Metadata of the chapter that will be visualized online

Chapter Title	A Comparative Analysis of Trophic Structure and Functioning in Large--Scale Mediterranean Marine Ecosystems	
Copyright Year	2013	
Copyright Holder	Springer Science+Business Media Dordrecht	
Author	Family Name	**Barausse**
	Particle	
	Given Name	**Alberto**
	Suffix	
	Division	Laboratorio di Analisi dei Sistemi Ambientali
	Organization	Università di Padova
	Address	via Marzolo 9, 35131, Padova, Italy
Corresponding Author	Family Name	**Palmeri**
	Particle	
	Given Name	**Luca**
	Suffix	
	Division	Laboratorio di Analisi dei Sistemi Ambientali
	Organization	Università di Padova
	Address	via Marzolo 9, 35131, Padova, Italy
	Email	lpalmeri@unipd.it
Abstract	The Mediterranean is a sea rich with many kinds of diversity: this hotspot of marine biodiversity covers many habitats and environmental conditions, and is surrounded by three continents, characterized by different cultures and degrees of socio-economic development, whose coastal human activities exert multiple pressures on the marine environment. Yet, surprisingly, the diversity in the structure and functioning of Mediterranean marine ecosystems has not been analyzed rigorously, especially on large spatial scales. Such information are critical to implement an Ecosystem Approach to the management of Mediterranean sub-basins. To fill this gap, a comparative analysis of the South Catalan, the Northern-Central Adriatic, the Northern Adriatic and the North Aegean Seas was performed. Trophic network models of the marine pelagic environment in each system were assembled with Ecopath software, based on published datasets. To facilitate the comparison, models had the same number and kind of trophic groups. Multiple indicators from ecological network analysis consistently highlighted similarities and differences among Mediterranean pelagic food webs. Shared traits included the key role of intermediate-trophic level species, the low overall impact exerted by large predators, and inefficiencies in the exploitation of phytoplankton and detritus production giving rise to high export flows fuelling the benthic compartment. Primary productivity markedly influenced food web properties, but additional	

differences in the global structure of trophic flows emerged, highlighting a great ecosystem diversity. The systems could be ranked in a clear order of development and maturity (from high to low): South Catalan, Northern-Central Adriatic, North Aegean, Northern Adriatic Sea.

24

A Comparative Analysis of Trophic Structure and Functioning in Large-Scale Mediterranean Marine Ecosystems

Alberto Barausse and Luca Palmeri

Abbreviation List

TST	Total system throughput
PPR	Primary production required (to sustain catches)
FCI	Finn's cycling index
PCI	Predatory cycling index
FMPL	Finn's mean path length
FSTPL	Finn's straight-through path length

Introduction

A Sea Rich with Diversity

The Mediterranean is a semi-enclosed sea with a relatively small area compared to other large marine ecosystems worldwide, yet its waters and coasts are characterized by a disproportionately huge diversity from the environmental and socio-economical points of view. Three continents (Europe, Asia, Africa) and 21 countries surround this basin, a number which alone suggests the great variety in human culture and socio-economic development found in Mediterranean coastal zones, which have been inhabited for millennia. Marine environmental and ecological conditions and habitats greatly vary: a wide range of depths is covered, and primary productivity displays a clear west-east and north-south decrease, similarly to fishery landings, a spatial pattern opposite to that of temperature and salinity (Caddy 1993; Caddy et al. 1995; Coll et al. 2010; Fig. 24.1). The Mediterranean Sea is also a hotspot of biodiversity: more than 17,000 marine species occur there, and about a fifth are endemic (Lejeusne et al. 2009; Coll et al. 2010).

This highly-diverse environment interacts with the numerous pressures generated by the heterogeneous coastal human activities, as well as with climate variability, in a complex, intriguing manner, to the point that the Mediterranean has been defined as a "miniature ocean" or a "giant mesocosm" where the effects of climate and anthropic pressures on the world's oceans could be studied (Lejeusne et al. 2009). Climate change should impact this region strongly, acting together and, possibly, synergistically with multiple anthropogenic pressures which are already high in the basin, such as fishing, habitat degradation and loss, pollution and nutrient enrichment. Invasions of alien species is another key impact, possibly driven by both climate and human factors (Halpern et al. 2008; Lejeusne et al. 2009; Coll et al. 2010). The Mediterranean appears to be one of the most human-impacted seas in the world (Halpern et al. 2008; Lejeusne et al. 2009).

The Need for an Ecosystem Approach in the Mediterranean Sea

Diversity, or variety, seems to be the keyword for the Mediterranean Sea. Thus, a sustainable management of human activities impacting the marine environment should be adapted the peculiarities of it local sub-basins and, also, integrated. The latter word means that management should adopt a network perspective, explicitly considering that the ecological impacts of different socio-economic activities can combine, that ecosystem components, both biotic and abiotic, are interconnected and this influences their response to human impacts, and that feedbacks exist between socio-economic and ecological systems: human activities impact marine ecosystems, but the subsequent ecological change can impact human welfare and activities. Such view of an integrated management strategy for human activities impacting the marine environment and its resources is known as the Ecosystem Approach (e.g. CBD 2000; Garcia et al. 2003). This approach has greatly influenced fishery science, which is currently switching from the classical management focus on single species towards multispecies and food web approaches taking predatory interactions into account (Garcia et al. 2003;

A. Barausse • L. Palmeri (✉)
Laboratorio di Analisi dei Sistemi Ambientali, Università di Padova, via Marzolo 9, 35131 Padova, Italy
e-mail: lpalmeri@unipd.it

S. Goffredo and Z. Dubinsky (eds.), *The Mediterranean Sea: Its history and present challenges*,
DOI 10.1007/978-94-007-6704-1_24,

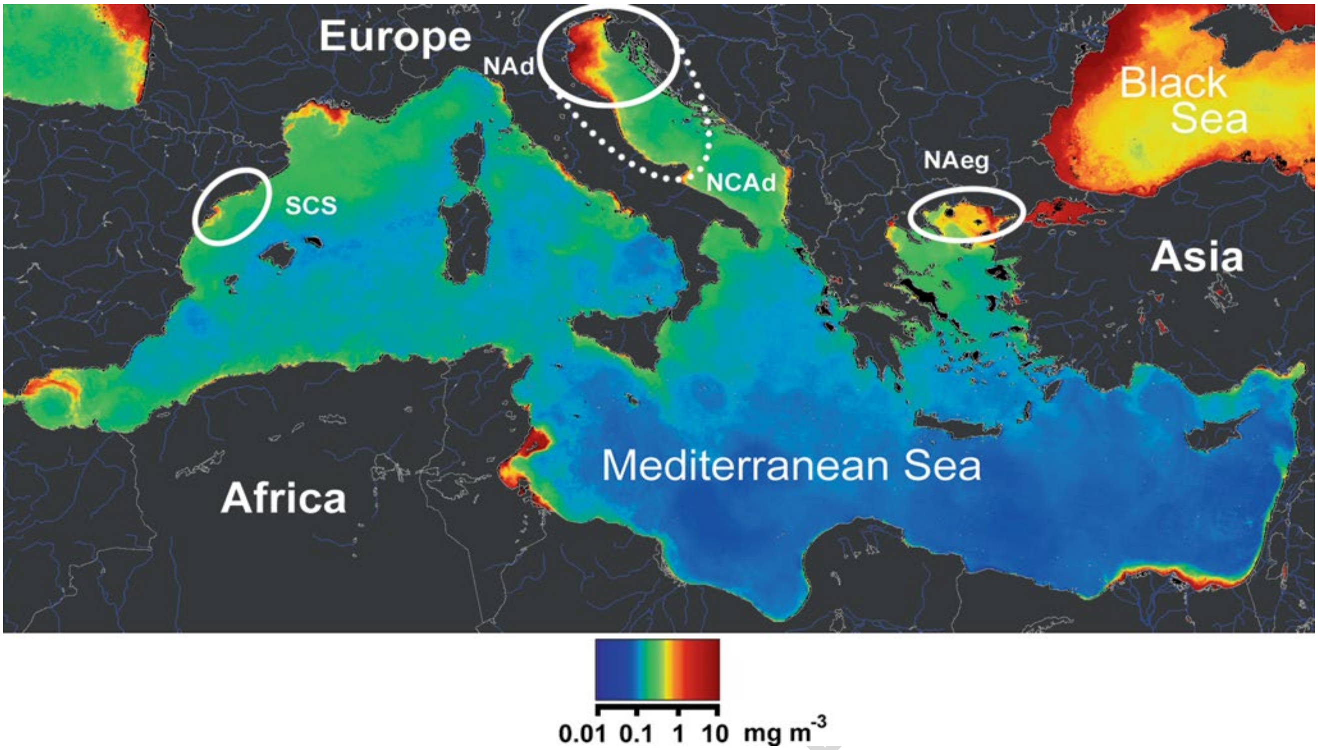

Fig. 24.1 The location of the four ecosystems analyzed, as indicated by the ovals. *SCS* indicates the South Catalan Sea; *NAd* is the Northern Adriatic Sea; *NCAd* is the Northern and Central Adriatic Sea (*dotted oval*, also including the *continuous oval* of the Northern Adriatic); *NAeg* is the Northern Aegean Sea. The *color map* represents satellite-based estimates of chlorophyll-a concentration in Mediterranean marine waters (mg m^{-3}, see scale bar; monthly composite of SeaWiFS data for June 1998; image downloaded from the OceanColour portal, Institute for Environment and Sustainability, European Commission – Joint Research Centre, http://oceancolour.jrc.ec.europa.eu/). The map is not supposed to mirror exactly the spatial patterns of primary productivity over one or multiple years, nevertheless marked differences in algal biomass can be seen across the basin

Worm et al. 2009). The Ecosystem Approach is becoming more and more popular and is being integrated into marine environmental policies worldwide, an outstanding example being the European Marine Strategy Framework Directive (EU 2008).

The Need for Ecological Network Analysis

As an Ecosystem Approach can only be applied based on a good knowledge of the integrated functioning of marine ecosystems and their response to human pressures and environmental forcing, several ecological questions appear to be of practical importance. For example: how strongly does one species influence the others? Are there species playing particularly important roles in the marine ecosystem? What are the main pathways through which energy flows from primary producers to other species? Is the ecosystem configuration resilient and resistant to external disturbances? Are whole-system properties such as productivity, efficiency and stability affected by human pressures? Is the ecosystem found in an early stage of ecological succession, e.g. is it overexploited and stressed, or is it mature and developed (Odum 1969, 1985; Ulanowicz 1997)?

To answer these questions, ecologists have studied the structure and function of food webs, i.e. the networks of trophic interactions linking ecosystem populations, by quantifying energy and material flows within them.[1] This approach to the study of ecosystems[2] is called Ecological Network Analysis and has partly been inspired by economics, a scientific field in which data on commodity flows are more frequently available than explanations concerning what caused such flows (Ulanowicz 1986, 1997, 2004; Baird et al. 1991).

The analysis of marine trophic networks is important because it helps to refine our conceptual models of how

---

[1] Such flow reconstruction results in a trophic network "model", see section "Materials and Methods".

[2] Although marine ecosystems are influenced by many factors besides predation, the assumption made when focusing on food webs is that, in phenomenological fashion, the status of a system is mirrored by the structure of its trophic flows. No direct causal relationship between system status and flows is claimed, much like temperature reflects, but is not the cause of the health or sickness of a person.

ecosystems function as a whole. A conceptual model is the first, key step to construct a quantitative model of an ecological system to be used for management purposes (Jørgensen and Bendoricchio 2001). It is well-known that the Mediterranean Sea encompasses greatly-diverse ecosystems, reflecting the abovementioned diversity in species, habitats, environmental conditions and pressures, but, surprisingly, the diversity in ecosystem structure and functioning has not been analyzed rigorously. Relatively few food web models and ecological network analysis applications have been published for Mediterranean marine systems, mostly during the last decade and covering limited areas of the basin. According to the review of Coll and Libralato (2011), only one publication dealt with the Southern Mediterranean, analyzing the Gulf of Tunis food web. Moreover, few comparisons of trophic networks from different Mediterranean sub-basins exist (Coll et al. 2008; Libralato et al. 2010; Tsagarakis et al. 2010; Coll and Libralato 2011). Comparative studies are vital to highlight differences in the functioning of Mediterranean ecosystems, which would result in different management plans depending on the local ecological peculiarities.

The goal of this work is to perform a comparative analysis of four trophic network models of large-scale marine ecosystems in the Mediterranean Sea during recent years, focusing on differences and similarities in their structure, functioning and development *sensu* Odum (1969). They are the South Catalan Sea (Coll et al. 2006), the Northern and Central Adriatic Sea (Coll et al. 2007), the Northern Adriatic Sea (Barausse et al. 2009) and the North Aegean Sea (Tsagarakis et al. 2010). These four models were carefully selected among published ones (Coll and Libralato 2011), based both on their quality and on common characteristics (e.g. system surface) needed to exclude artificial sources of bias from the comparison (see Materials and Methods). All the original trophic networks were standardized into a common structure, i.e. models were aggregated into the same number of network nodes, each node representing similar species or functional groups. Model standardization is fundamental because ecosystem indicators and properties from ecological network analysis can strongly depend on, and be biased by, the number of nodes in a network (e.g. Abarca-Arenas and Ulanowicz 2002). To our knowledge, very few papers have performed comparative analyses of standardized Mediterranean food webs. Coll et al. (2008) analyzed only the South Catalan and the North-Central Adriatic Sea, while Libralato et al. (2010) compared the North-Central Adriatic with a small marine reserve (1.2 km^2) in the Northern Adriatic Sea. Tsagarakis et al. (2010) compared three marine systems (South Catalan, North-Central Adriatic and North Aegean Sea), but the models showed some differences in the degree of aggregation. In this work, to ensure the best aggregation possible, only pelagic organisms (living in the water column) were included in the standardized model structure, while benthic and demersal ones (living on or close to the bottom) were excluded. Why only pelagic ecosystems? On large spatial scales, they seem to be better studied and understood with respect to benthic ones, possibly because data are more widely available and food webs are simpler. Thus, pelagic data were probably of better quality and it was easier to find a standardized model structure suitable for all systems. A forced and therefore partly-inadequate standardization of the benthic compartment would have been a potential source of artificial biases in the comparative analyses.

Materials and Methods

Models of Trophic Networks and the Ecopath Methodology

In a trophic network model, a food web is represented as a set of nodes (or groups) each representing some organisms, e.g. a population, taxon or functional group, and as the trophic flows leaving and entering such nodes. Flows include consumption and predation, i.e. flows from one node to another, imports and exports from the system (e.g. migratory flows, catches), respiration, and flows to detritus (e.g. excretion, egestion, dead organisms due to illness or old age). Each node is characterized by the total biomass of its organisms. When constructing a model, usually, information on flows and biomasses in that ecosystem is obtained from literature, but it can be difficult to collect the huge amount of data needed, especially with good precision. Approaches to tackle this issue and reconstruct the values of trophic flows and biomasses include inverse modeling (Vézina and Platt 1988) and the Ecopath methodology (Christensen et al. 2005), which, originally, was used to build the four models and, then, to standardize and analyze them.

Ecopath is based on the principle of mass conservation and the typical assumption that the food web is in an approximate steady state over the modeled period. Based on these considerations, two mass budgets can be written for each model group: (1) its production is equal to the sum of different mortality sources (predation, fishing, other mortality sources such as illness and old age) plus net exports and emigration from the system; (2) flows into the node (consumption) are equal to those leaving it, i.e. production plus respiration and unassimilated food. When written for all N groups in the network, these budgets result in a linear system:

$$B_i(P/B)_i = \sum_{j=1}^{N} B_j(Q/B)_j DC_{ij} + Y_i + B_i(P/B)_i \cdot \left(1 - EE_i\right) + E_i + Ex_i \qquad (24.1)$$

$$B_i(Q/B)_i = B_i(P/B)_i + B_i(R/B)_i + GS_i B_i(Q/B)_i \qquad (24.2)$$

B_i is the biomass of group i, $(P/B)_i$ is its production rate, $(Q/B)_i$ is the consumption rate, DC_{ij} is a matrix whose elements represent the fraction that group i represents in the diet of j, Y_i are fishery yields, EE_i is the ecotrophic efficiency and represents the fraction of production "used" in the system, so that $(1-EE_i)$ represents the fraction of production flowing into detritus due to mortality sources such as illness and old age, E_i is net emigration from the system, Ex_i represents net exports, $(R/B)_i$ is the respiration rate and GS_i the fraction of unassimilated food. The modeller has to specify all such data but two unknowns for each group, generally EE and R/B, which are estimated by solving the linear system. The model is considered acceptable if it is mass-balanced, i.e. $EE<1$ and $R/B>0$ for all groups, otherwise input data are mutually inconsistent and have to be varied within uncertainty ranges. Thus, the mass-balance approach reduces the uncertainty about input values, ensuring that the network is, at least, a physically-feasible representation of reality where mass is conserved and flows are non-negative.

The Four Trophic Network Models and Their Standardization

Only published and high-quality Ecopath models, whose construction was well-documented, were chosen for standardization and subsequent analysis. Also, models had to describe relatively-large marine systems (surface at least 1,000 km^2) during recent years (1990s or 2000s). These criteria restricted the number of systems for which models were available in the literature, but allowed us to select only the ones which were fully comparable, as ecosystem properties can be strongly influenced by surface and depth (Libralato et al. 2010) and by the intensity of anthropogenic pressures. For example Piroddi et al. (2010) described the Northeastern Ionian ecosystem in 1964, before the decline of most fishing resources due to overexploitation and changes in primary productivity. Such model was not included in this study because, most probably, it would have been exceedingly different from the others due to the relatively "pristine" state described.

The selected ecosystems (Fig. 24.1) are now briefly described. More details are found in the cited publications describing the original models. All systems represented continental shelves except the South Catalan Sea, which also included the upper slope. The model of the Northern Adriatic food web during 1996–1998 originally comprised 34 groups (Barausse et al. 2009). The basin has a surface of 32,000 km^2, depth range about 0–50 m and is very productive and eutrophic due to the nutrient loads discharged by Italian rivers. For this reason, the system has been strongly exploited for decades by fisheries targeting mostly small pelagic fish and invertebrates, and is one of the most fished Mediterranean basins (Barausse et al. 2009, 2011). Coll et al. (2007) constructed a 40-group model of the Northern and Central Adriatic Sea during the 1990s, covering a surface of 55,500 km^2 (depth range from 10 to 200 m) which partially overlaps with the area of the Northern Adriatic model. This second model was included to represent a deeper, more oligotrophic ecosystem where more large pelagic predators (e.g. tunas) were found with respect to the more productive Northern basin. Similarly to the Northern Adriatic, fishing pressure is intense in this system (Coll et al. 2007). The North Aegean Sea food web in the mid-2000s (Tsagarakis et al. 2010) had 40 groups and covered a surface of 8,374 km^2, depth range from 20 to 300 m. The ecosystem is oligotrophic but pelagic productivity is high compared to other sub-basins of the Eastern Mediterranean due to the influence of nutrient-rich Black Sea waters, river discharges and the extended continental shelf. A major fraction of trophic flows is originated in the pelagic compartment. Anchovy and sardine dominate fishery landings and the system is probably unsustainably fished (Tsagarakis et al. 2010). The 40-group network of the South Catalan Sea (Coll et al. 2006) represented the system during 1994; its surface was 4,500 km^2 and depth ranged from 50 to 400 m. The ecosystem is oligotrophic and has been highly exploited for a long time. Again, the pelagic domain dominates **trophic flows and biomasses** (Coll et al. 2006).

In all networks, biomasses were expressed as wet weight on a per area basis (t km^{-2}) and biomass flows as yearly averages (t km^{-2} y^{-1}). Food web models were digitized based on the original publications, imported into Ecopath software version 5.1.218 (www.ecopath.org) and standardized into a common structure of 13 groups (Table 24.1). Such structure comprised one detritus group, representing non-living bioavailable matter, and three plankton compartments: primary producers (phytoplankton), zooplankton and jellyfish. Fish were sorted according to size: three small pelagic fish groups, representing two abundant species in the systems (sardine and anchovy) and other small pelagics; medium-sized pelagics, such as mackerel or horse mackerel; large pelagics, representing species such as tuna, swordfish or sharks. A bentho-pelagic fish group was also included. Other groups were cephalopods (bentho-pelagic and pelagic, e.g. squid), sea-mammals and sea-birds. Model standardization involved the lumping of some groups in the original models, e.g. mackerel, horse mackerel and medium pelagic fishes in Tsagarakis et al. (2010) were aggregated into the medium pelagics group. Each aggregated group had biomass and flows (production, consumption, landings, etc.) equal to the sum of those of the groups aggregated to compose it. Unlike other models, the Northern Adriatic standardized network only included 12 and not 13 nodes, since large pelagics were not incorporated in the original model due to their low biomass. Such ecologically-meaningful difference among

Table 24.1 The common structure of the standardized models of Mediterranean trophic networks

Standardized network model	North Aegean Sea	Northern Adriatic Sea	Northern and Central Adriatic Sea	South Catalan Sea
1. Detritus	Detritus	Detritus	Detritus	Detritus
2. Phytoplankton	Phytoplankton	Phytoplankton	Phytoplankton	Phytoplankton
3. Zooplankton	Mesozooplankton	Zooplankton	Micro and mesozooplankton	Micro and mesozooplankton
4. Jellyfish	Jellyfish and *M. leidyi*	Jellyfish	Jellyfish	Jellyfish
5. Pelagic – benthopelagic cephalopods	Squids	Squids	Benthopelagic cephalopods	Benthopelagic cephalopods
6. Benthopelagic fish	Hake; Benthopelagic fishes; Picarels and bogue	European hake; Nectobenthic zooplanktivorous fish	Hake (1); Hake (2); Benthopelagic fish	Poor cod; Juvenile hake; Adult hake; Blue whiting; Benthopelagic fishes
7. Anchovy	Juvenile anchovy; Adult anchovy	Anchovies	European anchovy	European anchovy
8. Sardine	Juvenile sardine; Adult sardine	Sardines	European pilchard	European pilchard
9. Other small pelagic fish	Other small pelagic fishes	Other small pelagics	Other small pelagic fish	Small pelagic fishes
10. Medium-sized pelagic fish	Horse mackerels; Mackerels; Medium pelagic fishes	Mackerel; Horse mackerel	Horse mackerel; Mackerel; Atlantic bonito	Horse mackerel; Mackerel; Atlantic bonito
11. Large pelagic fish	Large pelagic fishes	–	Large pelagic fish	Large pelagic fishes
12. Seamammals	Dolphins	Dolphins	Dolphins	Dolphins; Fin whale
13. Seabirds	Seabirds	Seabirds	Seabirds	Audouins gull; Other sea birds

For each of the four ecosystems analyzed, the table reports which groups of the original model were used and, in some cases, lumped together to form the corresponding group of the standardized network

models did not introduce artificial biases into the results: even if a large pelagics node had been added to the Northern Adriatic model, its low biomass and flows would not have influenced the network analysis indicators computed for the inter-system comparison.

Exchanges of matter between living groups in the pelagic domain and those found in the original models but not included in the standardized version were represented as import or export flows through the system boundary. Such external groups included benthos and demersal fish, and groups which were found only in some of the analyzed food webs and thus, to obtain a common network structure, could not be included in the present analysis, e.g. ciliates for the North Aegean model, or sea turtles. No imports or exports for detritus were include in the standardized models. In the original networks there were groups representing fishery discards and by-catches, but here they were excluded since, generally, a large fraction of discarded catches was benthos or demersal fish. Consequently groups feeding on discard were assumed to feed on imports.

Indicators from Ecological Network Analysis

To compare the four models, indicators based on ecological theory, thermodynamics and information theory were computed for each network based on its flows and biomasses. The focus was on properties related to whole-system functioning or the global role of groups in the food web. Indicators based on trophic levels (Christensen et al. 2005) were not calculated, because the not-negligible imports from the benthic compartment in the diets of some groups could have led to biased assessments of trophic levels, misrepresenting the actual trophic positions.

Indicators Based on Flows, Biomasses and Their Ratios

Several types of flows were assessed in each network: total primary production, the sum of all consumption, of all respiratory flows, of all flows into detritus, of all production, of all catches, of all exports. The sum of all network flows, or Total System Throughput (*TST*), was computed to gauge the system activity and energetic size (Ulanowicz 1986; Christensen et al. 2005). The total biomass in the network was computed by summing over all living groups, i.e. excluding detritus.

Based on such values, other indicators were computed such as the net system production (primary production minus respiration flows) which, according to the theory of ecological succession, should approach zero in more mature ecosystems (*sensu* Odum 1969), where primary production is more efficiently exploited and more biomass is stored, as reflected by higher respiration (Odum 1969; Christensen et al. 2005).

Consequently, the primary production-total respiration ratio (dimensionless) should be close to one in mature systems. The primary production-total biomass ratio (y^{-1}) should be higher in ecosystems in their early developmental stages, when populations are characterized by high turnover rates (i.e. production-biomass ratios), and should decrease as systems mature and biomass is stored (Odum 1969; Christensen et al. 2005). For similar reasons, the total biomass-*TST* ratio (y), i.e. the biomass sustained by a unit of flow in the system, should be higher in developed ecosystems, where biomass is accumulated, K-selected organisms with lower metabolic rates dominate, and energy transfers in the food web are more efficient and organized (Odum 1969; Peters 1983; Ulanowicz 1997; Christensen et al. 2005).

Fishing

Fishery gross efficiency (dimensionless) was calculated as the ratio of catch (including discards) to primary production. High values can indicate that fishing pressure is high or, alternatively, that catches mainly consist of abundant low-trophic level species (Christensen et al. 2005). The equivalent units of primary production required (PPR) to sustain catches represented the sum of primary and detritus production consumed at the bottom of all the trophic chains leading to fished groups and associated catches, similarly to Odum's emergy (Christensen et al. 2005). Unlike fishery gross efficiency, PPR weights catches of high-trophic level predatory species more than the same amount of caught herbivorous species. PPR was expressed as percentage of the overall detrital and phytoplankton production in the ecosystem.

Food Web Structure and Cycling

Connectance (dimensionless) is the number of existing predator-prey links in the food web divided by the number of potential links, i.e. the fraction of realized links (Christensen et al. 2005), and it gauges the connectedness of the network. The System Omnivory index (dimensionless; Christensen et al. 2005) provides similar information, but it takes the magnitude of trophic flows into account: it is the average Omnivory index of consumer groups, weighted by the logarithm of their food intake. The Omnivory index of a group is the variance of the trophic levels of its preys. The System Omnivory index should increase with system maturity, as the flow structure changes from linear to web-like (Odum 1969).

The number of cycles in the network was computed, as well as their average length (the mean number of trophic interactions in a cycle, i.e. without taking the magnitude of flows involved in different cycles into account). The amount of cycled flows, i.e. passing more than once through the same compartment, was calculated, as well as its ratio with *TST*, named Finn's Cycling index (FCI). Such dimensionless fraction should be higher as systems mature, becoming less dependent on exogenous inputs, and trophic flows become more diverse (Odum 1969; Finn 1980; Ulanowicz 1986, 2004; Christensen et al. 2005). The Predatory Cycling Index (PCI; Christensen et al. 2005) is the ratio of cycled to total system throughput, but calculated after cycles involving detritus have been removed.

Finn's mean path length (FMPL) was computed as *TST* divided by the sum of exports and respiratory flows (Finn 1980; Christensen et al. 2005). FMPL represents the average number of compartments that a unit of inflow goes through before leaving the food web, and should grow with ecosystem maturity in response to increased flow and species diversity, connectedness and cycling (Odum 1969; Christensen et al. 2005). Finn's straight-through path length (FSTPL) has a similar meaning: it is the average path length in the network if cycles are neglected, i.e. the ratio of the throughput going straight through the system (i.e. *TST* minus cycled flows) to the sum of exports and respiration (Finn 1980).

Information Theory and Ascendency

Matter/energy flows in ecological networks can be translated into flows of information (Ulanowicz 1986). In general, information is carried by changes in observable physical quantities (e.g. matter or energy) through which it can be stored and propagated. In analogy with Shannon's definition of entropy, the diversity of flows in a trophic network is:

$$H = -K \cdot \sum_{i,j} P_{ij} \log_2 P_{ij} \tag{24.3}$$

$P_{ij} = J_{ij} / TST$ is the unconditional probability that flow J_{ij} from i to j occurs, and the sum is over all i, j combinations. H is related to the structure of the network of flows, but not to system size, which is measured by *TST*. Conversely, *TST* does not say anything about network organization. Since the scalar K in (24.3) defines the units of information (the scale) and *TST* is a feature of the network scale, Ulanowicz (1986) proposed $K = TST$ and termed (24.3) the network capacity C, which can be factorized as $C = A + \Phi$, where:

$$A = TST \bullet \sum_{i,j} P_{ij} \log_2 \frac{P_{i|j}}{P_j^*} \tag{24.4}$$

$$F = -TST \bullet \sum_{i,j} P_{ij} \log_2 \frac{P_{i|j} P_{ij}}{P_j^*} \tag{24.5}$$

A is called ascendency and Φ is the overhead. $P_{i|k} = J_{ik} / \sum_q J_{iq}$ is the conditional probability that a unit of medium enters k knowing *a priori* that it originated in i, and $P_k^* = \sum_q J_{qk} / TST$ is the *a priori* probability that one unit of medium flowing in the network enters k. C measures the maximum exchangeable information in all potential network configurations attainable with the available machinery (connections and flow intensities), while A accounts for the information actually realized in the current configuration. Φ measures the degrees of freedom available to the network, i.e. its capability to rearrange in response to external disturbances.

Ulanowicz (1986, 1997, 2004) proposed that ecosystems show a propensity to increase in *A*, because it measures both the growth (or activity, an extensive property represented by *TST*) and development (or organization, an intensive property given by the summation in (24.4), called average mutual information or *AMI*) of the system. An increase in *TST* means that the system has grown in the usual economic sense. An increase in *AMI* means that the system has developed new constraints to channel the flows into more specific and efficient pathways. Thus increasing *A* indicates that the system is experiencing growth and/or development (Ulanowicz 1997). Processes that increase *A* include a greater number of species, a higher retention of resources and the specialization of the food chain, which are among the primary signs that the ecosystem is maturing (Odum 1983). Such propensity to achieve an efficient, streamlined network configuration is accompanied by a trade-off: high *A* can mean low Φ, i.e. the system becomes vulnerable to perturbations, if their sum *C* is fixed (Ulanowicz 1986, 1997, 2004).

C, *A* and Φ can all be expressed as the sum of four contributions due to different flow types: flows between groups (internal flows), respiratory flows, imports and exports. In particular, the ratio of internal ascendency to internal capacity (A_i/C_i) is the realized fraction of the potential organization of prey-predator flows and measures system maturity, resistance and efficiency. The internal overhead-capacity ratio (Φ_i/C) originates from the redundancy of predatory connections and measures system resilience (Baird et al. 1991; Ulanowicz 1997, 2004).

Input-Output Analysis and Keystone Species

The global importance of different groups in the food web was evaluated using the mixed trophic impact matrix (Ulanowicz and Puccia 1990; Libralato et al. 2006), whose elements m_{ij} represent the total effect that an infinitesimal change in the biomass of one group *i* has on another group *j*. m_{ij} is the sum of all direct and indirect (i.e. mediated through trophic interactions) effects, and can be positive or negative. The overall impact of a group *i* on the ecosystem can be estimated as:

$$\varepsilon_i = \sqrt{\sum_{j \neq i} m_{ij}^2} \qquad (24.6)$$

Where impacts are summed over all living groups but *i*. To identify keystone species, i.e. groups having a disproportionately high total impact on the system with respect to the fraction p_i of the total living biomass that they represents, the keystoneness *KS* (Libralato et al. 2006) was calculated for each group *i*:

$$KS_i = \log_{10}\left[\varepsilon_i\left(1 - p_i\right)\right] \qquad (24.7)$$

Results

Flows and Biomasses

Table 24.2 reports indicators from ecological network analysis computed for the four standardized pelagic models. Absolute biomass flows showed that the Adriatic Sea was clearly the most vigorous and dynamic system, particularly the Northern basin, where *TST* was 1.6 times as large as that of the model including the Central basin, and nearly 4 times as those of the North Aegean and South Catalan networks, showing similar total flows. Primary productivity (Table 24.2) partly explained these differences: the last two systems are oligotrophic while the Adriatic is quite productive, and eutrophic in its Northern area (Barausse et al. 2009).

However, differences in total primary production and in net system production among systems were much larger than those in *TST*: in the Northern Adriatic, phytoplankton productivity was twice as large as that of the Northern and Central Adriatic, 4.3 times as that of the North Aegean and 6 times as that of the South Catalan Sea, while net system production was 2.2 times as large as in the Northern and Central Adriatic, 4.5 times as large as in the North Aegean and 14.8 times as large as in the South Catalan Sea. These results suggested that not only primary production, but also the flow structure differed among food webs, e.g. the South Catalan network was probably more complex and longer while the Northern Adriatic food web was shorter. Indeed, *TST* partitioning among flow typologies greatly varied across systems: absolute consumption flows were largest in the Northern and Central Adriatic Sea, where they represented about 27 % of *TST*, similarly to the North Aegean model. Consumption dominated total flows in the South Catalan Sea (47 % of *TST*), while in the Northern Adriatic Sea it corresponded only to 17 % of *TST*. In this last network, *TST* was dominated by exports (43 %), mainly unconsumed detrital production and predatory flows towards the benthic compartment (catches were negligible), and by flows to detritus (33 % of *TST*), suggesting that a large fraction of production in the system was not immediately consumed or not used at all. Similarly, flows to detritus and exports dominated total flows in the Northern and Central Adriatic (respectively, 35 and 28 % of *TST*) and in the North Aegean Sea (respectively, 24 and 42 % of *TST*). The sum of flows to detritus and exports was less than half of the total flows (respectively, 21 and 12 % of *TST*) only in the South Catalan model.

In line with these results, the ecotrophic efficiency of detritus, i.e. the fraction of pelagic flows into detritus which was consumed in the pelagic ecosystem, was high only in the South Catalan Sea (0.55), being 0.22 in the Northern and Central Adriatic, 0.17 in the North Aegean and only 0.08 in

Table 24.2 Indicators from ecological network analysis, computed for the four standardized trophic network models of Mediterranean marine ecosystems

Indicator	Currency	North Aegean	Northern Adriatic	North-Central Adriatic	South Catalan
Flows, biomasses and their ratios					
Consumption flows	t km^{-2} y^{-1}	316.2	801.4	846.0	606.6
Export flows	t km^{-2} y^{-1}	506.9	2068.3	876.5	148.7
Respiration flows	t km^{-2} y^{-1}	100.1	359.6	282.8	255.3
Flows into detritus	t km^{-2} y^{-1}	293.6	1612.8	1078.8	268.2
Total system throughput (*TST*)	t km^{-2} y^{-1}	1217.0	4842.0	3084.0	1279.0
Sum of all production	t km^{-2} y^{-1}	635.0	2553.0	1442.0	609.0
Total primary production	t km^{-2} y^{-1}	536.1	2310.0	1150.0	386.7
Tot. primary prod./tot. respiration	–	5.35	6.42	4.07	1.51
Net system production (p.p. – resp.)	t km^{-2} y^{-1}	435.9	1950.4	867.3	131.4
Total primary prod./total biomass	y^{-1}	35.44	71.89	30.63	11.88
Total biomass/*TST*	y	0.0124	0.0066	0.0100	0.0254
Total biomass (excluding detritus)	t km^{-2}	15.13	32.13	37.54	32.55
Fishing					
Total catches	t km^{-2} y^{-1}	1.45	2.95	1.17	4.45
Fishery gross efficiency (catch/p.p.)	–	0.0027	0.0013	0.0010	0.0115
PPR to sustain catches	%	4.39 %	3.31 %	2.92 %	18.03 %
Food web structure and cycling					
Connectance	–	0.35	0.40	0.30	0.30
System Omnivory Index	–	0.26	0.18	0.33	0.37
Finn's mean path length (FMPL)	–	2.00	1.99	2.66	3.17
Finn's straight-through path length (FSTPL)	–	1.91	1.96	2.48	2.68
Number of cycles in the food web	–	322	318	114	104
Mean length of cycles	–	5.30	5.82	4.91	4.82
Throughput cycled	t km^{-2} y^{-1}	59.9	78.2	206.0	196.3
Finn's cycling index (FCI)	% of *TST*	4.92 %	1.61 %	6.68 %	15.35 %
Throughput cycled (excl. detritus)	t km^{-2} y^{-1}	13.4	14.5	36.3	25.7
Predatory cycling index (PCI)	% of *TST* w/o detr.	2.13 %	0.89 %	3.92 %	3.46 %
Information theory					
Ascendency (*A*)	t bits km^{-2} y^{-1}	839.8	4025.7	3014.4	1149.9
Overhead (*Φ*)	t bits km^{-2} y^{-1}	3513.9	10267.2	6909.7	3584.4
Capacity (*C*)	t bits km^{-2} y^{-1}	4353.7	14292.9	9924.1	4734.3
A/*C*	%	19.3 %	28.2 %	30.4 %	24.3 %
Internal *A*/Internal *C*	%	11.8 %	22.1 %	18.7 %	19.7 %
Internal *Φ*/*C*	%	44.7 %	39.7 %	53.6 %	50.3 %

the Northern Adriatic Sea. Such system ranking was exactly opposite to that based on the fraction of *TST* represented by exports and detrital flows. The ratio of all production to primary production in the system suggested, similarly, that basal resources were used more intensively, or more efficiently, in the South Catalan Sea (ratio = 1.57) than in the Northern-Central Adriatic (1.25), the Northern Aegean (1.18) and, lastly, the Northern Adriatic Sea (1.11).

Total biomasses seemed to be only partially related to primary productivity or other flows in the systems (e.g. *TST*, production, consumption), suggesting differences in the development of the flow networks. Living biomass was highest in the Northern and Central Adriatic network, while the more productive Northern basin showed a similar value to that of the South Catalan Sea. The North Aegean Sea showed the lowest biomass, despite a primary productivity 1.4 times as large as that of the South Catalan ecosystem. The primary production-total biomass ratio, representing the algal production needed to sustain a unit of biomass in the food web, suggested that the systems could be ranked in this order of decreasing specific productivity and of increasing efficiency and maturity: Northern Adriatic, North Aegean, Northern and Central Adriatic, South Catalan Sea. The primary production-respiration ratio provided the same ranking, suggesting that the South Catalan Sea was the most mature system since, there, the largest fraction of energy fixed by phytoplankton was respired, i.e. used to sustain the living biomass stored in the ecosystem. Indeed, in the South Catalan Sea the total biomass-*TST* ratio, i.e. the biomass sustained by a unit of flow in the food web, was twice as large as in the North Aegean Sea, 2.5 times as large as in the Northern and Central Adriatic, and 3.8 times as large as in the Northern Adriatic Sea.

Fishing

Catches per unit of system surface greatly varied: by far, the highest values were observed in the South Catalan Sea, 3.8 times as large as the lowest catches of the Northern and Central Adriatic Sea. Such difference was even larger (11.5 times) when rescaling catches on primary production. PPR to sustain pelagic fisheries was markedly larger in the South Catalan Sea with respect to other systems, suggesting quite a strong fishing pressure: nearly a fifth of the whole primary production indirectly sustained exploitation. Again, the Northern and Central Adriatic Sea scored lowest in PPR among the four systems.

Pathways and Cycles

The Northern Adriatic and North Aegean networks were the most connected according to connectance, but the complexity of the food webs was ranked differently if the magnitude of flows along different pathways was weighted through the System Omnivory index. The South Catalan Sea had the most web-like network, as well as the longest average flow pathway (FMPL>3 only in this system), and this was true even if cycles were neglected (FSTPL). The System Omnivory index, FMPL and FSTPL consistently showed that the Northern and Central Adriatic had the second most complex network, while the Northern Adriatic and Aegean Sea had short (both path length measures<2) and linear flow structures.

The number of cycles and their mean length was markedly higher in the Northern Adriatic and North Aegean Seas, about 320, but, similarly to connectance, these indicators were not much informative because they did not weight the magnitude of flows along trophic pathways. FCI showed that cycling was actually most intense in the South Catalan network, followed by far by the Northern and Central Adriatic Sea, while it was lowest in the Northern Adriatic Sea. This rank was partly confirmed when detritus and the cycles involving it were not considered, but the top positions were exchanged: PCI was slightly higher in the Northern and Central Adriatic than in the South Catalan Sea, for which FCI >>PCI. Therefore, in the latter system, a large fraction of cycled flows involved the detrital pool. In general, cycling involved a small fraction of total flows, especially when neglecting detritus (mean FCI=7.14 %, mean PCI=2.60 %).

Indicators from Information Theory

System ranking according to ascendency, overhead and capacity mirrored exactly that based on *TST*, confirming that these indices weight disproportionately the magnitude of the scaling factor *TST* in Eqs. 24.3, 24.4 and 24.5 (Fath et al. 2001). When rescaling internal overhead on capacity (Φ_i/C), system ranking became the same as the one based on cycling (PCI), confirming that fewer redundant pathways were present in the North Aegean and Northern Adriatic pelagic food webs, while the other two networks were more complex. The other results were unexpected: the A/C ratio, i.e. the fraction of the potential system organization that is realized, identified the two Adriatic networks as the most developed ones. The North Aegean was ranked last among the four networks based on this index, as well as according to A_i/C_i. Surprisingly, A_i/C_i identified the Northern Adriatic network as the most efficient and mature among the analyzed models. However, A/C and A_i/C_i ratios did not generally differ much among systems.

Keystones and Overall Impacts

Indices of keystoneness and overall trophic impacts (Libralato et al. 2006) are reported on Fig. 24.2. Groups belonging to intermediate trophic levels such as zooplankton and medium-sized pelagics exerted strong impacts on the pelagic food webs, moreover disproportionately high ones with respect to their abundance in the system (*KS* index). To a lesser extent, other groups belonging to medium-low trophic levels appeared to influence the food webs noticeably, such as phytoplankton, cephalopods and anchovy or, alternatively, sardine (these two species have similar trophic roles and, typically, opposite abundance trends in marine ecosystems, Chavez et al. 2003). Other small pelagic fish had weak effects in all systems, indicating that anchovy and sardine were the dominating small pelagic fish species in these Mediterranean basins. These results were generally in line with previous findings for the original food web models including the benthic compartment (Coll et al. 2006, 2007; Barausse et al. 2009; Tsagarakis et al. 2010). Jellyfish, sea-birds, mammals and large pelagic fish also had generally-negligible ecosystem impacts. The only exceptions were dolphins and fin whales in the South Catalan Sea and large pelagics in the Northern and Central Adriatic Sea, representing keystone species with medium-high overall impacts on the pelagic system.

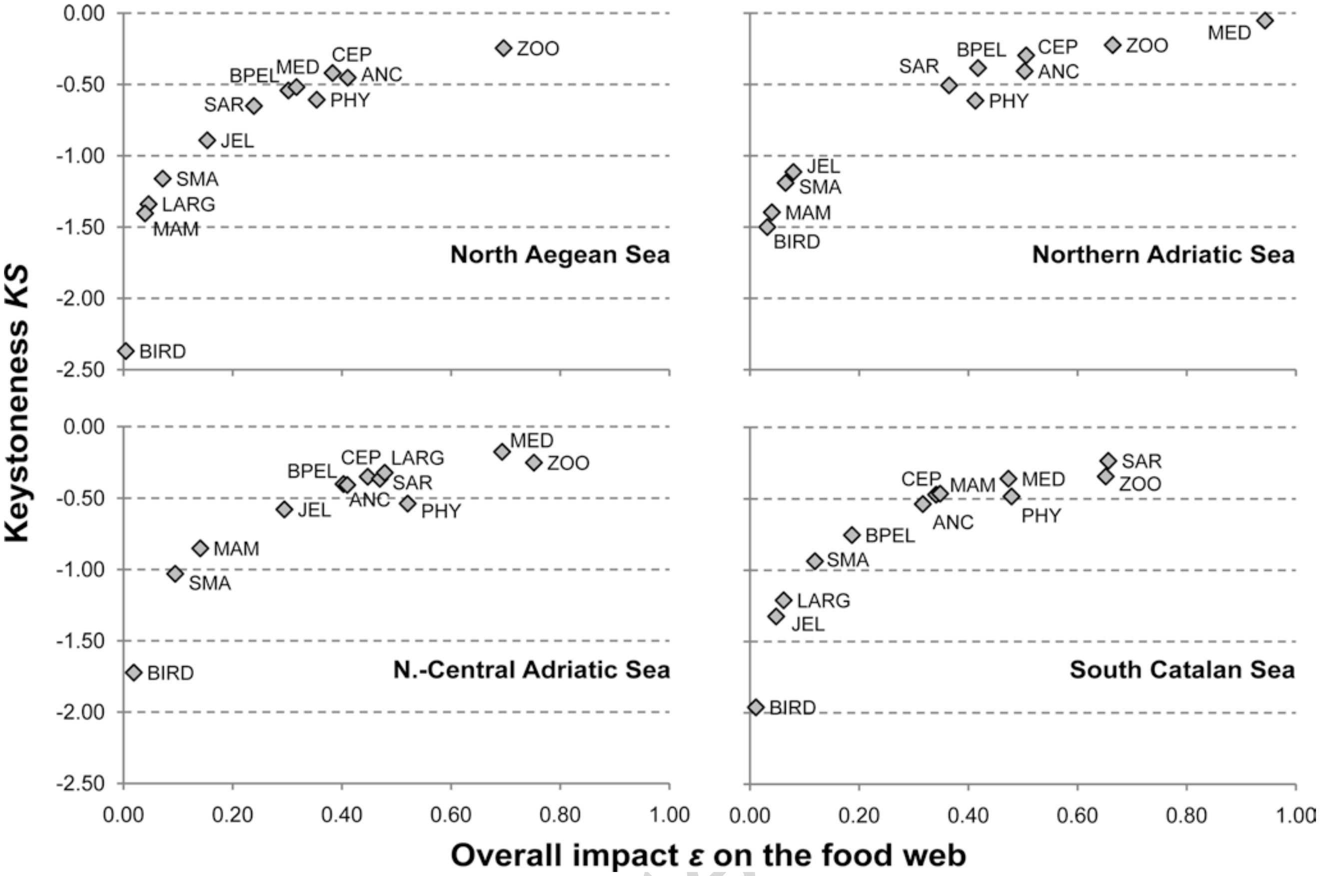

Fig. 24.2 Keystoneness *sensu* Libralato et al. (2006) plotted against the overall impact on the ecosystem for the living groups of the four trophic network models. Labels indicate phytoplankton (*PHY*), zooplankton (*ZOO*), jellyfish (*JEL*), cephalopods (*CEP*), bentho-pelagic fish (*BPEL*), anchovy (*ANC*), sardine (*SAR*), medium pelagics (*MED*), other small pelagics (*SMA*), large pelagics (*LARG*), sea-birds (*BIRD*) and sea-mammals (*MAM*). Generally, intermediate-trophic level organisms such as zooplankton, medium pelagics, anchovy and sardine had great impacts, both on an absolute scale and with respect to their relative biomass in the system, while sea-birds and sea-mammals ranked low

Discussion

To our knowledge, this is the first comparative analysis of (more than two) standardized trophic network models of large-scale Mediterranean marine ecosystems. To ensure a proper comparison, published models were standardized to represent the pelagic compartment of the food web through a common structure. Does this choice of focusing exclusively on the pelagic ecosystem provide a distorted picture of its functioning? In all systems, the pelagic compartment dominated the demersal one in terms of flows (Coll et al. 2006, 2007; Barausse et al. 2009; Tsagarakis et al. 2010), and phytoplankton was always, by far, the most important energy source: from a quantitative point of view the choice of focusing on the pelagic compartment would be justified. This consideration does not exclude, however, that the benthic compartment can influence the pelagic one through key trophic interactions, and a good benthic-pelagic coupling appears to be a characteristic of several large-scale Mediterranean marine systems (e.g. Coll et al. 2007; Tsagarakis et al. 2010). Therefore the present study only represents a first step to understand the functioning of Mediterranean ecosystems through comparative analysis, and future research should extend network standardization to include the demersal compartment.

The standardized networks were based on models which had previously been built according to different criteria and for different purposes, all factors that complicated the process of aggregation. Some standardization choices, such as the common model structure and lumped or excluded groups, were partly forced by data availability and could have been different if the networks had been built for the only purpose of comparing the functioning of their pelagic compartments. The effect of such bias on results was difficult to evaluate, but it was probably not big, since lumping did not involve many groups in the models (Table 24.1).

Structure, Functioning and Development of Mediterranean Ecosystems

The comparative network analysis highlighted clear differences in the trophic structure and functioning of Mediterranean marine systems. The South Catalan Sea emerged as the most developed and mature ecosystem *sensu* Odum (1969) according to several indicators: its food web sustained the largest amount of living biomass per unit of primary production or of flow in the network, its primary production-respiration ratio was the closest to one, it had the highest fraction of cycled flows, the longest pathways and the most web-like structure. Conversely, the Northern Adriatic Sea appeared to be in the earliest developmental stage, with high specific productivity and low sustained biomass per unit of flow, and a short, linear trophic network with low cycling. The North Aegean and the Northern and Central Adriatic Seas showed an intermediate degree of maturity with respect to these two extremes. According to most indicators (e.g. the primary production-respiration ratio, path lengths, System Omnivory index, cycling indices), the latter appeared to be more developed than the former, but this difference was not always clear, e.g. the total biomass-*TST* ratio was highest in the North Aegean Sea.

Primary production emerged as a key process, clearly visible in ecosystem properties such as the amount of total flows, but it did not explain every difference among systems. In particular, it did not mirror the maturity ranking, since the two Adriatic systems were much more productive than the others. Interestingly, the simple inter-system comparison of total primary production or net system production with other, equally-uncomplicated indicators such as *TST* or total production was able to anticipate some of the differences in development highlighted by more sophisticated analyses. Higher primary productivity corresponded to a comparatively-weaker increase in *TST* suggesting that, for example, the flow structure of the eutrophic Northern Adriatic had to be shorter and simpler compared to other systems, particularly the South Catalan Sea. In general, most indicators led to consistent interpretations, in line with the indicator redundancy expected from ecological theory and observed in past studies (Odum 1969; Christensen 1995).

The composition of *TST* in terms of exports and flows to detritus *versus* consumption confirmed the maturity ranking of the systems, and provided additional insights. The most mature ecosystem was again the South Catalan Sea, where consumption dominated, thus suggesting that resources were intensely and efficiently exploited in the pelagic compartment, followed in order of decreasing development by the Northern and Central Adriatic, the North Aegean and the Northern Adriatic Sea, where exports and flows to detritus were higher, symptomatic of low organization and inefficient resource exploitation. A large amount of unused or exported primary production could be a signal of systemic stress (Odum 1985) and of disruption of the predator-prey pathways transferring energy to higher trophic levels. Such high inefficiencies suggest that the demersal compartment in Mediterranean food webs is strongly dependent on the energy provided by the pelagic compartment. As previously discussed, the pelagic compartment dominates the demersal one in several Mediterranean sub-basins, and bentho-pelagic coupling based on detritus flows and an inefficient exploitation of production in the pelagic domain has previously been identified as a typical feature of Mediterranean marine systems (Coll et al. 2008; Barausse et al. 2009; Tsagarakis et al. 2010).

The analysis of cycles and connectivity highlighted the importance of weighting the magnitude of trophic flows when studying food webs. Most probably, the differences in connectance, number of cycles and mean cycle lengths among systems simply highlighted different approaches to the construction of the original models: more but weaker trophic interactions were included in the North Aegean and Northern Adriatic models. Only such interpretation can explain the nearly-threefold difference in the number of cycles between the two Adriatic systems.

Two information theory indicators, A/C and A_i/C_i, did not agree with the maturity ranking identified by other analyses. A justification is that differences among systems in the values of A/C and A_i/C_i are too small to be meaningful, and should not be interpreted. A different, speculative explanation is that, in the case of the Adriatic, the high value of these two ratios actually portrayed the long-term adaptation of the ecosystem to continuously-stressful conditions, rather than system maturity (Baird et al. 1991). The Northern Adriatic could have scored high among the systems in both ratios because its flow configuration has adapted to a long history of intense fishing and nutrient enrichment (Fortibuoni et al. 2010; Barausse et al. 2011), leading to a depressed state (Barausse et al. 2009) which could have become the usual system condition. Within such existing constraints, trophic connections have become efficient, organized and resistant (see Baird et al. 1991). Instead, attributes of maturity characterized by shorter-term dynamics, such as a low primary production-total biomass ratio, cannot be observed because the ecosystem is, indeed, continuously perturbed (Barausse et al. 2009).

Exploitation

The Adriatic systems appeared to be the least exploited ones. Indeed their high primary productivity, fuelled by anthropogenic nutrient loads especially in the Northern basin, is able to sustain large fisheries (Table 24.2; Barausse et al. 2009, 2011). The Northern and Central Adriatic food web appears less exploited than the Northern one, possibly because pelagic fisheries concentrate in the more productive Northern area. A bit surprisingly, the highest pelagic catches were observed in the oligotrophic South Catalan Sea, as well as the most intense exploitation (PPR). This was probably not in disagreement with its greatest development among the four Mediterranean networks: only a system where energy is efficiently channeled towards fishery resources can sustain a fishing pressure indirectly consuming 18 % of its primary production.

The analysis of overall impacts and keystones highlighted some similarities among Mediterranean pelagic food webs and, possibly, the impact of fishing: r-selected species with medium-low trophic levels appeared to play key roles in the functioning of all systems while, generally, large predators had negligible impacts, even when taking their low biomass into account, with partial exceptions in the more mature South Catalan and Northern and Central Adriatic Seas. Large predators are the first species to succumb to fishing pressure because they are less abundant, grow more slowly, mature later and are easier to catch than smaller species (Pauly et al. 1998). Indeed, several Mediterranean large predatory species have strongly declined because of overexploitation (e.g. Ferretti et al. 2008; Coll et al. 2008; Barausse et al. 2011), and the weak impacts of large predators could suggest that the analyzed ecosystems are all strongly impacted by fishing. The key role of zooplankton and small-medium pelagic fish may be related to their trophic position, as they represent the main channel through which energy from phytoplankton reaches pelagic food webs, and suggests that these Mediterranean ecosystems are wasp-waist controlled (Cury et al. 2001).

Conclusions

This comparative study highlighted that the Mediterranean is a sea rich with diversity also in the structure and functioning of its large-scale marine pelagic ecosystems. Multiple indicators from ecological network analysis provided consistent and, thus, robust indications concerning similarities and differences among Mediterranean pelagic trophic networks. Shared traits included the important role of intermediate-trophic level species, the low impact on the system exerted by large predators, and inefficiencies in the exploitation of phytoplankton and detritus production, which gave rise to high export flows fuelling the benthic compartment. Primary production was a fundamental process influencing the properties of the food webs, but other marked differences in the global structure of trophic flows emerged, unrelated to algal productivity. In particular, the ecosystems could be clearly ranked according to their maturity and development (from high to low): South Catalan, Northern and Central Adriatic, North Aegean and, lastly, Northern Adriatic Sea. Despite its higher maturity, the South Catalan ecosystem sustained a strong fishing impact: it was speculated that the higher efficiency of its trophic network made this possible. The Northern Adriatic appeared to be the system in the earliest developmental stage. This basin is heavily exploited and other anthropogenic pressures, such as nutrient enrichment, and environmental factors, such as climate variations, probably act synergistically with fishing and exert a strong stress on the ecosystem (Barausse et al. 2009, 2011).

Additional research is needed to relate anthropogenic pressures and ecosystem structure and functioning in the Mediterranean Sea on large spatial scales.[3] In particular, it remains to be seen whether the varying degrees of development in Mediterranean ecosystems highlighted by this work are directly related to the intensity of human pressures or, instead, mirror different natural conditions.[4] This is a complex research question deserving more analyses. Future work will also, hopefully, focus upon the Eastern and Southern Mediterranean areas, where few or no efforts have been made to construct food web models and study the structure and functioning of ecological networks. These information are critical in order to implement an effective Ecosystem Approach to the management of the Mediterranean Sea and its sub-basins.

Acknowledgments The research leading to these results has received funding from the European Community's Seventh Framework Programme (FP7/2007-2013) under grant agreement n° 226675, KnowSeas project.

References

Abarca-Arenas LG, Ulanowicz RE (2002) The effects of taxonomic aggregation on network analysis. Ecol Model 149:285–296

Baird D, McGlade JM, Ulanowicz RE (1991) The comparative ecology of six marine ecosystems. Philos Trans R Soc Lond Ser B 333:15–29

Barausse A, Duci A, Mazzoldi C, Artioli Y, Palmeri L (2009) Trophic network model of the Northern Adriatic Sea: analysis of an exploited and eutrophic ecosystem. Estuar Coast Shelf Sci 83:577–590

Barausse A, Michieli A, Riginella E, Palmeri L, Mazzoldi C (2011) Long-term changes in community composition and life-history traits in a highly exploited basin (northern Adriatic Sea): the role of environment and anthropogenic pressures. J Fish Biol 79:1453–1486

Caddy JF (1993) Contrast between recent fishery trends and evidence for nutrient enrichment in two large marine ecosystems: the Mediterranean and the Black Seas. In: Sherman K, Alexander LM, Gold BD (eds) Large marine ecosystems. Stress, mitigation and sustainability. American Association for the Advancement of Science, Washington, DC

---

[3] For a review of what has been done so far in the Mediterranean, see Coll and Libralato (2011).

[4] See Barausse et al. (2009) for the Northern Adriatic Sea.

Caddy JF, Refk R, Do-Chi T (1995) Productivity estimates for the Mediterranean: evidence of accelerating ecological change. In: Effects of riverine inputs on coastal ecosystems and fisheries resources. FAO Fisheries Technical Paper 349. FAO, Rome

CBD (2000) Conference of the parties to the convention on biological diversity. Report of the fifth meeting of the conference of the parties to the convention on biological diversity. Nairobi, 15–26 May 2000. UNEP/CBD/COP/5/23, Decision V/6

Chavez FP, Ryan J, Lluch-Cota SE, Niquen CM (2003) From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299:217–221

Christensen V (1995) Ecosystem maturity – towards quantification. Ecol Model 77:3–32

Christensen V, Walters CJ, Pauly D (2005) Ecopath with Ecosim: a user's guide. Nov 2005 edn. Fisheries Centre, University of British Columbia, Vancouver

Coll M, Libralato S (2011) Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea. Fish Fish 13:60–88

Coll M, Palomera I, Tudela S, Sardà F (2006) Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. J Mar Syst 59:63–96

Coll M, Santojanni A, Palomera I, Tudela S, Arneri E (2007) An ecological model of the Northern and Central Adriatic Sea: analysis of ecosystem structure and fishing impacts. J Mar Syst 67:119–154

Coll M, Lotze HK, Romanuk TN (2008) Structural degradation in Mediterranean Sea food webs: testing ecological hypotheses using stochastic and mass-balance modelling. Ecosystems 11:939–960

Coll M, Piroddi C, Steenbeek J et al (2010) The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. PLoS One 5(8):e11842. doi:10.1371/journal.pone.0011842

Cury P, Shannon L, Shin YJ (2001) The functioning of marine ecosystem. In: Reykjavik conference on responsible fisheries in the marine ecosystem, Reykjavik, 2001

EU (2008) Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008, establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). Official Journal of the European Union, L 164:19–40

Fath BD, Patten BC, Choi JS (2001) Complementarity of ecological goal functions. J Theor Biol 208:493–506

Ferretti F, Myers RA, Serena F, Lotze HK (2008) Loss of large predatory sharks from the Mediterranean Sea. Conserv Biol 22:952–964

Finn JT (1980) Flow analysis of models of the Hubbard Brook ecosystem. Ecology 61:562–571

Fortibuoni T, Libralato S, Raicevich S, Giovanardi O, Solidoro C (2010) Coding early naturalists' accounts into long-term fish community changes in the Adriatic Sea (1800–2000). PLoS One 5(11):e15502. doi:10.1371/journal.pone.0015502

Garcia SM, Zerbi A, Aliaume C, Do Chi T, Lasserre G (2003) The ecosystem approach to fisheries. Issues, terminology, principles, institutional foundations, implementation and outlook. FAO Fisheries Technical Paper 443. FAO, Rome

Halpern BS, Walbridge S, Selkoe KA et al (2008) A global map of human impact on marine ecosystems. Science 319:948–952

Jørgensen SE, Bendoricchio G (2001) Fundamentals of ecological modelling, 3rd edn. Elsevier, Amsterdam

Lejeusne C, Chevaldonné P, Pergent-Martini C, Boudouresque CF, Pérez T (2009) Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. Trends Ecol Evol 25:250–260

Libralato S, Christensen V, Pauly D (2006) A method for identifying keystone species in food web models. Ecol Model 195:153–171

Libralato S, Coll M, Tempesta M et al (2010) Food-web traits of protected and exploited areas of the Adriatic Sea. Biol Conserv 143:2182–2194

Odum EP (1969) The strategy of ecosystem development. Science 164:262–270

Odum HT (1983) Systems ecology. Wiley, New York

Odum EP (1985) Trends expected in stressed ecosystems. Bioscience 35:419–422

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F Jr (1998) Fishing down marine food webs. Science 279:860–863

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Piroddi C, Bearzi G, Christensen V (2010) Effects of local fisheries and ocean productivity on the northeastern Ionian Sea ecosystem. Ecol Model 221:1526–1544

Tsagarakis K, Coll M, Giannoulaki M et al (2010) Food-web traits of the North Aegean Sea ecosystem (Eastern Mediterranean) and comparison with other Mediterranean ecosystems. Estuar Coast Shelf Sci 88:233–248

Ulanowicz RE (1986) Growth and development: ecosystems phenomenology. Springer, New York

Ulanowicz RE (1997) Ecology, the ascendent perspective. Columbia University Press, New York

Ulanowicz RE (2004) Quantitative methods for ecological network analysis. Comput Biol Chem 28:321–339

Ulanowicz RE, Puccia CJ (1990) Mixed trophic impacts in ecosystems. Coenoses 5:7–16

Vézina AF, Platt T (1988) Food web dynamics in the ocean. I. Best-estimates of flow networks using inverse methods. Mar Ecol Prog Ser 42:269–287

Worm B, Hilborn R, Baum JK et al (2009) Rebuilding global fisheries. Science 325:578–585