



Effects of biomass changes in the supply–demand balance of energy in aquatic food webs



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ABSTRACT

Due to the complex interactions between the community and its environment, understanding the behaviour of ecosystems is a difficult and laborious task. In this paper, we study several aspects of the ecosystem characterised by food webs and how their energy balance is affected by changes in biomass and the availability of resources required for self-maintenance. Ecosystem behaviour, as expressed through the energy flows between compartments, and the respiration flows and biomass of 124 trophic models are analysed. The metabolism of food webs is characterised by measuring respiration flows and scaling biomass to the $3/4$ power. On the basis of this scaling, 16 food webs were selected to make a comparative analysis of the system dynamics, assuming that metabolism, relative to the size and independence of the environment, is the main source of change in the supply–demand balance of energy. The results demonstrate the importance of variation in the biomass of primary producers for the availability of resources in the system, which is related to bottom-up control, whereas a decrease in the supply of resources by top predators is associated with top-down control.

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1. Introduction

Studying ecosystems through an analysis of food webs allows for the complementary use of holistic and reductionist approaches, thus creating a synthesis between the general aspects and individual parts of a system. The aggregation of species into compartments or functional groups in the food web allows us to map a network of interactions that might initially hide key mechanisms in the functioning of ecosystems. To reveal these networks, there are a variety of ecological indicators that need to be considered in describing the behaviour of the ecosystem.

Bendoricchio and Palmeri (2005) proposed an index of supply–demand balance (SDB) to measure the energy state of an ecosystem. Using Ecopath software (Christensen and Pauly, 1992), they built trophic models assuming that food webs are systems that transport resources with an efficiency affected by the form and size of the network (Banavar et al., 1999). Bendoricchio and Palmeri (2005) indicate that the SDB index calculates the balance in the rates of supply and demand resources, thus reflecting the distance between the ecosystem and its possible optimal state.

The SDB index was recently proposed and has not been sufficiently explored. The work of Bendoricchio and Palmeri (2005) is

the only study in the literature describing relationships between the supply and demand of energy with population or ecosystem attributes. The authors take the theoretical framework of SDB index and assume that food webs with indices below 0.66 correspond to trophic models characterised by a poorly representation of the network due to the quality of data used or a mass imbalance of the modelled system. An index greater than 0.75 corresponds to food webs with a high proportion of supply/demand of resources, a high recycling, greater resilience and a high cost of network maintenance.

The energy flow of an ecosystem may be governed by different control mechanisms. Power (1992) provides a review about it, indicating the importance of limited resources at different trophic levels and their relationship to bottom-up and top-down forces. Polis and Strong (1996) developed a conceptual model positing the existence of a number of donor-controlled (sensu DeAngelis, 1980) resources and alternative pathways (allochthonous inputs) controlling the system flow, thus indicating that the dynamics expressed in a food web are primarily governed by the availability of resources (bottom-up control sensu Huxel and McCann, 1998). However, other studies have suggested that predation at higher trophic levels plays an important role in the flow control of the network from the top-down (Hairston et al., 1960; Oksanen, 1991 sensu Huxel and McCann, 1998). These ideas seem opposed to each other, but both limit the widespread influence of natural variability. As a single system, they offer either the possibility of bottom-up control when there are significant energy subsidies (allochthonous

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inputs) that prevent a decline in the abundance or renewal rate of prey by predators, or top-down control, when the subsidies are reduced or removed (sensu Polis and Strong, 1996).

Considering that the ecosystems have control mechanisms on the energy flow (Polis and Strong, 1996; Huxel and McCann, 1998), this leads us to ask if the flow control by certain functional groups might be related to the energy balance and consequently to the resources availability of the system. In this study, we test the sensitivity of the SDB index (Bendoricchio and Palmeri, 2005) to changes in the biomass of the compartments of 16 marine and freshwater aquatic food webs. Our aim is to determine if the balance in the supply and demand of energy is controlled by a particular group in the ecosystem, and if a pattern of control mechanisms between ecosystems could exist. The study ensures that the comparison between different types of ecosystems is relative to the ecosystems' metabolic state (explained below) and assumes an implicit and negligible influence from factors such as the taxonomic aggregation level of the functional groups and environmental variability.

2. Materials and methods

2.1. The food web model

The food webs analysed in this paper are based on the approach proposed by Polovina (1984) and improved by the Ecopath model of Christensen and Pauly (1992). The data were obtained using the Ecopath with Ecosim software (EwE version 5.1.218, Christensen and Walters, 2004). The Ecopath model is based on a system of linear equations that represent the mass-balance of species in an ecosystem through compartments and energy flows that are expressed quantitatively as,

$$B_i \left(\frac{P}{B} \right)_i EE_i - \sum_{j=1}^n \left(\frac{Q}{B} \right)_j B_j DC_{ji} - Y_i - E_i - BA_i = 0 \quad (1)$$

where B_i and B_j are the biomass of the prey and the predator group, respectively; P_i , Q_j , Y_i , E_i and BA_i are the rates of production, consumption, fisheries capture, net migration and biomass accumulation, respectively; DC_{ji} is the fraction of the prey i in the average diet of the predator j . The sum describes the predator consumption; for its prey, it is equivalent to the mortality rate of predation ($M2_i$); EE_i is the ecotrophic efficiency and indicates the proportion of production used in the system. The model is balanced under the following thermodynamic condition of consumption (Q_i):

$$Q_i = P_i + R_i \cdot D_i \quad (2)$$

Such that,

$$P_i = Y_i + M2_i \cdot B_i + E_i + BA_i + M0_i \cdot B_i \quad (3)$$

where R_i , D_i and $M0_i$ are the rates of respiration, waste and mortality from different causes related to fishing and predation, respectively. The energy units are expressed in terms of wet weight biomass.

2.1.1. The chosen models

Out of 124 available Ecopath trophic models (Table A1), we selected 16 to represent several types of aquatic ecosystems, such as oceans, the continental shelf, reefs, bays, coastal lagoons, rivers, lakes and reservoirs. These systems have several characteristics that might influence the comparison (Table 1) between their own implicit natural variability (space-time) and the criteria used for the construction of each model. The food web used to experiment with biomass changes of the functional groups were selected based on their biomass and respiration flow.

Table 1 Food web models used to analyse marine and freshwater ecosystems. For their selection, biomass and heterotrophic respiration attributes were considered.

Ecosystem	Food web	Functional groups	Biomass (t/km ²)	Respiration (t/km ² ·year)	B/P ^a	Study period (year)	Study area (km ²)	Longitude	Latitude	Water temperature (°C)
Continental Shelf	West Florida (Okey et al., 2004)	59	451.16	5977.33	0.051	Unknown	170,000	-83,250	27.250	Unknown
	Coast of Sarawak (Garces et al., 2003)	29	9.63	268.92	0.019	1972	76,668	112,500	3.260	Unknown
Oceanic	Central Pacific Ocean (Cox et al., 2002)	26	59.90	1574.90	0.015	1990–1998	36,290,000	170,000	20.000	25.2 ^b
	Bali Strait (Buchary et al., 2002)	14	12.85	466.65	0.034	1995–1998	3126	114,760	-8.570	27.7 ^b
Coral reef	Loos Keys (Venier and Pauly, 1997)	20	3876.92	24904.01	0.132	Unknown	30	-81,400	24.655	Unknown
	Mexican Caribbean (Alvarez-Hernández, 2003)	18	2401.60	13494.73	0.137	1990	Unknown	-87,240	19.300	27.5
Bay	Tongo Bay (Wolff, 1994)	18	183.34	3571.81	0.024	1978–1989	60	-71,548	-30.283	14.6
	Maputo Bay (De Paula et al., 1993)	10	51.81	1281.32	0.063	1972–1985	1100	32,766	-26.024	24.5
Coastal lagoon	Celestun Lagoon (Chávez et al., 1993)	16	76.17	1687.36	0.176	Unknown	28	-90,393	20.816	Unknown
	Sakumo Lagoon (Pauly, 2002)	13	10.10	318.63	0.024	1971	1	0.013	5.630	Unknown
River	Paraná River (Angelini and Agostinho, 2005)	40	7.21	249.73	0.084	1992–1995	933,000	-52,840	-22.360	Unknown
	Garonne River (Palomares et al., 1993)	10	30.08	315.86	0.021	1990–1991	5	1.319	43.761	4.0
Lake	Awassa Lake (Fetahi, 2005)	14	72.97	1619.64	0.157	2003–2004	90	38,443	7.064	25.5
	George Lake (Moreau et al., 1993)	14	41.45	856.37	0.041	1970s	250	80,200	0.000	16.5 ^c
Reservoir	Sri Lankan Reservoir (Moreau et al., 2001)	17	76.49	7188.10	0.026	1970	25	80,982	7.909	27.5 ^c
	Broa Reservoir (Angelini and Petreire, 1996)	11	1.25	59.42	0.300	1970s	6	-47,888	-22.192	24.7

^a B/P is the biomass/production ratio and reflects the average size of organism in a system (sensu Christensen et al., 2005).

^b Mean temperature obtained for the same area and period study through the Earth Science Information Partner Federation (Ocean ESIP: <http://poet.jpl.nasa.gov>).

^c Mean temperature from the International Lake Environment Committee (<http://wldb.ilec.or.jp/>). Biomass, respiration and B/P are estimates of the static model Ecopath.

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