

## NOTES

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### Allochthonous organic carbon decreases pelagic energy mobilization in lakes

**Abstract**—Over the past decade, it has been shown that unproductive lakes worldwide are net heterotrophic because bacterial respiration of allochthonous organic carbon (AOC) makes community respiration exceed primary production. Net heterotrophy means that aquatic systems are net sources of CO<sub>2</sub> to the atmosphere but also that bacterial utilization of AOC increases bacterioplankton production (BP) and bacterial uptake of limiting inorganic nutrients at the expense of phytoplankton production (PP). We studied 15 unproductive lakes in northern Sweden with dissolved organic carbon concentrations between 3 and 22 mg L<sup>-1</sup>. We found a highly significant negative relationship between the degree of heterotrophy and total pelagic energy mobilization (PP + BP based on AOC) per unit of limiting nutrient. We suggest that this is because the high cell phosphorous (P) requirement of bacteria makes energy mobilization per P unit considerably lower in bacterioplankton than in phytoplankton. We also suggest that the productivity of the entire pelagic ecosystem is determined by the availability of inorganic nutrients and AOC and by whether nutrients are allocated to BP or PP.

Pelagic production depends on biological energy mobilization from external energy sources. Photosynthesis by phytoplankton is here an important process. In addition to autotrophic production, there is also mobilization of energy by bacteria utilizing allochthonous organic carbon (AOC) as an energy source (Jones 1992). Bacterial utilization of AOC must be separated from the bacterial secondary production in the microbial loop (Azam et al. 1983) and should be regarded as mobilization of energy from an external source by analogy with photosynthesis (Jones 1992; Jansson et al. 2000). Consequently, the energy mobilization in pelagic food webs is based on both light energy and imported chemically bound energy in the form of AOC. The importance of heterotrophic energy mobilization relative to autotrophic energy mobilization increases with increasing input of AOC, and bacterial energy mobilization is often entirely dominant in brownwater lakes (Hessen 1998; Jansson et al. 2000) and can exceed phytoplankton primary production (PP) even in ultraoligotrophic clearwater lakes (Karlsson et al. 2002). Therefore, energy consumption in pelagic food chains in a large variety of unproductive systems might depend on energy mobilized by bacteria from C sources other than PP.

It can be hypothesized that pelagic systems dominated by bacteria should be less efficient in mobilization of energy and production of biomass than autotrophic systems. Bacteria can generally out compete phytoplankton for low concentrations of inorganic P (Vadstein 2000). Bacteria also have a very high P content (median, lower, and upper quartiles, respectively, from the review by Vadstein 2000: 32, 15,

55 μg P [mg C]<sup>-1</sup>) compared to phytoplankton (3.8, 2.5, 5.2 μg P [mg C]<sup>-1</sup>) and typically contain about 10 times (by weight) more P per C unit than phytoplankton (Vadstein 2000; Wetzel 2001). These differences are critical when P is a limiting inorganic nutrient for production of bacteria and phytoplankton, as it often is in lakes (Schindler 1977; Vadstein 2000), and imply that bacteria mobilize considerably less biomass C per P unit than phytoplankton. However, it is an open question whether, and to what extent, pelagic energy mobilization is lower with a heterotrophic than with an autotrophic base for the total production. Therefore, we tested the hypothesis that pelagic energy mobilization per unit of limiting nutrient is lower when dominated by heterotrophic bacterioplankton than by autotrophic phytoplankton.

We used data from 15 unproductive small (0.02–0.27 km<sup>2</sup>) lakes in northern Sweden, studied with identical methods. The lakes have low concentrations of N and P and concentrations of dissolved organic carbon (DOC) between 3 and 22 mg L<sup>-1</sup> (Table 1). Thus, the lakes represent a gradient from ultraoligotrophic clearwater lakes to highly stained brownwater lakes (i.e., the lake types that dominate the world population of unproductive lakes). Lakes 1–4 in Table 1 are located close to Örträsket (64°10'N, 18°55'E) in the temperate region of northern Sweden and lakes 5–15 are located close to Abisko (68°21'N, 18°49'E) in the subarctic region of northern Sweden. Sampling and analytical procedures have been reported in detail for lakes 1–4 by Jansson et al. (2001) and for lakes 5–15 by Karlsson et al. (2002). All lakes were sampled during the period June–September at intervals of every second to every fourth week.

Photosynthetically active radiation (PAR) was measured at every meter of the water column using a Windaus Luxmeter (Windaus Labortechnik, Clausthal-Zellerfeld) in lakes 1–4 and an IL-1400 Radiometer (International Light) in lakes 5–15. Attenuation coefficients and daily irradiation data from the Umeå Centre for Marine Sciences (lakes 1–4) and Abisko Scientific Research Station (lakes 5–15) were used to calculate daily effective light climate (mean light intensity in the mixed layer) for PAR in the lakes according to Blomqvist et al. (1981). Water temperature was measured at every meter of the water column with a Ruttner sampler thermometer (lakes 1–4) and a WTW multiline P4 instrument (lakes 5–15). Water for analyses of water chemistry, bacterial biomass, bacterioplankton production (BP), and phytoplankton species composition and biomass was gathered from composite samples collected with a tube sampler (1 or 2 m long, diameter 3.4 cm).

Each layer of the investigated water columns (epilimnion in stratified lakes and the whole water column in nonstrati-

Table 1. Physical, chemical, and biological characteristics of 15 lakes in northern Sweden: Water temperature (T), effective light climate for photosynthetic active radiation (PAR), total nitrogen (TN), total phosphorus (TP), bacterioplankton biomass (BB), phytoplankton biomass (PB), net primary production (PP), net bacterioplankton production (BP), pelagic energy mobilization (PEM), share of PEM corresponding to bacterioplankton energy mobilization from allochthonous carbon (PEM<sub>het</sub>), and pelagic energy mobilization in relation to total P concentration (PEM/P). Summer mean values  $\pm$  standard deviation.

Lake	T (°C)	PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	DOC ( $\text{mg L}^{-1}$ )	TN ( $\mu\text{g L}^{-1}$ )	TP ( $\mu\text{g L}^{-1}$ )	BB ( $\mu\text{g C L}^{-1}$ )	PB ( $\mu\text{g C L}^{-1}$ )	BP ( $\mu\text{g C L}^{-1} \text{d}^{-1}$ )	PP ( $\mu\text{g C L}^{-1} \text{d}^{-1}$ )	PEM ( $\mu\text{g C L}^{-1} \text{d}^{-1}$ )	PEM <sub>het</sub> (%)	PEM/ P ( $\text{C P}^{-1} \text{d}^{-1}$ )
1	13.7 $\pm$ 2.3	39 $\pm$ 36	22.3 $\pm$ 4.7	557 $\pm$ 121	26.8 $\pm$ 4.6	20.9 $\pm$ 13.9	6.1 $\pm$ 3.5	6.4 $\pm$ 4.1	1.8 $\pm$ 3.0	8.1	77	0.3
2	14.3 $\pm$ 2.3	29 $\pm$ 15	15.6 $\pm$ 1.8	481 $\pm$ 24	23.0 $\pm$ 3.9	18.4 $\pm$ 7.1	8.7 $\pm$ 6.7	5.0 $\pm$ 2.3	2.8 $\pm$ 2.7	7.5	62	0.3
3	14.0 $\pm$ 2.3	48 $\pm$ 27	12.6 $\pm$ 1.3	421 $\pm$ 39	21.8 $\pm$ 3.1	24.5 $\pm$ 10.1	93.9 $\pm$ 76.2	8.6 $\pm$ 3.5	6.4 $\pm$ 5.7	14.4	55	0.7
4	11.5 $\pm$ 2.1	62 $\pm$ 45	15.8 $\pm$ 2.9	441 $\pm$ 51	20.8 $\pm$ 2.7	20.3 $\pm$ 8.0	9.5 $\pm$ 7.4	5.0 $\pm$ 2.2	1.7 $\pm$ 1.4	6.5	74	0.3
5	12.7 $\pm$ 3.3	86 $\pm$ 48	9.0 $\pm$ 1.0	371 $\pm$ 67	11.3 $\pm$ 1.1	56.2 $\pm$ 4.7	44.5 $\pm$ 19.3	6.6 $\pm$ 1.8	4.7 $\pm$ 2.1	10.9	56	1.0
6	10.8 $\pm$ 2.1	73 $\pm$ 19	3.2 $\pm$ 0.5	113 $\pm$ 35	7.9 $\pm$ 1.1	28.2 $\pm$ 2.1	23.1 $\pm$ 5.5	1.7 $\pm$ 0.8	1.0 $\pm$ 0.2	2.6	63	0.3
7	10.9 $\pm$ 2.2	53 $\pm$ 24	3.6 $\pm$ 0.6	207 $\pm$ 136	7.9 $\pm$ 4.3	19.3 $\pm$ 3.5	16.0 $\pm$ 4.0	2.1 $\pm$ 1.1	0.9 $\pm$ 0.7	2.9	70	0.4
8	14.0 $\pm$ 3.5	59 $\pm$ 27	8.9 $\pm$ 1.0	420 $\pm$ 85	7.7 $\pm$ 3.7	32.3 $\pm$ 6.3	20.2 $\pm$ 9.1	2.7 $\pm$ 0.9	7.7 $\pm$ 2.5	9.6	21	1.3
9	8.0 $\pm$ 1.5	58 $\pm$ 5	3.5 $\pm$ 0.5	187 $\pm$ 17	6.8 $\pm$ 2.4	25.4 $\pm$ 3.6	25.5 $\pm$ 14.0	1.6 $\pm$ 0.5	1.2 $\pm$ 0.4	2.7	56	0.4
10	11.3 $\pm$ 1.5	30 $\pm$ 10	6.2 $\pm$ 0.8	209 $\pm$ 135	6.3 $\pm$ 1.5	27.5 $\pm$ 3.6	8.7 $\pm$ 0.9	2.1 $\pm$ 1.1	0.7 $\pm$ 0.3	2.7	75	0.4
11	7.9 $\pm$ 2.0	74 $\pm$ 23	3.3 $\pm$ 0.5	248 $\pm$ 103	5.9 $\pm$ 0.8	24.1 $\pm$ 3.4	17.2 $\pm$ 4.3	1.1 $\pm$ 0.5	1.3 $\pm$ 0.4	2.3	43	0.4
12	10.8 $\pm$ 3.9	147 $\pm$ 121	4.7 $\pm$ 0.7	305 $\pm$ 213	5.8 $\pm$ 1.5	16.6 $\pm$ 2.4	57.3 $\pm$ 5.3	2.5 $\pm$ 1.9	5.8 $\pm$ 2.2	7.8	25	1.4
13	8.0 $\pm$ 1.1	74 $\pm$ 28	2.7 $\pm$ 0.4	142 $\pm$ 34	5.5 $\pm$ 1.0	30.3 $\pm$ 3.9	21.5 $\pm$ 8.2	2.0 $\pm$ 0.6	1.2 $\pm$ 0.5	3.1	61	0.6
14	9.3 $\pm$ 3.9	131 $\pm$ 69	5.0 $\pm$ 0.7	244 $\pm$ 179	4.8 $\pm$ 1.9	22.5 $\pm$ 2.5	15.4 $\pm$ 2.5	2.0 $\pm$ 0.8	2.6 $\pm$ 1.7	4.3	40	0.9
15	13.3 $\pm$ 1.5	92 $\pm$ 46	6.4 $\pm$ 0.8	250 $\pm$ 94	3.4 $\pm$ 1.5	22.5 $\pm$ 1.9	26.5 $\pm$ 13.1	1.7 $\pm$ 0.6	7.0 $\pm$ 3.5	8.1	13	2.4

fied lakes) was sampled according to its relative volume of the water column. N and P were analyzed by standard methods at the Department of Limnology, Uppsala University (see Karlsson et al. 2002). Net BP in all lakes was determined by the leucine incorporation method (Smith and Azam 1992) according to a slightly modified procedure described by Karlsson et al. (2002). Samples for bacterial biomass were fixed with formaldehyde. Bacteria were then counted and measured with acridine orange staining and epifluorescence microscopy (Bell et al. 1983). PP in all lakes was measured during midday (4 h) incubations at different depths throughout the photic zone using the  $^{14}\text{C}$  method (Schindler et al. 1972) and is reported as net production of organic material per day as described by Jansson et al. (2001) for lakes 1–4 and Karlsson et al. (2002) for lakes 5–15. For both types of lakes, the calculated production for the 4-h incubation period was extrapolated to daily values using the ratio of incident PAR irradiation during the incubation in relation to whole-day irradiation of PAR. Calculated daily values in clearwater lakes were checked by comparison with values obtained by 24-h incubations (sum of six consecutive 4-h incubations) as described by Karlsson et al. (2002).

Species composition and biomass of phytoplankton preserved with Lugol's iodine were determined in all lakes using an inverted phase-contrast microscope after overnight sedimentation of the plankton in 10 ml of water. Biovolumes were obtained with geometrical formulas and transformed to biomass by assuming a density of  $1 \text{ g cm}^{-3}$ . Transformation to C equivalents was made according to Blomqvist et al. (1995). In lakes with a stable thermocline (lakes 1–4), we used data from composite samples representing the epilimnion only. The subarctic lakes (lakes 5–15) were never stably stratified, and for these lakes, we used data from composite samples representing the entire volume of water. All stratified lakes had shallow epilimnia that equaled the trophogenic layer. All nonstratified lakes had trophogenic layers that reached from the surface to the maximum depth. These characteristics are important when we compare BP with PP. By using data from the mixed layer in all lakes (i.e., from the epilimnion in the stratified temperate lakes and from the entire volume of water in the subarctic lakes), we compare water columns where both PP and BP takes place simultaneously.

We used summer mean values for the comparison of lakes. The relationship between parameters was analyzed using linear regression (SPSS 10.0 for Windows). When necessary for the regression analysis, data were log transformed to obtain normality.

BP in our study lakes depended on DOC generated by phytoplankton and on AOC (Jansson et al. 2001; Karlsson et al. 2002). The fraction of PP available to bacteria ( $\text{PP}_b$ ) was set equal to the sum of phytoplankton exudate production (assumed to be 30%; Baines and Pace 1991; Arvola et al. 1996) plus the DOC release from zooplankton grazing on phytoplankton (assumed to be 10% of particulate PP; Lamport 1978). Thus,  $\text{PP}_b$  can be expressed as Eq. 1.

$$\text{PP}_b = 0.3 \times \text{PP} + 0.1 \times (\text{PP} - 0.3 \times \text{PP}) \quad (1)$$

We assumed that bacterioplankton had a growth efficiency (BGE) of 26%, which is the mean value for freshwaters re-

ported by del Giorgio and Cole (1998) and close to what has been reported for lake water in northern Sweden (Wikner et al. 1999). With these assumptions, we calculated the extent to which the observed BP was supported by PP, and assumed that the residual BP was based on AOC ( $\text{BP}_{\text{AOC}}$ , Eq. 2).

$$\text{BP}_{\text{AOC}} = \text{BP} - \text{PP}_b \times \text{BGE} \quad (2)$$

By adding net PP (autotrophic energy mobilization) and net BP based on AOC (heterotrophic energy mobilization), we obtained a measure of the total pelagic energy mobilization ( $\text{PEM} = \text{PP} + \text{BP}_{\text{AOC}}$ ). The bacterioplankton contribution to PEM was denoted as  $\text{PEM}_{\text{het}}$  (Eq. 3).

$$\text{PEM}_{\text{het}} = \text{BP}_{\text{AOC}}/\text{PEM} \quad (3)$$

The calculation of PEM and  $\text{PEM}_{\text{het}}$  was based on assumptions concerning BGE, bacterial utilization of PP via exudates, and recirculation of phytoplankton carbon via zooplankton excretion. To estimate the uncertainties introduced by these assumptions, we used the upper and lower quartiles of BGE (37 and 20%, respectively) from the review of del Giorgio and Cole (1998) and the upper and lower limits of phytoplankton exudate production (40 and 20%, respectively) reported by Baines and Pace (1991).

Because BP and PP rates are determined by the availability of limiting inorganic nutrients, we expressed PEM in relation to concentrations of total P and used  $\text{PEM}/\text{P}$  as a measure of pelagic nutrient use efficiency. Nutrient use efficiency has been used to denote the amount of production relative to the amount of nutrients in plant tissues (Vitousek 1982), and nutrient use efficiency in lakes has been discussed in lakes in relation to availability of light and P (Sterner et al. 1997). By relating PEM to P, we presume that the production of biomass of both bacteria and phytoplankton was controlled by P. Experimental results from the lakes used in this study or nearby lakes have demonstrated that bacteria generally were P-limited and phytoplankton generally N-limited but the common situation was very close to colimitation by N and P for both bacterioplankton and phytoplankton (Holmgren 1983; Jansson et al. 1996, 2001; Karlsson et al. 2001). Even if BP and PP in some lakes were determined by both P and N, or slightly more by P, or slightly more by N, we do not consider this critical. Taking into account the relatively large gradient in total P concentrations ( $3\text{--}27 \mu\text{g L}^{-1}$ , Table 1) and the positive correlation between total P and total N ( $\text{TN} = -53.37 + 377.37 \log \text{TP}$ ,  $r^2 = 0.63$ ,  $n = 15$ ,  $p < 0.001$ ), we consider P concentration to be a good descriptor of the variation in inorganic nutrient availability between the lakes in this study.

The biomass of bacterioplankton and phytoplankton varied considerably between lakes (Table 1). Phytoplankton composition (lakes 1–4: Jansson et al. 1999; Jansson et al. 2001; lakes 5–15: Jansson unpubl. data) was rather similar in all lakes in spite of large variation in the concentration of DOC and inorganic nutrient concentration and was dominated by chrysophytes, cryptophytes, and chlorophytes.

There was a considerable span in PEM between the lakes, and bacterioplankton contributed between 13 and 77% to PEM (Table 1) which makes the data set very useful for an

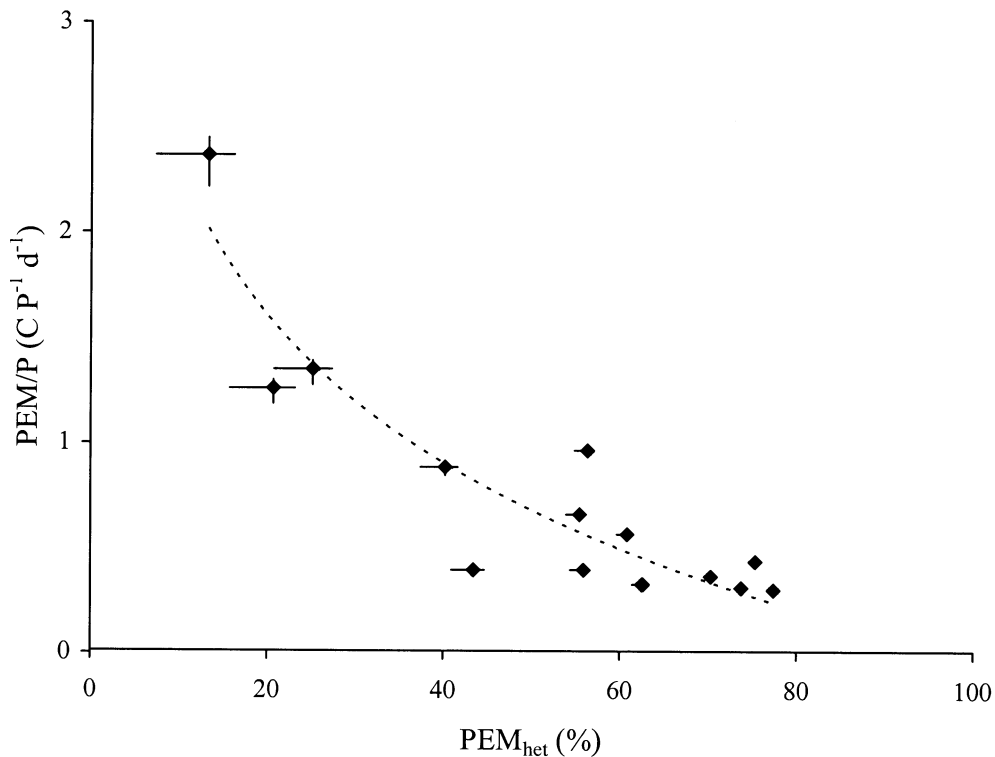


Fig. 1. The relation between PEM/P (pelagic energy mobilization per unit of total phosphorus concentration) and  $PEM_{het}$  (share of PEM corresponding to bacterioplankton energy mobilization from allochthonous carbon) in 15 lakes in northern Sweden ( $\log PEM/P = 0.43 - 0.012PEM_{het}$ ,  $r^2 = 0.76$ ,  $n = 15$ ,  $p < 0.001$ ). The error bars demonstrate the uncertainties introduced by assumptions about BGE and bacterial utilization of PP when calculating PEM (*see text*).

analysis of how PEM is affected by a shift from an autotrophic to a heterotrophic base for the food web. We obtained no significant correlation between summer mean water temperature or effective light climate and PEM or PEM/P, which shows that differences in temperature and light availability were not major determinants of differences in PEM between our lakes. Neither did we find any relationship between PEM and total P or total N, which is interesting considering the role of P and N as limiting inorganic nutrients. However, the lack of such clear relationships is predicted by our hypothesis, which states that PEM is determined not only by the limiting nutrients but also by the relationship between autotrophic and heterotrophic energy mobilization. Instead, we found a clear and highly significant negative relationship for the relation between PEM/P and  $PEM_{het}$  ( $\log PEM/P = 0.43 - 0.012PEM_{het}$ ,  $r^2 = 0.76$ ,  $n = 15$ ,  $p < 0.001$ , Fig. 1). The error bars in Fig. 1 show that uncertainties in calculation of PEM (and  $PEM_{het}$ ) introduced by assumptions on bacterial growth efficiency and bacterioplankton use of phytoplankton carbon via phytoplankton exudates and zooplankton excretion (*see above*) did not affect the correlation between PEM/P and  $PEM_{het}$  to any large extent. This was a fact even when we tested the extreme possibilities that bacteria used 0 and 100% of PP (not shown). Therefore, the regression in Fig. 1 is determined mainly by the measured values on BP, PP, and P concentration.

The slope of the regression in Fig. 1 demonstrates a tran-

sition from systems with high nutrient use efficiency to systems with low nutrient use efficiency as BP increases relative PP. PEM/P was about one order of magnitude higher when PEM was dominated by autotrophs than when dominated by heterotrophs in our data set (Fig. 1; Table 1). This transition agrees with our hypothesis that a heterotrophic base for pelagic production leads to low energy mobilization. We based our hypothesis on different P:C stoichiometry of bacterioplankton and phytoplankton. The results offer some support for the assumption that nutrient use efficiency is dependent on the P:C ratio. If, for example, P:C ratios are 10 times higher in bacteria than in phytoplankton (Vadstein 2000; Wetzel 2001) and bacteria and phytoplankton have similar growth rates, we should obtain a relationship similar to that in Fig 1. However, this interpretation cannot be approved uncritically. P:C ratios have been defined by studies of cultured organisms and can be highly variable between species and depending on P availability (Vadstein 2000). It is not possible to obtain adequate P:C ratios for bacterioplankton and phytoplankton in natural plankton assemblages. Therefore, we do not know the P:C composition of the organisms in our lakes.

Growth rates of bacteria and phytoplankton can be quite different. However, the production/biomass ratios given by data in Table 1 were similar for bacteria (mean for all lakes:  $0.14 d^{-1}$ ) and phytoplankton (mean for all lakes:  $0.15 d^{-1}$ ) which indicate that the growth rates of bacteria and phyto-

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plankton were rather similar in our lakes. It should also be stressed that if fixed P:C ratios of bacterioplankton and phytoplankton determined the relationship in Fig. 1, we should expect a linear regression instead of the logarithmic one given by our data. The deviation from a linear relationship can have several reasons even if we accept P:C ratios as a major determinant for nutrient use efficiency (e.g., that P:C ratios of bacterioplankton and phytoplankton vary because of differences in P availability, Vadstein 2000) or depending on the dominance of bacterioplankton relative to phytoplankton. Thus, even though our results to some extent support the assumption that cell P:C ratios determine the regression in Fig. 1, we do not consider them sufficient to define the role of P:C ratios in this respect. However, we conclude that pelagic nutrient use efficiency was about one order of magnitude lower when dominated by BP than when dominated by PP, and we suggest that this difference to a large extent is a reflection of the different P:C stoichiometry of bacteria versus phytoplankton.

Our result corresponds to the traditional opinion that brownwater lakes, now known to be dominated by bacterial energy mobilization, represent a special type of lake ecosystem with extremely low production that already ascribed to them the term “dystrophic” in the early 20th century (Thieneman 1925). However, the lake data set used in this study demonstrates that not just strongly colored humic lakes with a high input of AOC and reduced light transmission have low nutrient use efficiency. Several of the lakes with very low PEM/P are clearwater oligotrophic lakes (Table 1). The reason BP in these lakes, similar to that in brownwater lakes, is higher than PP was discussed in detail by Karlsson et al. (2002) and is explained by the support of bacterioplankton growth to a large extent by AOC and the similarity in proportions between supply of inorganic nutrients and AOC in both types of lakes. We therefore suggest that nutrient use efficiency and, thus, the productivity of the entire pelagic ecosystem is determined by the availability of inorganic nutrients and organic C and whether inorganic nutrients are linked primarily to production of bacteria or to production of phytoplankton. The regression in Fig. 1 shows that even small changes in conditions that determine the relationship between bacterioplankton and phytoplankton production can have dramatic effects on the nutrient use efficiency and thus on the energy mobilization and productivity of pelagic ecosystems.

Mats Jansson

Department of Ecology and Environmental Science  
Umeå University  
SE-901 87 Umeå, Sweden

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Department of Ecology and Environmental Science  
Umeå University  
SE-901 87 Umeå, Sweden

Climate Impacts Research Centre (CIRC)  
Abisko Scientific Research Station  
SE-981 07 Abisko, Sweden

Peter Blomqvist

Department of Limnology  
Evolutionary Biology Centre  
Uppsala University  
Norbyv. 20 SE-752 36 Uppsala, Sweden

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## Predicting herring recruitment from young-of-the-year densities, spawning stock biomass, and climate

**Abstract**—Because fish are key organisms in most aquatic ecosystems, we seek to understand what determines their highly variable reproductive success. From our work, it appears that year-class strength of Baltic Sea herring (*Clupea harengus* L.) can be predicted from young-of-the-year densities in a small coastal area (hydroacoustic data), a climate index (the North Atlantic Oscillation), and the spawning stock biomass. These three factors explained 93% of the variation in the number of age 2 herring during 1985–2000. By predicting year-class strength 3 yr before the fish enter the fishery, we provide managers with the opportunity to adjust fishing pressure per upcoming year classes and manage the fishery by multiannual catch quotas.

Overfishing is recognized as one of the most serious human impacts on marine ecosystems (e.g., Pauly et al. 1998; Jackson et al. 2001). This failure of management derives, at least in part, from uncertain stock size assessments and a poor understanding of variability in fish recruitment. Furthermore, year-class strength typically is only assessed on entry into a fishery, clearly too late to manage effort appropriately. The difficulty in understanding and predicting fish recruitment reflects a classical problem in fish biology and fisheries research (e.g., Ricker 1954; Beverton and Holt 1957; Cushing 1996).

Fish populations typically display large natural variations in abundance. Periods with unusually large populations can persist for decades (Alheit and Hagen 1997; Toresen and Östvedt 2001). For naturally short-lived marine species or intensively fished populations the time between high and low population size can be shorter and even based on a single or a few consecutive strong or weak year classes (e.g., Cushing 1996). These fluctuations can be self-perpetuating with large stocks of adult fish producing numerous offspring and

small stocks producing few. However, for most marine pelagic fish species, the stock–recruitment relationship is generally weak, as high fecundity is combined with high and variable egg and larval mortality. Early life stages suffer highest mortality, subject to variability in water temperature, feeding conditions, and wind stress (Houde 1994; Cushing 1996), suggesting that year-class strength is set generally by the time young fish have passed larval and early metamorphosed stages (Bradford 1992; Cushing 1996). Accordingly, in most marine pelagic species, year-class strength can be estimated after young fish have passed these stages.

Herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) are the dominant pelagic species in the Baltic Sea and are subjected to intensive fishing. Although the Baltic Sea is an open system and adult herring migrate extensively (e.g., Parmanne et al. 1994), a growth gradient from south to north reveals their sedentary nature within regions (Arrhenius and Hansson 1993). Herring is fished mainly offshore but spawn in shallow coastal areas, predominantly in spring and early summer, all along the Swedish east coast. In late summer, the archipelago areas support dense populations of young-of-year herring (Rudstam et al. 1992; Hansson 1993).

To predict recruitment of Baltic Sea herring shortly after spawning, we compared data on year-class strength (YCS) of age 2 herring with young-of-the-year herring densities (YOY) and herring spawning stock biomass (SSB, fish age  $\geq 3$  yr). Because mild winters can positively affect year-class strength (e.g., Briemann 1989; Rajasilta et al. 1996; Laine et al. 1998), we also included climate data (the North Atlantic Oscillation index, NAO) in our analysis.

**Material and methods**—Our data were derived from sub-division 27 (SD27, 26,700 km<sup>2</sup>), a standard assessment area