

OCEAN FOOD WEBS AND TROPHIC DYNAMICS

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Keywords: Food web, food chain, trophic level, ecological efficiency, phytoplankton, zooplankton, fish production, jellyfish, benthic food webs.

Contents

1. Introduction
2. The pelagic food web
 - 2.1 The structure of the pelagic food web.
 - 2.2 Phytoplankton community structure.
 - 2.2.1 Bottom up determinants of phytoplankton size structure.
 - 2.2.2 Top-down determinants of phytoplankton size structure.
 - 2.3 Zooplankton of marine pelagic food webs
 - 2.3.1 Protozoa.
 - 2.3.2 Copepoda.
 - 2.3.3 Tunicata.
 - 2.3.4 Mesozooplankton feeding selectivity.
 - 2.3.5 Herbivory by protozoa versus herbivory by metazoa
 - 2.4 The configuration of the lower food web.
 - 2.5 The jellyfish-fish interaction.
 - 2.6 Future research questions.
3. Benthic food webs
 - 3.1 Euphotic benthic communities
 - 3.2 Aphotic benthic communities
- Glossary
- Bibliography

Summary

Populations within a community are bound by trophic interactions. The simplest presentation of these connections is the food chain, a more realistic but also more complex presentation is the food web.

Pelagic food web configurations are proposed for three different types of marine nutrient regimes: (1) upwelling systems, (2) oligotrophic oceanic systems, (3) eutrophicated coastal systems.

Upwelling systems are characterised by high levels of plant nutrients and high ratios of Si to N and P. Most phytoplankton falls into the food spectrum of herbivorous, crustacean zooplankton. Therefore, herbivorous crustaceans occupy trophic level 2 and zooplanktivorous fish occupy trophic level 3.

Phytoplankton in oligotrophic, oceanic systems is dominated by picoplankton. Most of the primary production is channelled through the “microbial loop” (picoplankton – heterotrophic nanoflagellates – ciliates). Herbivorous crustaceans feed on heterotrophic nanoflagellates and ciliates, thus occupying a food chain position between 3 and 4, which leads to food chain position between 4 and 5 for zooplanktivorous fish.

By cultural eutrophication, N and P availability are elevated while Si concentrations remain unaffected or even decline. Diatoms decrease in relative importance while summer blooms of inedible algae prevail. The production of the inedible algae enters the pelagic energy flow via the detritus food chain: Carbon release by cell lysis – bacteria – heterotrophic nanoflagellates – ciliates. Accordingly, crustacean zooplankton occupy most of the season food chain position 4 to 5.

Benthic food webs follow the same ecological principles as pelagic food webs. Benthic food webs can differ in the energy source they depend on. Benthic communities of euphotic areas are supported by benthic plant growth. Communities of aphotic regions (about 90% of the seafloor) need allochthonous energy input which comes mostly from overlaying pelagic food webs. Communities at hydrothermal vents are supported by H₂S as energy source for purely bacterial primary production.

1. Introduction

Organisms within a community are bound by a network of interactions. Most important are trophic interactions, that is eat and be eaten. If this network of interactions are presented graphically, predator-prey interactions of trophic nature are portrayed vertically and competition relationships are portrayed horizontally. The simplest presentation of the vertical connections within a community is the food chain. Food chains are linear arrangements showing the transfer of energy and matter through various trophic levels. A trophic level is composed of organisms that obtain their energy in a similar manner. Food chains begin with primary producers. Primary producer are organisms which build organic material from inorganic elements and most primary producers are plants. The next trophic level is made up from organisms feeding these plants, they are referred to as primary consumers. Subsequent trophic levels are carnivorous and are called secondary consumers, tertiary consumers and so on. The highest trophic level is occupied by those adult animals that have no predators of their own. The number of trophic levels vary with locality and with the total number of species in the community. The question of what factors determine the length of a food chain is still unanswered and one of the large enigmas in ecology.

Elements such as carbon, nitrogen or phosphorus which become incorporated in organic components of plant and animal tissues have a cyclical flow through food chains. Bacteria and fungi decompose waste materials and tissues of dead organisms and release inorganic forms of elements which again become available for uptake by autotrophic organisms. In opposite to elements, energy has a unidirectional flow. Possible energy sources for food chains include sunlight, reduced inorganic chemical bounds or allochthonous input of organic matter. On a global scale sunlight is by far the most important energy source and oxic photosynthesis is by far the most important initial process in the flow of energy. Nearly all pelagic food chains of the oceans get their initial energy from sunlight. A few ecosystems exist where chemolithotrophy is the primary initial process of energy flow such as hydrothermal vents in the deep ocean

bottom that supply H_2S . Food chains that use allochthonous organic compounds as an energy system must depend on other ecosystems. An example are the food chains of most of the ocean seafloor which depend on material produced in euphotic pelagic food webs sinking downwards to the bottom.

Energy leaves the food chains by each transfer to the next trophic level. This is because much of the chemical energy incorporated in organic compounds is converted to heat or respired when organic carbon is broken down to CO_2 . A consequence of that process is that total energy diminishes at each trophic level and this places a finite limit on the possible number of trophic levels in any community. The efficiency with which energy is transferred between levels is called the ecological efficiency. It is defined as the amount of energy extracted from a given trophic level divided by the energy supplied to that trophic level. It is often approximated from the transfer efficiency which is defined as the production at trophic level t divided by the production at trophic level $t-1$.

Populations within a food chain directly affect their neighbors through trophic interactions and thereby indirectly influence other populations with which they are integrated. Effects of population interactions can travel through the food chain, although the effects may be dampened. Species with especially far reaching effects are called keystone species. However, such keystone species need not to be associated with major pathways of energy and matter as for example a disease vector with negligible energy flow could dramatically alter the composition of a community. Such a flow of controlling influence in food chains can start from the bottom of the food chain – the available nutrients – and all the trophic levels depend on the fertility of the habitat (bottom up control). Additionally, a controlling influence can also flow downward in the food chain and biomass and species composition of each trophic level is determined as those species left over by predation of the upper trophic level (top down control). In marine biology, pelagic research is traditionally more focussed on the investigation of bottom up effects in food chains, whereas benthic research resulted in detailed investigations of top down controlling effects in food chains. Both flows of controlling influence are operating in each food chain, however the strength of each flow will vary between ecosystems and in time and scale.

In reality the establishment of food chains is most often an attempt to reduce a complex natural system to simple dimensions. Communities are seldom arranged in a simple linear way. The trophic connections are more accurately portrayed as a food web with multiple and shifting interactions between the organisms. Because many species do not fit into distinct trophic levels and are for example omnivorous, detritivorous or parasitic and change their food items during development organisms are more complex connected with each other than a linear arrangement could represent. However, in spite of that lack of realism in food chain arrangement of interacting trophic levels there is evidence that still some pelagic communities may operate more as parallel independent food chains than as one complex food web.

Although food webs are often more realistic than food chains, they are more difficult to quantify in ecological terms. Hence, similar as in a food chain an important property of a food web is the ecological transfer efficiency (ETE), expressing the conversion efficiency of material/energy bound into biomass between successive trophic steps. However, it is more difficult to follow the energy input from primary production channeled into different trophic levels and pathways of a food web. Measurements of

ETE are difficult to do in the field. Most measurements of ETE are therefore very rough estimates. However, this parameter is of crucial importance as it is needed to predict the yield of a certain food web. The number of transfer steps from the base of the food web to a certain trophic level and the efficiency at each step would allow to predict the production of a certain food web compartment from a relatively simple estimate of primary production.

2. The pelagic food web

Marine pelagic food webs are the most common type of food webs on earth and the organisms bound in them are the most abundant on earth. The dynamics of pelagic food webs have strong impacts on world food production, the world climate and the global carbon cycle. This article starts therefore with a detailed introduction to this type of food webs.

In marine pelagic ecosystems, the processes taking place between the resource-controlled production of the basal trophic level, and the harvestability on the top links, determine within a wide range the ratio between primary (PP) and fish production (FP). A recent compilation shows a >3-fold difference in FP/PP between low productive and high productive marine environments, with increasing system ETE (from phytoplankton to fish) with increasing PP. This means that in ocean areas with good nutrient supply a higher amount of fish is produced per amount of primary production than in areas with low nutrient supplies. The number of trophic levels, and the ETE between these, is an obvious explanation. Functional groups dominant at each trophic level can vary significantly in their 'functional biology and resource dynamics', and their food value or accessibility for the next step, ranging from inedibility (toxic species) and 'low quality' to 'high quality' food via altering ETE and food web structure.

Classic ecological common-sense has started from 2 assumptions: an ecological efficiency of 10% and planktivorous fish at the 3rd trophic level. This would predict, that fish production should amount to 1% of primary production. Some early authors have even assumed a considerable amount of herbivory by planktivorous fish of upwelling areas, which would place the trophic position of fish below 3 and the FP:PP quotient to >1%. A more recent analysis leads to considerably lower estimates. This regression equation predicts, that nekton production (fish plus squid production) should be non-linearly related to primary production. NP:PP amounts to ca. 1% in eutrophic upwelling areas but to <0.5% in the oligotrophic ocean. This dependence of NP:PP on PP could have two reasons: A lower ecological efficiency under more or longer food chains under more oligotrophic conditions. The first assumption seems improbable, because the ecological efficiency at the phytoplankton:zooplankton link has been found slightly higher under more oligotrophic conditions.

In this article, the available knowledge about the phytoplankton response to nutrients and about mesozooplankton food selection is used to develop some hypotheses about differences in the food web structure at different levels of nutrient richness. Instead of just contrasting oligotrophic and eutrophic conditions, three scenarios will be developed. A low nutrient scenario for the oligotrophic ocean, a high Si - high N - high P scenario for upwelling regions and temperate/boreal seas immediately after winter circulation, and a low Si – high N –high P scenario for summer stratification under the eutrophication influence from land-borne nutrient sources.

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