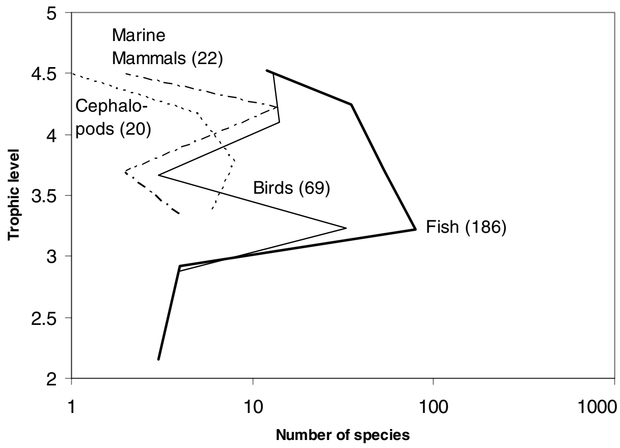

Fig. 6. – Number of species per trophic level for four groups of organisms in the North Sea.

Fig. 7 shows the sum of species per trophic level across the considered groups, resulting in the pyramid structure that is commonly encountered when plotting individual numbers (LINDEMAN, 1942), or biological production (CHRISTENSEN & PAULY, 1992) by trophic level. Looking at Fig. 7 from a phylogenetic perspective, it appears that the four groups jointly dominating the upper trophic levels of marine ecosystems (i.e., fish, marine mammals, sea birds and cephalopods) tend to be highly derived, predatory representatives of their class or phylum, while the organisms abundant at the lower trophic levels (<3), tend to belong to stem groups, and to feed mainly on phytoplankton, benthic algae and detritus (though other invertebrates are also consumed, and cnidarians, chaetognaths and other groups of carnivorous zooplankton are actually restricted to trophic levels above 3).

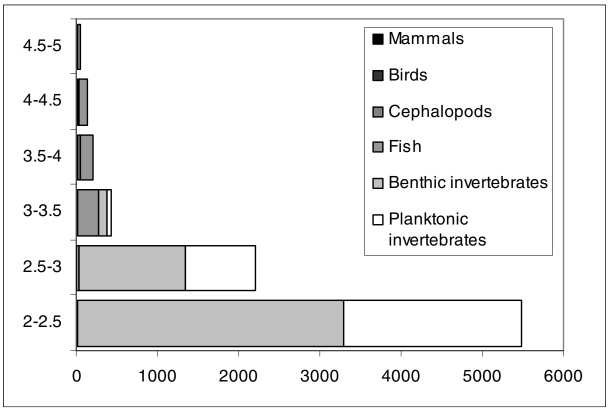

Fig. 7. – Numbers of Mediterranean species per trophic level. Note that about 7800 invertebrates are assumed, with most being herbivores, fewer being omnivores, and very few being first-order predators.

This suggests that overfishing, which tends to remove upper-trophic level animals (PAULY et al., 1998) will tend to reverse the implied evolutionary sequence, as noted in PAULY (1979), and further developed in PARSONS (1996).

Feeding studies exist only for a fraction of the invertebrates in the Mediterranean or other LMEs, and thus the distribution to trophic levels shown in Fig. 7 is hypothetical. Detailed trophic studies on invertebrate species, as well as generalizations by higher taxa such as families and orders, are urgently needed for a better understanding of the foundation of LME food webs.

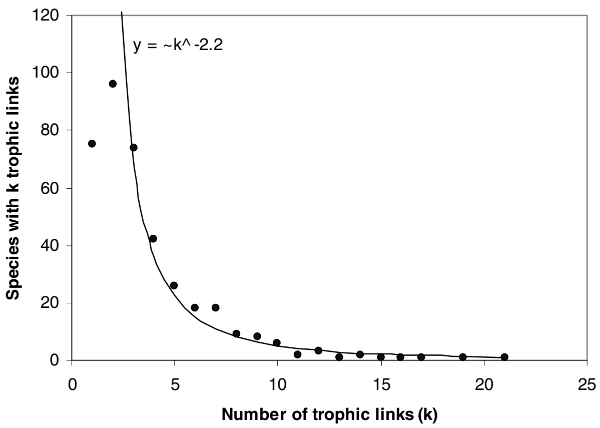

Fig. 8. – Frequency distribution of species with k trophic links, with eye-fitted curve. Note that number of species with one link is probably too high and number with two links probably too low because of a bias caused by 'understudied' species.

Fig. 8 shows a frequency plot of the number of trophic link categories per Mediterranean fish species. The plot shows the typical shape of a scale-free network which is roughly described by a power-law function of the form k^{-y}, and where y typically takes values between 2 and 3 (here $y = 2.2$). Thirty-two fishes (8%) preyed directly on other Mediterranean fishes and the shortest distance between them was thus one link. Analysis of ten randomly selected species showed that they had, on average, 54% of species (208.1, SE +/-16.7) within 2 links, 99% of species (380.9, SE +/-0.10) within 3 links, and all species (384) within 4 links distance from themselves. The weighted mean path length in the food web was 2.38 (SE +/-0.033) links. This agrees well with other food-web analyses, where path lengths between 1.4 and 2.7 have been found (WILLIAMS et al., 2000). Knowledge about mean path length is important as it quantifies the average number of links necessary for an effect to propagate from one species to other species. Significant effects have been shown to propagate often two and sometimes three links away from manipulated species, whereas species more than three links away from each other are functionally disconnected (BRETT & GOLDMAN, 1997; PACE et al., 1999).

It has been suggested that the removal of 5% of the nodes starting with those with highest numbers of links can double path length (COHEN, 2002). In our data set such removal of species with highest numbers of trophic links increased mean path length to 2.43 (SE +/-0.066), which is not significantly (t-test, n=740, $P<0.05$) different from 2.38. To choose a more realistic scenario we removed 38 Mediterranean fishes that were marked in FishBase as 'highly commercial,' many of them upper-trophic level species with many (median=5) trophic links. This removal increased mean path length to 2.45 (SE +/-0.033), which is also not significantly (t-test, n=712, $P<0.05$) different from 2.38. Thus, it appears that food webs are relatively robust towards removal of 5-10% of highly connected species. This might explain the observation that many ecosystems have apparently withstood very strong fishing pressure for a very long time. We want to stress that our application of scale-free network theory to food-web data of Mediterranean fishes is preliminary and a more thorough study of trophic relationships including non-fish species is needed to confirm or reject our results.

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