

An overview of studies on trophic ecology in the marine environment: Achievements and perspectives

Um panorama sobre os estudos de ecologia trófica em ambientes marinhos: Resultados e perspectivas

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Abstract

Classical approaches to trophic ecology of marine species has focused on trophic structure, trophodynamics, dominant and keystone species, ecosystem maturity, energy transfer, and anthropic effects. A recent breakthrough for evaluating the structure of communities has been the application of phylogenetic methods to community ecology. This recent approach is known as community phylogenetics. Although this perspective is still not common in trophic studies, phylogenetic methods promise new insights into the old ecological question on how communities are assembled in time. Integrating phylogenetics and ecosystem function creates the possibility of predicting ecological consequences of biodiversity shifts in a changing world. Once we understand the structure and functioning of the ecosystem in a historical context, we should be able to avoid human or natural disturbances that draw a system away from its state of maximum complexity.

Key words: trophic structure, trophodynamics, keystone species, ecosystem maturity, energy transfer, anthropic effects, community phylogenetics.

Resumo

Abordagens clássicas para estudos de ecologia trófica de espécies marinhas focam a estrutura trófica, a trofodinâmica, espécies dominantes e espécies-chave, maturidade de ecossistemas, transferência de energia, e efeitos antrópicos. Um avanço recente para avaliar a estrutura de comunidades foi a aplicação de métodos filogenéticos à ecologia de comunidades. Esta abordagem recente é conhecida como filogenia de comunidades. Embora esta perspectiva ainda não seja comum em estudos tróficos, métodos filogenéticos prometem novas abordagens à velha questão ecológica de como entender a organização de comunidades ao longo do tempo. A integração de filogenia com o funcionamento de ecossistemas cria a possibilidade de prever as consequências de alterações na biodiversidade num mundo em mudança. Uma vez entendida a estrutura e o funcionamento do ecossistema num contexto histórico, deveremos poder evitar alterações naturais ou humanas que tendem a desviar o sistema ecológico do seu estado de complexidade máxima.

Palavras-chave: estrutura trófica, trofodinâmica, espécies-chave, maturidade de ecossistemas, transferência de energia, efeitos antrópicos, filogenia de comunidades.

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Introduction

Most studies on marine macrobenthic communities have been conducted in north temperate regions. Tropical and subtropical macrobenthos is less known, especially the South Atlantic fauna (Santos and Pires-Vanin, 2004). In relation to temperate regions, tropical systems are typically dominated by smaller species (Froese *et al.*, 2004, 2005). There is a reduced biomass in low latitudes, compared to middle and high latitudes (Chardy and Clavier, 1988). In the tropical zone this kind of study is more complex since a large number of species are present and are frequently represented by only a few individuals. The high biological diversity obscures the recognition of specific food webs responsible for the larger part of the energy flow (Paiva, 1993; Santos and Pires-Vanin, 2004). Trophic structure of tropical fish communities in particular contrast with those from temperate regions in terms of more efficient use of relatively low-quality food resources (Harmelin-Vivien, 2002; Floeter *et al.*, 2004; Ferreira *et al.*, 2004).

Coastal ecosystems are relatively rich in nutrients and play a significant role in the development of many species of economic interest. Studies on the feeding habits of macroinvertebrates and demersal fish, even those of a descriptive character, provide basic information for understanding the trophic relations of species (Rocha *et al.*, 2007; Gasalla and Soares, 2001). Coastal systems such as lagoons, sea grass banks and estuaries are characterized by high eco-physiological capacities of biological communities against extremely varying environmental conditions, in space and time (Villanueva *et al.*, 2006; Bascompte, 2009; Ings *et al.*, 2009). The instability of the coastal zone affects the benthic community, determining the patterns of distribution and density and the trophic relationships among the species (Santos and Pires-Vanin, 2004). The existence of gradients of

trophic functions in coastal systems represent the best way the communities can adapt to exploit the existing resources as a response to physical gradients (Carvalho *et al.*, 2010).

Marine biodiversity is higher in benthic rather than pelagic systems. The best way to conserve marine diversity is to conserve habitat and landscape diversity in the coastal area. Feeding relationships may cause invasions, extirpations, and population fluctuations of a species that dramatically affect other species within a variety of natural habitats (Williams *et al.*, 2002). Macrobenthic communities are now used worldwide as bioindicators (Diaz and Rosenberg, 1995; Belan, 2003; Carvalho *et al.*, 2006; Cardoso *et al.*, 2007).

Food webs, descriptions of who eats whom in ecosystems, provide complex yet tractable depictions of biodiversity, species interactions, and ecosystem structure and function (Dunne *et al.*, 2002). Strong and weak trophic links are responsible for ecological dynamics among diverse assemblages of species. The use of trophic groups to characterize the role of macrobenthos in marine communities is advantageous since it incorporates estimates of macrobenthic community structure, and assesses or infers community functioning (Gaston *et al.*, 1995; Boaventura *et al.*, 1999). On the other hand, feeding patterns of macrobenthic organisms have been frequently used to distinguish ecological zones (Pearson and Rosenberg, 1987; Boaventura *et al.*, 1999; Dias *et al.*, 2001). Knowledge of both web structure and interaction strengths is a key to understanding how ecological communities function (Berlow *et al.*, 2004).

The feeding roles of species are thus important tools for the evaluation of the structure and functioning of ecosystems (Krebs, 1989). Species occur at top, intermediate and basal trophic levels (Williams and Martinez, 2000). Food chains tend to be short, typically with only three or four kinds

between basal and top species. Chains involving more than six species are rare (Hutchinson, 1959; Pimm, 1982; Cohen *et al.*, 1986). The knowledge of diet is important for the establishment of its nutritional needs and of the interactions with other organisms (Albertoni *et al.*, 2003). W. Odum and Heald (1975) used effective trophic level to group various taxa into common feeding categories. The emphasis in all of these studies has been at the ecosystem level (Christian and Luckovich, 1999).

The analysis of the trophic structure of benthic communities is also a useful way to determine the main energy flow at the ecosystem level. Most ecological research has relied on trophic groups as a classification scheme for defining functional diversity (Micheli and Halpern, 2005). Food web analysis has also been a well-documented tool to achieve a fisheries ecosystem approach and to understand the ecosystem under various scenarios (Abarca-Arenas *et al.*, 2007; Pauly *et al.*, 1998, 2000).

Both abiotic (temperature, salinity, substrate) and biotic factors (competition, predation) play a role in shaping macrobenthic communities (Angermeier and Winston, 1998). Food availability plays an important role in the structure of coastal communities in addition to abiotic factors (Vaslet *et al.*, 2010). Predation functions in resource limitation (Verity, 1998). Trophic interactions are one of the determinants of distribution and abundance of organisms (Duarte and Garcia 2004). Trophic ecology of macrobenthic communities in estuaries may be used not only to infer community function, but may also provide insights into community responses following disturbances (Gaston *et al.*, 1998). Trophic structure has thus become one of the primary ways by which ecologists organize communities and ecosystems (Christian and Luckovich, 1999).

In this paper we overview the accomplishments of classical approaches to

the study of trophic structure in marine environments, and then point out present developments and future directions in community phylogenetics.

Macrobenthos

Temporal and spatial patterns of microhabitat used by fishes and decapods in a Louisiana estuary were shown to determine overall community structure in the system (Baltz and Jones, 2003). The role of fish predation in determining the benthic community structure was specifically studied by Gilinsky (1984). In coastal lakes of West Africa, detritivore and piscivore trophic guilds had most species (Adite and Winemiller, 1997). Spatial and temporal separation in the distribution and/or dietary preferences of fish in salt-marshes in South Carolina was found to probably reduce the potential for resource competition (Allen *et al.*, 1995).

Trophic structure

Trophic interactions are web-like, with the strongest flows occurring in the lower part of the trophic web (Manickchand-Heileman *et al.*, 1998). Nets have multiple connections and organisms take food from different trophic levels, denoting opportunistic generalists (Polis and Strong, 1996). Trophic levels range from herbivores to predators (Froese *et al.*, 2004). Top species are those which prey upon other species but are not themselves preyed upon. Intermediate species have both prey and predators. Basal species have predators but no prey (Briand and Cohen, 1984).

Primary producers and detritus are placed in trophic level 1. Herbivores and detritus consumers are level 2. The remaining predators are placed in level 3 and up (W. Odum and Heald, 1975). Trophic levels higher than five rarely exist in nature (Pimm, 1982). However, second and third-level predators typically exploit a wide range of prey, from herbivores to other second or third-level predators (Froese *et al.*, 2004).

Assigning of feeding types to each species is sometimes ambiguous and not consensual (Chardy and Clavier, 1988). The general importance of omnivory in regulating predator-prey interactions and in predicting the relative importance of indirect predator effects was analyzed by Posey and Hines (1991). The omnivory index represents the variance of the effective trophic levels of a consumer's preys (Christensen and Pauly, 1992). Most consumers feed on several trophic levels, as shown by omnivory indices (Manickchand-Heileman *et al.*, 1998). Complex predator-prey interactions prevail within an estuarine benthic community. The diversity of trophic levels of prey fed upon by a predator increases with the index value. Organisms at higher trophic levels seem to feed over a broader range of levels than do organisms at lower levels. Also, as trophic level increases, the energy flow of an average compartment at any trophic level decreases (Christian and Luckzkovich, 1999).

A species' trophic group is a determinant of that species' role in the energy transfer within the assemblage. Changes in species diversity lead to changes in functional diversity (Micheli and Halpern, 2005). Food webs in nature have multiple, reticulate connections between a diversity of consumers and resources. Such complexity affects web dynamics (Polis and Strong, 1996). Trophic groups in coastal habitats in Portugal were assigned to four distinct categories (filter feeders, detritivores, herbivores, and carnivores) (Boaventura *et al.*, 1999). Six trophic categories were recognized for mangrove shoreline fish communities in Caribbean lagoons: piscivorous, omnivores, carnivores 1 and 2, herbivores, and planktivores (Vaslet *et al.*, 2010). Demersal communities in the Gulf of Mexico were organized into three guilds: ichthyophagous, carcinophagous, and omnivorous. In general, juvenile stages showed a narrower trophic spectrum than adults (Torruco *et al.*, 2007).

Luczkovich *et al.* (2003) defined trophic role similarity as species that play the same structural roles, even if they are not directly consuming the same prey or if they do not share the same predators. This information is useful for measuring the trophic roles of species in food web models, for measuring similarity in trophic relations of two or more species, for comparing food webs over time and across geographic regions, for aggregating taxa into trophic groups that reduce complexity of ecosystem feeding relations without obscuring network relationships, and for predicting the outcome of predator-prey interactions in experimental studies. Aggregations of biological species on the basis of trophic similarity have been called trophospecies and are the basic units of study in food web and ecosystem research (Yodzis and Winemiller, 1999).

Group-specific trophic signatures have been established as plots of number of species per trophic level. Froese *et al.* (2004) used these signatures to identify similarities and discrepancies between taxonomic groups and ecosystems. Trophic signatures are similar for ecosystems previously known to share major features, and different for dissimilar ecosystems. Trophic signatures may be useful tools for better understanding the roles that different groups of organisms play in different ecosystems (Froese *et al.*, 2004). One type of trophic signature is generated by a plot of species frequency in relation to their number of trophic links (Williams *et al.*, 2002).

A feeding guild is defined as a set of organisms that exploit food resources in a similar intake mechanism, independently of their phylogenetic relationships. Feeding guilds of a benthic community can be broadly divided into deposit feeders, suspension feeders, herbivores, carnivores, and omnivores (Cheung *et al.*, 2008). Determining the trophic guilds of fishes and macroinvertebrates in coastal habitats should greatly improve the develop-

ment of future network models of food webs by providing an objective procedure for aggregating trophic groups (Luczkovich *et al.*, 2002). Multiple trophic levels have been identified in soft-bottom communities (Commuto and Ambrose, 1985). Linkage density, the number of trophic links per species, once thought to be constant, is now known to increase with the number of species in the web (Cohen *et al.*, 1990).

The existence of gradients of trophic functions in these systems may represent the best way the communities can adapt to exploring resources as a response to physical gradients (Cancella da Fonseca *et al.*, 2001). Duarte *et al.* (1990) questioned whether trophic group patterns of macrobenthos represent a good tool to understand macrobenthos communities. Clustering species by trophic group overlooks well known variation in the functional roles of species within a trophic guild. But a species' trophic group, in combination with its size, can be a determinant of that species' role in energy transfer within a food web and in controlling other species within the assemblage (Micheli and Halpern, 2005).

Finally, trophic box models of aquatic ecosystems have been established by Christensen and Pauly (1993). Such models were applied to coastal fish communities in the Gulf of Mexico (Arreguín-Sánchez *et al.*, 1993), and for a coastal system in northwest Africa (Diallo *et al.*, 2003).

Trophodynamics

Ecosystem models have not always been successful for predicting the future development of complex ecological systems (Ulanowicz, 1993). Attempts have therefore been made to develop structural dynamic models – which change parameters, even species composition, over time (Jørgensen, 1986, 1988, 1992).

The trophic dynamic concept in ecology was established by Lindeman (1942). Food web dynamics showed a variable

structure among the different seasons of the year (Abarca-Arenas *et al.* 2007). Trophodynamic aspects of fish in Yucatan have been studied, for example, by Vega-Cendejas *et al.* (1987).

Dominant and keystone species

Dominance is the appropriation of potential niche space of certain subordinate species by other dominant species and so can be manifested most clearly only within a trophic level. In other words, a producer cannot dominate a decomposer or predator because the immediate sources of their energy and inorganic nutrients are not overlapping. Dominant species tend to be generalists (McNaughton and Wolf, 1970).

It may sometimes be interesting to identify those species that play an important role in the ecosystem, also known as keystone species (Dunne *et al.*, 2002; Luczkovich *et al.*, 2003). Keystone species are those that have large impacts on communities or ecosystems out of proportion to their abundance (Power *et al.*, 1996).

Species that have both large abundances and large impacts are considered dominant species instead of keystones. Species with few trophic connections that have large effects on community structure may act as the structural equivalent of keystone species, whereas species with many trophic linkages may be more conceptually similar to dominant species (Dunne *et al.*, 2002). Jordan *et al.* (1999) and Jordan (2001) proposed a method to identify a keystone species using weighted trophic networks.

In keystone-dominated systems, species other than the keystone species have only minor, if any, effects on the rest of the community, and thus might be cited by some as "redundant species". However, after loss of a keystone species, previously "redundant" species can partially compensate for the reduced predation and adopt a major role in the altered system. Such

responses are potentially an important force in stabilizing communities. The term "redundant species", thus, conveys an inaccurate image of the potential importance of weak interactors and should thus be abandoned (Navarrete and Menge, 1996). Following Yodzis and Winemiller (1999), we prefer the use of trophic similarity or trophospecies for these trophic equivalences.

A keystone predator crops down the dominant competitor from reaching a competitive equilibrium. Thus, predation constitutes an important factor that disturbs the trend of competition and curbs it, counteracting dominance (Raghukumar and Anil, 2003). Keystone predation demonstrated that unweighted link structure by itself is not a good predictor of species and population dynamics (Paine, 1969, 1974, 1980). For example, Gasalla *et al.* (2010) evaluated the keystone role of the squid *Loligo plei* in a southwestern Atlantic ecosystem. The studied squid represents an important link between pelagic and demersal energy pathways, with high indices of keystoneity.

The idea that communities may be dominated by a few keystone species has a long history in ecology (Mills *et al.*, 1993). Yet McCann *et al.* (1998) and Berlow (1999) provide an alternative viewpoint, based on weak trophic interactions. For the intertidal habitat, Menge *et al.* (1994) propose that it is variation in interaction strength that determines community structure, questioning the usefulness and generality of the keystone concept. Because we expect all complex ecosystems to be structured similarly, this type of analysis could help conservation managers identify connected keystone species that should be the focus of conservation efforts (Parrott, 2010).

Ecosystem maturity

Biodiversity and community structure are now recognized to be important determinants of ecosystem functioning. High diversity leads to greater

community stability and productivity (Raghukumar and Anil, 2003). And changes in species diversity lead to changes in functional diversity (Micheli and Halpern, 2005).

Predation can maintain high local species diversity if the predator consumes a competitively dominant prey species (Paine, 1966, 1971; Menge and Sutherland, 1987). In this situation, the predator will have a fundamental influence at the community level by structuring interactions between species and reducing the impact of each, thereby permitting coexistence that would not occur in the absence of the predator (Calil *et al.*, 2009). Predators commonly show a variety of trophic strategies and prey selectivity (Brögger and Penchaszadeh, 2008).

Food-web structure mediates dramatic effects of biodiversity loss, including secondary and cascading extinctions. Food webs are more robust to random removal of species than to selective removal of species with the most trophic links to other species. Robustness increases with food-web connectance but appears independent of species richness and omnivory. Removing species with few trophic connections generally has little effect on biodiversity loss. Thus, the number of species removed affects ecosystems differently depending on the trophic functions of species removed (Dunne *et al.*, 2002).

We should expect decline in diversity to accelerate the simplification of ecological communities. Diversity can be expected, on average, to give rise to ecosystem stability. Weakly interacting species stabilize community dynamics by dampening strong, potentially destabilizing consumer-resource interactions (E. P. Odum, 1953). Decreasing biodiversity will be accompanied by increases in average interaction strengths within ecosystems, and a concomitant decrease in ecosystem stability. Simplified communities are consequently more vulnerable to invasion (McCann, 2000). Weak interactions may thus be the

glue that binds natural communities together (McCann *et al.*, 1998).

Thus, the more trophic links that a species has to other species in a food web, the more potential it may have to affect community structure (Dunne *et al.*, 2002). Community stability will increase as the number of links in a food web increases (MacArthur, 1955). Highly connected communities will tend to be more robust to species losses (Dunne *et al.*, 2002). On the other hand, secondary extinctions occur due to removal of highly connected species. Unfortunately, the degree to which taxonomic and functional diversity are correlated is unknown for most ecosystems (Naeem, 2002). Given the high diversity that characterizes tropical regions, the study of dominant species has been a widespread research strategy. This approach can identify important ecological interactions among members of a diverse demersal fish community, acting both as sources of information of the members themselves, and of other species with similar behavior (Sánchez-Gil *et al.*, 2008).

The relationships of species richness and other measures of complexity to ecosystem properties need to be further explored, such as in network topology and related food-web studies (Solé and Montoya, 2001; Williams *et al.*, 2002; Dunne *et al.*, 2002; Montoya and Solé, 2002). To determine food web complexity, four statistics are commonly used: species richness, number of trophic species in the food web, links per species, and omnivory (Dunne *et al.*, 2002).

Many have tried to define stability (May, 1975; Rutledge *et al.*, 1976; Pimm, 1979, 1984; Johnson, 1981; Mauriello, 1983), buffer capacity (Jørgensen, 1990) and resilience of communities and ecosystems (Berryman, 1983). But the whole idea of energy flow ruling ecosystem interaction has also been questioned on the basis of chaos theory (Måansson and McGlade, 1993).

The relationship between trophic complexity and community stability

was first established by Paine (1969). The diversity-stability debate continued with May (1973), with early multi-species models, and may help identify the role of weak or positive interactions in community structure (McCann, 2000). The interacting webs should provide more accurate characterizations of the complex structural signatures of ecosystems. Recent research continues to confirm the presence of temporal, spatial, and structural signatures that share common characteristic patterns across all types of complex ecosystems. Ecological complexity often represents a link to concepts such as ecological resilience and ecological integrity (Levin, 1999; Harris, 2007).

The degree of complexity of an ecosystem is correlated with its health or integrity, both of which very likely increase a system's resilience and robustness (Loreau *et al.*, 2001; Hooper *et al.*, 2005). Functional and structural redundancy increases system complexity in space and time, and provides increasing robustness and tolerance to disturbance (Carlson and Doyle, 2002).

Stability has been based typically on local stability analysis. Local stability does not guarantee persistence of food webs in stochastic environments. Global stability and permanence could be better criteria of community persistence. The relationship between stability and complexity of food webs remains a central issue in theoretical ecology. May (1972) suggests that complexity reduces stability. Many efforts have been made towards incorporating structural features of real food webs into the pool of community matrices of dynamic models (DeAngelis, 1975; Yodzis, 1981; Pimm, 1982).

Communities with more omnivory links have more prevalent permanent paths and communities of high connectance are more ready to reassemble themselves (Law and Blackford, 1992; Law and Morton, 1993). Thus, complex communities may also be less vulnerable to disturbance than

simple ones. Within stochastically assembled food webs, complex food webs are less likely to be permanent than simple webs; in other words, in these simulation analyses, permanence actually decreases as food web complexity increases (Chen and Cohen, 2001).

Food webs of high connectance are shown to rebuild themselves more readily than those of low connectance, and therefore recover more readily from disturbance (DeAngelis, 1975; Law and Blackford, 1992). Connectance remains surprisingly constant, while the fractions of top and basal species decreased, and the fraction of intermediate species increased (Martinez *et al.*, 1999). Species redundancy (Naeem, 1998), or species diversity (Naeem and Li, 1987), which we refer to as trophic similarity, or trophospecies, enhance ecosystem reliability.

Ecosystem development is seen by E. P. Odum (1969) as a process that involves structural changes in the system that are orderly, directional and therefore predictable. The development is to culminate in a stable system with maximum biomass and/or information content. In this climactic system widespread symbiotic interactions will tend to optimize energy utilization (Christensen, 1995). Unfortunately, the lack of general prediction seriously impedes the maturation of ecology as a scientific discipline. Martinez (1994) found that scale-dependent food-web structure only predicts properties of new, high-quality food webs successfully, when more than 54 species are present.

The Connectance Index and the number of possible links in the food web can be used to assess the maturity of the ecosystem (Manickchand-Heilman *et al.*, 2004). Another descriptor system is path length, which is the average number of groups that a flow passes through (Finn, 1980). Path length also increases with maturity (Christensen and Pauly, 1993). Competition may be a third useful indicator of the state and health of an

ecosystem (Parrott, 2010). Complexity may serve as a fourth indicator of the degree of maturity or organization of an ecosystem (Müller, 2005). Complexity of natural ecosystems increases with maturity (Parrott, 2010). The relationship between respiration and production represents a final measure of the maturity of the ecosystem (E. P. Odum, 1969).

Energy transfer

Transfer of energy from one trophic level to another is only about 10% efficient. Trophic relationship studies of macrobenthos show that primary production of the overlying water is not a limiting factor for benthic production (Joydas and Damodaran, 2009). Populations with higher effective trophic levels would be expected to contribute less to the energetics of the ecosystem than those with lower levels.

The links between the primary producers and the top consumers are often poorly understood. Aggregation of species into trophic guilds is required for network analysis of most, if not all natural ecosystems (Christian and Luckzkovich, 1999).

Trophic relations follow a pyramid of flows (Lindeman, 1942). The efficiency of trophic transference diminishes gradually towards the higher trophic levels, due to the increase in the rate of respiration (Christensen and Pauly, 1993). The peak in transfer efficiency at level 3 is due to the consumption of high-quality food by carnivores (Manickchand-Heileman *et al.*, 1998). Trophic structure is determined by competitive and predator-prey interactions. It is trophic structure that controls the fraction of energy consumed at each trophic level, rather than being energy that controls trophic structure (Hairston and Hairston 1993).

Anthropic effects

Human interventions or natural disturbances can draw a system away from the state of maximal complexity. Con-

versely, restoration efforts may help the system to self-organize towards a state of higher complexity (Parrott, 2002), once we understand the structure and functioning of the ecosystem. For successful fisheries management, we need to take into account not only prey and predators of a target species, but also their role in an overall ecosystem context (Christensen, 1996). Trophic relations of fish in northwestern Atlantic were studied to determine the role that predation plays in determining ecosystem structure and the possible long-term effects of various fisheries exploiting regimes (Bowman *et al.*, 2000).

Trophic structure of macrobenthic assemblages is closely linked to environmental characters and serve as indicators of environmental conditions (Gaston and Nasci, 1988), permitting the assessment of anthropic perturbation in marine and estuarine systems (Gaston *et al.*, 1998). A common approach to assess risks to ecosystem health is to identify stressors and their potential effects through the use of indicators (Fisher *et al.*, 2001).

Macrobenthic communities are now used worldwide as bioindicators (Diaz and Rosenberg, 1995; Belan, 2003). Community structure, trophic functional analysis and several biotic metrics should be tested in order to assess their effectiveness in discriminating potential impacts of fish production (Carvalho *et al.*, 2010). Comparative analysis of trophic structure in four temperate estuaries was conducted in Europe and South Africa. The Finn (1980) cycling index and the whole system average path length were shown to be highest in the most polluted estuaries (Baird and Ulanowicz, 1993).

Biological metrics for environmental monitoring show a faster and more sensitive response to changes in the quality of benthic environment and ultimately of the water column (Edgar *et al.*, 2005). Average fisheries operate around two trophic levels above the primary producers (Christensen,

1996). Fisheries tend to switch from species with high trophic levels to species with low trophic levels in response to changes of their relative abundances (Pauly *et al.*, 2000).

Humans have historically tended to impact higher trophic levels through overfishing and hunting of shellfish and large coastal marine invertebrates, with associated cascading trophic and non-trophic effects. Trophic cascades result in inverse patterns in abundance or biomass across more than one trophic link in a food web (Carpenter and Kitchell, 1993). Alternative predatory regimes can thus instill powerful organization forces in the marine zone (Pace *et al.*, 1999). However, trophic cascades and top-down community regulation as envisioned by trophic-level theories are now regarded as relatively uncommon in nature (Polis and Strong, 1996).

Feeding relationships and other direct and indirect effects need to be taken into account when considering the effects of species loss (Jackson *et al.*, 2001). Trophic structure of macrobenthic assemblages are closely linked to environmental characteristics and serve as indicators of environmental conditions (Gaston and Nasci, 1988) and for the assessment of anthropic perturbations in marine and estuarine ecosystems (Gray, 1974; Gaston *et al.*, 1998; Lucero *et al.*, 2006). Cardoso *et al.* (2004) have used macrobenthos feeding guilds distribution to assess impacts.

Parasites in food webs: the penultimate frontier

Parasitism is the most common animal lifestyle among organisms. Notwithstanding, attempts to incorporate parasites and hyperparasites (parasites of parasites) into food webs are recent (Huxham and Raffaelli, 1995; Marcogliese and Cone, 1997; Holt and Hochberg, 1998). This neglect of parasites is due to the difficulty of quantifying them by standard ecological methods (Lafferty *et al.*, 2005).

For example, multiple co-occurring parasites can show different feeding strategies and thus lead to complex and cryptic trophic relationships. This complexity and dimensionality of host-parasite interaction networks is difficult to disentangle (Gómez-Díaz and González-Solís, 2010). Furthermore, parasites are small and invisible, hidden inside their hosts, and tend to remain unnoticed unless you actively seek them out with the necessary expertise. Advances in molecular genetics are now helping to increase the taxonomic resolution of food webs. For example, DNA barcoding is aiding in the automated identification of possibly every parasite species within one isolated host (Besansky *et al.*, 2003).

Parasites have been demonstrated to strongly affect food web structure, parasite links being necessary for measuring ecosystem stability (Lafferty *et al.*, 2006). In the first place, the inclusion of parasites and pathogens significantly increases the diversity of species in food webs (Dobson *et al.*, 2006). There is accumulating evidence that parasites have the capacity to affect food-web topology, increasing chain length, connectance and robustness, as well as stability, interaction strength and energy flow (Margogliese, 2002; Lafferty *et al.*, 2006, 2008; Warren *et al.*, 2010). These results show that food webs are very incomplete without parasites. A variety of theoretical studies suggest that parasites have properties that will allow them to play major roles in stabilizing the long-term dynamics of food webs (Dobson *et al.*, 2006). Parasite species composition may change in heavily exploited areas (Marcogliese, 2002), while keystone parasites will affect important predator or prey species (Minchella and Scott, 1991). Food-webs contain many more host-parasite links than predator-prey links (Lafferty *et al.*, 2006). Biodiversity and production are thus enhanced by parasites, and healthy ecosystems or food webs should thus have a di-

verse parasite fauna (Hudson *et al.*, 2006). Parasites have a prominent role in ecological networks and may substantially alter food-web structure and functioning (Amundsen *et al.*, 2009). Incorporating parasites into food webs should become the standard procedure in the future (Byers, 2009). In food web studies the key feature is now to understand the complex interactions among hosts, parasites, predators and prey. Unraveling the relationship between food web complexity and ecosystem stability is becoming increasingly important in a world of biodiversity loss, invasive species and climate change (Wood, 2007). Parasites are far from randomly distributed in relation to the underlying predator-prey food web (Chen *et al.*, 2008). For example, a prey and its predator are more likely to be hosts to the same parasite species (Warren *et al.*, 2010). Poulin and Leung (2011) found that small fish are more vulnerable to predation, and thus make better hosts for larval parasites.

Given how central food webs are to fundamental ecological concepts such as stability, diversity and complexity of ecosystems (Pascual and Dune, 2006), it is important to understand the influence of parasites on the structure, dynamics and function of food webs. Because parasites augment the flow of energy, alter the strength of interactions, change productivity and cause trophic cascades, the inclusion of infectious agents in food web studies might permit a better understanding, evaluation and mitigation of human impacts on ecosystems, including biodiversity loss, climate change, exotic species, pollution, bioremediation, pest control and fishery exploitation (Lafferty *et al.*, 2008). Marcogliese (2002) found that parasite species composition changes in heavily exploited areas to reflect modifications in fish and invertebrate communities. Integrating parasites into food webs even changes the paradigmatic view of ecosystems, because top predators are conceivably no longer the high-

est trophic level, as few species completely lack parasites (Lafferty *et al.*, 2006). According to Kevin Lafferty, “food-web theory is now the framework for modern ecology. Parasites have been missing from this framework, and as a result, we know relatively little about the role of parasites in ecosystems. It’s like driving with a highway map, but with no knowledge of the smaller road network. To reach most destinations, you need a map with both” (Maender, 2006).

Further Perspectives

Ecosystems evolve through time, since the living world is the product of evolution (Gould, 1980). Whichever variables are chosen for study of ecological interactions, it is important to place them in an evolutionary context, relating them to their historical development. Since the pioneering effort of Brooks and McLennan (1991) to integrate ecology and behavior with phylogenetics, the importance of studying ecology in a phylogenetic context has been gradually increasing.

However, this perspective is still rare in trophic studies. The way communities are assembled is an old ecological subject currently experiencing renewed interest thanks to the recent advances in molecular biology and phylogenetics (Pausas and Verdú, 2010). Webb *et al.* (2002) provided a novel framework in which phylogenetic information from co-occurring species is used as an indicator of the two main assembly processes of ecological communities (competition and habitat filtering).

The incorporation of phylogenetics to the classical approaches has laid the foundation of the emerging research area of community phylogenetics. Many tools are being developed for detecting the underlying forces structuring communities (Cavender-Bares *et al.*, 2009; Vamossi *et al.*, 2009). Phylogenetic information will permit a better understanding not only of the historical relationships between species, but also

of the genetic signature of both ecological (e.g., filtering) and evolutionary processes (e.g., diversification).

Phylogenetic methods predict ecosystem function on the basis of relatedness. For example, plant community biomass was found to be better predicted when considering species relatedness of the community than by traditional biodiversity indicators such as number of species or functional groups (Cadotte *et al.*, 2008).

Phylogenetic relatedness can also act effectively as a proxy for species’ responses to disturbance, and thus these methods can be applied to temporal slices in order to detect changes in phylogenetic structure (Helmus *et al.*, 2010). Integrating phylogenetics and ecosystem function opens up the possibility of predicting ecological consequences of biodiversity shifts in a changing world.

Phylogenetics may help to guide better taxon sampling of key traits for scaling from organism to global processes (Edwards *et al.*, 2007). Phylogenetics clearly represents the next breakthrough for studies of trophic ecology.

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