From Biomass Towards Chemical Ecology: Progress and New Perspectives for the Study of Food Webs in Marine Ecosystems

Thesis

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From biomass
towards chemical ecology:
progress and new perspectives for the study
of food webs in marine ecosystems

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Abstract

Changes of paradigms in the study of food webs in the last decades summarize a fast evolution of concepts: starting from a mechanistic vision of life, scientists recently approached to the emergent properties of ecosystems and started to investigate the informational functions of foods. The development of concepts is illustrated in this thesis by means of various papers, starting from a numerical evaluation of fluxes, moving then to biomasses and energy and approaching finally to several examples of “functional foods” influencing the ecology of key species in complex ecosystems. This exercise also permits comparison of the results with a model-based vision of ecosystems and the development of a general equation linking biodiversity with the availability of trophic resources. The equation, derived from mathematical analysis of networks, is proposed to be applicable to any network of organisms or cells, at various structural levels. It is based on an exponential decay function and it has been here tested on field data obtained in such different environments as a temperate harbour, seagrass beds and coral reefs. Results are encouraging, since a good fitting of the function to the experimental data has been demonstrated.
Acknowledgements

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Further, I urge to thank the kindness, the tolerance and the partnership of many colleagues, often in competition for resources and ideas: without the daily struggling relationships with them I could not develop the weapons to produce some of the ideas herein proposed. As well, the stimulating relationships with several students were sources of new thoughts and challenges.

Finally, I need to thank my family, for their patient tolerance of my busy moments, and the supervisors of this thesis, Dr. W. Kooistra and Dr. L. Mander: they generously did find the time to read it, finally, permitting me to overcome this essential step and look forward to higher scientific goals.
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Section 1. General introduction
**Summary of the Section**

The study of food webs summarizes the fast evolution of several ecological concepts in the last decades. Starting from a mechanistic vision of life and a static concept of natural communities, it evolved through concrete steps towards the present vision of functional foods and emergent properties of ecosystems. Thus, following some ancient and modern ideas it will be shown that, starting from numbers and energy, general laws may be reached ruling communities at different organization levels – *from cells to ecosystems*– taking into account the abundance of trophic resources and the way they are distributed among individual consumers. Following this synthesis, the main objectives of the thesis will be outlined.
Chapter 1. History and importance of food web investigations

1.1 Historical milestones in ecological research: the genesis of ideas and their time evolution

The idea of this research grew out of several conversations with students, when it emerged that they had limited knowledge of the standard theory upon which our present ecological exploration is based. The question of whether the understanding of history is important to ecologists conducts to philosophical issues, about how theory changes actually proceed fast in ecology and which critical changes of paradigms characterized the second half of the previous century. The starting point of this change of paradigms was the need, felt in the first half of the century, to demonstrate that ecology may be considered a numerical science, with the same intrinsic dignity of mathematics and physics. In fact, previous ecological research was limited to structural characters of communities, unable to produce canonical hypotheses and test them experimentally. Thus, following the success of the International Geophysical Year (1957-1958), the British Rudolph Peters and the Italian Giuseppe Montalenti started discussing the need for an international program of biological studies focused on the productivity of biological resources and the human adaptability to environmental changes (Hillmann et al, 1989). A Planning Committee was established in 1964, proposing an International Biological Program (IBP), implemented in the wake of the successful International Geophysical Year, with G. Montalenti as the chairman. The committee recommended to be focused on the effects of environmental changes on natural communities and on the conservation and growth of natural resources for human benefits. Quite a modern topic, after all! This demonstrates how the program influenced further steps of ecological research and definitely made feeding relationships one of the core thematic frameworks in ecological sciences (Layman et al., 2015).
Accordingly, during a General Assembly held in Paris in 1964 and attended by 150 lead participants from worldwide scientific academies, a special committee was established for the IBP, for directing the program. The activities of the program ended in 1974, but the advancements it produced in our ideas are still influencing ecological research. The first critical results, however, emerged immediately in the first years of the IBP activities. In 1968 Odum published its “Energy flow in ecosystems: a historical review”, that changed the mind of thousands of young ecologists, included the writer. Here, some revolutionary (for the time) concepts were introduced, as the fact that “trophic levels are not primarily applicable to species” and that ecosystems could be analysed by means of “computer models”, simulating their activities by means of the flows of matter and energy. Fundamentally, this meant the possibility for realizing models (thanks to the first diffusion of electronic calculators), hypothesise basic relationships derived from field evidences, then test assumptions and reach conclusions that could evolve in time, just like physicists did with their theoretical systems. What a change!

The basic concepts bringing the attention of scientists on food came from far, since the concept that food is important in ecology as a limiting factor for animal populations and a regulating element for benthic communities was commonly accepted (Sousa et al., 1981; Garrity and Levings, 1983; Fairweather et al., 1984). The localized effects of predation, including grazing (Tegner and Levin, 1983; Penny and Griffiths, 1984; Thayer, 1985), were among the most extensively studied and important causes of spatial variability. As a matter of fact, the behaviours of all evolutionarily successful organisms are constrained by two major dictates (Yeakel and Dunne, 2015):

1) they must pass down their genetic material, and

2) they must acquire the necessary energy to do so.
Thus, feeding relationships have important implications for ecology, evolution and persistence of plants and animals. It has been demonstrated that even mass extinctions of the Cretaceous-Paleocene were influenced by the structure of trophic relationships and the continuous evolution of species is paralleled by an evolution of the trophic structure of ecosystems (Barnosky et al., 2011; Lotze et al., 2010). Older studies demonstrated that manipulations and experimentations could lead to concrete changes of paradigms. For example, some experiments demonstrated that specific perturbations resulted in loss of a key benthic predator, causing the community to shift to a totally different configuration (Barkay and McQuaid, 1989). Thus it was clear that comprehension and modelling of matter and energy fluxes in any ecosystem enable to comprehend its internal dynamics and built provisional models to calculate the effect of events that may modify the community structure (MacFaiden, 1964). These studies conducted to immediate results in simple ecosystems and, while computer platforms evolved, becoming more powerful, they led to interesting hypotheses in ecosystems of increasing complexity.

At the time, ecology could be defined, according to Odum (1959), as “the study of the structure and function of nature”. Energetics was concerned with energy transformations occurring within ecosystems, including feeding: a plant may be eaten by one animal that, in its turn, is eaten by another, and so on. Such a sequence of events was termed a “food chain”. However, it became progressively more evident that food and feeding relationships of plants and animals in any ecosystem are rarely, if ever, as simple as a single food chain.

For example, in the case of seagrasses, the problem was even more complex, due to the role played as both refuge for animals and food source, by such different interacting compartments as leaf stratum, rhizome layer, detritus, epiphyte layer (Irlandi and Peterson, 1991; Mazzella et al., 1992). First researches were performed on the importance of detritus feeder species in P. oceanica ecosystem (Verlaque, 1981; Tenore and Rice, 1980; Tenore, 1981; Velimirov et al., 1981). Studies were also performed to define the influence of grazers on leaves of P.
oceanica and other seagrasses (Asmus and Asmus, 1985; Klumpp and Nichols, 1983; Verlaque, 1990; Stenek, 1982). The importance of the epiphytic layer for macrozoobenthic vagile organisms, however, was initially underestimated (Verlaque and Boudouresque, 1984), although we know, now, that the total epiphytic biomass produced in a year at a shallow stand off Lacco Ameno d’Ischia (Italy) is high and accounts for 109 grams (dry weight) per square meter (Mazzella and Ott, 1984). Actually there was no information about the fate of this biomass; consequently we did not know the structure of this important path of energy transfer.

The complexity of feeding relationships in ecosystems could be illustrated taking into account the high number of producers (e.g., seagrass standing stocks, different species of epiphytic macrophytes, microphytes), first consumers (fishes, echinoderms, decapods, amphipods, polychaetes, molluscs, etc.), secondary consumers (crustaceans, echinoderms, fishes), and last consumers (fishes, large decapods) cooperating for its stability. The large number of species interacting each other produce a complex “web”, which regulates and integrates the system. Therefore it was clear that the simple food chain could not be considered as an isolated linear system; in contrast, it interconnects with a large number of other food chains. This interconnection leads to the trophic relationships of organisms expressed diagrammatically as a web. The discovery and description of a food web in any given habitat must be considered to be an enormous task (Phillipson, 1964; 1966).

Species and communities associated to various compartments of any ecosystem, their feeding mechanisms, reproductive features and rates of growth had to be analysed in the first phase of researches. This qualitative approach represented the background to the investigation of any system and led to the application of quantitative methods for estimating the abundance of common organisms and, ultimately, of the total amount of living matter or biomass. An example of such a survey is given by some older studies (e.g., Mazzella et al. 1990; Gambi et al., 1992) on Lacco Ameno d’Ischia P. oceanica bed. In addition it is interesting to
consider the foreword to the new edition of the Pimm’s Food web text (2002) because it contains an historical review of the main phases leading to the analysis of multi-species models based on population dynamics, consumption and growth rates of various elements in each compartment. The parameterization of multi-species models, made easy by the application of simple spreadsheet programs, made possible the production of predictive models based on a large portion of the literature published in the last decades. Also, the work by Pimm (2002) provides evidences for the definition of various fixed properties of food webs, based both on mathematical assumptions and field data. For example the “connectance”, i.e., the fraction of possible inter-specific links that is realized in a real web (May, 1972), depending on the number of species (biodiversity) and their trophic preferences may determine the stability of ecosystems. A related parameter, the “linkage density” appears to be as a constant feature of several ecosystems, being:

\[ L = dn \]  \hspace{1cm} (1)

Where L is the total number of trophic links; d is the linkage density; and n is the number of species, so that food webs are likely to be “scale invariant” in this and in other key properties.

On average, the number of trophic linkages was demonstrated to be about double the number of species in a range of ecosystems (Pimm et al., 1979). Very interesting is the finding that connectance declines hyperbolically with the number of species. In fact, this mathematical relationship is in accordance with our field data (still unpublished) indicating that the biodiversity is inversely related to the abundance of trophic resources, following a trend of hyperbolic decline:

\[ C = \frac{L}{s^2} \]  \hspace{1cm} (2)
where $C$ is the total connectance, $L$ is the total number of trophic links and $S$ is the number of species in the system. This relationship, for values of $S>0$ brings to the trend reported in figure 1: this is what we could expect, from a simple mathematical point of view, in the representation of the connectance $C$ according to increasing values of $S$ (namely, alpha diversity).

![Graph of function (2) for values of $S>0$.](https://www.desmos.com/calculator)

Different methods were employed for determining food chains and food webs. In some instances, simple observations were sufficient as a first approximation. For example, given molluscs might be restricted to certain species of tunicates and it was demonstrated that many of these molluscs were eaten by a few crustaceans. However, simple observations never assured that all possible links in food webs had been considered.

A second approach was to collect representatives of all species occurring in a given system and to analyse their gut contents. Provided that a sufficient number of individuals of each species was examined, it was possible to state which animals fed upon what and, thus, build a food web (Zupo and Fresi, 1984). This type of investigations required taxonomic knowledge not only for whole organisms, but also for their separate parts. Radioactive isotopes and precipitine
tests started to be used to identify digested parts of organisms without skeletal parts. These last methods, however, were tedious and the results obtained did not always justify the amount of work performed. The simple analysis of gut contents was often considered as a good balance between research effort and quality of results.

However, a need for producing generalized representations or models of food webs emerged, even after detailed investigations had been made, as the more knowledge was available about a particular food web, the more complex it apparently became. It is possible to group together animals with similar feeding habits and similar predators, to build “ecothropic groups” (as used in Ecopath models: www.ecopath.org). Furthermore, it demonstrated to be quite difficult to compare food webs in one situation with another, because different species were involved in each case. For this purpose, feeding indices were proposed, which allowed comparisons of species and ecosystems based on their trophic features (Zupo, 1993).

The interdependence of various parts of food webs was made clear by dividing the flows into further trophic levels, starting with the primary producers which use solar energy and fix inorganic nutrients (first trophic level), passing through the herbivores (second trophic level), the carnivores (third trophic level), and reaching ultimately the decomposers (Odum, 1959; Phillipson, 1966, Fenchel, 1970). Some authors (Elton, 1927) noted that the animals at the base of a food chain were relatively abundant while those at the top were relatively few in number and there was a progressive decrease between the two extremes. This "pyramid of numbers" was found in several animal communities all over the world and the widespread occurrence of such a phenomenon provided a common denominator by which different communities could be compared. The most comprehensive form of investigations, however, was the measurement of the flow of organic matter and energy throughout each component of the ecosystem. In fact, it came clear that a simple numerical approach was not enough informative, due to the
different sizes of animals and plants. The difficulties were overcome by using the biomass of organisms rather than their number (pyramids of biomass).

Biomass is defined as the amount of living substance composing studied organisms. Alternative terms are standing crop or standing stock. The biomass of aquatic organisms is measured by weighing them after removing the excess water. A more accurate method consists in measuring the dry weight, after excluding those parts that are not living (external skeleton, calcareous parts, shells, etc.). Measurements of biomass alone, however, were quite inadequate for the purpose of predicting yields on a time basis. The rates of production of organic matter by various members of natural communities and their trophic dependence on one another or on sources outside the community had to be known. Measurements of biomass, in terms of energy released from tissues, when they are fully oxidized to water and carbon dioxide, overcame the problem of defining what are the living and non-living parts of a consumer or a prey. Furthermore, energy units were the same for all organisms. The measurements of energy contained in the tissues of organisms (pyramid of energy), gave information about the process rates (turnover time) and overcame the problems arising with the pyramids of numbers and biomass. Energy units provided a unifying concept, a means of expressing the productivity of an individual organism or all the organisms within an ecosystem. Further, the concept permitted comparisons of the productivity of regions as different as a desert and a marine environment. Energy flow refers to rates of change of biomass. The whole flow is divisible into a number of separate processes, which together indicate the passage of matter or energy throughout organisms, populations or ecosystems under investigation.

Hence, when food was finally measurable in terms of energy, computations of energy flow could be employed to assess actual and potential yields of exploitable benthic species, to predict means of increasing productivity, and to estimate the contributions made by benthic or planktonic communities to predators occupying other habitats. In addition, in order to determine the amount
of energy used by herbivores over a given period (Lubchenko and Gaines, 1981), it was important to investigate the use they made of energy. Since energy is a conservative item, energy changes between parts of an ecosystem had to be accountable by the first law of thermodynamics: Conservation of Energy.

A convenient and frequently used unit of biomass in terms of energy is the Kilo gram-calory (Kcal) expressed per unit of surface. When biomass was to be measured in energy units, it was usually necessary to measure the calorific content -or heat of combustion per g dry weight- of the biological material either directly, by burning it in a bomb calorimeter, or indirectly, by determining its approximate chemical composition as proteins, carbohydrates and lipids. Known average values of calorific contents for each component were applied. The first method, which is more accurate and direct, was often applied.

Interestingly, energy mainly flows in the benthos of aquatic communities at the second and third trophic levels (previously described), which are among the easiest measurable components of an ecosystem and also the most interconnected (in terms of connectance) according to Pimm (2002). A simple method of “icons” was proposed by Odum (1959) to indicate each intermediate of the system (e.g., primary producers, consumers, etc.) and formulate simple graphical representations of ecosystems, described by energy flows within each intermediate. Furthermore, this method described the efficiency of energy transfers between trophic levels and the use of energy to overcome environmental constraints. These subjects were important not only to define basic principles underlying the functioning of ecosystems, but also to suggest methods of preservation and exploitation of natural environments (Zupo et al., 2016).
1.2. **Energy as the key descriptor of ecosystems**

Given the previous assumption, the research was further concentrated on energy as the main descriptor of relationships in any ecosystem. The first researches tried to answer fundamental questions as:

- *What proportion of stocked energy is used to increase the overall standing crop of herbivores?*
- *How much is passed to carnivores?*
- *Is the remainder dissipated as heat of respiration?*

It was necessary to assess the number, biomass, mortality, moulting losses, and respiratory rate of each main species of animals in order to answer these questions in any natural environment. For these studies the terminology of IBP (International Biological Programme) was used, according to Holme and MacIntire (1984). The appropriate IBP terms and symbols for components of energy flow for heterotrophic organisms are still quite informative:

**Production (P):** That part of the assimilated food or energy that is retained and incorporated in the biomass of the organism, but excluding the reproductive bodies released from the organism. This may also be regarded simply as "growth". It is useful to reserve the term "productivity" for the potential rate under ideal or stated conditions, and use the term "production" for the actual rate of incorporation of organic matter or energy (Davis, 1963).

**Egesta (F):** The part of the consumption that is not absorbed but is rejected as faeces;

**Absorption (Ab):** The part of the consumed energy that is not rejected as faeces;
Excreta (U): The part of the consumption that is absorbed and later passed out of the body as secreted materials, usually in an unwanted form as, for example, in the urine, or exudates as milk, mucus, nematocysts, etc. The combined energies of F + U are sometimes referred to as Rejecta;

Assimilation (A): That part of the consumption that is retained for physiological purposes as production (including gonoproductions), and respiration, but excluding rejecta;

Respiration (R): That part of the assimilated energy that is converted into heat, either directly or through mechanical work performed by the organism;

Gonad output (G): That part of the absorbed energy that is released as reproductive bodies. Because of its great importance in survival and recruitment, this part of the energy flow is separated from excreta (U) and production (P); some authors might regard it as being a contribution toward either of these elements of energy flow (Bagenal, 1978);

Yield (Y): The part of the production or excreta (in a varied sense) used by mankind or other predators. It may refer to only part of the organism or it may refer to a fraction of the individuals in a population, which are consumed by a predator or harvested by man;

Mortality (M): The mortality due to all causes, including any yield Y;

Efficiency of assimilation: The ratio of the food absorbed into the organism to the total amount of food ingested;

Growth efficiency: the total energy of production of body tissues and gonads, as a fraction of the food ingested;

Coefficient of ecological efficiency: the measure of the efficiency of energy transfer from one trophic level to the next. The simplest definition is the fraction of the energy consumed at a given trophic level (n) that is exploited by a predator at the next trophic level (n+1), referring to the yield to the predator as Yn.
Hence, assuming conservation of energy, we are able to set the following fundamental equations:

\[
\begin{align*}
(3) \quad & C = P + R + G + U + F \\
(4) \quad & Ab = C - F = P + R + G + U \\
(5) \quad & A = P + R + G \\
(6) \quad & Ab/C = (C-F)/C \\
(7) \quad & (Yn/Cn) = (Cn+1/Cn)
\end{align*}
\]

The equation (3) is interpreted as the fundamental equation of total energy budget and it was applied to any system where all energy sources and all energy sinks were known. This budget could be applied to a species and, with increasing difficulty and complexity, to a population or to all the organisms constituting an ecosystem. Since an energy budget must balance, should any of the terms be particularly difficult to measure, it was omitted and found by difference. However it was preferable, whenever possible, estimating all the terms of the equation, and use them as a check of the accuracy of the flow-sheet.

For some practical purposes the production term (both as primary and secondary) in the energy budget (P), was the only essential one. It was also the most important quantity to be measured in fundamental studies of ecosystems and productivity.
1.3 Secondary production measured by energy budgets: historical and methodological issues

There are two different approaches in the measurement of the total secondary production by a population, which must be clearly distinguished. The first is to take into account the growth increments of all members of the population during a given period (e.g., 1 year). The second is to take into account the fate of the biomass that has been produced during a given survey.

If the biomass is expressed in energy units, it must be conserved and the above relations remain true. If the biomass is expressed as weight, the loss of biomass due to respiration and excretion is usually not taken into account and the above equations are not applicable, since they involve R and U. The changes of biomass in the energy flow can be referred either to a given area of the system or as a fraction of the existing amount of standing crop present. Investigations tried to measure the previous constants and calculate, on the basis of cited equations, the other variables of energy flow in any ecosystem.

If $B_0$ is the standing crop biomass at the start of experiment and $B_1$ is the standing crop biomass after a given period, then:

$$P = (B_1 - B_0) + M = dB + M \quad (8)$$

The previous equation implies, generally, that population dynamic studies must be performed and applied to the energetic data in order to obtain a yearly standing crop and a total energy budget for an ecosystem or a given compartment. In fact, productivity measurements require knowledge of the rates of growth in terms of dry weight or energy and this information, about whole compartments of a food web, can be obtained from population dynamics (e.g., based on size-frequency histograms of monthly data).

Population estimates were normally obtained by taking random samples of fauna at time intervals (e.g., 1 month). Animals could be counted, weighed, and their energy value determined by chemical processes or by means of bomb-
calorimeters. Also the energy contained in foods and the energy residual in faecal pellets was measured. Respiration rates were measured by respirometry sets and O₂ electrodes.

The heat of combustion of foods, faecal pellets and animal bodies was used to calculate some of the above-mentioned variables. Heat of combustion was measured in bomb calorimeters, usually made of steel and filled with oxygen under pressure. For some biological work, a sufficient quantity of dry tissue was not easily available (e.g., faecal pellets produced by small benthic organisms) and thus, micro-bomb calorimeters were used instead. The Phillipson (1964) micro-bomb calorimeter had a capacity of 8 ml and took samples of 5-10 mg.

Faecal pellets, due to their low calorific content, burned too slowly. Since it was most important that the samples burned completely and smoothly, some improvements were normally achieved by compounding a known amount of benzoic acid of standard thermodynamic quality into the pellet. For these kinds of substances, an alternative to direct calorimetry was the use of indirect chemical methods. These approaches, however, were not sufficiently accurate for small amounts of substances.

The ingestion and egestion were difficult to measure, especially in small organisms, and there were a few satisfactory studies of energy flow applied to benthic species. Rates of ingestion and egestion were normally measured in the laboratory. There were, in principle, two types of methods available:

1) **direct methods**: the food ingested and the faeces produced by the animal, over an adequate period of time to establish continuity, were measured directly.

2) **indirect methods**: the concentration of an indigestible marker present in, or artificially incorporated into the food, was measured in both food and faeces, together with the rate of faecal production.
The simplest marker was the organic ash content of the food itself, although the method was very inaccurate and perhaps unreliable if the amount of ash present was small. Conover (1966) employed this technique for measuring the ingestion rates of copepods; it was assumed that all the ash absorbed in the food was present in the faeces, and this influenced results. However, other inorganic compounds (e.g. salts, and calcareous substances) and markers added to the food (e.g., vital dyes like Methylene blue) could be partially assimilated. Thus, the method of ash measure represented a good balance between the accuracy of results and the influence of the food quality on the organism to be tested.

Energy losses by respiration were directly measured by respirometry, although the values obtained accounted, generally, only for a fraction of the actual amount of energy to be considered as “cost of maintenance”. In fact, anaerobic respiration and heat losses contribute to this value. For general ecological purposes, the value obtained was considered accurate enough. According to Elliot & Davidson (1975) and Ivlev (1934), in view of other experimental errors involved in the measurements of energy losses through respiration, the assumption that 1 ml of oxygen at normal pressure and temperature is equivalent to 29 J, was sufficiently close for all practical purposes. The knowledge of chemical composition of foods ingested was useful to reduce the error in the conversion of oxygen uptake into energy losses. The energy lost per mg of oxygen was variable according to the elementary composition of foods and tables were available (Elliott & Davidson, 1975) to calculate oxycalorific equivalents of different compounds. On the basis of previous considerations methods were devised to calculate the energy budget in various environments.
1.4. Various types of theoretical models and their consequences

1.4.1 The shape of food webs

In general terms, food webs are networks of interactions among species, groups of organisms, populations, or aggregate trophic units (Winemiller and Polis, 1996). Different approaches were proposed by scientists, according to the features of target ecosystems, available instruments of study and aims of the research (Dunne, 2009), whether they were predictive, descriptive or simply theoretical. Yet in 1927 Elton suggested that food webs are a central topic in the field of animal ecology, although at his time food chains were considered as the basic concept in this field, presently almost deprived of importance in most complex ecosystems. At the time, simple models of trophic interactions (Bronmark, 1985) offered the most direct framework to understand how entire ecosystems functioned and several concepts relevant for food webs were emphasized, as the role of body size (Thayer et al., 1984), the pyramid of numbers, the concept of niche, and various indirect effects of food webs. Some of these topics are still interesting fields of scientific discussions, as a demonstration of the key importance of the concepts linked with food webs and interactions (Brose et al., 2006). In fact, the concepts presented by Elton, as the introduction of “pyramids of numbers”, influenced ecological sciences for decades, and most notably Lindeman (1942) and Odum (1953) ideas on ecology, while Elton (1927) initially tried to balance the search for simple theories with the recognition of ecological complexity in natural systems. This concept is recurrent in present research trends.

1.4.2. The vision of Elton

The initial vision of Elton (1927), in terms of interactions between prey and predators, evolved rapidly into the Lindeman (1942) vision of prisms of energy and nutrients: a concept that directly generated, after some time, the above
mentioned ideas of the IBP (Nicholson, 1961). Energy networks permitted the definition of a common currency for studying and comparing diverse aquatic ecosystems (Lindeman, 1942). A key advancement of his characterisation of ecosystems was the recognition of abiotic and biotic compartments through which organic matter is transformed. This vision brought to the first reference to the concept of “ecosystem”, as “the association of abiotic and biotic components” (Golley 1993): another demonstration of food webs as an underpinning concept for the ecology theory... and it continues to expand today.

1.4.3. The visions of Gardner and May

In fact, the theory further expanded through the IBP, as above referred, to reach full maturity, demonstrated that —at list in part- ecosystems may be modelled using energy networks and considering “animal characters” as energy transducers (Gardner and Ashby, 1970; Williams and Martinez, 2000). However, only after the end of the Program it was possible to foresee how the concept of “food webs” was closely interconnected with some key features of ecosystems, as their stability and diversity (May, 1972; McCann, 2000). In addition, various further evolutions of these concepts indicated interrelationships, demonstrating that biodiversity influences stability of natural communities and vice-versa (Dunne, 2006; Ives, 2005; McCann, 2000; 2005). In a mechanistic (not totally accepted) view of ecosystems, the number of nodes (system size), the number of links among nodes (system complexity), and the interaction strength among nodes influence the relative degree of stability of ecosystems (Gardner and Ashby, 1970). In fact, generating small perturbations to equilibrium values of nodes, and checking whether values return to the previous equilibriums, the stability levels of various ecosystems are assessed.
1.4.4. Emergent properties

Alternative parameters and “emergent properties” (Novak, 2006) were further proposed in the never-ending search for an easy assessment of system’s stability, as the ascendancy (Banerjee et al. 2017), the biodiversity (Bastolla et al., 2005) and the connectance levels (Liu et al., 2017). Various authors demonstrated other emergent properties of ecosystems (Novak, 2006) according to the structure of their food webs (May, 1972), as the inverse relationship between connectance (a measure of the food web complexity, based on the proportion of realized ecological interactions among the potential ones; Poisot and Gravel, 2014) and species richness (directly related to biodiversity, ruled by the equation (2) above mentioned). Various groups (Briand, 1983; Briand and Cohen, 1984; Cohen et al., 1981) further investigated these patterns. As above indicated, not all the conclusions of May were generally accepted and some of them are still discussed, in the light of modern theories. However, his studies revolutionized this scientific field, in terms of theory and practice, and they continue to impact and inspire investigations on food webs, especially through quantitative analyses of their structural properties. In addition, present research in evolutionary ecology still proposes individual-based stochastic models, where ecological communities are considered “emergent structures” derived from interactions between organisms.

1.4.5. The TaDa model

A very interesting and modern view of this concept is the TaDa model (Tangled Nature model) proposed by Christensen et al. (2002). According to this model, individuals are vectors in a genotype space and their reproductive success is determined by the fitness of each individual to his own environment. Some conclusions of this model, as the exponential extinction of the node degrees according to the density of species, will be further discussed along with my general model of species diversity related to the abundance of resources.
His theories on the effects of connectance received attention by further authors (Gardner and Ahsby, 1970) that re-defined the properties of ecosystems. The models attempted to mathematically establish their levels of stability and complexity. In particular, they modulated the number of nodes (system size), the average number of links among nodes (system complexity), and the strength of interactions (effects of strength of nodes).

The first pure theorization of ecosystem properties led to a useful process of hypothesis and test, considered to be a milestone in the study of food webs and, more generally, in ecology. For example, it was demonstrated that structural properties of networks affect the stability of ecosystems and, in particular, an increase in the number of nodes, complexity, and interaction strength represents a destabilization factor for natural networks. Also, researches by May and his followers demonstrated that if the interaction strength in a stable system is kept constant while species richness is increased, the system might remain stable only if the overall connectance decreases. Thus, an inverse relationship between connectance and species richness was demonstrated. This assumption was further investigated and obtained subsequent support from investigations on natural food webs (Briand, 1983; Cohen et al., 1985; Pimm, 1982; Yodzis, 1980). We will use these relationships to propose a general model linking species richness to the abundance of trophic resources.

1.4.6. Measuring web properties

As above specified, the theorization of specific properties of food webs primed further analyses based on hypotheses and these focused on specific metrics measuring the web properties, as the measures of connectance, food chain length, degree of omnivory, proportion of species at given trophic levels, population densities, etc. (Pimm, 1979, 1982, 1984). Going deeper in the results of these analyses would be redundant here, but it is worth to observe that, very simply, the introduction of ecological realism in mathematical models (e.g., non-random trophic structure imposed to the system), implies that predictions on food
web stability diverge from results based on randomly assembled mathematical models. This evidence primed researches in next years (e.g. Cohen, 1978) on real-world food webs aiming at predicting their structure based on quantitative metrics. One of the most interesting theories, in this view, was the so called “cascade model”, based on just two variables represented by:

a) species richness
b) linkage density (total number of links divided by species richness).

The hypothesized system had two constraints only:

1) species are randomly assigned to a one-dimensional feeding hierarchy;
2) species can only feed on lower elements in the established hierarchy (Cohen and Newman, 1985).

This very simple model, based on two basic assumptions, was effective in reproducing the structure of food webs in a range of ecosystems, indicating that similar underlying structure could rule several ecosystems.

Next advancements of food web theory indicated that a network model could answer several questions about the stability and functionality of ecosystems and allow for a simulation of food web dynamics (Dunne et al., 2002a; 2013; Thompson et al., 2012). Similar to small world networks, investigations indicated that food webs tend to have short path lengths (Williams et al., 2002), while deviation from scale-free structures in networks indicated that food webs should be more robust to species extinction than other forms of networks, as a result of high levels of connectance. In contrast, food webs with lower connectance are more sensitive to species extinctions. For example, it was demonstrated (Dunne et al., 2002b) that extinctions are more likely to propagate throughout networks with abundance of trophic specialists.

1.4.7. The conclusions by Winemiller

However, empirical data used to set and test food webs were insufficient to depict real-world feeding relationships and in often underestimated the actual strength of species interactions (Winemiller and Layman, 2005), making the
prediction somewhat weaker and uncertain, from a mathematical point of view. First examinations of tropical basin’s food webs demonstrated quite higher number of interactions and here it has been demonstrated, for the first time, a central concept that will be expanded throughout the present thesis: the completeness and the resolution of simulations is a basic attribute to obtain clear demonstrations of food web properties (Winemiller, 1990; Winemiller, 1989; Winemiller and Polis, 1996; Winemiller et al., 2007).

However, in-deep investigations require huge amounts of research work. For example, Winemiller (1990) examined about 4800 guts in each tropical watercourse to obtain sufficient conclusions on the degree of connectance in his empirical research. Actually, most investigations on food webs took into account only a limited number of nodes/animal groups, often from a single point of view (e.g., without considering the actual surface area or the volume where species lived), using different metrics, sometimes taking into account “suspected” but unverified feeding relationships. This led to easy generalizations and simplifications about the actual complexity of ecosystems (Cohen et al., 1993). This concept will be further used to propose a general model for evaluation of actual resources available for food web characters (the so called RAFI Index; Zupo et al., 2017). Actually, the spatial and temporal boundaries of food webs are arbitrary and each author investigated subsets of feeding interactions in a given region, generally chosen for practical reasons (a seagrass meadow, a portion of coral reef, etc.), not considering that ecosystems are interconnected and any boundary is an (indispensable) artefact influencing the conclusions of any study.

Another important corollary deriving from the researches by Winemiller (1990) was the demonstration of a positive relationship between connectance and species richness, such that more diverse webs had higher connectance. This conclusion derived from quantitative analyses, that contrasted prior assumptions (Briand, 1983; Pimm, 1982), and indicated an inverse relationship between connectance and species richness. The discussion continued up to the present,
with opposite visions. Hence the concept is worth to be investigated, because from it may depend our comprehension of life expansion and biodiversity.

The investigations contained in this thesis partially diverge from those of Winemiller and it will be demonstrated, based on empirical data and mathematical simulations, that species richness is inversely related to the abundance of resources. This is the fundamental concept that will be expanded within this thesis to reach higher assumptions and demonstrations on the consistent properties characterizing assemblages of natural life, extensible to communities at various organizational level, from single cells to the largest ecosystems (Shoener, 1986; 1989).

1.4.8. The classical vision of Polis

However, prior to conclude the general presentation of the history of food webs it is important to consider some fundamental studies conducted mainly on sub-aerial systems, whose conclusions may be extensible to marine ecosystems, claiming for the need of direct assessment of real-world webs (Polis, 1991; Polis and Hurd, 1995; 1996; Polis et al., 1997; Polis et al., 2004). For the first time the interactions among ecosystems (e.g., how terrestrial inputs affect ecosystem functions in freshwater ecosystems, or the impacts of marine productions on terrestrial food webs) were measured and quantified, demonstrating that the theoretical elimination of habitat boundaries brings to a better understanding of food web dynamics and to concepts important to investigate the landscape ecology.

Probably, due to the need of generalizations to afford food web studies (as above referred, we need to hypothesize hypothetical boundaries, reduce the number of connections due to lack of information, underestimate the flows of detritus, etc.), further studies tended to approach the problem from an alternative heuristic point of view, generalizing empirical information to compile energy flow through webs. For example a modern frame of research uses stable isotopes and molecular descriptors, in order to define time- and space-integrated properties of
food webs, avoiding the “snapshot of recently ingested prey items” provided by classical gut content analyses (Layman et al., 2012; Hobson and Welch, 1992). In fact, stable isotopes provide time-integrated estimates of trophic positions avoiding the need for extensive diet analyses performed on individual consumers (Vander-Zanden and Rasmussen, 1999). Stable isotope analyses are surely useful to produce information on bioaccumulation and help understanding the fate of trophic resources within the pathways of food webs. However, they do not allow detailed modelling of fluxes and of resource partitioning (van Valen, 1965), as previous studies did, and this makes unfeasible the evolution of mathematically formulated theories on the relationships between biodiversity, connectivity and abundance of resources.

For example, it has been recognized that individuals within a population vary according to their trophic roles (Roughgarden, 1972; Schoener, 1986). The importance of this concept was maximized by studies demonstrating that some “generalist” taxa are actually composed of several individuals each characterized by a specialized diet (Bolnick et al., 2003). Investigations on the “ecology of individuals”, in fact, led to newer assumptions, but also complicated our ability to model real-world food webs, in respect to the above mentioned stable isotope studies. In addition, they are only partially important to discuss the thesis herein contained. Thus this theory will not be afforded in deep, here. A single important point determined by this theory is that individuals of the same species may exhibit high overlap in resources use at low population densities, but at a higher conspecific density individuals will diverge in trophic ecology to minimize intraspecific competition (Bolnick et al., 2011).
1.4.9. Synthesis of fundamental approaches

On the whole, all the above-mentioned researches indicate two fundamental approaches to the problem of food webs:

a) webs of energy flows and
b) functional webs (Paine, 1980).

For example, it was demonstrated that the experimental removal of the starfish *Pisaster ochraceus* (Asteriidae, Forcipulatida) resulted in a local decrease of species richness, because the population size of a dominant competitor, a bivalve mollusc, increased excluding lower competitors (Paine, 1966, 1969a, 1969b, 1974). Thus, again, a significant effect was pinpointed, indicating a relationship between structure of food webs, abundance of trophic resources and biodiversity of the target community. In particular, an increase of the target “food” for a starfish (i.e., bivalve molluscs) was translated into a decrease of biodiversity for that specific trophic level. In addition, this theoretical advancement also led to the establishment of the concept of “keystone species”, in this case referred to the starfish, strong and highly influential for local food web dynamics.

In parallel, the dynamics of trophic cascades indicated that nutrient inputs determine the productivity of a system and cascading effects have broad implications for understanding food web dynamics and ecosystem functions (Carpenter et al., 1985; 1987; 2001).

1.4.10. Moving towards non-trophic interactions

Since this step, the attention of scientists was further attracted towards new horizons, represented by non-trophic interactions. In fact, the food web structure is definitely a function of the total sum of direct feeding interactions between consumers and their resources, but indirect effects, like density-mediated indirect interactions or allochemical and infochemical substances, may tune the efficiency
of trophic cascades (Schmitz, 1998; Schmitz et al., 2000; Schmitz et al., 2004; Werner and Peacor, 2003). These initial observations opened the way to the idea of “functional foods” and to the “emergent” (Novak, 2006) properties of food webs (anticipated by the TaDa model previously introduced), to explain how direct feeding interactions are insufficient to completely explain the complexity of food webs, and why behaviour, chemical interactions and life cycles, often co-evolved between plants and animals living in the same ecosystem, may be critical to understand the structure of food webs and the temporal dynamics of trophic fluxes.

Finally, as above referred, co-evolution of species (Post and Palkovacs, 2009) and evolutionary biology, in general, may be crucial to understand contemporary developments and relationships among mathematical and structural properties of food webs (Schoener, 2011). As a consequence, the attention of food web investigators definitely moved from simple observations of their structure to an experimental approach aiming at the comprehension of emergent properties, as those revealed by chemical interactions among species. In addition, the above considerations demonstrate how food webs have implications in species, population, community and ecosystem dynamics, involving mathematical modelling, physiology studies and chemical relationships, up to co-evolutionary dynamics. Thus, in the last decades scientists approached the study of food webs and debated about the right scientific perspectives according to divergent and continuously changing viewpoints, as indicated, alternating empirical and theoretical approaches.

1.4.11. **Food webs and biodiversity**

The scopes of this thesis go beyond the aforementioned points of view since it aims at identifying general patterns of food webs, to be applicable to a large range of plant and animal associations, even at various organisational and structural levels, as some previous authors attempted (Riede et al., 2011; Layman et al., 2015). For this reason, the next chapters of introduction will summarize the
work of various authors addressing the interactions between biodiversity and resource availability, in order to detect fundamental mathematical relationships to support the main hypothesis. These relationships will be further tested, according to the model for rapid detection of trophic resources to reach the conclusions of the thesis.

However, prior to start the description of the time evolution of the notion of food webs in the last decades, it is important to define key premises indispensable to transform the next chapters into a hypothesis to be tested and validated on field data to answer the main question of this thesis. To this end, some mathematical relationships of networks will be introduced in order to show how complex ecological patterns may be modelled into simple equations, whose validation will represent the main output of the thesis.
1.5. Evolution of concepts and the need for a “model”

In the next chapters examples of the evolution of the concept of food webs in the last decades will be provided. Several studies performed on this topic exhibited a “hope” for a synthetic model able to reproduce the complex patterns of energy and matter circulation in nature. Scientific research moved towards multiple aims, individually important to understand key processes; however, they were insufficient to find a general law consistently linking the availability of resources to the biodiversity measured in natural environments. In fact, part of the research explored the possibility to describe key mechanisms and processes, as the strength of trophic links, the patterns of presence of different types of predators and prey and the distribution of species among trophic levels (Zupo, 1993). Another sector of the research explored emergent (Novak, 2006) properties of food webs, as the changes over time of trophic relationships within complex and stable ecosystems and the role of information, often overcoming the importance of energetic relationships (Zupo, 1993; Zupo, 2000): this produced a critical shift from the sciences of energy to the concept of emergy. Finally, an important output of recent researches was the discovery of common features characterizing the food webs of such different environments as tropical reefs and temperate seagrass meadows (Zupo and Mazzocchi, 1988). Thanks to this discovery we can finally model, with good degree of approximation, the actual abundance of trophic resources available for various groups of consumers and this opens up new chances to investigate the relationships between biodiversity and trophic resource availability (Zupo et al., 2016).

Due to the lack of punctual and comparable data on the availability of trophic resources, most studies linking biodiversity and food webs investigated mainly local effects of biodiversity on the stability of ecosystems and the total biomass of consumers reached (May, 1972). In contrast, studies relating the effect of trophic resource availability on the biodiversity of consumers are almost absent because the abundance of trophic resources has been constantly investigated using a range of methods, adopting variable measures and was based on a range of
volumes or area units to evaluate stability and complexity of ecosystems (May, 1973). All this made generally impossible the comparisons of biodiversity and resource availability in different environments, to test hypotheses derived from mathematical models (Rosenzweig et al., 1999). In addition, the newest chances offered by modern computers revive the challenge to obtain complex models simulating the actual properties of natural ecosystems (May, 1999) in order to forecast their development according to global changes. However, taking advantage of the information contained in further chapters and crossing them with the most advanced modelling techniques, an attempt will be made here to find general equations and trends explaining the effects of trophic resource availability on the biodiversity of the communities of their consumers.
1.6. Modelistic approaches to trophic interactions

It is demonstrated that many species of animals directly interfere with each other through chemical, physical or other interactions (Mazzella et al., 1991), but besides these, the food web theory shows that community dynamics and structure are mainly controlled by trophic interactions (Rossberg et al., 2005). We will further analyse the consequences of these types of interactions on the levels of biodiversity of various ecosystems and a search for common laws ruling different environments will be performed, even at very different structural levels.

Most researches aimed at understanding the extent to which biodiversity is important in the functioning of ecosystems and, in order to quantify this effect, investigations were concentrated on empirical relationship between biodiversity and ecosystem efficiency to perform given functions, directly or indirectly relevant to their services supporting human activities (Rossberg et al., 2006). Investigations and mathematical models often demonstrated a close relationship between biodiversity vs. biomass and productivity of ecosystems; these relationships were also related with the stability of ecosystems (e.g., Millennium Ecosystem Assessment; Hassan et al., 2005).

Thus, mathematical models were developed to describe and forecast food web functions and properties although, according to Box (1979), “models are all wrong but some of them are useful”. Many different useful models of complex systems (including food webs) exist. A conceptual reduction of ecological communities to “food webs” is commonly considered acceptable (Jennings et al., 2002) and any area of science may invest in theoretical research aimed at constructing useful ecological models and improving them according to experimental evidences. Very simple and effective models, as the Lotka-Volterra (Lotka, 1922; 1956) simulation for competition, may exemplify scenarios of community assembly using elegant simplifications, as:

\[
\frac{d B_j}{dt} = (s_j - \sum_k C_{jk} B_k) B_j \quad (9)
\]
where $B_j$ is the biomass of a predator species, $s_j$ is the size of its population, $C$ is the consumption according to the biomass $B$ of its prey and we impose $s_j$ and $C_{jk} \geq 0$ for all $j$, $k$.

This model is a generalization of the logistic growth model, where several competing species hamper each other’s growth. In addition, periodic invasion-fitness distributions may complicate the model and permit evaluations of the trends of biodiversity over time. Natural quantitative limits exist to keep sustainable the species richness of a food web. Thus, species richness must be a consequence of intrinsic processes operating within food webs, not controlled by the influence of speciation, invasion, etc. However, to produce an effective model, we should also consider invasion processes, possibly leading to the extirpation of other species from a given community. Previous papers (Zupo et al., 2015) demonstrated that the community is chemically defended (Sieburth and Conover, 1965) against the attack of invader species (competition avoidance), because the community owns knowledge shared among the residents- that invaders have not incorporated in their strategy yet- about the toxicity of some prey. However, even when saturated and chemically protected, communities are not closed to invasions and an extirpation may eventually be due to a direct knock-out of a resident species by an invader or it may result from more complex interactions within the community, indirectly facilitating the process of extirpation (Yackulic et al., 2014). Thus, the natural turnover of communities also results from a continuous process of alien invasions and resident defences, leading to progressive (slow) changes of species composition, including possible changes of species diversity. Due to climate change influences, further and faster invasions of alien species support the functioning of communities. It has been demonstrated (Maibam et al., 2015) that environmental modifications due to climate changes may influence the chemical relationships among organisms and increase the vulnerability of the chemical defences protecting natural associations (Zupo et al., 2015), so facilitating an easier admission for invader species. Fixed mathematical limits constrain the number of species naturally assembled in a community, even
if species composition was progressively modified by climate changes. Interestingly, the biodiversity has space constraints: since there is less space at higher than at lower latitudes, less species may be predicted to globally co-exist, as the planet warms up and oceans acidify (Descombes et al., 2015; Zupo et al., 2015).

### 1.7. Essential mathematical simulations: noticeable relationships

#### 1.7.1 How species diversity influences the community biomass

Mathematical simulations permit to evaluate the relationships between total biomass of the community ($B_{tot}$) and species diversity ($S$) according to Wilson et al. (2003) and Wilson and Lundberg (2004), using approximation techniques, as the mean-field approximation, often reported by physics. According to the mean-field approximation we can forecast:

$$B_{tot} = \frac{SK}{1+(S-1)C}$$

where $I$ represents the invasion rates and $C$ represents the competition rates, which indicates a continuous increase of species richness, up to a plateau, normally expected in any community, until the rate of competitive exclusions of species is balanced against the rate of invasions.

This trend proceeds in time in accordance with increments of biomass, as reported in the Figure 2 (Hooper et al., 2005) and this simulation represents, indeed, an indirect demonstration that a higher diversity ($S$) corresponds to a higher biomass ($B_{tot}$).

In fact, the maximum value of $B_{tot}$ obtained at saturation must correspond to the value obtained by the mean-field approximation for infinite values of $S$. Thus, again, the increase of species richness is naturally correlated to an increase of biomass of the community, up to a plateau imposed by space constraints,
confirming the assumptions of several authors (May, 1972; Gardner and Ashby, 1970; Hooper et al., 2005).

Figure 2. Relationship of $B_{\text{tot}}$ and $S$ along time, according to Hooper et al. (2005)

Figure 3. Known relationships (right) and hypothesis of this thesis (left)
1.7.2 How community biomass influences species diversity

Unfortunately, the relationships described in the previous chapter about the effects of biodiversity on the biomass of resources does not add much information about the main question above stated (Figure 3), that in contrast aims at understanding:

*Does the relative abundance of trophic resource influence (positively or negatively) S?*

As a matter of fact, most theories tend to provide measures of biomass in order to detect the effects of biodiversity on the productivity of ecosystems and evaluate their services. An opposite theoretical approach is proposed in the present study, to forecast the diversity of an ecosystem (or part of it) according to the abundance and availability of trophic resources. In this case, should we expect that a higher availability of resources triggers a higher diversity of species, as instinctively one could forecast? Will a large amount of available plant biomass trigger an explosion of species diversity for vegetarians? Does a high abundance of organic detritus sustain a large diversity of detritivores? The answer is not trivial, since a higher availability of “prey” could theoretically both induce an increase of species number, or an increase of (larger) individuals deriving from a few species. In both cases, a good efficiency of energy transfer between levels is assured, but the effects in terms of biodiversity are quite different. This question also imposes to establish if an increase of trophic resources available for given categories of consumers will lead to a different type of interference competition, exploitation competition, or apparent competition. Interference competition is commonly associated with direct (somewhat aggressive) interactions between organisms; exploitation competition (often included under indirect competition as well) is associated with the exploitation of biotic or abiotic resources; apparent competition (sometimes called indirect competition) is associated with the resistance of two competitors to mortality by a consumer, parasite or pathogen.
they share. A numerical increase and/or a biomass increase of a few species feeding on a given resource will produce low competition and increase of the productivity. In contrast, an increase of diversity of species feeding on the same resource will lead to an increase of competition and relatively low productivity of their populations (MacArthur, 1969; MacArthur and Levins, 1964).

In both cases (increase of individuals of a few species or increase of the total number of species “S”) a large availability of feeding sources could produce a higher biomass of consumers, but the effects on the general levels of diversity might be contrasting (MacArthur, 1955). As an alternative, a higher abundance of feeding sources could theoretically have no effects on the biomass of consumers, because it could be only partially consumed (e.g., chemically defended resources) and the theory of feeding interactions may be applied to various kinds of feeding interactions (Maibam et al., 2014). Finally, various competition strategies may be theorized for producers (allochemical relationships, competition for nutrients and light, etc.) and again we should be able to predict if an increase of resources (e.g., inorganic nutrients), sufficient to trigger an increased productivity, will also facilitate variations in the biodiversity of primary producers and eventually, in which direction (positive or negative effect). May a trend be forecasted, according to the theory of networks and the data deriving from empirical studies on ecosystems? Inorganic fertilization and increase of light irradiance will lead to a simple increase of production for the plants already present (increased exploitation of shared resources), or conduct to an increase/decrease of biodiversity of plants (Makarieva et al., 2008) sharing the same resource, according to an increase of resource-mediated competition?
1.8. Mathematical networks and their properties

1.8.1. Predictable effects of production and competition

To obtain indications about this central question, we will start now by examining some fundamental mathematical properties of networks (Case and Gilpin, 1974) and we will compare them with empirical data obtained in ecological communities. For example, we do know that consumer-mediated competition is strong when producers exhibit a high carrying capacity (K) and are aggressively consumed by species efficient in the foraging upon their resources. In contrast, consumer-mediated competitive exclusion decreases when producers exhibit low carrying capacity and/or are eaten by inefficient consumers. If the abundance of consumers is constrained by internal competition, they will not have strong effects over productive communities.

Different theories were developed to address this problem. They all imply an upper limit $S_{lim}$ of the number of competing species $S$, over which the coexistence becomes increasingly difficult (Bastolla et al., 2005). Species that efficiently exploit their resources keep the abundances of producers low (Chesson, 1994). For this reason, small abundances of available resources are normally recorded, even if they are intensively produced at high rates (May, 1972). Less aggressive consumers tend to be less influential on the population size of their prey (top-down effect). However, the actual issue herein raised (bottom-up effect) is if a larger abundance of “potential” feeding sources (i.e., theoretically present in the community in the absence of their consumers) may trigger positive or negative variations of species richness $S$ within the pool of their competitive consumers (Bastolla et al., 2005).
1.8.2. Species abundance distributions

A property of ecological communities, fundamental to develop several models, is the distribution of numerical abundances of species (namely, the Species Abundance Distribution, SAD). The leading concept is that although a natural community may be dominated by a few species, we normally detect the presence of several less common and rare species. SAD is low-demanding with respect to criteria for properties and in fact McGill et al. (2007) reviewed 27 different models to reproduce and explain empirical SADs, concluding that most of them perfectly reproduced the field data, even though the ecological mechanisms considered were quite different. Sometimes we define the “complexity of a system” as the possibility to be described by a variety of different models. In this view, food webs are complex, because they fall into this category, being multi-dimensional entities. However, according to Rossberg (2012), while being guided by mathematical techniques because theory-driven ecology goes one step further, we need in-deep knowledge and data of empirical systems, but much theoretical work is just a matter of trial and error. In particular, community food webs classically describe networks of flows of energy and biomass between populations of various species, as resulting from feeding interactions.

1.8.3. Networks

From a mathematical point of view, food webs are networks because consumers (generally) do not feed on all species present in a community. This concept is quite clear and easy from a formal point of view, but it is scarcely defined and precise when we observe the actual rules in nature. In fact, a species might consume a large number of “potential” resources (several potential links) but most of the energy reaching its population could derive from a limited number of preys (main preys, due to active choice or seasonal availability of resources). This concept is difficult to be synthesized into a general theory because “theoretical flexibility” is hardly needed. This brings to various generalizations, simplifications and types of models containing large or small numbers of nodes for the
description of the same ecosystem. Different types of models may take into account the chemical composition of bodies, the spatial structure of food-webs or specific features of networks, as the connectance or the seasonal variability, the trophic transfer efficiency between levels and the number of trophic levels. For example, Lindeman (1942) proposed a relationship for trophic transfer between two next levels as follows:

\[
\text{Transfer Efficiency} = \tau = \frac{c_{r}}{c_{A}}
\]

(11)

where \(\tau\) is the ratio of production rates at adjacent trophic levels, \(c_{r}\) is the constant of respiration and \(c_{A}\) is the assimilation efficiency for a given species. According to this equation, it is interesting to observe that the energy content of farmed salmons and the transfer efficiency of their commercial feeds, described by Tyedmers (2000), exhibiting transfer efficiencies between 15% and 19%, was in total agreement with the data reported by Brett (1986) for wild populations of salmons and their natural foods.

As expected, the proportional changes in abundance (availability, biomass, and population size) resulting from bottom-up effects, increase at each trophic level. A small increase or decrease in primary production, for example, triggers large increases or decreases of populations at higher trophic levels. The ecological reason, sustained also by the above reported equation, is that a decreased resource abundance induces less biomass being available for consumers, at each level, crossed by the assimilation efficiency, leading to a proportional decrease in consumer abundances (Rossberg, 2012). A corollary of this rule is that small perturbations of a food chain (in given top-down or bottom-up effects) might be combined, without affecting each other. From this perspective, some aspects of the historical debate of top-down vs. bottom-up control in ecosystems may appear scarcely effective to describe ecosystems (Gross et al., 2004).

Thus the “rates” each model provides are often referred to different kinds and dimensions of physical quantities. Sometimes they indicate a flow rate (having
1.8.4. Species richness and resource availability

The number of species present in an ecosystem is normally considered as the species richness “S” and it is only partially related to the number of trophic links “L”. The population dynamics of a species may be modelled as:

\[
\frac{dN(t)}{dt} = rN(t) \tag{12}
\]

where \( n(t) \) is the number of individuals (population size) and \( r \) is a reproduction constant (growth rate of the population size). The size of a population, for a given species, is (approximately) proportional to its reproductive value and it is, in its turn, related to the body mass of individuals (Rossberg, 2012), which also depends on the availability of trophic resources and the rates of predation and competition. The value of \( r \) is positive when individuals of a given population reproduce faster than they die. In addition, the above equation establishes that the larger the population size \( N(t) \), the faster it increases over time. The equation has a possible solution represented by:

\[
N(t) = N_0 \exp(rt) \tag{13}
\]

where \( N_0 \) is an arbitrary constant that equals the population size at the time \( t = 0 \). The population becomes very large rapidly due to the exponential function
Its effects on plant and animal associations will quickly become stronger and the population will drastically modify its environment. Thus the conditions that determine the population growth rate $r$ will change due to the depletion of the resources necessary for reproduction, reaching a plateau. The rates of reproduction and death depend on the composition (in terms of sex, age and genotype) of the population of $N_{i(t)}$ individuals, on the health of individuals and their spatial distribution. If, on the other hand, the population growth rate $r$ is negative, the population size $N_{i(t)}$ will sooner or later reach just a few individuals, and subsequently the species will extinct after stochastic demographic fluctuations in $N_{i(t)}$.

1.8.5. Allee effects and alien invasions

The rates of reproduction might be limited by the probability of finding mates in a species with sexual reproduction, present in a given population at a low abundance. Consequently, $r$ will decrease with $N_{i(t)}$ (a process called dispensatory dynamics or Allee effect). Besides this, several other mechanisms may impact life cycles and species populations can be disrupted at low abundances, thus leading to “Allee effects” (Berec et al., 2007). Since many communities are regularly invaded by new species (White et al., 2006), the Allee effect does not represent a critical reason for population disruption at low abundance. A noticeable mechanism for overcoming such limits in the life cycles of species is the invasion of habitats by alien species along fronts. Before invading a given front, the new species cannot be considered as an invader, but after the front the populations are above the threshold of the Allee effect. Dispersion of individuals around the front can help overcoming the threshold. Such a front may move forward and the invasion proceeds when the Allee threshold is lower than half of the system carrying capacity for the invading species (Lewis and Kareiva, 1993). However, in our treatment of data to demonstrate relationships between resource availability and biodiversity (Chesson, 2000), we will not consider spatial effects; thus, Allee
effects (including issues of mate finding) will not be taken into account either, for simplicity.

1.9. Biodiversity and common laws of functioning

1.9.1. Complex models
The maintenance of biodiversity implies the maintenance of individual populations within a community. Several mathematical models calculate the theoretical survival of a given population or groups of species over time, depending also on their food availability and abundance. However, we would need to calculate the survival of each life stage (larvae, juveniles, adults, etc.) over the timeline, also according to reproduction cycles and seasons, for each species present in a given ecosystem, and finally the biodiversity of the studied environment. These complex computations may lead to frequent errors, especially when repeated for several species (de Roos and Persson, 2013; Blanes et al. 1998) since the size of populations of each species (in each stage) depends on the population size of every other species. These relationships, instead of being based on numbers of individuals, may be modelled based on total biomass (or energy units) of species and their populations, but the formal complexity of simulations remains, even using mathematical simplifications as the Quasi Normal Approximation techniques (QNA; Rossberg and Farnsworth, 2011).

1.9.2. Modelling individual features
Due to the increasing complexity of models, overcoming the performances of even larger computers, several authors found easier and more useful to abandon the goal of obtaining such detailed models of simulation and heuristically concentrate on single features of food webs, even starting from empirical sets of data, to find common laws of functioning. For example, the depletion of resources according to the species consumption may be modelled.
The time variation of a trophic resource according to the presence of a species of consumers may be modelled as (Rossberg, 2013):

\[
f(x(t),y(t)) = \frac{v^t L(x(t),y(t)) w}{v^T w} = 0.46 \, y^{-1} x(t) + 0.54 \, y^{-1} y(t) - 1 \, yr^{-1}
\]

This equation was computed as a model for the resource-dependent rate of change of the population size of *Rana catesbeiana* as a whole. The coefficients 0.46 yr\(^{-1}\) and 0.54 yr\(^{-1}\) characterized the strengths of resulting trophic interactions. This relationship leads to the patterns of abundance or *R. catesbeiana* reported in Figure 4:

Another key parameter to be taken into account for modelling the size of an animal population is its reproductive value \(r\). For several species, including fish and marine invertebrates, the reproductive value roughly equals their body mass (Rossberg, 2012). In addition, the realized community structure and dynamics may be influenced (or even be a direct consequence) of the strength of trophic links. Trophic link strengths are “dyatic” data (Kenny et al., 2006) because they depend on the phenotypes of two species, i.e., the resource and the consumer species. They are both described by the trophic traits of species (e.g., the combination of the vulnerability and the foraging traits of each species or, in other words, their descriptions as both resources and consumers). The functional response of a consumer population (Stenek and Watling, 1982) is represented by the rate at which consumers remove the biomass of their resources through foraging,
depending on the actual availability of the resource (Rossberg, 2012). The functional response of a population of consumers may be modelled as the sum of their functional responses to their resources, multiplied by an assimilation efficiency that is approximately evaluated to be between 0.1 and 0.6 (Jeschke et al., 2002). We should consider, in parallel, that consumers tend to eat much more of the most abundant resources, according to the prey-switching model. Thus, a faster depletion of the most abundant resources should be forecasted, because all possible consumers will tend to switch their choices towards them. Notwithstanding all the above-mentioned relationships, however, we should consider that in stable ecosystems, at the equilibrium, the sums of body masses in a population (i.e., the population biomass for each species) should not change, independently from the initial population structure.
1.10. Dietary diversity and proportions

1.10.1 Basic indices of diet partitioning

Several indices of dietary diversity have been proposed (Ulanowicz and Wolff, 1991; Bersier et al., 2002). The diet partitioning function (DPF) for example depends (Quince et al., 2005) on the dimensionality of niche space and a power law with exponent -0.74 (named dietary partitioning exponent) and it has been proposed to describe the sizes of diet proportions (Quince et al., 2005). Interestingly, several quite different food webs exhibited similar DPF exponents. Here it is worth to consider also the Gini-Simpson index of dietary diversity (dd), which is defined as:

\[ Gini - Simpson \; dd = 1 - \sum_j p_j^2 \]  \hspace{1cm} (15)

where \( p_j \) (ranging from 0 to 1) represents the proportional contribution of species \( j \) to the total biomass of a community.

Often an index \( Z_{c(p)} \) is computed to evaluate the DPF of a community, by counting all links \( l \) contributing proportions of at least \( p \) to the diet if some consumers and dividing by the number of consumers:

\[ Z_{c(p)} = \frac{l}{sc} \]  \hspace{1cm} (16)

Where \( Z \) is the number of links \( l \) divided by the number of species in a food web. Consequently, \( Z_{c(p)} \) is the number of links above the threshold \( p \), divided by the number of consumers \( c \) in a food web. The Diet Partitioning Function \( Z_{c(p)} \) is a function of a threshold value with \( 0 < p < 1 \) and it is defined as the number of food items contributing at least a biomass proportion \( p \) to the diet of a consumer, averaged over all consumers in a community (Berlow et al., 2004).
The DPF largely depends on the niche-space dimensionality and diet efficiency indices, as indicated in Figure 5. From this computation we conclude that the number of links contributing proportions of biomass $Z_{c(p)}$ to consumers, is characterized by a logarithmic decay shape for the DPF, when related to the abundance of diet proportions $r$ (Connolly et al., 2005) and according to the same equation, we can expect that the biomass $B_j$ of resource $j$ is lower if its trophic link strength $A_{jk}$ with consumer $k$ is large:

$$p_{jk} = \frac{A_{jk}B_j}{\sum_{i=1}^{s} A_{ik} \theta_i} \tag{17}$$

Differently, the diet ratio $r_{jk}$ is defined as the ratio between the contribution of the species $j$ and the contributions of all other resources to the diet of the consumer $k$. Thus, diet proportions derive from a relationship that can be evaluated as:

$$r_{jk} = \frac{p_{jk}}{\sum_{i \neq j} p_{ik}} = \frac{p_{jk}}{\left(\sum_{i=1}^{s} p_{ik}\right) - p_{jk}} = \frac{p_{jk}}{1-p_{jk}} \tag{18}$$

However, inter-specific competition plays an essential role in ecological relationships since, in the context of community ecology as well as in the frame of the global evolution on the planet, interactions between two species may produce an increase in the population of the first, that is in its turn detrimental to the second, and vice versa. Contemporaneously, several features of the
population, as its mortality, consumption and growth rate, follow an allometric scaling law in the form:

\[ am^{3/4} \Delta t \]  \hspace{1cm} (19)

where \( a > 0 \) is a constant. This means that the amount of body mass \( m \) gained in a short time \( t \) is \( am^{3/4} t \).

**1.10.2 Relationships of resources vs. consumers**

Here it is also worth to consider that the number of links connecting one node to others may be called “degree” and the *degree distribution theory* may explain other features of food webs. Since food web topologies are graphs with indication of flow directions, we can distinguish the “in-degree” as the number of food-species resources and the “out-degree” as the number of consumers. A mathematical analysis of this niche model indicates that it generates distinctive distributions of in- and out-degrees according to the distribution of scaled numbers of resources \( k/Z \) (Camacho et al., 2002a; b). Following to this analysis, the probability that a species has \( m \) consumers is the following:

\[ P[m \text{ consumers}] = \frac{1}{2Z} \int_0^{2Z} \frac{t^m e^{-t}}{m!} dt \]  \hspace{1cm} (20)

and contemporaneously, the probability to reach \( k \) resources is:

\[ P[k \text{ resources}] = \frac{1}{2} E_1\left(\frac{k}{2Z}\right) \]  \hspace{1cm} (21)

From this also derives the integral exponential function that we will encounter in various models for the evaluation of resources in the form:

\[ E_1(x) = \int_x^{\infty} \frac{e^{-t}}{t} dt \]  \hspace{1cm} (22)
All the previous are quite general mathematical laws of models, since the distribution of scaled number of resources $k/Z$ is independent of model parameters. The same applies to the scaled number of consumers $m/Z$ (if $Z$ is not too small). Thus, the corresponding universal cumulative distribution functions shown in Figure 6 can be explained taking into account that the cumulative distribution of out-degree is approximately triangular, while that of the in-degree has a fatter tail, analogous to the shape of an inverse exponential function.

Figure 6. Universal cumulative distribution functions for consumers and their resources in any environment follow an exponential decay pattern (From Camacho, 2002).
1.10.3. A starting point to model biodiversity according to the abundance of resources

For the same reason, the following relationship has been proposed (Chamacho et al., 2002b; Stouffer et al., 2007) to predict the shape of the functions explaining the probability to increase the number of trophic links (cumulative distributions) and the number of resources, as well (and very interestingly for our hypothesis!) as the diversity of consumers and the abundance of resources:

\[
Cumulative\ distributions = \exp(-x) - x E_1(x) \quad (23)
\]

with \(x = k/(2Z)\).

According to the above relationship, the number of trophic links, that is closely related to the diversity \(S\) of consumers, depends on the abundance of resources according to the \(\exp(-x)\), as a possible answer to our main question. This is then the model we will test, through the indices RAFI (Zupo et al., 2017), and validate on trophic data collected in various environments, in the next sections. Following these two trends, we could approximately hypothesize that:

\[
S = K \times \exp(-R) \quad (24)
\]

Where \(S\) is the number of species (alpha diversity), \(R\) is the abundance of resources and \(K\) is a constant of the considered ecosystem (depending on genetic diversity, turnover rates, temperature, etc.). In this case, the expected trends for the levels of biodiversity of consumers, expressed according to the abundance of their resources, should follow a typical exponential decay pattern (Figure 7).
A question clearly arises (Rossberg, 2007): what is the underlying mechanism for these apparently universal trends? The equation above might simply be a consequence of the lower-triangular structure of food webs (Figure 8) and in fact the same out-degree distribution applies to cascade models. Since links connecting in the niche model a given species to its consumers are statistically independent and they have equal probability of occurrence (except for the triangularity constraints), this approximate independence is maintained in nature (Rossberg et al., 2006b), evidently.
Similar conclusions may be reached when a variant of the niche model is considered Guill (2010). Thus, there is not only evidence for phylogenetic patterns in food webs, but also indications that (at least according to the principle that in most cases “the larger eats a smaller one”) phylogenetic correlations dominate the processes structuring food-web topologies.

However, and most importantly, the mathematical nature of these geometric distributions helps assuming that they may be applicable to a range of systems at various structural levels, from whole ecosystems down to the physiology of individual multi-cellular organisms, where phylogenetic and size constraints meet the triangular shape of prey-predator distributions according to the abundance of resources (Milo et al., 2002; Arim and Marquet; 2004; Bascompte and Meliàn, 2005; Stouffer et al., 2007; Kondoh, 2008). Ecological communities are dynamical systems, just like assemblages of cells within organized tissues, and this explains why we expect that the diversity of (consumer) forms observed along a range of resources may be reproduced at any organizational level with similar patterns of distributions derived by the mathematical forecasts for such networks.

A confirmation comes from the analysis of networks using the coefficient of variation of scaled abundance, expressing CV as a coefficient of variation of trophic resources. In this case, according to Rozdilsky and Stone (2001) we can expect (Vandermeer, 1970) a distribution shaped as the one in the figure 9.

This is interesting because once again it indicates that species richness in an ecosystem increases according to a quasi-exponential function, with CV. Thus, an increase of species richness contributes an exponential increase of CV up to a plateau (limit for species richness), due to competitive interactions among species. The relationship demonstrates once again that S may be related to the abundance and distribution of the trophic resources.
Figure 9. A numerical test of competition mean-field theory performed according to Rozdilsky and Stone (2001) indicating the patterns of variation of the coefficient of variation of scaled abundance of resources according to species richness.
### 1.11. Expected relationships with trophic level

Several studies took into account the abundance of trophic resources along what is named a “trophic level”, although this is a generalization useful for scientists since it has not an actual realization in nature, given the network structure of food webs (Zupo, 1994). However, while analysing trophic levels, we can attempt some predictions useful to address our main question, as above stated. In fact, we do know that the abundance of resources changes at different trophic levels. In particular, when we move to higher trophic levels the abundance of resources decreases according to the efficiency of conversion of prey biomass. Thus, examining the changes in biodiversity over increasing trophic levels will provide another evidence about the possible effects of prey biomass (expressed as well as number of individuals or in energy units) on the diversity of consumers.

For example, the distribution of species over trophic levels was investigated by Petchey et al. (2004) in UK. Although in their study the diversity of producers is probably underestimated, since some taxa were excluded to improve data comparability, they demonstrated a regression of species richness against levels with good agreement of the regression slope with a ratio to the richness of 1/3 as expected for multi-level food webs (Figure 10).

![Figure 10: Species richness by trophic level in freshwater ecosystems (from Petchey et al., 2004). Circles, squares, and triangles are geometric averages of data sets. The solid line is a linear regression of log S. The dash-dotted line indicates the theoretical slope.](image-url)
In a similar study, the ratio between the richness of level-2 and level-3 of consumers in British and North American freshwaters were computed (Jeffries and Lawton, 1985). They reported a high correlation, and a mean richness ratio of 0.36 with a tendency for lower values in communities characterized by higher $S_l$. Given the quantitative agreement between richness ratios observed in several types of natural communities and those predicted using random-matrix models, and observing the apparent absence of alternative explanations, we can now summarize the implications that theory of random-matrix competition has for the interpretation of community structure. These implications follow from key assumptions made in developing the theory itself. In fact, according to these simulations, at higher trophic levels (lower theoretical availability of biomass of food sources) a lower $S$ is recorded. If this is true, it represents another demonstration of the expectation, herein proposed, that higher biomass available for consumers should be related to lower diversity of their communities. And given the above mentioned concepts about allometric scaling laws and slopes of about 1/3 of the regressions “species richness vs. trophic levels” (directly related with gross resource availability) we should expect that regressing $S$ against the relative abundance of trophic resources in various systems, a pattern of exponential decay with negative exponent close to 1/3 should be observed. In addition, given the premises, we should expect as well that this pattern will be recorded at any structural level of an analysed systems, from the physiology of individual organisms up to complex ecosystems.

In fact, several characters of naturally complex food webs may be reconstructed starting from purely mathematical models, as the so-called “PDMM” (population-dynamical matching model, Rossberg et al. 2008). Recent evolutions of the PDMM (Fung et al., 2013; Shephard et al., 2012) combine switching functional responses and a multi-dimensional trophic-niche space, with simple Euclidean geometry and allometric scaling laws for biological rates. It was called “matching model” because of the matching of vulnerability traits with foraging traits indispensable for the establishment of strong trophic links. The model provides
not only the community structure and its internal relationships, but also insights about size, biomass and diversity of various organismic groups. The theory explains these patterns on the assumption (not always justified) that the mechanisms underlying the process could operate not only in the simplified models studied, but also at higher levels. In some cases, in fact, the PDMM answers questions regarding general relationships between community dynamics, structural stability, productivity, exploitation and biodiversity, and dependencies of these on size or trophic level.

However, in general terms we may state that two mechanisms regulate biodiversity in food webs, and they are both associated with competition: the first is resource-mediated and the second is consumer-mediated (resembling the top-down and bottom-up mechanisms often considered in the past). Both mechanisms limit biodiversity through constraints to the feasibility (rather than the stability) of equilibrium communities. The reason for this evidence is that distributions of trophic link strengths in food webs have large spreads, while variations in species biomasses appear not important. Both mechanisms naturally co-occur in models and both play the role of determining species richness at a given trophic level. Resource-mediated competition in food webs with multiple trophic levels restricts richness in one trophic level to a fraction of the richness at the lower trophic level. This fraction is approximately 1/2 in food webs with only two trophic levels, while it is 1/3 in food webs with many trophic levels: this brings back to the concept of the exponential functions exhibiting this ratio along a trend of decrease of resources. The reason why the richness ratio in multi-trophic food webs is as small as 1/3 is that resource overlap matrices are scarce and random, so that even with a comparatively small number of competing consumers, strong competitive interactions are possible. On the other end, when resources are very abundant and consequently, consumers may easily invade communities, the resulting consumer-mediated competition may still limit and regulate the richness of resource.
1.12. Expected relationships with size of organisms

The above mentioned laws also have implications on the size of organisms, when the considered resources are not (totally) protected by chemical or physical defences and they are thus regularly consumed to increase the biomass $C$ of associated communities of consumers. In fact, if the first hypothesis above-stated was true (no effect on the number of species $S$ feeding on them) then we should expect that an increase of biomass is due to either an increase of the number of individuals of consumers, or an increase of their body mass, or both. The same applies if there is an effect on $S$ and it is negative (increased biomass $Q$ of resources paired with decrease of $S$). Also in this case, in fact, if $Q$ increases and it is regularly consumed, producing an increase of $C$, then we should hypothesize either (or both) an increase in the number of individuals $N$ or an increase of individual size $B_c$.

From a modelistic point of view, a characterization of the community size structure (Blanco et al., 1994) makes use of $\beta_{\geq m}$, defined as the biomass of living individuals with body mass larger or equal to $m$. The “size spectrum” of an aquatic community may be defined as the value of $\beta(m)$ (Platt and Denman, 1977; Rodriguez and Mullin, 1986):

$$\beta(m) = \frac{d\beta_{\geq m}}{d\ln m} = -\frac{md\beta_{\geq m}}{dm}$$  \hspace{1cm} (25)

Naturally, each species has a specific size spectrum (from juveniles to adults) and the average size spectrum may vary seasonally. However, if the above mentioned relationships result to be true (exponential decay of the number of species according to increases of biomass of $Q$) then we should expect that communities feeding on abundant food sources are composed by a large number of (larger?) consumers, while communities feeding on scarcely abundant food sources should be composed by lower number of (smaller?) consumers, to assure conservation of mass.
The theory developed here gives an answer to the question of what ultimately determines absolute species richness. Previous analyses indicated that resource-mediated competition links the richness at one trophic level to richness at the next lower level. At the lowest trophic level another mechanism must be active and this could be consumer-mediated competition via the second trophic level. In various communities a top-bottom mechanism was demonstrated (Fuhrman, 1999; Thingstad, 1998) and in this case the biodiversity must be due to consumer-mediated competition.

![Graph showing trophic levels and species richness](image)

Figure 11. Trophic levels of species against rank in order of falling values (From Rossberg, 2013). Dotted lines correspond to integer levels, the dash lines has a slope as predicted by the above reported equations.

Low-level biodiversity is required to sustain the species richness at higher trophic levels in natural communities. According to this theory, species richness naturally declines along with trophic levels, and usually also with species sizes. These evidences should be taken into account when quantifying biodiversity, e.g. by measuring species richness in each trophic level or size class (Figure 11).
Section 2. Aims and Objectives
Chapter 2.1. Thesis aims (expected results)

All the reported relationships tend towards a clear forecast, i.e., the diversity of consumers $S$ should exponentially decrease according to the increase in the abundance of resources $R$ and it could follow a typical exponential decrease pattern (equation 24) or, alternatively, it may be viewed in terms of connectance and in this case it should follow a trend as that reported in equation (2). In both cases, for positive values of resources a typical exponential decay pattern should be recorded.

If the relationship between resource abundance and $S$ in a given ecosystem will be straight, we could even consider a linear trend and in this case, given the above mentioned concepts about allometric scaling laws, a negative slope of about 1/3 of the regression “species richness vs. trophic resource availability” should be estimated.

These predictions might sound somewhat atypical, since one could instinctively expect that an increase of resources leads to an increase of biodiversity of consumers. However, as demonstrated in the previous chapters and although the reverse relationship has been well demonstrated (i.e., a high biodiversity of the community leads to its increased productivity) there are clear indications that this trend should be expected. In the next chapters some investigations will be reported to trace the discoveries of various features of benthic and planktonic ecosystems, and the above mentioned hypothesis will be tested and validated on field data.
Chapter 2.2 Objectives

This thesis has two main objectives, both equally important:
(1) To illustrate, from an historical perspective, the evolution of the science of food webs, from mechanistic approaches to the modern vision of emergent properties of ecosystems, based on researches published in the last 30 years.
(2) To propose, based on recent research, a general equation of life, able to evaluate and forecast the biodiversity of organism’s associations at various structural levels, from cells to ecosystems.

To this end, some published papers have been combined to follow the theoretical evolution of investigations on food webs, moving from numerical descriptions (cpt. 2.1), trophic guilds and energetics (cpt. 2.2), and modelistic approaches (cpt. 2.3). Some key findings on the information delivered by functional foods are reported (cpt. 2.4) to exemplify the shift toward a modern vision of food webs, and highlight the importance of chemical ecology relationships among benthic organisms. This concept is deepened (cpt. 2.5) by means of some recent papers, demonstrating that food may represent information, and this step is fundamental to understand the actual functioning of natural communities associated with Posidonia oceanica meadows. In this case, wound-activated compounds trigger vital chemotactic reactions in invertebrate grazers, demonstrating that information may be as important as energy, in ecology. Finally, to reach the objective (2), the results of recent publications on a model of availability of trophic resources are reported (cpt. 2.6), because this is an indispensable step to obtain comparable trophic data on a range of ecosystems, and compare them with the biodiversity levels measured in different environments. Thus, starting from established mathematical relationships between diversity of consumers and abundance of their trophic resources, the general shape of biodiversity trends has been hypothesized and formalized into two general “equations of life”. The first equation describes the levels of biodiversity expressed according to the abundance of trophic resources, while the
second equation describes size and abundance of consumers according to the levels of food availability. The results of the proposed general equations have been validated using the model reported in cpt. 2.6 and compared with field data. They permit to forecast the trophic structure of any ecosystem and the results could be extended to other networks of live structures at various hierarchical levels (from cells to ecosystems), but further experiments will explore this hypothesis and eventually extend the validity of the two equations to a wider range of biological systems.

Thus, in the experimental chapters (Section 3), it will be indicated how:

1) The structure of food webs may be assessed based on numerical analyses and semi-quantitative data on gut contents (Chapter 3.1). Some papers have been considered that investigated the food webs of Posidonia oceanica and they demonstrated how, starting from numerical analyses of prey frequencies, it has been possible to extrapolate some key pathways of flow from the plant to higher predators. These relationships represent the pavements for further improvements of the theory.

2) The use of feeding guilds and energetics may provide a synthetic representation of the main functions in any ecosystem (Chapter 3.2). Since most studies in that period were taking into account feeding groups and a large scientific debate was alive about the possibility to agree on homogeneous group, to avoid an heuristic approach that led to the assignment of same species to different groups, due to personal opinions of scientists. For this reason, a new index has been proposed to classify species in homogeneous trophic groups. The introduction of the index is representative of an attempt to conduct “opinions” on food webs towards a quantitative analysis of fluxes and paths.

3) Primary production studies and investigations on plant-animal interactions started to indicate the importance of “information” within the structural properties of food webs (Chapter 3.3). This has been a critical stage in the history of food webs. The strong mechanistic convictions that led studies
up to this stage started to appear weaker when compared to the value of informational relationships among organisms. This step is important to highlight the value of information within the food webs of coastal complex ecosystems, which will be further demonstrated in the next chapter.

4) The above-mentioned topic will be further explored with newer techniques, demonstrating through the example of a shrimp co-evolved with a benthic diatom, how chemical interactions determine the ecosystem functioning (Chapters 3.4 – 3.5). The case of Hippolyte inermis and his diatom food, in fact, is emblematic to demonstrate that food may represent mainly a source of information, more than simply playing the role of “fuel” for consumers. In fact, this proterandric herbivorous opportunistic species may find plenty of food in the epiphytic layer of P. oceanica, but specific diatoms of the genus Cocconeis are indispensable to “tell” information about the right time to change the sex and the presence of possible predators. More recently (Zupo et al., submitted) the infochemicals produced by Cocconeis spp. have also been demonstrated to be a chemical cue for H. inermis larvae, to detect the right substrates for settlement.

5) Finally, a model for rapid prediction of the available trophic resources was proposed (Chapter 3.6) and, using mathematical predictions derived from simple analyses of webs, tested on empirical data on food webs, it will be demonstrated that biodiversity is inversely related to the abundance of resources and that this law is valid for any system, at any level of complexity.
Section 3. Experimental \textit{(published papers)}
Chapter 3.1 Synthesis of methods used

3.1.1 Published papers

This thesis on published papers involves a range of methods used over time to reach various types of food web representations. The pathways of energy transfer numerically described in Cpt. 1 are obtained by collecting benthic organisms in seagrass meadows, using a trawl trained by a boat, and counting the organisms present in their gut contents identified, after dissection, up to the lowest possible taxonomic levels. Multifactorial statistical analyses were applied to obtain trophic structures of ecosystems. Trophic guilds described in Cpt. 2 use a similar methodological approach, and the research is based on the techniques developed in Cpt. 1, but new statistical tools have been developed in order to obtain comparable data in different ecosystems. To this end, preys were classified according to their size and type (either plant or animal). In contrast, the modelistic approach used for the researches described in Cpt. 3 involves field experimentations, because the leaves of *Posidonia oceanica* have been mechanically marked and monthly sampled to evaluate their growth rhythms, while various physical properties of their environments have been recorded. A further statistical treatment permitted to identify the main factors involved in the growth rates of individual leaves and the time patterns of leaf growth and decay. The results were used to build a mathematical model (Buia et al, 1992), to predict the primary production in various conditions and in any season, as a base to predict the circulation of energy in a seagrass ecosystem. The research described in Cpt. 4, in its turn, takes into account the life cycle of a benthic shrimp, exemplifying the importance of diatom food as a metabolic regulator. In this case shrimps were collected by divers over fixed surfaces of a seagrass by means of an airlift, identified, measured and counted prior to determine their sex based on the size and shape of the appendices on their second pleopods, dissected and observed under the optical microscopy. The techniques described in Cpt. 1 and 2 are applied here to detect the effects of individual gut contents on the process of
sex reversal. In Cpt. 5 a typical approach of chemical ecology was applied. Volatile organic compounds (VOCs) were extracted from benthic algae (epiphytes of *P. oceanica*) typically fed by benthic invertebrates (as demonstrated in Cpt. 1, 2 and 3). VOCs were concentrated by loop-stripping and incorporated into agarose blocks, further proposed to target invertebrates (collected over leaves of *P. oceanica*) to record their chemotactic reactions. Finally, in Cpt. 6 a model of trophic compartmentalization is presented, applicable to virtually any marine ecosystem and based on literature data. In this case, a large data-base has been built and filled with the abundance of trophic resources characterizing various environments, as described in previous chapters. This permitted to establish a specific index of relative abundance of food items (RAFI) useful to predict the availability of trophic sources for various categories of consumers. The RAFI index takes into account the trophic categories identified in Cpt. 2 and it is the base for the validation of the “equations of life” developed in this thesis.

### 3.1.2 Statistical treatment of data in this thesis

In order to reproduce the structure of food webs in a range of ecosystems and quantitatively predict the relationships existing between abundance of resources and biodiversity of plant and animal communities, various models of trophic resource partitioning have been examined, according to network theories. Interestingly, various models and geometric distributions, as the Universal Cumulative Distribution functions for consumers and resources, follow an exponential decay pattern (Camacho et al., 2002b). According to this trend, it has been hypothesized that the number of species $S$ present in a given trophic compartment is inversely related to the abundance of their trophic resources ($R$) according to such an exponential decay function.

To demonstrate this hypothesis, the relationships between theoretical food availability (RAFI) and the species diversity according to feeding guilds were compared in various environments and in particular, in 13 stations distributed into the bay of Naples and in additional 41 world sites. Final scores indicating the
Relative Abundance of Food Items (RAFI%) for each of the considered environments have been obtained taking advantage of specific indices (Zupo et al., 2017; Cpt. 6 of this thesis). Thus, the shape of biodiversity has been evaluated in a range of ecosystems and the results have been compared with the trends expected according to the above mentioned exponential decay relationship in order to validate the model here proposed, using both field data and mathematical forecasts.
Chapter 3.2. Food numerical abundance and pathways in seagrass food webs

Summary

3.2.1 A study on the food web of Posidonia oceanica ecosystem: analysis of the gut contents of echinoderms. (cited by 38. IF=n.d.)
The analysis of the gut contents of 23 species of echinoderms indicates that this taxon is fundamental for the circulation of energy produced by Posidonia oceanica leaves. However this analysis is uniquely based on numerical abundance of prey.

3.2.2. A study on the food webs of Posidonia oceanica (L.) Delile ecosystem: analysis of the gut contents of decapod crustaceans. (cited by 19. IF= n.d.)
Here the food webs of a key taxon for the ecology of Posidonia oceanica is studied based on the numerical abundance of prey in the gut contents. The study indicates that decapod crustaceans are generally to be considered as opportunistic detritivores and they play a key role in the transfer of energy to higher trophic levels.

3.2.3. Depth and seasonal distribution of some groups of the vagile fauna of Posidonia oceanica leaf stratum: structural and trophic analyses. (cited by 193. IF= 1.79)
The crustacean decapods living in a protected area are important links between primary producers and final consumers in local food webs and their gut contents were analysed evaluating their numerical abundance. The results have been correlated to the functional algal groups in order to detect their influence in the structure of decapod communities. Therefore, both the influence of algae on the taxon and the influence of decapods on their environment were considered by taking into account the numerical abundance of prey in gut contents.
A STUDY ON THE FOOD WEB OF POSIDONIA OCEANICA ECOSYSTEM: ANALYSIS OF THE GUT CONTENTS OF ECHINODERMS

A STUDY ON THE FOOD WEB OF POSIDONIA OCEANICA (L.) DELILE ECOSYSTEM: ANALYSIS OF THE GUT CONTENTS OF DECAPOD CRUSTACEANS

DEPTH AND SEASONAL DISTRIBUTION OF SOME GROUPS OF THE VAGILE FAUNA OF POSIDONIA OCEANICA LEAF STRATUM: STRUCTURAL AND TROPHIC ANALYSES
Chapter 3.3. Trophic guilds and energetics as a mean to investigate food webs

Summary

3.3.1. Decapod and algal associations from “Banco di Santa Croce” (a protected area in the bay of Naples): a key pathway in local food webs. (Cited by 6. I.F.=n.d.)
A new index is proposed to classify species in homogeneous feeding groups. Macrozoobenthic species sampled in Posidonia oceanica meadows are used to test the method and demonstrate the correctness of theoretical assumptions.

3.3.2. The use of feeding indices for the study of food webs: an application to a Posidonia oceanica ecosystem. (Cited by 11. I.F.=1.23)
The gut contents of fish in three Posidonia oceanica meadows off the island of Ischia (Bay of Naples, Italy) were investigated and numerical abundance of prey was recorded. Seasonal variations in the diets of fish, also at prey-species level, were demonstrated. The fish taxon plays essentially a macro-carnivore trophic role. In the investigated seagrass meadows the main trophic fluxes start from plant detritus, macrophyta, and microphyta (as primary producers) towards crustacean decapods, copepods, ostracods, and gammarid amphipods (as secondary producers) to fish. A low recycling rate (4%) within the fish community was observed. Larger fish predators (e.g., Sparidae), swimming over the leaf canopy, are the main exporters to adjacent coastal systems.

3.3.3. Diet of fish populations in Posidonia oceanica meadows off the island of Ischia (Gulf of Naples, Italy): assessment of spatial and seasonal variability. (Cited by 15. I.F.=1.42)
A close interaction among various disciplines is necessary for a comprehensive analysis of food webs. In this case gut contents were analysed using the feeding indices above mentioned (previous research) to find out the pathways of energy transfer from primary producers to the last consumers.
Pages 107-141 are redacted and contain the published articles:

DECAPOD AND ALGAL ASSOCIATIONS FROM “BANCO DI SANTA CROCE” (A PROTECTED AREA IN THE BAY OF NAPLES): A KEY PATHWAY IN LOCAL FOOD WEBS

THE USE OF FEEDING INDICES FOR THE STUDY OF FOOD WEBS: AN APPLICATION TO A POSIDONIA OCEANICA ECOSYSTEM.
https://www.jstor.org/stable/43461109

DIET OF FISH POPULATIONS IN POSIDONIA OCEANICA MEADOWS OFF THE ISLAND OF ISCHIA (GULF OF NAPLES, ITALY): ASSESSMENT OF SPATIAL AND SEASONAL VARIABILITY
http://dx.doi.org/10.4236/ns.2010.211154
Chapter 3.4. Determination of primary production and models

Summary

3.4.1. A production model for Posidonia oceanica based on temperature. (Cited by 41. I.F.= 2.61)
To produce feasible models of food webs a sufficient knowledge about the rates of primary production is indispensable, in order to define the initial budget of biomass entering the various trophic pathways. Since seagrasses are important models for coastal ecology and management, this study presents a model of production of the Mediterranean seagrass Posidonia oceanica based on weight. Temperature appears to be the main factor modulating biomass production during the year, while other factors, as light irradiance and nutrient availability are scarcely important to determine the seasonal growth rhythms.

3.4.2. Culture conditions influence the growth dynamics and the production of Cocconeis scutellum (Bacillariophyta). (Cited by 5. I.F.= 3)
Microalgae are also important primary producers and play a fundamental role both in planktonic and benthic environments. Their trophic role is comparable to the one of seagrasses for macrozoobenthic organisms, since they play both a trophic function and a structural function as first colonizers of benthic substrata. In addition, some diatoms are quite important because they produce secondary metabolites influencing the physiology of their consumers. The optimal conditions for the growth of two conspecific benthic diatoms were defined through factorial experimentation. The roles of light spectrum, nutrient availability, and culture conditions on the laboratory production of Cocconeis scutellum scutellum Ehrenb. and C. scutellum parva Grunow were investigated. Results permitted to devise adequate culture protocols to produce a biotechnologically important substance: an apoptogenic compound that specifically destroys the androgenic gland of a shrimp and could find novel
applications in human medicine.

3.4.3. **Feeding of *Penaeus japonicus* Bate (Decapoda: Penelidae) in pond cultures: size descriptors and food selection. (Cited by 3. I.F. = 0.83)**

Various characters of food, as calorimetry, biometry, type, may influence the preferences of consumers and this may have importance also for cultured organisms. In this study weight data are coupled with the numerical abundance of prey to apply the (previously developed) index of food type and evaluate the trophic behaviour of prawn.
Pages 144-175 are redacted and contain the published articles:

A PRODUCTION MODEL FOR POSIDONIA OCEANICA BASED ON TEMPERATURE.  
https://doi.org/10.1006/ecs.1996.0137

CULTURE CONDITIONS INFLUENCE THE GROWTH DYNAMICS AND THE 
PRODUCTION OF COCCONEIS SCUTELLUM (BACILLARIOPHYTA) 
https://doi.org/10.1111/j.1529-8817.2011.01073.x

FEEDING OF PENAEUS JAPONICUS BATE (DECAPODA: PENEIDAEA) IN POND 
CULTURES: SIZE DESCRIPTORS AND FOOD SELECTION.  
https://doi.org/10.1080/00222939800771321
Chapter 3.5. Food as a physiology regulator in marine invertebrates

Summary

3.5.1. *Strategies of sexual inversion in Hippolyte inermis* Leach *(Crustacea, decapoda)* from a Mediterranean seagrass meadow. *(Cited by 48. I.F.= 1.79)*

The shrimp *H. inermis* exhibits an unusual strategy of sexual inversion as an adaptation to overcome problems related to predation pressure and seasonal food availability in *P. oceanica*. This strategy is based on two reproductive periods showing different types of females. In this study the effect of food on sexual development was not yet hypothesized.

3.5.2. *Effect of microalgal food on the sex reversal of Hippolyte inermis* *(Crustacea, Decapoda)*. *(Cited by 52. I.F.= 2.62)*

The effect of diatoms of the genus *Cocconeis* on the sex reversal of the shrimp *Hippolyte inermis* Leach was examined in the laboratory. The results provide an explanation of the patterns observed in the field, demonstrate that microalgal food is involved into the sex change of the shrimp and are in accordance with the seasonal abundances of diatoms in the leaf stratum of *Posidonia oceanica*.

3.5.3. *Influence of diet on sex differentiation of Hippolyte inermis* Leach *(Decapoda: Natantia)* in the field. *(Cited by 40. I.F.= 2.05)*

Here for the first time an indication appears of a direct effect of a food in the sex reversal of an invertebrate, in the field. The diets of immature and adult individuals were compared to detect any influence of food on sex differentiation, since previous investigation indicated a correlation of the life cycle of this protandric species with the abundance of algal food in the environment. The influence of microalgal food on the sex reversal mechanism of this species, previously detected through laboratory experiments, was demonstrated to
control the life cycle of *H. inermis* in the field.

3.5.4. **Do benthic and planktonic diatoms produce equivalent effects in crustaceans?** (Cited by 18. I.F.= 0.91)
Various diatoms produce apoptosis both in benthic and planktonic crustaceans and their influence on the reproductive ecology and life cycles of decapods and copepods has been demonstrated. However, the effects appear deleterious for copepods and regulative for shrimp populations. This study indicates that diatom food does produce an apoptogenic effect on the two taxa and the two environments, but these effects are due to different classes of compounds and, probably, to different evolutionary patterns and relationships.

3.5.5. **How do dietary diatoms cause the sex reversal of the shrimp *Hippolyte inermis* Leach (Crustacea, Decapoda).** (Cited by 40. I.F.= 2.39)
Several congeneric diatoms influence the sex reversal of a shrimp and their activity is very specific. The ingestion of diatoms and the effect of their infochemicals are limited to a time window between the 5th and the 12th day of post-larval development.

3.5.6. **Experimental evidence of a sex reversal process in the shrimp *Hippolyte inermis*.** (Cited by 15. I.F.= 1.05)
*Hippolyte inermis* has been object of literature debates: some authors considered it as a proterandric species, other as a gonochoristic. Since this point is essential to the issue of the influence of food on its sexual maturation, this research provides a conclusive experimental evidence of the sex reversal process in this species.

3.5.7. **Apoptogenic metabolites in fractions of the benthic diatom *Cocconeis scutellum parva*.** (Cited by 15. I.F.= 4.38)
Various bioassay-directed fractionations have been performed in order to determine the apoptogenic compounds influencing the sex reversal of *Hippolyte*
*inermis*. The lipophilic fraction was purified, which led to the characterization of an active sub-fraction containing a highly lipophilic compound, whose molecular structure has not yet been identified. The results also point to the possible medical uses of the active compound. Once the molecular structure will be identified, the study and modulation of apoptotic processes in various types of cells will be possible.
Pages 179-265 are redacted and contain the published articles:

STRATEGIES OF SEXUAL INVERSION IN HIPPOLYTE INERMIS LEACH (CRUSTACEA, DECAPODA) FROM A MEDITERRANEAN SEAGRASS MEADOW
https://doi.org/10.1016/0022-0981(94)90229-1

EFFECT OF MICROALGAL FOOD ON THE SEX REVERSAL OF HIPPOLYTE INERMIS (CRUSTACEA, DECAPODA)
https://doi.org/10.3354/meps201251

INFLUENCE OF DIET ON SEX DIFFERENTIATION OF HIPPOLYTE INERMIS LEACH (DECAPODA: NATANTIA) IN THE FIELD
https://doi.org/10.1007/978-94-017-0645-2_13

DO BENTHIC AND PLANKTONIC DIATOMS PRODUCE EQUIVALENT EFFECTS IN CRUSTACEANS?
https://doi.org/10.1080/10236240701592930

HOW DO DIETARY DIATOMS CAUSE THE SEX REVERSAL OF THE SHRIMP HIPPOLYTE INERMIS LEACH (CRUSTACEA, DECAPODA)
https://doi.org/10.1007/s00227-006-0524-9

EXPERIMENTAL EVIDENCE OF A SEX REVERSAL PROCESS IN THE SHRIMP HIPPOLYTE INERMIS
https://doi.org/10.1080/07924259.2008.9652276

APOPTOGENIC METABOLITES IN FRACTIONS OF THE BENTHIC DIATOM COCCONEIS SCUTELLUM PARVA.
https://doi.org/10.3390/md12010547
Chapter 3.6. Food is information: the role of wound-activated infochemicals

Summary

3.6.1. Odour compounds of the diatom Cocconeis scutellum: effects on benthic herbivores living on Posidonia oceanica. (Cited by 33. I.F.= 2.62)
Food is information and wound-activated infochemicals generate a web of communication among diatoms and benthic invertebrates. The effects have been identified through experiments on the chemotactic behaviour of invertebrates to detect the meaning of their evolutionarily evolved choices.

3.6.2. Ecological role of diatoms as regulators of invertebrate physiology and behaviour. (Cited by 6. I.F.= n.d.)
Diatoms play fundamental trophic roles both in the marine benthos and plankton. The knowledge about their regulatory influences on benthic invertebrates is discussed since they are demonstrated to be both physiologic regulators (through the food webs) and infochemicals perceived by chemosensory structures and triggering defined chemotactic reactions.

3.6.3. Chemoreception of the seagrass Posidonia oceanica by benthic invertebrates is altered by seawater acidification. (Cited by 12. I.F.= 2.45)
Food is energy and food is a physiology regulator. However food is also information. Several plants and invertebrates interact and communicate by means of volatile organic compounds (VOCs). These compounds play the role of infochemicals, being able to carry complex information to selected species, thus mediating inter- or intra-specific communications.
The VOCs have been extracted and tested on a set of 13 species of associated invertebrates to identify their specific chemotactic responses in order to determine if: a) seagrasses produce VOCs playing the role of infochemicals, and b) their effects can be altered by seawater pH. Results indicate that several invertebrates recognize the odour of wounded *P. oceanica* leaves, especially those strictly associated to the leaf stratum of the seagrass. Thus, leaf-produced infochemicals may influence the structure of *P. oceanica* epifaunal communities, and their effects can be regulated by seawater acidification.

### 3.6.4. Relevance of wound-activated compounds produced by diatoms as toxins and infochemicals for benthic invertebrates. (Cited by 14. I.F.= 2.39)

Plants evolved the production of toxic wound-activated compounds (WACs) to reduce grazing pressure. In addition, several plant-produced WACs are recognized by invertebrates, playing the role of infochemicals. The specific toxicity of WACs is inversely correlated to the perceptive ability of invertebrates towards volatile compounds liberated by the same algae. Hence, when the recognition of specific algae by a given invertebrate species evolves, their detrimental effects on the receiving organism may be lost.

### 3.6.5. *Centropages typicus* (Crustacea, Copepoda) reacts to volatile compounds produced by planktonic algae. (Cited by 9. I.F. = 1.79)

The ability of the copepod *Centropages typicus* to perceive the odour of three planktonic diatoms (*Skeletonema marinoi, Pseudonitzschia delicatissima* and *Chaetoceros affinis*) and a dinoflagellate (*Prorocentrum minimum*) was investigated. This information is ecologically relevant for orientation, habitat selection, predator avoidance and communication. In addition, as the pH of the medium influences the perception of chemical
cues in aquatic environments, the effect of seawater acidification resulting from increasing levels of CO₂ was tested, along with its influences on the olfactory reactions of copepods. Seawater acidification induces changes in copepods’ perception of odours. These findings highlight the sensitivity of chemically-mediated interactions to global changes.
Pages 269-342 are redacted and contain the published articles:

ODOUR COMPOUNDS OF THE DIATOM COCCONEIS SCUTELLUM: EFFECTS ON BENTHIC HERBIVORES LIVING ON POSIDONIA OCEANICA.
https://doi.org/10.3354/meps08381

ECOLOGICAL ROLE OF BENTHIC DIATOMS AS REGULATORS OF INVERTEBRATE PHYSIOLOGY AND BEHAVIOUR
https://ebookcentral.proquest.com/lib/open/detail.action?docID=3018022

CHEMORECEPTION OF THE SEAGRASS POSIDONIA OCEANICA BY BENTHIC INVERTEBRATES IS ALTERED BY SEAWATER ACIDIFICATION.
https://doi.org/10.1007/s10886-015-0610-x

RELEVANCE OF WOUND-ACTIVATED COMPOUNDS PRODUCED BY DIATOMS AS TOXINS AND INFOCHEMICALS FOR BENTHIC INVERTEBRATES.
https://doi.org/10.1007/s00227-014-2448-0

CENTROPAGES TYPICUS (CRUSTACEA, COPEPODA) REACTS TO VOLATILE COMPOUNDS PRODUCED BY PLANKTONIC ALGAE.
https://doi.org/10.1111/maec.12254
Chapter 3.7. Trophic resources may be predictable and influence biodiversity: a general model

Summary

3.7.1. Relating trophic resources to community structure: a predictive index of food availability. (Cited by 5. I.F.= 2.51)

The abundance and the distribution of trophic resources available for consumers influence the productivity and the diversity of natural communities. Here an index of food abundance has been proposed, the framework of which can be adapted for different ecosystems. The relative available food index (RAFI) is computed by considering standard resource conditions of a habitat and the influence of various generalized anthropogenic and natural factors. RAFI tables can be applied to a range of marine ecosystems for predictions of the potential abundance of food available for each trophic group. They will be critical to demonstrate the validity of the general model relating the availability of feeding resources to the biodiversity of ecosystems.
Pages 344-360 are redacted and contain the published article:

RELATING TROPHIC RESOURCES TO COMMUNITY STRUCTURE: A PREDICTIVE INDEX OF FOOD AVAILABILITY.
https://doi.org/10.1098/rsos.160515
Section 4. General Discussion
4.1. Food webs: an historical perspective

The investigations reported in the Section 2 indicate the advantages and the constraints of various methods of investigation of food webs. It is interesting to observe that even simple numerical analyses of gut contents data (Cpt. 1) indicate a disproportion in the diversity of consumers feeding on different layers of a seagrass meadow. In particular, the relatively small biomass of epiphytic algae sustains a large variety of (small) consumers, including polychaetes, crustaceans, molluscs, echinoderms and fish. In contrast, the large biomass stored into the leaves of the seagrass itself is consumed only by a few species of (large and numerically abundant) echinoderms and fish. The classification of species in trophic guilds (Cpt. 2) permits a better definition of various categories of consumers exploiting the above-mentioned resources and fundamentally confirms this general picture. In addition, the data obtained on trophic guilds will be critical to develop the RAFI index (Cpt. 6), as a further step to reach the final result of this thesis, i.e., finding an equation linking biodiversity and resource availability.

A primary driver of patterns of biodiversity is the heterogeneity in the amount of energy available, or the primary productivity measured at a given location (Lotka, 1956; Mittelbach et al., 2001). Biodiversity itself is heterogeneously distributed across the Earth (Gaston 2000) and ecological theory (Oksanen & Oksanen, 2000) suggests that food webs are structured by the interaction of resources (Chase, 2000) and their consumers (Leibold, 1977; Persson, 1999; Polis, 1999). For example, the abundance of herbivores and their predators increase along a gradient of primary productivity (Chase, 2000). Although the shape of the relationships between productivity and species diversity is variable (Waide et al., 1999; Gross et al., 2000), the abundance and availability of food
may influence the patterns of biodiversity in natural systems (Sokolowski et al., 2012).

For this reason, studies reported in Cpt. 3 are fundamental to confirm the actual productivity of a seagrass itself (*Posidonia oceanica*) and of its epiphytes, along with the factors modulating the seasonal patterns of production because this helps understanding also the seasonally variable trends of production as compared to the biodiversity exhibited by various trophic compartments. Studies on plant communities suggest that species diversity is correlated to productivity and that the hump-shaped productivity-diversity relationship is correlated to the amount of nutrients in the soil (Tilman and Pacala, 1993). These investigations demonstrate that “diversity is a unimodal function of productivity and other measures of nutrient supply rates”. Similarly, ecological models predict that species diversity is correlated to productivity as well as to the abundance of trophic resources, and that the productivity-diversity relationship should be unimodal (Tilman, 1993; Rosevzweig, 1995).

Part of these relationships may be explained in the light of the information contained in various food items, since the biomass of the seagrass may be considered “chemically protected” in respect to that of epiphytic algae and the latter may contain information able to influence the life cycles of consumers (Chapters 4, 5).

Finally, we know that body size is an important factor in the competition for natural resources (Bagchi and Ritchie, 2012) and that a smaller consumer should be competitively superior across a wide range of supplies of the two resource types (Persson, 1985). Productivity, trophic resource availability and body size must thus be interrelated in natural systems (Schoener, 1976; Schroeder et al., 2009); however previous research has been focused mainly on the influences of predators on the populations of prey, through a top-down approach (Polis and Strong,
Here we wish to explore the relationships between species diversity and the abundance of trophic resources at various sites around the world, taking into account a variety of environments (hard and soft bottoms, seagrass meadows, caves, etc.), along a range of anthropic impacts, to test the hypotheses above reported, i.e., that:

1) a relationship exists between abundance of trophic resources and biodiversity;

2) that this relationship has the shape of exponential decay, as indicated by network theory;

3) that in case of exponential decay the exponent is close to 1/3 due to allometric scaling and

4) that the higher availability of trophic resources (evaluated according to Chapter 6), coupled to lower $S$, must be accompanied by higher number of individuals or higher individual biomass (or both) to provide full exploitation of available resources.

Evidences for dependence of biodiversity patterns on the local partitioning of food resources will be also presented, in order to clarify the relationships between functional biodiversity and allocation of resources, according to a theoretical relationship derived from mathematical treatment of network data, represented by the scaled numbers of resources and consumers (as reported in Section 1), and roughly represented by a function of exponential decay (derived from the equation (24):

$$Diversity\ of\ consumers = K \ast \ exp^{(-R)} \quad (26)$$

Where $K$ is a variable depending on the life cycle and turnover of consumers according to their feeding guilds and $R$ could be roughly
evaluated to be close to 1/3. If all the above will be demonstrated true, we should also hypothesize, as indicated in previous chapters, that the larger abundances of trophic resources, eventually used by a low diversity of consumers (scaled numbers) will correspond to an increase in numerical abundance of consumers, or an increase of their body size, to be efficiently exploited (if not physically or chemically protected) according to a linear relationship in the shape of:

\[ Nr.\text{consumers} \times \text{Size consumers} = r \times \text{trophic resource biomass} \quad (27) \]

Also in this case “r” is a variable depending on the turnover and the life cycles of consumers. The above-mentioned two relationships have been tested over actual field data to validate our hypotheses. In conclusion, we tried to answer the questions:

i) Is biodiversity influenced by the abundance of trophic resources in different marine systems?

ii) Can we predict the level of functional redundancy in a given system taking into account the relative abundance of the main prey for each trophic group?

iii) Does compartmentalization and diversification of trophic resources within a system allow for a spread of species diversity?

To test these hypotheses, relationships between theoretical food availability and the species diversity according to feeding guilds were compared. In particular, to check the possibility for a wide application of the relationships above reported, the following experimental data were taken into account:

- extensively (to test the above mentioned hypotheses): 13 stations distributed into the bay of Naples and 41 world sites comprised in a large
coral fish data-base, for which large datasets of biodiversity were available from direct measurements and from literature;

- **intensively** (to validate the model obtained): two Mediterranean sites for which detailed data on size of individuals and actual abundance of food items were collected by means of different techniques.

### 4.2. The RAFI% index

One of the main constraints to compare trophic resources across different environments is the lack of equivalent information on their actual abundance. For this reason, we developed a procedure to evaluate the trophic resources theoretically available for each trophic group in any marine ecosystem. Using specific indices (Zupo et al., 2017; Chapter 6 of this thesis), we obtained final scores indicating the Relative Abundance of Food Items (RAFI%) for each of the considered environments. The same scores are applicable to any marine environment, by classifying it according to the ecosystem (hard bottoms, soft bottoms, seagrasses, kelps, etc.), and local site deviations from the conditions of “standard” inshore ecosystems (e.g. exposed, eutrophic, deep, shallow, etc.). Consequently, a score was obtained for each trophic group and for each ecosystem and it indicates the theoretical abundance of a given food item (not the actual rate of ingestion by its consumers). In fact, a seagrass meadow may contain, for example, a huge abundance of plant biomass, but this is not directly consumed in the majority of cases, being chemically protected. As well, a rocky bottom may contain a large abundance of food items available for carnivores, but they may be not consumed due to the lack of larger fish in the specific area (Zupo and Stübing, 2010). For this reason, the RAFI scores are representative of the “theoretical” food availability, not of the real consumption by various feeders.
4.3. The shape of biodiversity

Species diversity had a statistically significant, inverse exponential relationship with food abundance (Fig. 12a), consistently in all Mediterranean sites. Similar relationships were found when individual environments are investigated (Fig. 12b and 12c). The highest diversity corresponds to species feeding on “less abundant” food items and vice-versa. In contrast, average size of species within a trophic group correlated with the abundance of their food items ($R^2 = 0.73; p<0.01$). While this last result appears obvious and in accordance with specific literature (McClain and Boyer, 2012; McClain et al., 2012), because an increased availability of food positively influences individual biomass and total abundance of consumers in natural populations, the previous results on the inverse relationships between diversity and food availability may look in contrast with instinctive assumptions (Sokolowski et al., 2012). Since species diversity is positively related to productivity (Mittelback et al., 2001; Gross et al., 2000), one would expect a similar pattern in the local abundance of food resources. However, as demonstrated in the previous chapters, this evidence confirms the results of the modelistic approach.

Several instances, at least in benthic systems, confirm this trend. For example, two main sources of primary production are available in a *Posidonia oceanica* meadow (Mazzella and Zupo, 1995): the leaf tissues and the epiphytes living on the leaf stratum. Leaf growth is slow, while the productivity of epiphytes is high (Gacia et al., 2009). The standing crops of these two main food sources per unit area are very different, as the biomass of *Posidonia* leaves exceeds by three orders of magnitude that of epiphytes (Terrados and Medina-Pons, 2011), but studies on the diversity of species classified into trophic groups, and feeding on the leaves of the
seagrass or on its epiphytes, demonstrated that only a few grazers feed directly on seagrass tissues (Vizzini, 2009), while a complex and diverse grazer community feeds on the “scarcely abundant” epiphytes (Gacia et al., 2009). Such evidence, which could easily be replicated for hard-bottom environments as well as for sand-bottoms and caves, explains our results about the inverse relationship of biodiversity with trophic resources. Highly eutrophic lakes provide a further non-marine example, as these are characterized by low diversity of species, large abundance of organic matter available for feeders and high productivity (Mukherjee et al., 2010).

These results, on the whole, may be explained in the light of the arguments raised by Bagchi and Ritchie (2012). They developed equations able to provide predictions on the “diversity” of diet reaching large size or small species in the same environment and, interestingly, the graphical representation of their equations predicts that smaller consumers are ordered in the left-top part of the diagram and are characterized by a higher dietary diversity, as compared to larger consumers, whose diet is dominated by a single resource (right, down part of the graph; Figure 12d). This theoretical diagram fits both the theoretical model and our experimental findings. Thus, the constant trends of biodiversity we found may be viewed in the light of this set of body size-based allometric constraints (Bagchi and Ritchie, 2012).
Figure 12. (a) Relationship between % alpha diversity versus % RAFI for trophic groups at 13 Italian sites. Dashed line represents 95th log-linear regression quantile (Cade et al., 2003). R² for 95th regression quantile = 0.373 (p<0.001). (b) Food availability versus diversity in trophic groups at comprehensively surveyed seagrass meadow Lacco Ameno. Species list accumulated over multiple surveys. Abundance of food items calculated on actual data of numerical abundance of food items per unit area and results of gut content analyses. Multiple R-squared: 0.8521 (p<0.001). (c) Relationship between alpha diversity and food availability for hard-bottom site Banco Santa Croce. Food resources were produced using Ecopath-Ecosim. Each point represents a trophic group (n = 5) at a sampling station (n = 4) for a seasonal survey (n = 4). Multiple R-squared: 0.3477 (p<0.005). (d) Mathematical predictions about the distribution of trophic resources between small and large consumers are perfectly superimposable to the experimental results. Most data points (Figures 12 a, b, c) for small consumers are ordered in left area of this figure, while a few larger species consume the most abundant resources, and they are ordered in the lower area (From Bagchi and Ritchie, 2012).
4.4. Experimental validation of the model

Alpha diversity at Lacco Ameno (Island of Ischia, Italy), a continuous seagrass meadow, is significantly correlated to the abundance of food items ($R^2 = 0.81$; $p<0.01$). The analysis in this case was based on observed data on the numerical abundance of food items per unit area and results of the gut content analyses. Taxonomical analyses indicated that filter feeders and micro-omnivores were the most diverse groups in the system (120 and 63 species, respectively) and they fed on the lowest abundant trophic resources (number of prey equals 1.04 m$^2$ and 2.08 m$^2$, respectively). In contrast, detritus feeders, herbivores and detritus feeder-herbivores were the least diverse feeding groups (3, 4 and 5 species, respectively) and they fed on the most abundant trophic resources (number of prey equals 21.0 m$^2$, 21.0 m$^2$ and 17 m$^2$, respectively). Size of individuals and number of individuals per square meter, as expected, were directly correlated to the abundance of food items ($R^2 = 0.63$ and 0.58, respectively). In fact, filter feeders and micro-omnivores had the lowest average size (2.7 and 2.9 mm respectively), and the lowest number of individuals (0.2 and 1.4 ind./m$^2$, respectively), while detritus feeders, herbivores and detritus feeder-herbivores had higher average size (6.5, 7.3 and 4.9 mm, respectively) and higher number of individuals (4.8, 6.2 and 3.9 ind./m$^2$, respectively). A similar picture was obtained at Banco di Santa Croce. In this case, Alpha diversity evaluated on a benthic hard-bottom system demonstrated a trend with the abundance of food items that is ($R^2=0.35$; Figure 12c) consistently described by an exponential equation.

The use of actual data on the abundance of food items (kJ m$^2$, according to the Ecopath model) represents an experimental confirmation of the results obtained by means of the extensive study at Banco di Santa Croce, but original data do not allow the fine definition of macro-consumers and
micro-consumers, as needed for applying the RAFI index (Zupo et al., 2017). However, the inverse relationship indicates that higher diversity is correlated to lower abundance of food items, obtained in this case by direct measures. The most diverse groups in this specific hard bottom environment are herbivores (85.7 species, on average, in the 4 stations) and carnivores (79.7 species, on average), and they fed on minor (less abundant) food items for this environment: the abundance of food items in this case reaches average values (in 4 sampling stations) of 51.2 kJ m⁻² for herbivores and 15.5 kJ m⁻² for carnivores. In contrast, filter feeders and detritus feeders are the least diverse groups (24.7 and 40.5 species, on average, into the 4 stations representing the site “Banco”) and they fed on the most abundant food items: the abundance of food items reached average values of 55.6 kJ m⁻² and 70.4 kJ m⁻², respectively. These data confirm previous findings indicating that biodiversity patterns are in accordance with the trends of environmental energy availability (Gaston, 2000).
Figure 13. (a) Biomass of trophic groups linearly increased with food availability on a log-log scale. Food resources were produced using Ecopath-Ecosim. Each point represents a trophic group (n = 5) at a sampling station (n = 4) for a seasonal survey (n = 4). Multiple R-squared: 0.7657 (p<0.001). (b) Number of individuals in trophic groups linearly increased with food availability on a log-log scale. Food resources were produced using Ecopath-Ecosim. Each point represents a trophic group (n = 5) at a sampling station (n = 4) for a seasonal survey (n = 4). Multiple R-squared: 0.4424 (p<0.001)
Total biomass (expressed as kJ m\(^{-2}\)) and number of individuals per square meter are, as well, directly correlated to the abundance of food items (Figures 13a and 13b): herbivores and carnivores have lower biomass, on average (340.7 and 126.5 kJ m\(^{-2}\) respectively), and lower number of individuals (456.5 and 187.9 ind/m\(^{2}\), respectively), while filter feeders and detritus feeders have the highest biomass (3336.7 and 699.3 respectively) and higher number of individuals (226.6 and 229.7 ind./m\(^{2}\), respectively).

### The RAFI table

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**Table 1.** Computation of RAFI indices for various environments, according to trophic categories. (a). RAFI (relative food availability) developed in Zupo et al., 2016 as a tool to analyse any coastal ecosystem. (b). Table of site specific features to be assigned to individual environments, to further tune the theoretical data contained in table A (after Zupo et al., 2016). To calculate the theoretical abundance of food items in a given environment the user identifies in table A the substrate corresponding to specific sites (e.g., high canopy seagrass) and in table B one or more specific features, if applicable. The corresponding scores must be multiplied among them to obtain the RAFI value of each food item.
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Table 2 (a). Site specific features. Each site is indicated by its main characteristics, as reported in tables 1 A and 1 B. The 13 Mediterranean sites (on the left) and 8 of the 41 RLS sites are shown.
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**Table 2 (b).** RAFI (relative abundance of food items) calculated for each of the above sites, according to the previous tables.
The application of the RAFI% scores (Table 1 a and b) to 41 ecosystems described in the global diversity data-base confirmed the inverse relationship Alpha versus RAFI% (Figure 14), as well as the significant direct relationships RAFI% versus size and RAFI% versus numerical abundance, so demonstrating its global applicability. Hence, the peculiar relationships detected on 13 Mediterranean sites and validated by intensively studying two very different benthic ecosystems (a seagrass meadow and a rocky bank, as above described) have been confirmed on 41 different environments (from sandy bottoms to coral reefs) located in a wide portion of the globe. This process of development, validation and confirm demonstrates the possibility to use the RAFI% tables (Zupo et al., 2017) as a general tool applicable to any environment, to provide comparisons of the general trends of biodiversity as related to the abundance of food items locally present.

Figure 14. Limiting influence of increasing food availability on alpha diversity of trophic groups for 41 sites representing shallow benthic habitats around the world. R² for 95th log-linear regression quantile = 0.158 (p<0.001).
Section 5. General Conclusions
5.1. The equations of life

In conclusion, biodiversity is inversely correlated to the abundance of food items according to the exponential relation (26), while the size of individuals and their numerical abundance are linearly correlated to the levels of food availability according to the relation (27), confirming the findings of previous investigations (McClain & Boyer, 2012; McClain et al., 2012). Two groups of species appear to be consistently recognizable in any marine ecosystem (Fig. 15), according to their trophic features: a first group, feeding on "abundant" food items, characterized by low taxonomical diversity, large abundance and, generally, large size, and a second group, feeding on less abundant food items, characterized by high taxonomical diversity, low abundance and, generally, small size. The presence of the two groups may be understood as a result of variable defence abilities by the preys (Speed and Ruxton, 2007), since some species may invest energy in the production of structural or inducible defences, and they drastically reduce the diversity of their consumers, while other species may invest most energy in the production of new biomass (turnover) and in this case their crop is totally available for a large diversity of consumers (Stanley, 2007). Following this pattern, the consumers able to feed on "defended" species have only a few competitors and they can thus rely on a large abundance of trophic resources: their populations reach large biomass and numerical abundance. In contrast, the consumers of "secondary" items, exhibiting a higher turnover and a lower level of defence, may have several competitors (high alpha diversity in the same trophic group) that limit the potential expansion (numerical and in terms of biomass) of their populations. In fact, according to Stanley (2007), "the basic idea that competition can set a limit for marine animal diversity is incompatible with
basic tenets of marine ecology”. In addition, Basset and Angelis (2007) suggested that smaller consumers can counter the competitive advantage of a larger competitor by their ability to reduce resource densities to a low level and, in this view, a higher diversity of smaller consumers could be forecasted for less abundant resources, in any ecosystem, as demonstrated by our findings, although previous studies have never explicitly connected body size to mechanisms of competitive coexistence of the consumers. According to the assumption of our theoretical model, however, we do know that the widely documented patterns of size-related niche partitioning may be due to relationships of competitive coexistence (Figure 15).

![Diagram](image)

**Figure 15.** Graphical sketch of the main results of this study. Two groups of species are consistently found in all ecosystems, the first represented by cryptic species of small size, characterized by high diversity, the second represented by larger species, characterized by low diversity.

These conclusions open the possibility for testing various hypotheses in selected ecosystems. For example, we demonstrated that biodiversity is inversely correlated, in each trophic group, to the maximum size reached
by species (Figure 16a). Since global patterns of biodiversity indicate an increase of species diversity from higher latitudes towards the lower ones (Gaston, 2000), can we accordingly forecast a decrease of size moving from poles to the equator? An analysis of the global biodiversity database confirms this hypothesis and shows that also this trend is confirmed.

As well, taking into account single trophic groups, since our model forecasts a decrease of diversity according to the availability of trophic resources, can we demonstrate a decreasing trend for the species diversity in the group of herbivores, in various environments, according to the percent cover of various plants? Also in this case the Global Biodiversity data-base allowed to confirm this hypothesis (Figure 16b).
Other hypotheses could be formulated, about the role of small sized organisms (Figure 15) present in a given environment (feeding on secondary items?), the exceptional biodiversity recorded in some areas (importance of secondary prey?), or the quick disappearing of large size species according to dramatic modification of the food webs (disappearance of “structural” food items?).

Even more interestingly, considering once again that our model of biodiversity was based on mathematical properties of networks, the trends observed of biodiversity and abundance of trophic resources should be transferable to any other biological system in which a network of cells or organisms is connected by trophic relationships. In this view,
we could forecast that, in agriculture, the addition of fertilizers will trigger larger production of a few crops, while the scarcity of resources will facilitate the increase of biodiversity, with the introduction of several (generally undesirable) species. Similarly, we can forecast that in a single organism, an abundance of trophic resources for cells (e.g., plenty of sugars, aminoacids and fatty acids) will facilitate the production of a single type of cells (eventually pathological?), while the “biodiversity” in the tissue homeostasis could be promoted by the scarcity of trophic resources.

The aforementioned hypotheses and several others will be tested in further investigations, in order to establish the actual limits of the model herein developed, linking the biodiversity levels to the availability of trophic resources and based on the above stated function of exponential decay. This will also facilitate a general interpretation of biodiversity patterns observed in any ecosystem, and a thorough comparison of their trophic structures. Since the equations here tested were derived from a mathematical evaluation of networks and further tested on ecosystem data, it is likely that they can find confirmation and validity also in other networks of live structures (cells, tissues, species, ecosystems) at various organization levels. Further studies will explore this hypothesis and eventually extend the validity of the two equations to a range of biological systems.
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List of Figures
(not including those of the published researches)

Figure 1: plot of the function (2) for values of $S>0$. (Graphical representation produced using https://www.desmos.com/calculator)

Figure 2. Relationship of $B_{tot}$ and $S$ along time, according to Hooper et al. (2005)

Figure 3. Known relationships (right) and hypothesis of this thesis (left)

Figure 4. Patterns of abundance of *Rana catesbeiana* (according to Rossberg, 2012) evaluated through the time trends of the coefficients $x$ and $y$ of the above equation

Figure 5 (From Rossberg, 2013). Index $Z_{C(p)}$ evaluated for increasing values of $D_{eff}$ of 1, 1.6, 4.6, 19, 3 respectively and reported over logarithmic axes

Figure 6. Universal cumulative distribution functions for consumers and resources in any environment follow an exponential decay pattern (From Camacho, 2002)

Figure 7: study of the generic function $S = K^* \exp(-R)$ according to the above considerations on the cumulative distributions and their relationship with the diversity of consumers.

Figure 8: matching-model food webs underlying the simulated distributions of in- and out-degrees according to (Rossberg et al., 2006b).

Figure 9. A numerical test of competition mean-field theory performed according to Rozdilsky and Stone (2001) indicating the patterns of
variation of the coefficient of variation of scaled abundance of resources according to species richness

Figure 10: Species richness by trophic level in freshwater ecosystems (from Petchey et al., 2004). Circles, squares, and triangles are geometric averages of data sets. The solid line is a linear regression of log $S_l$. The dash-dotted line indicates the theoretical slope.

Figure 11. Trophic levels of species against rank in order of falling values (From Rossberg, 2013). Dotted lines correspond to integer levels, the dash lines has a slope as predicted by the above reported equations.

Figure 12. (a) Relationship between % alpha diversity versus % RAFI for trophic groups at 13 Italian sites. Dashed line represents 95th log-linear regression quantile. $R^2$ for 95th regression quantile = 0.373 ($p<0.001$). (b) Food availability versus diversity in trophic groups at comprehensively surveyed seagrass meadow Lacco Ameno. Species list accumulated over multiple surveys. Abundance of food items calculated on actual data of numerical abundance of food items per unit area and results of gut content analyses. Multiple R-squared: 0.8521 ($p<0.001$). (c) Relationship between alpha diversity and food availability for hard-bottom site Banco Santa Croce. Food resources were produced using Ecopath-Ecosim. Each point represents a trophic group ($n = 5$) at a sampling station ($n = 4$) for a seasonal survey ($n = 4$). Multiple R-squared: 0.3477 ($p<0.005$). (d) Mathematical predictions about the distribution of trophic resources between small and large consumers are perfectly superimposable to the experimental results. Most data points (Figures 12 a, b, c) for small consumers are ordered in left area of this figure, while a few larger species consume the most abundant
resources, and they are ordered in the lower area (From Bagchi and Ritchie, 2012).

**Figure 13.** (a) Biomass of trophic groups linearly increased with food availability on a log-log scale. Food resources were produced using Ecopath-Ecosim. Each point represents a trophic group (n = 5) at a sampling station (n = 4) for a seasonal survey (n = 4). Multiple R-squared: 0.7657 (p<0.001). (b) Number of individuals in trophic groups linearly increased with food availability on a log-log scale. Food resources were produced using Ecopath-Ecosim. Each point represents a trophic group (n = 5) at a sampling station (n = 4) for a seasonal survey (n = 4). Multiple R-squared: 0.4424 (p<0.001)

**Figure 14.** Limiting influence of increasing food availability on alpha diversity of trophic groups for 41 sites representing shallow benthic habitats around the world. R^2 for 95th log-linear regression quantile = 0.158 (p<0.001).

**Figure 15.** Graphical sketch of the main results of this study. Two groups of species are consistently found in all ecosystems, the first represented by cryptic species of small size, characterized by high diversity, the second represented by larger species, characterized by low diversity.

**Figure 16.** (a) World trends of size for fish and invertebrates, along a latitudinal scale, show that the predictions of our trophic model (higher biodiversity is related to lower size) are confirmed. (b) RLS sites. Relationship between algae percent cover and richness of fish species calculated using the Global Biodiversity data-base. Dashed line = 90th regression quantile. R^2 for 95th log-linear regression quantile = 0.120 (p<0.001)