

Partitioning of microbial biomass in pelagic aquatic communities: maximum resiliency as a food web organizing construct

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ABSTRACT: Application of the principle of maximum resiliency to a pelagic food web model leads to the conclusion that the ratio of heterotrophic bacterial biomass to phytoplankton biomass is greatest under oligotrophic conditions. This prediction is in accord with the results of several field studies. Under eutrophic conditions, model results indicate that the same ratio is positively correlated with temperature, and that microbial biomass is dominated by phytoplankton at low temperatures and high production rates. Predictions of heterotrophic bacterial biomass based on the model and information on temperature and photosynthetic rates or phytoplankton biomass are in excellent agreement with field data from a wide variety of limnetic and marine habitats with depths ≥ 6 m. The model consistently underestimated heterotrophic bacterial biomass in systems impacted by riverine throughput and in hypereutrophic systems in which the euphotic zone was less than 3 m deep. In systems less than 3 to 4 m deep the model was less successful in predicting heterotrophic bacterial biomass than in deeper systems, although there was no apparent bias in the results. Because of the short generation time of aquatic microbes, pelagic food web behavior that is determined primarily by the activity of these organisms may tend to display characteristics expected of the mature stages of ecological succession. Maximum resiliency, a characteristic expected of such mature stages, may therefore prove to be a useful construct in modeling the response of pelagic food webs to environmental change.

KEY WORDS: Bacteria · Model · Food web · Stability · Phytoplankton

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INTRODUCTION

Ecologists have hypothesized for many years that the evolution of biological systems is driven by fundamental principles or forces. Lotka (1922), for example, argued that natural selection tended to maximize the energy flux through a system, at least insofar as this was compatible with the constraints to which the system was subject. Odum (1983) expanded on Lotka's ideas. He argued that systems that prevail develop designs that maximize the flow of useful energy. 'They maximize power, and theories and corollaries derived from the maximum power principle explain much about the structure and processes of systems' (Odum 1983, p. 6). Odum's ideas have been sharply criticized by some authors. Fenchel (1987, p. 17), for example, argued that Odum's approach, 'had an appeal for some time, I suppose, only because it was sufficiently

obscure and incomprehensible to appear profound.' In reacting to such comments, Patten (1993) observed, 'The admissibility of virtually any system configuration, within given physical and resource constraints, does not mean the processes of ecosystem organization are lawless. The challenge is to find the laws, and that is the central thrust of Odum's work.'

Recently Cropp & Gabric (2002) used a genetic algorithm to simulate the adaptation of the biota in a simple linear food chain consisting of a limiting nutrient, autotrophs, and heterotrophs. Four basic selection pressures were formulated by considering thermodynamic (entropy, exergy, and ascendancy) and ecological (sustainable biomass, primary productivity, and productivity per unit biomass) imperatives that influence ecosystems. Interestingly, their simulations suggested that, within the constraints of the external environment and the genetic potential of their con-

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stituent biota, ecosystems evolve to the state most resilient to perturbation.

The words 'most resilient to perturbation' here mean that, following a small perturbation, the system returns to its equilibrium configuration most rapidly. The rate of return to equilibrium is determined by the real parts of the eigenvalues of the so-called community matrix, whose elements consist of partial derivatives of the deterministic equations describing the temporal dynamics of the system evaluated at the equilibrium point. The more negative the real part of the least negative eigenvalue, the more rapidly the system returns to equilibrium. May (1974) provides a lucid discussion of these topics. Laws et al. (2000) applied the assumption of maximum resiliency to the more complex pelagic food web depicted in Fig. 1. All but 2 parameters in the model were assigned values based on deterministic equations. Two independent adaptive characteristics of the model, the relative growth rates of the large phytoplankton and the biomass of filter feeders, were assigned values that maximized the resiliency of the steady-state system to perturbations at the given temperature and photosynthetic rate. The predictions of the model with respect to the behavior of the export ratio (Downs 1989, Murray et al. 1989), phytoplankton biomass, and heterotrophic bacterial biomass were in remarkable agreement with field observations encompassing a broad range of environmental conditions.

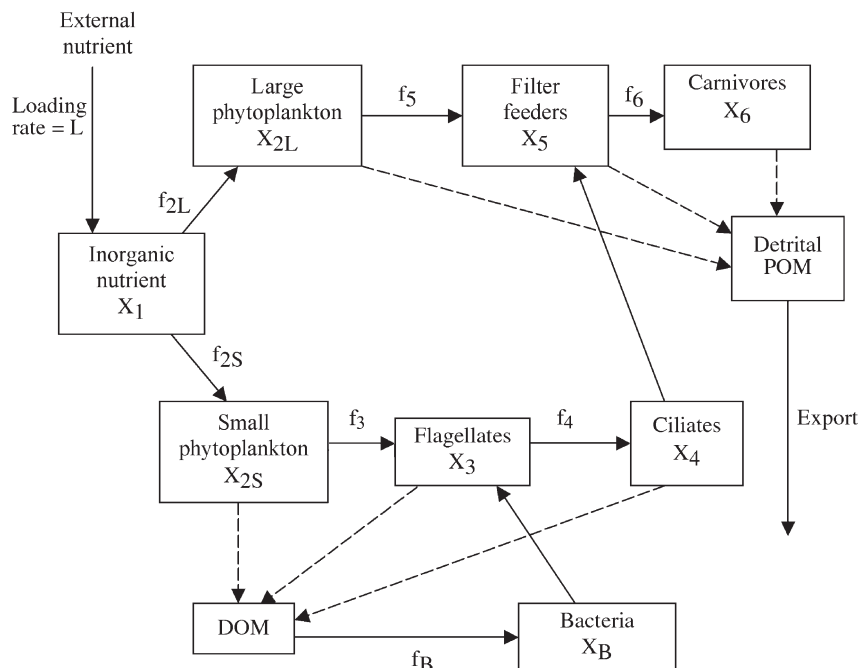


Fig. 1. Feeding and excretion relationships in a model pelagic food web in which photosynthetic production is partitioned between small and large phytoplankton cells (Laws et al. 2000). f : fluxes between boxes associated with nutrient uptake or grazing; dashed arrows: excretion; solid arrows: nutrient uptake or grazing

According to the model, photosynthetic rate and temperature are the primary determinants of community composition and system behavior.

Several authors have commented on the patterns of heterotrophic and autotrophic biomass in aquatic systems (Pomeroy & Deibel 1986, Li et al. 1992, Simon et al. 1992, Legendre & Rassoulzadegan 1995, Gasol et al. 1997, Biddanda et al. 2001, Cotner & Biddanda 2002). Empirically one observes that the ratio of heterotrophic bacterial biomass to microalgal biomass decreases as systems become more eutrophic (Li et al. 1992, Simon et al. 1992, Gasol et al. 1997, Biddanda et al. 2001, Cotner & Biddanda 2002). Biddanda et al. (2001) commented (p. 732), 'The underlying cause of this relationship is unclear.' They suggested 2 possible explanations: (1) heterotrophic bacteria are selectively grazed by bacterivores at the eutrophic end of the gradient, and (2) heterotrophic bacteria are better able to acquire nutrients at low ambient concentrations in oligotrophic systems. Pomeroy & Deibel (1986) have also noted that the ratio of heterotrophy to autotrophy is positively correlated with temperature. They argued that this pattern was due to differences in the temperature dependence of photosynthesis and respiration.

Fig. 2 shows the ratio of heterotrophic bacterial biomass to phytoplankton biomass predicted from the model of Laws et al. (2000), with temperature and photosynthetic rate as the independent variables. In accordance with the observations of Li et al. (1992), Simon et al. (1992), Gasol et al. (1997), and Biddanda et al. (2001), the ratio of heterotrophic bacterial biomass to phytoplankton biomass is highest in oligotrophic systems. The ratio is relatively insensitive to temperature in oligotrophic systems, but is strongly and positively correlated with temperature in eutrophic systems, consistent with the observations of Pomeroy & Deibel (1986). Laws et al. (2000) found that predicted and observed heterotrophic bacterial biomass were in excellent agreement in 10 marine ecosystems ranging from the equatorial Pacific to the Ross Sea and Greenland polynya.

METHODS

In order to more rigorously test the predictions of the Laws et al. (2000) model relative to the role of bacteria in aquatic ecosystems, I have examined data on bacterial biomass, phyto-

plankton production and/or biomass, and temperature from a wide variety of freshwater and marine ecosystems. The data set includes results from a total of 39 studies, 8 in freshwater and 31 in marine systems (Table 1). The data are taken primarily from results reported in the last 10 yr, although a few of the results analyzed by Laws et al. (2000) were reported as long as 15 yr ago. Although Fig. 2 treats temperature and photosynthetic rate as the independent variables in the model, the latter is less frequently reported than the concentration of chlorophyll *a* (chl *a*). Because the model predicts a one-to-one relationship between photosynthetic rate and phytoplankton carbon, I treated phytoplankton carbon and temperature as independent variables and used these to predict heterotrophic bacterial carbon (C_{HB}) from the output of the model in cases where photosynthetic rates were not reported. I excluded studies in shallow systems (depth <5 m) from the initial analysis, since the Laws et al. (2000) model envisions a strictly pelagic ecosystem. This fact accounts for the relatively small number of freshwater systems included in the data set. The depths of the freshwater systems ranged from 5.9 to 100 m. I also excluded hypereutrophic systems having chl *a* concentrations $>100 \text{ mg m}^{-3}$ from the initial analysis, since the Laws et al. (2000) model assumes nutrient limitation.

Since the model predicts phytoplankton and heterotrophic bacterial biomass in terms of carbon, it was necessary to convert heterotrophic bacterial cell counts and/or cell volume and chl *a* concentrations to carbon equivalents. In cases where only data on heterotrophic bacterial cell counts were reported by the authors, I assumed a carbon content of 12 fg cell^{-1} for open ocean bacteria and 30 fg cell^{-1} for coastal, estuarine, and limnetic bacteria (Fukuda et al. 1998). To convert chl *a* concentrations to phytoplankton carbon, I assumed a C:chl *a* ratio of 50 by weight (Fuhrman et al. 1985, Chróst et al. 1989, Cho & Azam 1990).

RESULTS

I found a high degree of correlation between C_{HB} predicted by the model and C_{HB} estimated from field data (Fig. 3). The model accounts for 84% of the variance in the log-transformed data, which span almost 2 orders of magnitude in C_{HB} . A total of 67% of the data

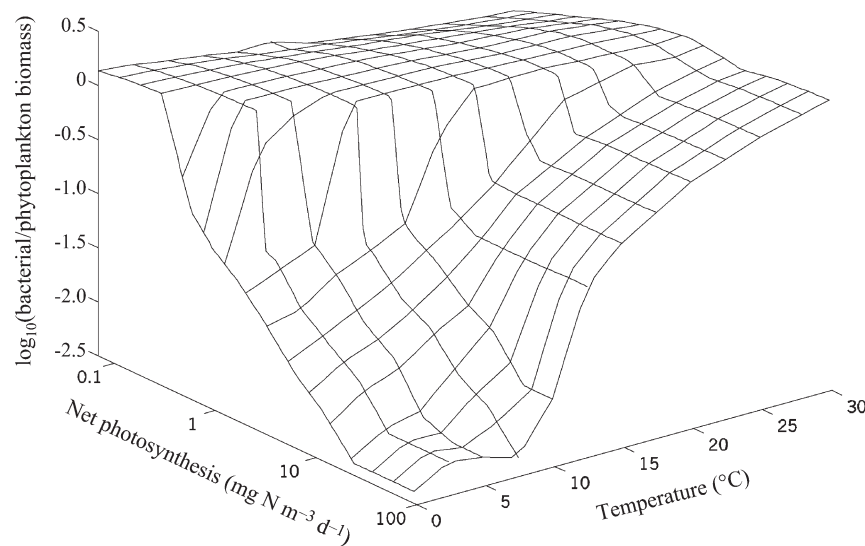


Fig. 2. Ratio of heterotrophic bacterial biomass to phytoplankton biomass as a function of photosynthetic rate and temperature for the pelagic food web model shown in Fig. 1. Adjustable parameters were chosen to produce a steady state with maximum resiliency

lie within a factor of 1.6 of the 1:1 line, i.e. heterotrophic bacterial biomass can be predicted to within a factor of ± 1.6 by the model. There was no systematic difference in the predictions of the model for marine and limnetic systems, but C_{HB} was predicted more accurately when photosynthetic rate and temperature were the independent variables ($r = 0.96$) versus phytoplankton carbon and temperature ($r = 0.78$).

Following this analysis, I examined the ability of the model to predict C_{HB} in 3 types of aquatic systems that do not, strictly speaking, conform to the assumptions of the model. In 3 hypereutrophic lakes (Table 2), C_{HB} was much less than the model predictions based on chl *a* concentrations. In the one case where both chl *a* concentrations and photosynthetic rates were reported, the discrepancy was greatly reduced when photosynthetic rate and temperature were the independent variables in the model. In shallow (mean depth 1.1 to 3.6 m) ecosystems (Fig. 4), the 3 lowest and 4 highest predicted C_{HB} values lay below and above the 1:1 line, respectively. Given the small number of data points, it is hard to say whether this pattern represents a systematic bias. There is certainly more scatter in the data, the standard deviation of the log-transformed data being twice as large in Fig. 4 compared to Fig. 3. Finally, in systems impacted by river throughput (Table 3), the predictions of the model were consistently higher than the observed C_{HB} . The discrepancy was most pronounced in the case of inner shelf waters off the mouth of the Yangtze River, PR China.

Table 1. Characteristics of aquatic systems in which heterotrophic bacterial carbon (C_{HB}) was estimated using the model of Laws et al. (2000). C_{HB} estimated using (A) temperature and photosynthetic rate or (B) temperature and phytoplankton carbon as independent variables. BATS: Bermuda Atlantic Time Series; NABE: North Atlantic Bloom Experiment

(A)	Photosynthetic rate (mg C m ⁻³ d ⁻¹)	C_{HB} (mg m ⁻³)	Predicted C_{HB} based on temperature and photo- synthetic rate (mg m ⁻³)	Source
Body of water (temperature)				
N. Atlantic, Canary Islands, Zone A (20°C)	2.5	4.6	4.8	Bode et al. (2001)
N. Atlantic, Canary Islands, Zone B (20°C)	1.7	4.4	3.1	Bode et al. (2001)
N. Atlantic, Canary Islands, Zone C (20°C)	2.7	5.4	5.3	Bode et al. (2001)
Sargasso Sea, BATS (21°C)	3.3	2.2	4.1	Carlson et al. (1998)
Ross Sea, Antarctica (0°C)	34.5	11	9.6	Carlson et al. (1998)
Lawrence Lake, MI, USA (21°C)	41	72	53.5	Coveney & Wetzel (1995)
North Atlantic, NABE (12.5°C)	31.5	20	23.1	Ducklow et al. (1993)
Equatorial Pacific, La Niña (24°C)	12.3	12	13	Ducklow et al. (1995)
Equatorial Pacific, El Niño (27°C)	8.0	10	7.3	Ducklow et al. (1995)
Arabian Sea (25°C)	17	19.6	16.7	Ducklow et al. (2000)
Strait of Georgia (17.3°C)	190	183	231	Harrison et al. (1991)
N. Pacific, Stn ALOHA (25°C)	3.1	3.9	3.1	Karl & Dobbs (1998)
Subarctic Pacific, Stn Papa (6°C)	8	14.2	22.7	Kirchman et al. (1993)
Unnamed lake, Ziegler Island, Franz Joseph Land (1.5°C)	22	14	10	Panzenböck et al. (2000)
North Sea, Transect 1, May 1992 (9°C)	12.3	38.7	23.1	Richardson et al. (1998)
North Sea, Transect 2 (9.5°C)	9.0	39.7	34.9	Richardson et al. (1998)
North Sea, Transect 3 (10°C)	9.1	59.8	33.4	Richardson et al. (1998)
North Sea, Transect 1, August 1991 (12°C)	13.8	26.9	28.9	Richardson et al. (1998)
East China Sea, mid-shelf (27°C)	6.5	3.5	7.9	Shiah et al. (2001)
East China Sea, outer-shelf (29°C)	3.2	3.2	3.3	Shiah et al. (2001)
Lake Constance, Germany (13.4°C)	72	95	62.9	Simon et al. (1998)
Peru upwelling system (16.8°C)	179	126	163	Sorokin & Kogelschatz (1979)
Greenland polynya (0°C)	7.2	7.2	7.8	Yager (1996)
(B)	Phytoplankton carbon (mg C m ⁻³)	C_{HB} (mg m ⁻³)	Predicted C_{HB} based on temperature and phyto- plankton carbon (mg m ⁻³)	Source
Body of water (temperature)				
Menai Bridge, North Wales, UK (12°C)	250	60	26.2	Blight et al. (1995)
Lake Plußsee, Germany (7°C)	1975	25.3	24.8	Chróst et al. (1989)
Eagle Mountain Lake, TX, USA (18.5°C)	875	120	390	Chrzanowski & Grover (2001)
Joe Pool Lake, TX, USA (18.5°C)	250	105	109	Chrzanowski & Grover (2001)
Ria de Aveiro, Portugal, Stns N1 and I2 (19.6°C)	425	123	226	Cunha et al. (2000)
Delaware Estuary, upper region (15°C)	560	90	132	Hoch & Kirchman (1993)
Delaware Estuary, middle region (15°C)	750	99	177	Hoch & Kirchman (1993)
Delaware Estuary, lower region (15°C)	540	111	128	Hoch & Kirchman (1993)
Maliakos Gulf, Greece, Inner Gulf (19°C)	62.5	30	31	Kormas et al. (1998)
Maliakos Gulf, Greece, Middle Gulf (19°C)	50	11.3	28.7	Kormas et al. (1998)
Maliakos Gulf, Greece, Outer Gulf (19°C)	25	9	22	Kormas et al. (1998)
Crooked Lake, Antarctica (1.2°C)	15	6.4	13.8	Laybourn-Parry et al. (1992)
English Channel (12°C)	100	20	19.3	Rodríguez et al. (2000)
St. Lawrence estuary (4.7°C)	160	44	12	Sime-Ngando et al. (1995)
Piburger See, Austria (12.3°C)	150	48	21	Sommaruga & Psenner (1995)
Ría de Vigo, Spain (15°C)	175	100	41.6	Zdanowski & Figueiras (1997)

DISCUSSION

At least some of the variance of the relationship between observed and predicted C_{HB} can be attributed to uncertainty in the factors used to convert chl *a* and cell counts to carbon. Phytoplankton C:chl *a* ratios depend on a variety of factors, including temperature, irradiance, species composition, and nutritional status

(Shuter 1979, Chan 1980). C:chl *a* ratios reported from field work have ranged between roughly 20 and 125 by weight (Sakshaug & Holm-Hansen 1986, DiTullio & Smith 1996, Smith et al. 1996, Karl & Dobbs 1998). Assuming a C:chl *a* ratio of 50 by weight is a reasonable approximation but could produce errors of as much as a factor of ~2. This fact probably accounts for the poorer correlation between the model and field

Table 2. Heterotrophic bacterial biomass in hypereutrophic lakes estimated using the Laws et al. (2000) model

Lake (temperature)	Chl <i>a</i> (mg m ⁻³)	Photosynthetic rate (mg C m ⁻³ d ⁻¹)	C _{HB} (mg m ⁻³)	Predicted C _{HB} based on chl <i>a</i> (mg m ⁻³)	Predicted C _{HB} based on photosynthetic rate (mg m ⁻³)	Source
Lake Rodó, Uruguay (18.9°C)	223		210	4956		Sommaruga (1995)
Lake Kauhak, Molokai (24.5°C)	105		105	5396		Donachie et al. (1999)
Lake Nesjøvatn, Norway (16°C)	232	330	66	3204	376	Vadstein et al. (1988)

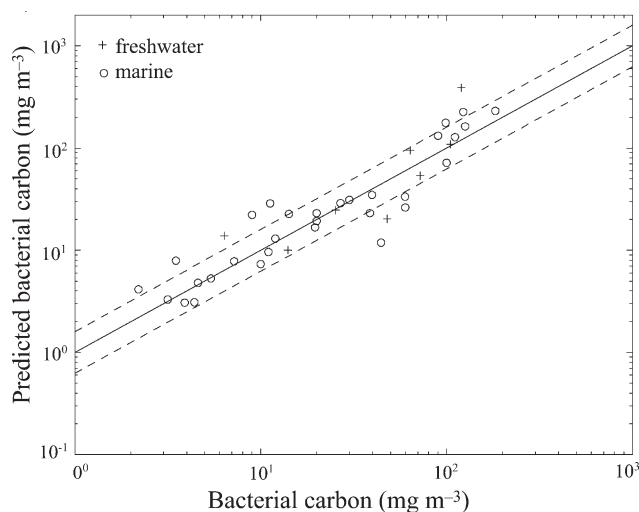


Fig. 3. Relationship between measured and predicted heterotrophic bacterial carbon (C_{HB}) from the systems in Table 1. The straight line is the 1:1 line. Dashed lines are ± 1 SD from the 1:1 line

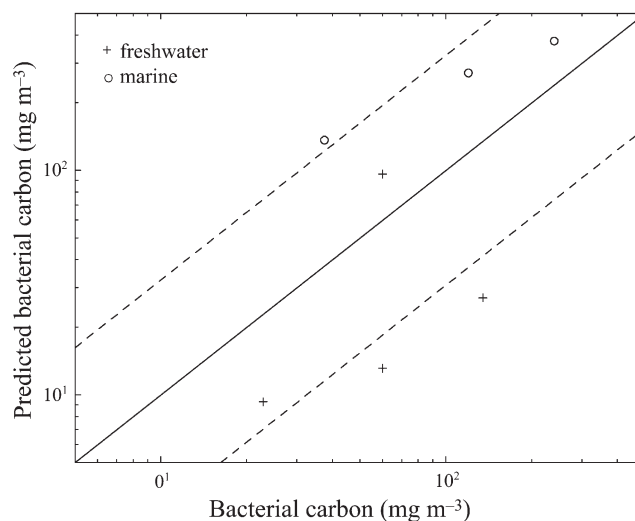


Fig. 4. Relationship between measured and predicted C_{HB} for shallow systems (freshwater: Butler et al. 2000, Kisand & Tammert 2000, Revilla et al. 2000, Vörös et al. 1996; marine: Reiter et al. 1997). The straight line is the 1:1 line. Dashed lines are ± 1 SD from the 1:1 line

results when chl *a* and temperature are the independent variables.

Fukuda et al. (1998) have pointed out that the use of 20 fg C cell⁻¹ (Pedrós-Alió & Brock 1982, Fuhrman et al. 1985, Hessen 1985) as a conversion factor between cell counts and C_{HB} can lead to an overestimation of C_{HB} by as much as 330% in open oceans and an underestimation by as much as 40% in coastal environments. My use of different conversion factors for open ocean

and coastal/limnetic systems has probably reduced the level of noise caused by uncertainty in this factor, but it seems fair to say that the abscissa in Fig. 3 is associated with a nontrivial amount of noise.

Estimates of photosynthetic rates are also subject to error, both from measurement error and natural variability. Most reported estimates of photosynthetic rates are based on the ¹⁴C method originally developed by Steemann Nielsen (1952). Still, 50 yr later, there is

Table 3. Heterotrophic bacterial biomass in shallow/riverine eutrophic systems estimated using the Laws et al. (2000) model

System (temperature)	Chl <i>a</i> (mg m ⁻³)	C _{HB} (mg m ⁻³)	Predicted C _{HB} based on chl <i>a</i> (mg m ⁻³)	Source
Ria de Aveiro, Stn I4 (22.7°C)	17	157	671	Cunha et al. (2000)
Ria de Aveiro, Stn I6 (22.7°C)	19	189	748	Cunha et al. (2000)
Ria de Aveiro, Stn I8 (25.2°C)	26.5	256	1379	Cunha et al. (2000)
Ria de Aveiro, Stn Rio Boco (25.7°C)	27.6	255	1502	Cunha et al. (2000)
Yangtze River estuary, inner shelf (21°C)	3.93	7.1	123	Shiah et al. (2001)

uncertainty over exactly what the ^{14}C method measures (Marra 2002). Even if photosynthetic measurements could be made with no analytical error, rates vary naturally over space and time, and any set of discrete measurements will therefore be subject to error when integrated over space and time. Finally, temperature also varies with space and time, and in temperate and polar ecosystems, the range of temperature over the course of a year can easily be 20°C (Sommaruga & Psenner 1995).

The model itself (Fig. 1) is a considerable simplification of the interactions in a pelagic food web, and the assumption of steady state is clearly an approximation that in some cases may be reasonable only when system behavior is integrated over appropriate time and space scales.

Considering the various sources of error in the data and model, the level of noise evident in Fig. 3 seems not unreasonable. The assumption of maximum resiliency leads to predicted system behavior that explains much of the variability of C_{HB} across a wide range of pelagic aquatic ecosystems. The limitations of the model are apparent in Tables 2 & 3 and Fig. 4. In the 3 hypereutrophic lakes the concentrations of heterotrophic bacterial carbon estimated using the model with temperature and chl *a* as independent variables are 20 to 50 times higher than the observed C_{HB} . Some of this discrepancy may be attributed to the fact that in these systems the concentration of phytoplankton carbon estimated using an assumed C:chl *a* ratio of 50 is undoubtedly too high. However, it is unlikely that the true C:chl *a* ratio is much less than 20. Reducing the assumed C:chl *a* ratio from 50 to 20 reduces the predicted C_{HB} by a roughly proportionate amount, i.e. much less than the factor of 20 to 50 discrepancy. For Lake Nesjøvatn, central Norway, photosynthetic rates were reported along with chl *a* concentrations. When C_{HB} is predicted using temperature and photosynthetic rate as the independent variables, the discrepancy between observed and predicted C_{HB} is reduced by almost an order of magnitude. In this case at least, the predictions of the model appear much more robust when photosynthetic rate is substituted for phytoplankton biomass as the second independent variable. The implication is that C_{HB} is determined primarily by the activity and not the biomass of the phytoplankton. However, there is still a 5.6-fold discrepancy between observed and predicted C_{HB} , which is about 3 times the standard deviation of the data in Fig. 3.

The average spectral extinction coefficient of chl *a* and associated pigments is about $0.016 \text{ m}^2 \text{ mg}^{-1} \text{ chl } a$ (Bannister 1974). At chl *a* concentrations of 100 to 200 mg m^{-3} (Table 2), the 1% light level occurs at depths of ~1.5 to 3.0 m. In such turbid systems photosynthetic rates are limited primarily by light rather

than nutrients. The implication of the results in Fig. 3 and Table 2 is that the relationship between phytoplankton activity and C_{HB} is fundamentally different in nutrient- and light-limited systems. This difference may reflect the tendency of photosynthate to be released as dissolved organic carbon in the former and to accumulate as particulate organic carbon in the latter (Carlson & Ducklow 1996, Carlson et al. 1998, Biddanda et al. 2001). The model (Fig. 1) accounts for this behavior by routing more photosynthate through the microbial loop, but this is apparently insufficient to explain the difference between the behavior of nutrient- and light-limited food webs.

Except under hypereutrophic conditions, the metabolism of shallow aquatic ecosystems is dominated by benthic processes (Scheffer 2001). In such systems, the interaction between the benthos and water column can have a major impact on the composition of the planktonic community (Scheffer 1999). Benthic filter feeders, in particular, can structure the plankton through top-down control, and benthic larvae may contribute substantially to the biomass of the planktonic community. The release of nutrients associated with benthic respiratory activity can be a major source of nutrient loading to the water column. While it is fair to say that the benthic community competes with the pelagic community for resources (Scheffer et al. 2000) and reduces its overall biomass, it is not obvious from the foregoing considerations that the existence of the benthos would systematically alter the relative numbers of phytoplankton and bacteria in the water column. Based on this logic, the larger amount of scatter in Fig. 4 compared to Fig. 3 is not surprising. Speculation about bias in the predictions is compromised by the small number of data points.

The consistent bias apparent in the case of systems impacted by river discharge (Table 3) probably reflects an advective throughput of microbial biomass that is not allowed for in the model (Fig. 1). In the model, all living biomass is produced *in situ*. In addition to being impacted by riverine throughput, the Ria de Aveiro stations in Table 3 are shallow, with mean depths ranging from 0.9 to 2.5 m (Cunha et al. 2000). However, as noted above, shallowness per se does not appear to create a systematic bias in the predictions. The mean salinity of the inner shelf stations off the mouth of the Yangtze River was 28 psu (Shiah et al. 2001), which implies that ~20% of the water was river throughput. This undoubtedly accounts for the anomalous autotrophic/heterotrophic microbial biomass ratio at the inner-shelf stations compared to the mid- and outer-shelf stations (Table 1), where mean salinities were 32.6 and 34.2 psu, respectively (Shiah et al. 2001).

Simon et al. (1992) have argued that limnetic systems support more bacterial biomass relative to phytoplank-

ton biomass than marine systems. The basis for this statement is the fact that in the 6 limnetic and 6 marine systems analyzed by Simon et al. (1992), limnetic systems tended to have a higher concentration of C_{HB} at comparable concentrations of chl *a*. This is not, however, the case in the more recent and extensive studies summarized here (Fig. 5). When chl *a* concentrations as abscissa are plotted against C_{HB} as ordinate and a model II geometric mean regression line is drawn through the data (Fig. 5), only 3 of the 8 freshwater data points lie above the regression line. The scatter in the data in Fig. 5 is much greater ($r = 0.79$) than in Fig. 3 ($r = 0.91$), and several of the largest deviations can easily be explained on the basis of temperature effects. The Ross Sea, Antarctica (Asper & Smith 1999) and Lake Plußsee, Germany (Chróst et al. 1989) studies were carried out at temperatures of 0 and 9°C, respectively. The concentration of chl *a* was relatively high in both cases, but at these low temperatures and moderate to high production rates the ratio of C_{HB} to phytoplankton carbon is much less than at temperatures of 20 to 25°C (Fig. 2). The largest deviations above the regression line were associated with data collected from the Peru upwelling system (Wilkerson et al. 1987) and Strait of Georgia (Harrison et al. 1991). In these 2 cases, temperature (16.8 and 17.3°C, respectively) was not responsible for the large positive deviations. Both systems were studied during upwelling/bloom conditions when the phytoplankton were turning over rapidly. Merely relating C_{HB} to phytoplankton biomass does not allow for differences in turnover rates, and in these 2 cases the differences in turnover rates were evidently great enough to cause large deviations from the regression line. The Laws et al. (2000) model does a much better job of predicting C_{HB} in these 4 cases (Table 1): in the first two (Ross Sea and Lake Plußsee) because the model explicitly accounts for temperature effects, and in the second two because information was available on photosynthetic rates, which are the product of turnover rate and biomass. Hence, in the case of the Peru upwelling and Strait of Georgia data, it was possible to implement the model in a way that accounted for turnover rate effects.

Finally, it is noteworthy that the slope of the geometric mean regression line in Fig. 4 is 0.78. This result implies that, other factors being equal, the ratio of C_{HB} to chl *a* decreases with increasing chl *a* concentration. This conclusion is consistent with earlier studies (Cole et al. 1988, Simon et al. 1992, del Giorgio et al. 1997, Biddanda et al. 2001).

The implication of this analysis is that the underlying cause of the relationships between heterotrophic bacterial biomass and microalgal biomass observed by previous investigators (Pomeroy & Deibel 1986, Cole et al. 1988, Li et al. 1992, Simon et al. 1992, Legendre &

Rassoulzadegan 1995, del Giorgio et al. 1997, Gasol et al. 1997, Biddanda et al. 2001) may be the tendency of natural pelagic ecosystems to evolve toward a condition of maximum resiliency. This tendency is believed to be a characteristic of the mature stages of ecological succession (Odum 1969). Because plankton have short generation times, it may also be a characteristic of systems whose behavior is largely controlled by the dynamics of the plankton community. As noted by Hutchinson (1967, p. 376), 'The annual cycle [of the plankton] is thus, in terms of generation time, the equivalent of perhaps up to ten thousand years in the successional history of organisms which are replaced as some forest trees every fifty or one hundred years.' However, even if maximum resiliency proves to be a characteristic of many natural planktonic ecosystems, it is certainly possible that other ecological laws influence the behavior of these systems. The first law of thermodynamics is a cornerstone of thermodynamic theory, but not all of thermodynamics can be explained on the basis of conservation of energy.

Systems with unstable steady states are not likely to persist in nature. Furthermore, systems that require a long time to return to their equilibrium configurations following a perturbation are unlikely to be found near their equilibrium point in other than very stable environments. In the simple linear food chain modeled by Cropp & Gabric (2002), the conditions associated with various selection pressures are easily identified, and the selection pressures suggested by Lotka (1922) and Odum (1983) lead to essentially the same system behavior as does maximum resiliency. Fath et al. (2001) have likewise noted an equivalency of system behavior

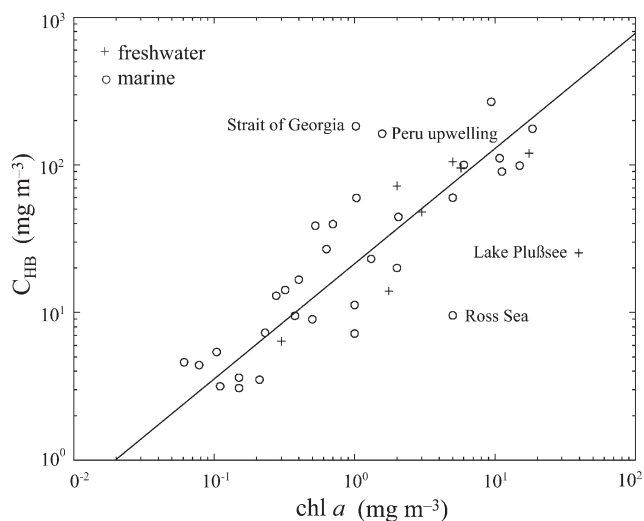


Fig. 5. Chl *a* versus C_{HB} from systems in Table 1 in which information on both was available. The straight line is a geometric mean model II regression line

governed by seemingly disparate ecological goal functions. In more complex systems, application of thermodynamic analogues as selection pressures to determine ecosystem behavior has met with mixed success. Månsson & McGlade (1993), for example, point out that the flows of carbon in 6 marine ecosystems studied by Baird et al. (1991), 'were contrary to what Odum has suggested, in that the aggregate amount of cycling was an indication not of maturity but rather of the type of dynamics and levels of stress.' On the other hand, Cropp & Gabric (2002) observe that in some cases thermodynamic approaches have met with considerable success in estimating parameters to describe real ecosystems (Jørgensen & Straskraba 2000).

Is it possible that very similar predictions concerning the partitioning of microbial biomass could emerge from the model in Fig. 1 if a criterion other than maximum resiliency were applied? To explore this hypothesis, I simply tried to average the ratio of heterotrophic bacterial biomass to phytoplankton biomass ($C_{HB}:C_P$) over all stable steady states at various temperatures and allochthonous nutrient loading rates and compared the average $C_{HB}:C_P$ ratio to the ratio associated with maximum resiliency. The result of this exercise showed that at high temperatures (e.g. 25°C) the ratio associated with maximum resiliency was little different from the ratio averaged over all stable steady states. This conclusion was especially true under oligotrophic conditions. Under eutrophic conditions and at high temperatures, the discrepancy was at most 10 to 20%. The discrepancy became much greater at low temperatures (e.g. 5°C). The model (Fig. 2) predicts a range of roughly 2 orders of magnitude in the $C_{HB}:C_P$ ratio at 5°C, with the lowest ratios under eutrophic conditions and the highest under oligotrophic conditions. If the ratio is simply averaged over all stable steady states at a given allochthonous nutrient loading rate, the average ratio ranges between roughly 0.6 and 0.7. Since the predictions of the model are in good agreement with field data at low temperatures over a wide range of C_P (e.g. Crooked Lake, Antarctica, and Lake Plußsee, Table 1), I conclude that applying the criterion of maximum resiliency considerably improves the predictive ability of the model as opposed to simply requiring that the steady state be stable.

I agree with Patten (1993) that the important thrust of Odum's (1983) work was his search for laws that govern the organization of ecosystems. Maximum resiliency may well be one of those laws. Indeed, Odum (1969) concluded more than 30 yr ago that ecological succession leads to mature stages characterized by good resistance to external perturbations. As noted by Jørgensen & Straskraba (2000), ecological systems are flexible. This property will need to be taken into consideration if models are to reliably predict the behavior

of ecosystems in response to changing forcing functions. Predicting the response of both aquatic and terrestrial ecosystems to environmental change (Mackenzie 1998) will ultimately require awareness and recognition of the laws that govern the response of ecosystems to their environment. Maximum resiliency may be a useful construct for pelagic food webs.

Acknowledgements. This work was supported by National Science Foundation grant OCE-97-25966. I am indebted to 3 anonymous reviewers for their constructive comments on this paper. This is SOEST contribution number 6149.

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Editorial responsibility: Fereidoun Rassoulzadegan, Villefranche-sur-Mer, France

*Submitted: June 5, 2002; Accepted: November 4, 2002
Proofs received from author(s): April 24, 2003*