Stable versus unstable planktonic food webs in oceans

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ABSTRACT

It is hypothesised that the multivorous and microbial food webs generally dominate marine pelagic waters. This hypothesis is tested using data from a wide range of marine environments and trophic conditions. The first step consists of computing the matching between production and losses of phytoplankton (M). The frequency distribution of M in oceans is dominated by values close to one, which indicates that there generally is a tight coupling between net phytoplankton production and losses (i.e., consumption and sinking). In the second step, frequency distributions of several ecological variables are constructed for three classes of M values. Analysis of these distributions indicates that $M \neq 1$ generally corresponds to dominance by the herbivorous food web, and $M \approx 1$ to dominance by the multivorous and the microbial food webs. It follows that the prevalence of values $M \approx 1$ in oceans supports the above hypothesis. Using data obtained from another study, it is further concluded that, in most oceans most of the time ca.60 to 80% of the phytoplankton production is respired in the euphotic zone, ca. 20 to 30% is transferred to the pelagic food web, and ca. 10% is exported downwards.

Introduction

Legendre and Rassoulzadegan [3] proposed that there is a continuum of trophic pathways in the pelagic environment, from the herbivorous food web, to the multivorous food web, to the microbial food web, and to the microbial loop. They defined the four pathways as follows. At one end of the continuum, the microbial loop is an almost closed system of heterotrophic bacteria and zooflagellate grazers, in which the latter release dissolved organic matter (DOM) used as substrate by the former [1, 2]. At the other end of the continuum, the herbivorous food web is dominated by large phytoplankton and herbivorous grazing. The microbial and multivorous food webs are located at the centre of the continuum: the former includes the same components as the microbial loop plus small phytoplankton [6]; in the latter, the herbivorous and microbial trophic modes both play significant roles. Legendre and Rassoulzadegan [3] also proposed that planktonic systems dominated by the herbivorous food web or microbial loop are of transient nature and thus inherently unstable, and that systems dominated by the multivorous and microbial food webs are longer lasting and thus more stable than the two extreme types. Hence, stability in the present paper refers to the transient vs. lasting nature of food webs.

Legendre and Rassoulzadegan [4] described a model to compute, for the four trophic pathways in the continuum, the partitioning of phytoplankton production (P) among three main fluxes of biogenic carbon, i.e., remineralization within the euphotic zone, transfer to the pelagic food web, and downward particulate organic carbon (POC) flux. The independent variables of the model are two food-web characteristics, the size structure of primary production (P_L/P_T, where L is the large size fraction, e.g., >5 µm; and T is the

Microbial Biosystems: New Frontiers
Proceedings of the 8th International Symposium on Microbial Ecology
Bell CR, Brylinsky M, Johnson-Green P (eds)
Atlantic Canada Society for Microbial Ecology, Halifax, Canada, 1999.

total) and the matching between primary production and grazing (M', a dimensionless variable, ranging from 0 to 1). Legendre et al. [5] proposed an approach, described below, to quantify the matching between production and losses of phytoplankton (M) using field estimates of chlorophyll *a* (Chl) and P. When the loss term includes sinking of intact phytoplankton in addition to grazing, the coefficient M is not the same as M'.

Because the herbivorous food web and the microbial loop are of transient nature, it is hypothesised that the longer-lasting multivorous and microbial food webs will dominate the pelagic environment in most oceans most of the time. This hypothesis is tested below using M values from a wide range of oceanic and coastal environments and trophic conditions. Our approach is to: (1) compute M at stations that cover a wide range of environments and trophic conditions; (2) use the frequency distribution of M to divide the range of observations into central and outlying values; (3) construct, for the various classes of M values, the frequency distributions of ecological variables (which were collected simultaneously to M); (4) use (3) to identify which food web each class of M corresponds to and; (5) by combining (1) and (4), identify which food web(s) generally dominate(s) the pelagic environment.

Materials and Methods

Computation of M

In oceans, the change in phytoplankton biomass (B_p) per unit time ($\triangle B_p/\Delta t$) reflects the difference, over time interval Δt, between P and the total losses of phytoplankton (L) in the euphotic zone:

$$\Delta B_p/\Delta t = P - L \qquad (1)$$

All terms in equation (1) have units of mass of C per unit area (or volume) and time. The L term includes grazing, lysis, remineralization, sinking, and advection of phytoplankton cells (the latter may be positive or negative). The matching between P and L is defined as:

$$M = 1 - [(\Delta B_p/\Delta t) / P] \qquad (2)$$

Equation (2) is conceptually quite simple. The estimation of M from field data requires consideration, however, of some practical aspects, which are discussed in Legendre et al. [5]. These concern: the choice of a C:Chl ratio to obtain B_p from Chl (in the present paper, the ratio C:Chl is equal to 30 in all cases); the maximum interval (Δt) between observations, which must be short (in the present study 1 day < dt < 7 days) because, as Δt increases, the likelihood of missing transient phytoplankton production and loss events also increases; cases where $\Delta B_p/\Delta t$ and P do not refer to the same time interval and; smoothing out of random variations in B_p.

Equation (2) shows that, when there is no loss of production, then $\Delta B_p/\Delta t = P$ and $M = 0$, i.e., a complete mismatch. When all production is lost, then $\Delta B_p/\Delta t = 0$ and $M = 1$, i.e., a perfect match. It however happens that, because of uncontrolled factors such as estimation errors in B_p and/or P, and advection of water at the sampling station, short-term field $\Delta B_p/\Delta t > P$; hence, $M < 0$. Conversely, there are situations where short-term phytoplankton losses are higher than production, i.e., field $\Delta B_p/\Delta t < 0$ and, hence, $M > 1$.

Legendre et al. [5] designed coefficient M to assess the dominance of physics (M near 0) vs. that of biology (M near 1). Hence, they replaced values $M < 0$ by $M = 0$, and $M > 1$ by $M = 1$. In other words, as a practical tool for extracting ecologically relevant information from Chl and P data, $0 \geq M \leq 1$. The present paper uses M as a tool to determine the dominance of marine systems by various food webs. In this specific case, values $M > 1$ are meaningful, so that the restrictions $M \geq 0$ and $M \leq 1$ are not implemented in the following analysis.

Equations (1) and (2) show that $M = 0$ corresponds to a complete mismatch between P and L, and $M = 1$ to a perfect match. It however happens that, because of uncontrolled factors such as estimation errors in B and/or P, and advection of water at the sampling station during Δt, field $\Delta B/\Delta t > P$; hence, $M < 0$. Since a negative M has no ecological meaning, the most conservative assumption in such a case is that $\Delta B/\Delta t = P$; hence, values $M < 0$ are replaced by $M = 0$. Conversely, there are situations where L is greater than P, i.e., field $\Delta B/\Delta t < 0$ and hence $M > 1$. By definition, a situation where $L > P$ must be transient, because it depletes B. Values $M > 1$ may be of interest for analysing phytoplankton dynamics, but they offer no special advantage within the context of the present paper. This is because our specific aims, as indicated in the introduction, are to develop a conceptually and practically simple method to extract ecologically relevant information from Chl and P data, and to test the hypothesis that M characterises the dominant processes (physical vs. biological) in pelagic marine ecosystems. The coefficient M being designed to assess the dominance of physics (M near 0) vs. that of biology (M near 1), values of $M > 1$ are replaced by $M = 1$.

Data Sources

Data used in the present study were taken from 24 published papers and cover a wide range of environments, both oceanic (subtropical and subpolar gyres, anticyclonic eddies, polynyas) and coastal (marginal seas, shelf and upwelling areas, estuaries, bays and inlets, and fjords), and trophic conditions (from eutrophic to oligotrophic). The general characteristics of the 24 data sets and the references are given in Table 1 of Legendre et al. [5].

Results and Discussion

Fig. 1 shows the frequency distribution of M values computed from the data presented in the 24 studies and, for each frequency interval, the number of values belonging to either oceanic or coastal (including estuarine) waters. The latter show that the two broad types of environments are well distributed over the range of M values. In other words, although it is easier to obtain repeated short-term samples in coastal than in oceanic areas, the data set is not unduly biased toward coastal waters. The M values tend to cluster around $M = 1$ ($0.8 < M < 1.2$), i.e., among the 536 M values, 163 (30%) are <0.8, 279 (2%) are between 0.8 and 1.2 and 94 (18%) are > 1.2. Hence, the frequencies of the outlying values are lower than the frequency of $M \approx 1$. Values $M \approx 1$ occur when the changes in phytoplankton biomass are commensurate with primary production. The outlying values correspond to increases ($M < 0.8$) or decreases ($M > 1.2$) of phytoplankton biomass out of proportion to primary production. The dominance of the frequency distribution of M by values close to one indicates that, in oceans, there is generally a tight coupling between net phytoplankton production and losses (i.e., consumption and sinking).

Fig. 2 shows the frequency distributions of four ecological variables, for the three classes of M values ($M < 0.8$, $0.8 < M < 1.2$, and $M > 1.2$), and Table 1 summarises the

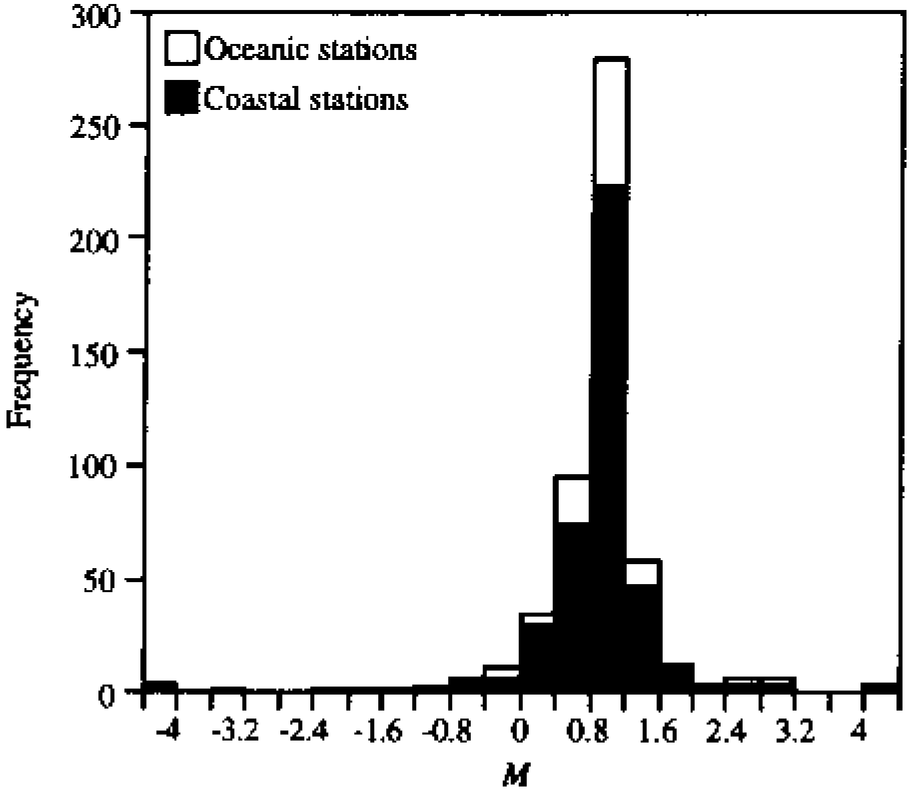

Fig. 1. Frequency distribution of the 536 *M* values computed from the 24 studies in Table 1 of Legendre et al. [5].

general characteristics of these distributions and those of the two ratios. The ecological variables in the Fig. 2 (and Table 1) are those for which the numbers of published data, in the papers used to construct Fig. 1 (Table 1 in Legendre et al. [5]), were high enough to obtain meaningful distributions. Even then, the total number of values for the bacterial biomass (31) may be too small to draw general conclusions. It is remarkable that, for the four variables, the distributions for the central values of *M* (0.8 to 1.2) are different from those for the outlying values (< 0.8 and > 1.2). When $0.8 < M < 1.2$, there are numerous cases in which the *f*-ratio is low (< 0.7). Most cases have low values of phytoplankton

Table 1. General characteristics of the frequency distributions of four ecological variables, for three classes of *M* values ($M < 0.8$, $0.8 < M < 1.2$, and $M > 1.2$; see Fig. 2). The ecological variables are: *f*-ratio ($\rho NO_3 / [\rho NO_3 + \rho NH_4]$ where ρ is the transport rate of N-nutrients by phytoplankton); phytoplankton biomass (B_p; g Chl m^{-2}); ratio of bacterial biomass (B_b; g Cm^{-2}) to $B_{p\,(C)}$ where $B_{p(C)} = B_p \times 30$ g C g^{-1} Chl and; ratio of mesozooplankton biomass (B_{mz}; g C m^{-2}) to $B_{p(C)}$.

Ecological variables	M < 0.8	0.8 < M < 1.2	M > 1.2	No. data
f-ratio	Most values >0.7	Numerous values <0.7	Most values >0.7	174
B_p (g Chl m^{-2})	Some values >0.05	Almost all values <0.05	Some values >0.05	536
B_b / $B_{p©}$	All values <1	Most values >1	Most values <1	31
B_{mz} / $B_{p(C)}$	Some values >1	Almost all values <1	Some values >1	98

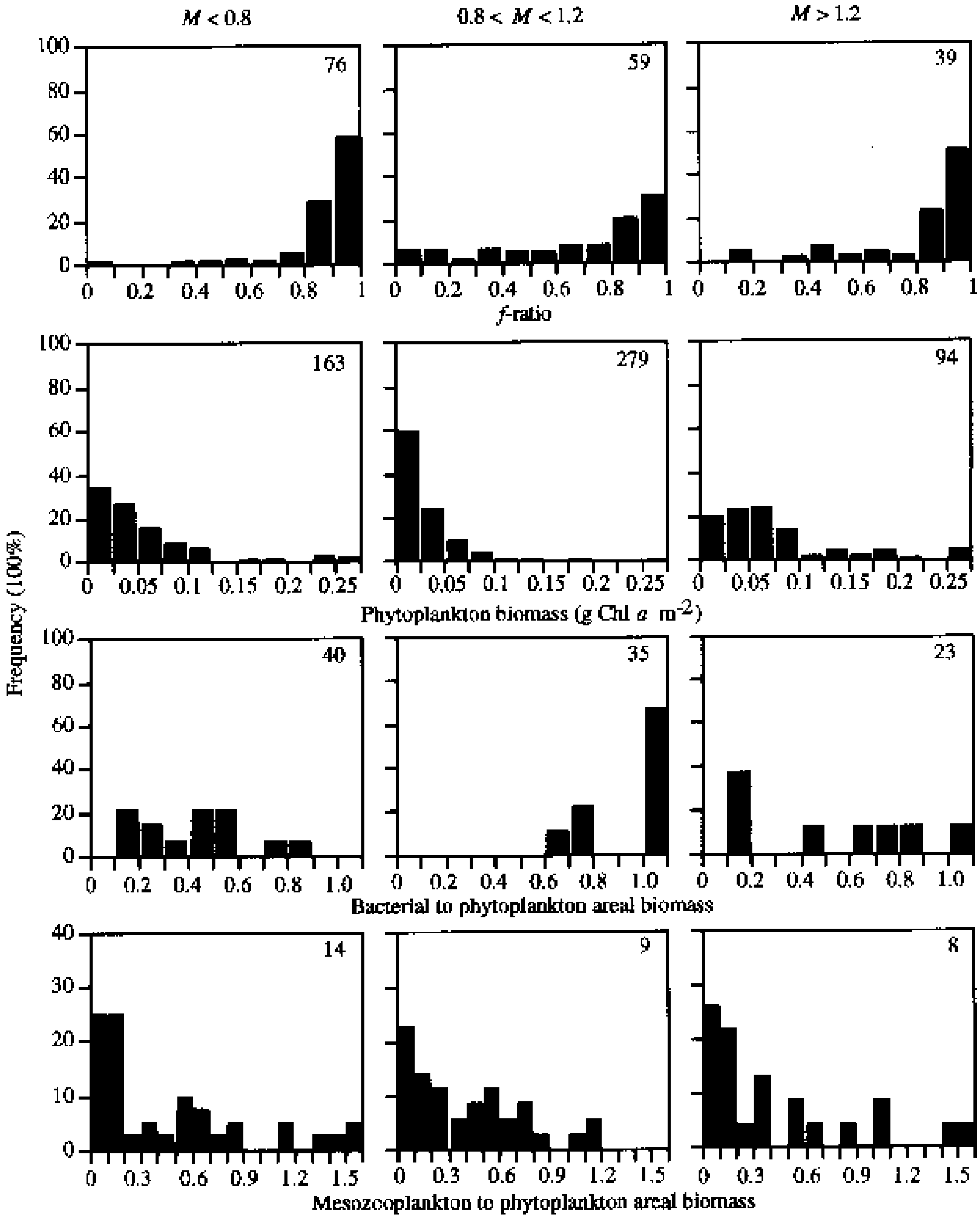

Fig. 2. Frequency distributions of four ecological variables for the three classes of *M* values. Numbers in each panel represent number of data. The general characteristics of the frequency distributions are summarised in Table 1.

biomass (<0.05 g Chl m^{-2}), high values of bacterial / phytoplankton biomass (> 1), and low values of mesozooplankton / phytoplankton biomass (< 1). When $M < 0.8$ and $M > 1.2$, most cases have high *f*-ratios (> 0.7), and low values of bacterial / phytoplankton biomass

(< 1); there are some cases with high values of phytoplankton biomass (> 0.05 g Chl m^{-2}), and mesozooplankton / phytoplankton biomass (> 1).

In situations where $M \neq 1$ ($M < 0.8$ and $M > 1.2$), the phytoplankton biomass either increases ($M < 0.8$) or decreases ($M > 1.2$) out of proportion with primary production. In such situations, phytoplankton production and losses are not matched. According to Legendre and Rassoulzadegan [3], planktonic systems away from equilibrium correspond to dominance by the herbivorous food web or the microbial loop. The present study considers changes in B_p over time scales ranging between one day and one week. Such a time scale is appropriate for the herbivorous food web, but it may be too long for the microbial loop. The herbivorous food web occurs under conditions of high phytoplankton production and grazing (and often high particle sinking). Because the processes of production and export are seldom perfectly matched in the short term, i.e., there are periods of excess production and periods of excess export, this results in the occurrence of both $M < 0.8$ and $M > 1.2$. It follows that dominance by the herbivorous food web should generally lead to both low and high M values. Dominance by the herbivorous food web is consistent with the frequency distributions (Fig. 2 and Table 1), for $M < 0.8$ and $M > 1.2$, of values observed for the *f*-ratio, which are generally high (> 0.7), and the bacterial biomass, which is generally low ($B_b/B_{p(C)} < 1$). Hence, values of $M \neq 1$ generally correspond to dominance of the planktonic system by the herbivorous food web.

In situations where $M \approx 1$ ($0.8 < M < 1.2$), the changes in phytoplankton biomass are commensurate with primary production. Such situations reflect an equilibrium between phytoplankton production and losses. According to Legendre & Rassoulzadegan [3], in oceans planktonic systems at equilibrium correspond to dominance by the multivorous or the microbial food web. Dominance by these two food webs is consistent with the frequency distributions (Fig. 2 and Table 1) for $0.8 < M < 1.2$, of values observed for the biomass of bacteria, which are generally high ($B_b/B_{p(C)} > 1$), and the biomasses of phytoplankton and mesozooplankton, which are generally low (B_p <0.05 g Chl m^{-2}, and $B_{mz}/B_{p(C)} < 1$). Hence, values of $M \approx 1$ generally correspond to dominance of the planktonic system by the multivorous or the microbial food web.

Conclusion

As indicated in the introduction, Legendre & Rassoulzadegan [3] proposed that planktonic systems dominated by the multivorous and the microbial food webs are stable. This led to the hypothesis, presented here, that the two food webs should generally dominate the pelagic environment. The analysis of data from a wide range of marine environments and trophic conditions indicates that values of $M \approx 1$ generally correspond to dominance of planktonic systems by the multivorous and the microbial food webs. Hence, the prevalence of values of $M \approx 1$ in oceans supports our hypothesis. According to Table 2 of Legendre & Rassoulzadegan [4], the dominance of planktonic systems by the multivorous and microbial food webs means that, in most oceans most of the time, ca. 60 to 80% of the phytoplankton production is respired in the euphotic zone, ca. 20 to 30% is transferred to the pelagic food web, and ca. 10% is exported downwards.

Acknowledgements

The authors thank Lawrence Pomeroy and one anonymous reviewer for useful suggestions, and Josée Michaud for assembling the data base, conducting preliminary analyses of the data, and preparing the figures. Grants from the NATO International Scientific Exchange

Programmes (F.R. and L.L.), the Natural Sciences and Engineering Research Council of Canada (L.L.), and the EEC MAST III (Project MAS3-CT96-0051, Mater-MTPII; F.R.), and a Killam Research Fellowship (L.L.) were instrumental in the completion of the work. This is a contribution to the programs of GIROQ (Groupe interuniversitaire de recherches océanographiques du Québec) and the Laboratoire d'Écologie du Plancton Marin (Université Pierre et Marie Curie, Paris VI, and CNRS/SDU URA 2077).

References

1. Azam FT, Fenchel T, Field JG, Meyer-Reil LA, Thingstad, F (1983) The ecological role of water-column microbes in the sea. Mar Ecol Prog Ser 10:257-263
2. Hagström Å, Azam F, Andersson A, Wikner J, Rassoulzadegan F (1988) Microbial loop in an oligotrophic pelagic marine ecosystem: possible roles of cyanobacteria and nanoflagellates in the organic fluxes. Mar Ecol Prog Ser 49:171-178
3. Legendre L, Rassoulzadegan F (1995) Plankton and nutrient dynamics in marine waters. Ophelia 41:153-172
4. Legendre L, Rassoulzadegan F (1996) Food-web mediated export of biogenic carbon in oceans: environmental control. Mar Ecol Prog Ser 145:179-193
5. Legendre L, Rassoulzadegan F, Michaud J (In prep) Identifying the dominant processes (physical vs. biological) in pelagic marine ecosystems from field estimates of chlorophyll *a* and phytoplankton production.
6. Rassoulzadegan F (1993) Protozoan patterns in the Azam-Ammerman's bacteria-phytoplankton mutualism,. In: Guerrero R, Perdos-Alio C (eds) Trends in microbial ecology, Spanish Society for Microbiology, Barcelona, pp 435-439