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Ecological stoichiometry of N and P in pelagic ecosystems: Comparison of lakes and oceans with emphasis on the zooplankton–phytoplankton interaction

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Abstract

By using an elemental-stoichiometry approach to zooplankton–phytoplankton interactions, we compare elemental composition and aspects of nutrient deficiency across a variety of marine and freshwater ecosystems. During 1992 and 1993 we sampled a total of 31 lakes (in northern Wisconsin and Michigan and the Experimental Lakes Area of northern Ontario) and 21 marine stations (at seven estuarine, coastal, and open-ocean sites in the Atlantic and Pacific) for elemental composition of zooplankton, seston, and dissolved components. Relative degree of nutrient deficiency was assessed by phytoplankton dark uptake of ammonia and phosphate, as well as growth response of phytoplankton to N and P addition. Marine and freshwater systems differed greatly in N and P concentrations, N:P stoichiometry, and the distribution of N and P within dissolved, seston, and zooplankton pools. Particularly notable was the high proportion of N and, especially, P that was incorporated in the particulate fraction (seston + zooplankton) of lakes compared to marine sites. In freshwater systems, *Daphnia* spp., which have low body N:P, dominated zooplankton communities when seston C:P and N:P were also low, and calanoids that tend to have high body N:P dominated when seston C:P and N:P was high. This relationship between zooplankton community composition and seston elemental stoichiometry supports arguments for the importance of food quality constraints on zooplankton growth in freshwater systems. Such patterns were not seen in marine systems.

Interest in comparative analyses of ecosystems seems to be increasing (Cole et al. 1991). Such a trend is arguably a sign of maturation in the science of ecology, as scientists evaluate the generality of the principles of ecosystem structure and function suggested by intensive study of individual ecosystems or a narrow range of ecosystem types. Peters et al. (1991) delineated a variety of benefits arising from ambitious comparative study of ecosystems, including sizable improvements in scale, breadth, generality, economy, and timeliness, compared to the accumulation of disaggregated information arising from an explosively expanding ecological research literature (Root 1987). Aquatic scientists have also recognized the need for comparative study, emphasizing in particular the need for a more complete understanding of the nature of marine and freshwater ecosystems (Nixon 1988). For example, delineation of similarities or differences in the functioning of pelagic ecosystems in lakes and oceans may be critical in determining whether insights obtained at the more manageable scale of lakes may be extrapolated validly to marine pelagia. In addition, comparative studies of diverse aquatic ecosystems may help counteract effects of disciplinary specialization (Nixon 1988), reducing the potential for intellectual isolation of oceanographers, lake ecologists, and stream ecologists.

Despite the intellectual benefits of comparative ecology, several factors complicate its application. One of the primary constraints on comparative ecology is identification of a conceptual or analytical framework that can be applied in analysis of diverse ecosystems and ecosystem types (Downing 1991). Common approaches include multivariate compressions of diverse ecosystem data (e.g. Vitousek 1977), analyses of energy flow (primary or secondary production) or energy storage (biomass of autotrophs or heterotrophs) such as those accomplished during the International Biological Program (e.g. O'Neill et al. 1989), and univariate considerations of biotic responses to nutrient (especially P) loading (e.g. Vollenweider 1976). Such studies have provided numerous insights into important similarities and differences between ecosystems. We propose ecological stoichiometry of biologically important elements as an additional perspective that offers promise in comparative ecology. Ecological stoichiometry traces its intellectual history to Lotka (1924) and its most explicit articulation to Reiners (1986). This approach focuses on the relative abundance (ratios) of critical elements (such as C, N, and P) during ecological interactions as means for insight into diverse phenomena such as foraging behavior of individuals, population regulation, resource competition, and nutrient limitation of primary production (Sterner et al. 1992). Ecological stoichiometry may be especially appropriate for comparative ecology, because all biotic and most abiotic components of ecosystems can be

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characterized with respect to ratios of nutrient elements such as C, N, and P.

The difficulty of obtaining comparable data from a variety of ecosystems also potentially interferes with successful comparative analyses of ecosystems (Peters et al. 1991). Broad comparative studies of ecosystems have generally compiled data from the literature, where selective data reporting and differences in sampling approaches, analytical techniques, and data analysis potentially introduce biases in data that are difficult to diagnose. In this study we seek to compare the ecological stoichiometry of C, N, and P in the lower pelagic food web of marine and freshwater pelagic ecosystems and use standardized sampling and analytical procedures to obtain data from a variety of lake and coastal and off-shore pelagic ecosystems. We wished to evaluate the degree of N and P limitation of microplankton growth in marine and freshwaters by assessing N and P ratios in major nutrient pools and by performing nutrient deficiency bioassays. By doing so, we could directly test a paradigm of aquatic ecology in which lake phytoplankton growth is considered to be limited primarily by P and marine phytoplankton growth by N (*see* Hecky and Kilham 1988). We also present detailed data on the association of stoichiometric imbalance between zooplankton and phytoplankton N and P with relative N and P deficiency in lakes and oceans. We thus test the hypothesis that differences in relative phytoplankton N and P deficiency in lakes and oceans are driven by differences in zooplankton body N:P, and therefore relative rates of N and P recycling, of dominant zooplankters in marine and freshwaters (Elser et al. 1988). Alternatively, food-quality constraints, reflected in differences in seston C:N, C:P, and N:P relative to zooplankton body composition, could be a key factor in driving zooplankton community composition (Sterner 1990*b*; Sterner et al. 1992). General patterns regarding these parameters have been reported previously (Elser and Hassett 1994).

In this paper we address several questions regarding stoichiometric relationships among pelagic ecosystems. Does the quantity and relative amount of limiting nutrient (N or P) stored in major pelagic pools differ for marine vs. freshwater ecosystems, for estuaries vs. coastal/offshore marine waters, or for lakes from different lake districts or with differing food-web structures? Are shifts in zooplankton community structure associated with shifts in zooplankton N:P and pelagic stoichiometry in marine and freshwater systems? Does the degree and nature (N vs. P) of algal nutrient deficiency differ for marine vs. freshwater pelagic systems or for lakes with differing food-web structure?

Methods

Sampling locations—Freshwater samples were collected from 25 lakes in Wisconsin (NTL—North Temperate Lakes LTER), Michigan (UNDERC—University of Notre Dame Environmental Research Center), and Ontario, Canada (ELA—Experimental Lakes Area). Marine samples were collected from estuarine stations in South Carolina (North Inlet LTER), New York (Stony Brook Harbor and Flax Pond, Long Island), and Maine (Damariscotta River estuary), and coastal-oceanic sites in the Gulf of California (off Puerto Peñasco, Sonora, Mexico), southeast Pacific Ocean, and Atlantic Gulf Stream (10–40 km off Melbourne, Florida). More detailed information on station locations and characteristics is presented in Table 1. For the data analysis, marine sites were subdivided as estuarine sites and coastal-oceanic sites. Freshwater sites were analyzed both by location (ELA vs. NTL-UNDERC area of Wisconsin and Michigan) and by food-web structure (piscivore dominated [primarily bass and pike], planktivore dominated, fishless, and trout-stocked or native trout dominated). Information on lake food-web structure was taken from Tonn and Magnuson (1982) and Rahel (1984).

Determination of N and P pool sizes and elemental ratios—Before field collections, temperature profiles were taken to determine the depth of the mixed layer/epilimnion. Duplicate water samples were then taken from bottom, midpoint, and top of the mixed layer with a 6-liter horizontal van Dorn water bottle. Water samples were prescreened through 83-μm mesh to remove most larger zooplankton and each vertical series was combined to produce two pooled mixed-layer samples (PMLs). Duplicate vertical zooplankton tows were taken with a 0.5-m, 160-μm mesh plankton net equipped with a General Oceanics flowmeter from 0.5 m above the bottom to the surface in lakes and shallow marine sites and from the entire surface mixed layer for deeper marine sites. Zooplankton samples were held in a cooler in 1-liter jars until processed.

Samples for dissolved nutrients were first filtered through 0.2-μm polycarbonate filters and then frozen for later analysis of total dissolved nitrogen (TDN) and phosphorus (TDP) (American Public Health Association 1992). Water samples were stored in 250-ml polyethylene bottles that were first acid-washed and rinsed in distilled, deionized water. Particulate samples were collected onto precombusted (24 h at 450°C) glass-fiber filters (Gelman GF/F, 0.7-μm porosity) and dried at 60°C. Particulate matter was analyzed for P content colorimetrically after persulfate oxidation (American Public Health Association 1992), for C and N with a Perkin-Elmer model 2400 CHN analyzer, and for Chl *a* fluorometrically following overnight extraction in cold absolute methanol (Marker et al. 1980; Strickland and Parsons 1972). Seston samples include particulates between 0.7 and 83 μm and potentially include phytoplankton, bacteria, microzooplankton, and detritus. We assessed potential detrital contribution to high C:P lake samples (which might be reflecting a high C:P detrital contribution) by using a C:Chl ratio characteristic of P-limited phytoplankton (200:1 by mass; Healey and Hendzel 1980) and calculating the percentage of the seston C that is attributable to phytoplankton C. This calculation indicated that 90% of the seston C could be attributed to chlorophyll-containing particles (Elser and Hassett 1994).

Zooplankton samples were sequentially split with a threeway plankton splitter until an appropriate amount of zooplankton for chemical analyses was present in the split. One split was preserved with Lugol's preservative for later enumeration. In the freshwater samples, *Chaoborus* spp. were removed from the splits used for elemental analysis and were

Table 1. Summary of sampling locations. Net haul depth is maximum depth of zooplankton net haul. Chl *a* (μg liter^{-1}) is averaged from three depths within epilimnion–surface mixed layer. Chl *a* for Maine sites estimated from seston carbon based on carbon : Chl *a* ratio of 36 (avg. of marine sites, excluding North Inlet low tide sites).

Site	Date	Notes	Net haul depth (m)	Surface temp. (°C)	Chl *a*
Freshwater					
Wisconsin, Northern Lakes LTER					
Trout Lake	4 Jul 92	Piscivore	—	15.0	8.9
	8 Jul 92		25	16.4	5.4
	10 Aug 93		14	21.5	7.1
Allequash Lake	7 Jul 92	Piscivore	8	17.1	5.1
Big Muskellunge Lake	7 Jul 92	Piscivore	15	17.2	16.8
Sparkling Lake	7 Jul 92	Piscivore	10	17.4	3.7
Blueberry Lake	10 Jul 92	Piscivore	4	20.3	9.8
Crystal Lake	10 Jul 92	Piscivore/trout stocked	18	18.7	2.3
Spruce Lake	13 Jul 92	Piscivore	3	19.4	12.3
Mystery Lake	13 Jul 92	Planktivore	2	19.0	58.9
Firefly Lake	13 Jul 92	Piscivore/trout stocked	11	19.7	5.9
	2 Aug 93		5	21.7	3.4
Little Rock Lake (north)	19 Aug 92	Piscivore	4	21.9	4.9
Little Rock Lake (south)	19 Aug 92	Piscivore	3	21.2	5.6
Trout Bog	19 Aug 92	Planktivore	3	20.8	6.0
Nebish Lake	4 Aug 93	Piscivore	8	24.2	5.3
Little John Jr. Lake	2 Aug 93	Piscivore	5	22.4	8.9
Pauto Lake	9 Aug 93	Piscivore/trout stocked*	13	22.2	5.7
Bug Lake	12 Aug 93	Planktivore	3	24.3	28.0
Michigan, UNDERC Lakes					
Peter Lake	16 Aug 92	Piscivore	10	21.5	7.2
Long Lake (east)	16 Aug 92	Planktivore*	11	20.3	17.2
	6 Aug 93		12	20.1	5.7
Long Lake (west)	16 Aug 92	Piscivore	12	20.3	3.9
Long Lake (central)	16 Aug 92	Fishless*	3	20.3	15.2
Tuesday Lake	6 Aug 93	Planktivore	12		10.6
Tender Bog	16 Aug 92	Fishless	7	18.5	13.3
Ontario, Experimental Lakes Area					
Lake 109	10 Jun 93	Planktivore	9	16.3	1.2
Lake 110	22 Aug 93	Piscivore	10	21.6	1.7
Lake 224	10 Jun 93	Lake trout	26	16.7	1.0
Lake 227	29 Aug 93	Piscivore	9	20.2	22.4
Lake 239	24 Jul 93	Piscivore	30	20.3	1.1
Lake 240	22 Aug 93	Piscivore	12	22.1	1.0
Lake 261	24 Jun 93	Planktivore	8	18.8	—
Lake 305	11 Aug 93	Lake trout	28	22.0	0.6
Lake 428	13 Aug 93	Planktivore	13	21.1	2.6
Marine—estuarine					
South Carolina, North Inlet LTER					
Oyster Landing	7 Aug 92	Low tide	1	25.0	53.8
	13 Aug 92	High tide			29.1
Clambank Landing	7 Aug 92	Low tide	1		36.2
	13 Aug 92	High tide			22.5
Town Creek	10 Aug 92	Low tide	4	28.3	41.8
	13 Aug 92	High tide		27.2	43.8
Inlet Mouth	10 Aug 92	Incoming tide	5	28.5	43.4
Long Island, New York					
Stony Brook Harbor	17 Aug 92	Incoming tide	3	19.4	3.9
Flax Pond	17 Aug 92	High tide	1	19.4	3.0
Damariscotta River, Maine	26 Aug 92	Estuary mouth, ebbing tide	16		9.8
	26 Aug 92	Mid-estuary, low tide	3		16.2
Gulf of California	8 Apr 93	5 km off Puerto Peñasco, Sonora	16	18.8	9.2
	8 Apr 93	5 km off Puerto Peñasco	25		10.8

Table 1. Continued.

Site	Date	Notes	Net haul depth (m)	Surface temp. (°C)	Chl *a*
	8 Apr 93	10 km off Puerto Peñasco	30		5.9
	3 Jun 93	25–31.277N, 123–01.120W	30	22.2	1.2
	4 Jun 93	26–32.109N, 122–17.084W	30		1.1
Southeast Pacific Ocean	4 Jun 93	27–12.080N, 121–46.117W	30	21.2	1.0
	9 Jul 93	40 km off Melbourne, Florida	40	27.5	1.1
	9 Jul 93	36 km off Melbourne	40		0.9
	9 Jul 93	18 km off Melbourne	30		0.7
Florida, Gulf Stream	10 Jul 93	4 km off Melbourne	20	27.7	0.7

* Lake status uncertain; in the case of the UNDERC lakes the intended food-web structure is indicated.

not used in the species composition analysis. When zooplankton samples contained appreciable densities of large phytoplankton cells, zooplankton were separated from phytoplankton by narcotization and settling. Known aliquots of zooplankton were placed on precombusted, preweighed Gelman GF/C glass-fiber filters under gentle vacuum. Marine samples were rinsed briefly with distilled water while under vacuum to remove salts. Filters with animals were dried (60°C), reweighed, and analyzed for P or N with the same methods used for seston. Zooplankton N:P was then calculated for each duplicate net tow based on %P and %N per unit dry weight.

For each site the elemental imbalance and predicted recycling ratio was calculated from the seston and zooplankton elemental ratios. Elemental imbalance was calculated as seston N:P − zooplankton N:P (Sterner 1990*b*), so that a positive imbalance indicates seston N:P > zooplankton N:P. Recycling ratio is the N:P predicted to be recycled by zooplankton at each site given the measured zooplankton and seston N:P. When N:P imbalance >0, $N:P_{recycled} = N:P_{seston} - N:P_{zoopl}L/(1 - L)$, where L is the maximum accumulation efficiency of the element (Sterner 1990*b*). When N:P imbalance ≤0, $N:P_{recycled} = N:P_{seston}(1 - L)/(1 - LN:P_{seston}/N:P_{zoopl})$. An accumulation efficiency of 0.75 was used for the calculations of recycling ratio. For comparison, we also calculated recycling ratios for accumulation efficiencies of 0.5 and 0.9. Accumulation efficiencies are assumed to be the same for both elements.

Zooplankton species composition—Preserved zooplankton samples were counted to species or genera for the major components of the plankton. To assess the contribution of the different components of the zooplankton to the total biomass, we also measured individual sizes for each sample. About 20 individuals of the dominant species within each sample were measured for length, and these lengths were converted to biomass using length/weight regressions. Regression equations for freshwater cyclopoid and calanoid copepods were from Malley et al. (1989), and regressions for cladoceran species were calculated directly from samples collected at ELA. Regression equations for *Oithona* spp. were taken from Sabatini and Kiørboe (1994) and *Acartia* spp. from Landry (1978). Regressions for calanoid copepods and nauplii were calculated from data of Davis (1984); for ostracods, chaetognaths, decapods, amphipods, medusae, and ctenophores, data were from Miller (1966). To convert wet weight data of Miller (1966) to dry weight, conversion factors were taken from Curl (1962), Beers (1966), and Omori (1969). Carbon was assumed to be 40% of copepod dry weight when a conversion factor was necessary (Beers 1966; avg. for May–August). For marine cladocerans, the freshwater *Bosmina* equation was used, as this yielded a value equal to the single length–weight data point for a marine cladoceran in Miller (1966). To assign average weights to minor components of each sample that were not sized, we took the average weights of these components for all relatively similar sites (e.g. NTL or Atlantic marine stations) and applied them to the minor components. These minor taxa generally contributed <1% of total biomass. The biomass data were used to determine the biomass-weighted average size of the zooplankton community for each site (ZM_B; Elser et al. 1988). Biomass-weighted size of the zooplankton community was calculated as $ZM_B = \Sigma(bm_i \times C_i)/\Sigma C_i$, where bm_i is average weight for species i in μg and C_i is zooplankton concentration for species i in μg liter^{-1}.

Indices of nutrient deficiency—The relative degree of nutrient deficiency in the phytoplankton community was assessed by both nitrogen/phosphorus-debt experiments and dilution bioassays. N- and P-deficient phytoplankton in culture have been shown to take up greater quantities of the deficient nutrients than non-nutrient-deficient phytoplankton (Healy and Hendzel 1980). N–P debt experiments were performed with the PML samples by inoculating 125-ml bottles with 25 μM NH_4 and 5 μM PO_4 and measuring dark uptake after ~18–25 h of incubation. Nutrient uptake was found to be nonlinear, occurring primarily during the first few hours of the experiment, so we simply expressed nutrient uptake as the total change in μM N(P), normalized to seston carbon. Results were expressed as the fraction of sites demonstrating nutrient uptake to total sites, as well as for those sites demonstrating uptake, the average μM uptake of N or P, and the ratio of N debt to P debt, i.e. μM N taken up per μM P. For each of the duplicate PMLs we used three controls with no enrichment, three +N, three +P, and three +N+P. To consolidate the ammonium and phosphorus measurements, we prepared initial samples by filtering water samples and holding them until the end of the experiment and then adding nutrients immediately before assaying. Phosphate was analyzed colorimetrically by the phosphomolybdate method

(American Public Health Association 1992) and ammonium by the indophenol-blue method (Solórzano 1969). When samples for phosphate and ammonium could not be processed within a few hours, they were frozen and analyzed within 3 d.

Size-fractionated N–P debt experiments were performed at a limited number of sites in 1993 (seven freshwater and seven marine) to determine which size fractions (>1 μm and <1 μm) were responsible for the observed changes in nutrient concentrations during the incubations. In these experiments, a parallel set of incubations was prepared with water filtered through a 1.0-μm polycarbonate filter, with the same nutrient treatments as above. Samples were handled as in the standard N–P debt experiments.

Bioassay experiments evaluated Chl *a* response to nutrient additions after 48-h incubations. PMLs from each site were combined for the bioassays, and water was filtered through a 0.2-μm Gelman cannister filter to prepare a 90% dilution. To this dilution were added enrichments as in the above N–P debt experiment, so that 12 500-ml experimental bottles were prepared for each site. Initial Chl *a* samples were taken at the start of the experiment ($n = 5$), and after the incubation period the bottle contents were filtered on Gelman GF/F filters and assayed for Chl *a* content following overnight extraction of the filter in cold methanol. Incubations were conducted under ambient light conditions that varied from site to site. Thus, comparisons can only be made within sites and not between sites.

Statistical analysis—Statistical analyses were performed with Statview (Abacus Concepts). ANOVA analysis was performed on concentration, elemental ratio, percent composition, and nutrient-deficiency experiment data grouped by four regions (NTL, including the UNDERC lakes, ELA, marine estuarine sites, and marine coastal and oceanic sites). Because only one site was truly oceanic (three stations in the southeast Pacific), marine coastal (Gulf of California and Atlantic Gulf Stream) and oceanic sites were treated as a group. Data for the ANOVA analyses were tested for homogeneity of variance and were transformed where appropriate by either in $(1 + x)$ or square root (x) (the latter for percent composition data). Regional comparisons were tested by Scheffé's *F*-test. Multiple regression analyses were performed on the zooplankton community composition data for different stoichiometric parameters. Freshwater zooplankton were grouped into four taxonomic categories (*Daphnia* spp., nondaphnid cladocerans, calanoid copepods, and cyclopoid copepods). Marine zooplankton were grouped into seven categories (calanoid copepods, cyclopoid copepods, harpacticoid copepods, crustacean nauplii [predominantly barnacle nauplii], other crustaceans [cladocerans and decapods], salps and larvaceans, and miscellaneous predators [predominantly chaeotognaths]). These groupings accounted for >95% of the estimated biomass in our sites.

Results

Pool sizes and elemental ratios—Freshwater and marine sites differed greatly in a broad range of the parameters measured. Dissolved N and P (TDN and TDP) were greater in marine sites, and seston and zooplankton N and P were, in general, greater in freshwater sites. Differences were much more pronounced for P than for N, with the only nonsignificant difference among P pools being between ΣP in the NTL lakes and coastal-oceanic sites. There was no difference between lake and coastal-oceanic sites in ΣN, as well as no difference between lakes and estuarine sites in seston C or N. In general, more differences were observed comparing freshwater to marine sites than in comparing the two lake (NTL-UNDERC vs. ELA) or two marine (estuarine vs. coastal-oceanic) regions (Table 2). However, several differences stand out in the latter comparisons. First, ELA lakes had significantly lower TDP and ΣP than did NTL-UNDERC lakes (Fig. 1). Estuarine sites had a significantly greater quantity of C, N, and P in the seston pool, as well as greater ΣP, than did oceanic-coastal sites.

Expressing the N and P concentrations in terms of percent contribution to the different pools (dissolved, seston, and zooplankton) illustrates the pronounced differences both between marine and freshwater systems and between N and P. ELA and NTL-UNDERC lakes were differentiated only by the lower %P in the dissolved pool of ELA lakes (Table 2, Fig. 2). Estuarine sites had a higher proportion of N and P in the seston pool, as well as a smaller proportion of N and P in the dissolved fraction, compared to the coastal-oceanic sites. Marine and freshwater sites differed particularly in the proportion of P incorporated in the dissolved, seston, and zooplankton pools (Table 2, Fig. 3). Twice as much P as N was incorporated in particulates (seston plus zooplankton) in all regions, both freshwater and marine. In lakes, nearly two-thirds of the P was incorporated in the combined seston and zooplankton fractions, with 17% of this in the zooplankton. The fraction of P in the zooplankton pool was as high as 53% (ELA Lake 109). ELA lakes had relatively more P in the seston and zooplankton pools and less in the dissolved pool compared to the NTL-UNDERC lakes. There was a marginally significant (ANOVA, $P = 0.065$) effect of food-web structure on the fraction of total phosphorus in the zooplankton, with fishless and planktivore-dominated lakes having a relatively low fraction and trout-dominated lakes a large fraction of the P in the zooplankton pool. In the marine sites, the maximum amount of P tied up in the zooplankton at any station was 4% (Gulf Stream Sta. 1). In this regard, estuarine sites were intermediate between the oceanic marine and freshwater sites, having a considerable amount of P in the seston pool but still very little in the zooplankton. Most of the N was in the dissolved pool in both freshwater and marine sites and did not differ significantly between different regions.

Comparing various ratios, the two lake regions were differentiated by the significantly higher ΣN:P (all pools combined) and seston C:N and C:P in the ELA lakes (Table 2, Fig. 4). Estuarine sites had lower ΣN:P than did coastal-oceanic sites. Both estuarine and coastal-oceanic sites had significantly lower N:P and C:P in the seston than did freshwater sites. Seston C:N was lower in estuaries than in either lake region but in the ocean regions was only significantly lower compared to the ELA lakes, not the NTL lakes. The only significant difference among regions in zooplankton N:P was between the NTL-UNDERC lakes and the

Table 2. Results of ANOVA model of regions vs. stoichiometric parameters. Part a presents differences in concentrations; part b presents differences in elemental ratios and imbalances, percent composition, and results of nutrient-debt experiments. EST—marine estuarine sites, OCE—marine coastal and oceanic sites. ZM_B is biomass-weighted zooplankton size; s-z imb is the imbalance between seston and zooplankton N:P; recyc.—recycled; %N(P)—d(s,z) refers to percent nitrogen (or phosphorus) in the dissolved (or seston, zooplankton) fraction. Significant differences for comparisons between regions are shown with an asterisk; ns—nonsignificant.

a)

	Dissolved		Seston			Zooplankton			Total nutrients			
	TDN	TDP	C	N	P	C	N	P	N	P	ZM_B	Biomass
P-value	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Comparisons												
NTL-ELA	ns	*	ns	ns	ns	ns	ns	ns	ns	*	ns	*
NTL-OCE	*	*	*	*	*	*	*	*	ns	ns	*	*
NTL-EST	*	*	ns	ns	*	*	*	*	*	*	*	*
ELA-OCE	*	*	*	*	*	*	*	*	ns	*	ns	*
ELA-EST	*	*	ns	ns	*	*	*	*	*	*	*	*
OCE-EST	ns	ns	*	*	*	ns	ns	ns	ns	*	*	ns

b)

	Σ Nutrients N:P	Seston C:N	Seston C:P	Seston N:P	Zoopl. N:P	s-z imb	Recyc. N:P	%Nd	%Ns	%Nz	%Pd	%Ps	%Pz	N debt	P debt
P-value	0.001	0.001	0.001	0.001	0.008	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	ns	0.02
Comparisons															
NTL-ELA	*	*	*	ns	ns	ns	*	ns	ns	ns	*	ns	ns	ns	ns
NTL-OCE	ns	ns	*	*	*	*	*	*	*	*	*	*	*	ns	*
NTL-EST	*	*	*	*	ns	*	*	ns	ns	*	ns	ns	*	ns	ns
ELA-OCE	*	*	*	*	ns	*	*	*	*	*	*	*	*	ns	ns
ELA-EST	*	*	*	*	ns	*	*	ns	ns	*	*	ns	*	ns	ns
OCE-EST	*	ns	ns	ns	ns	ns	ns	*	*	ns	*	*	ns	ns	ns

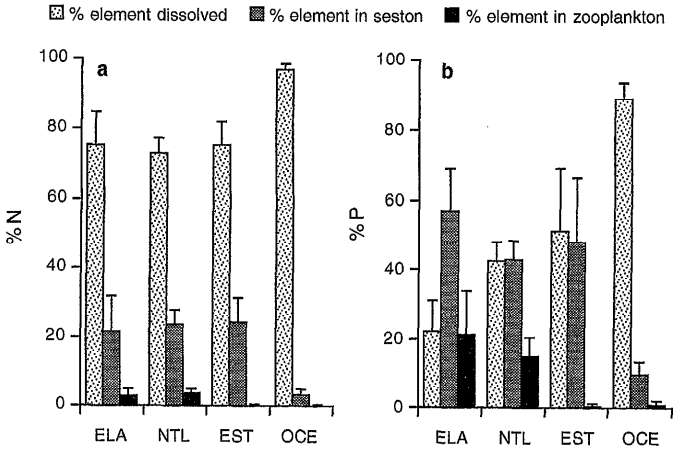

Fig. 1. Concentrations of nitrogen (N) and phosphorus (P) (in μm liter^{-1}) within different pools in the four freshwater and marine regions sampled. ELA—Experimental Lakes Area; NTL—North Temperate Lakes LTER and UNDERC lakes, northern Wisconsin and Michigan; EST—marine estuarine sites; OCE—marine coastal and oceanic sites. TDN and TDP—total dissolved N and P, respectively; ΣN and ΣP—combined (dissolved + seston + zooplankton) N and P. Sample sizes: ELA n = 9, NTL n = 25, EST n = 11, OCE n = 10.

coastal-oceanic sites. However, overall zooplankton N:P was significantly lower in lakes than in marine sites (Elser and Hassett 1994). The elemental imbalance between seston and zooplankton did not differ significantly between the ELA and NTL-UNDERC freshwater sites or between coastal-oceanic and estuarine sites (Fig. 4f). However, freshwater and marine sites differed greatly in elemental imbalance (Elser and Hassett 1994). Both freshwater regions had a positive (seston N:P > zooplankton N:P) imbalance, and coastal oceanic sites had a negative (seston N:P < zooplankton N:P) imbalance. Estuarine sites were essentially in stoichiometric balance (seston N:P = zooplankton N:P). These differences in the N:P imbalances led to pronounced differences in the N:P ratio that would be recycled by zooplankton (assuming a maximum accumulation efficiency of 0.75). Marine zooplankton would recycle at about the Redfield ratio of 16 and freshwater zooplankton at a much higher N:P (≈100) (Fig. 5). In freshwater systems there was a positive correlation between the N:P imbalance and the ΣP in the system, such that lakes with a high P content tended to show the greatest imbalance between seston and zooplankton N:P (Fig. 6).

Recycling ratios were also calculated for accumulation efficiencies (ae) of 0.5 and 0.9 (Fig. 5). The trend among

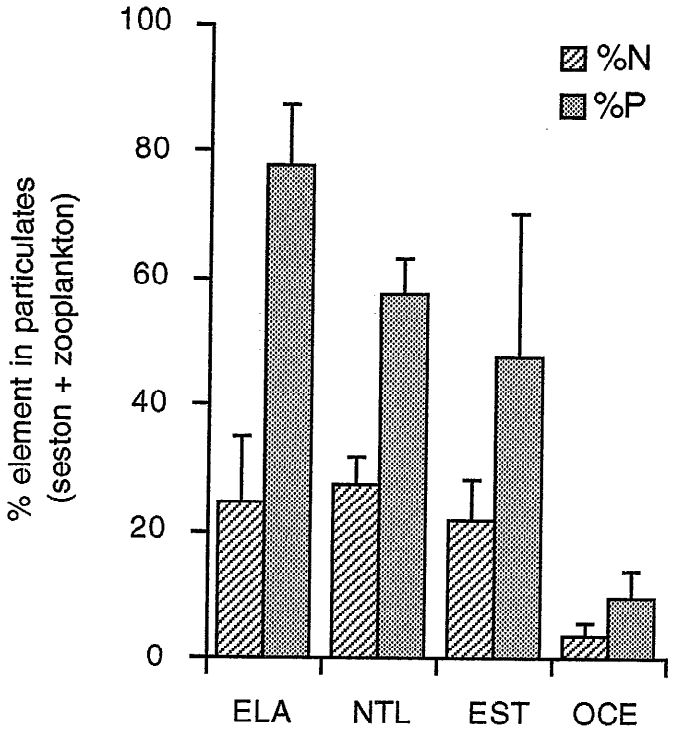

Fig. 2. Percent of element within each pool (dissolved, seston, zooplankton) in the four freshwater and marine regions. Abbreviations and sample sizes as for Fig. 1.

regions was not affected by using a different *ae* in the calculation. However, changing *ae* did affect the magnitude of the calculated recycling ratio. The recycling ratio in lakes was sensitive to the choice of *ae,* with high recycling ratios associated with high *ae,* but ocean, and to a lesser extent estuarine, sites were relatively unaffected by changing *ae.*

Zooplankton species composition—Tables 3 and 4 summarize data by site for zooplankton composition, with data combined into major taxonomic groupings. In freshwater sites (Table 3), major taxa were calanoid and cyclopoid copepods and *Daphnia* spp., with other cladocerans contributing significantly in a number of sites. When the freshwater sites are categorized according to food-web structure (planktivore, piscivore, trout-stocked [or native lake trout dominated], and fishless), the notable feature is the dominance of calanoid copepods in the trout-dominated lakes (ANOVA, significant $P = 0.003$). In marine sites (Table 4), most of the zooplankton biomass was contributed by calanoid copepods, although Stony Brook Harbor was overwhelmingly dominated by a ctenophore bloom. Cyclopoid copepods were often important contributors and dominated at several sites (Flax Pond and Gulf Stream Sta. 3). Cyclopoid dominance at the Gulf Stream site was due to an abundance of large *Corycaeus* spp. Zooplankton biomass was significantly higher in the NTL-UNDERC freshwater sites than in either the marine sites or the ELA freshwater sites (Table 2, Fig. 7).

Biomass-weighted average individual size (ZM_B) at each site is presented for aggregate samples in Table 4. If primarily carnivorous groups are excluded from the calculation of ZM_B (e.g. ctenophores, chaeotognaths, and cyclopoid copepods), the ZM_B at several sites is significantly affected, most notably Stony Brook Harbor (due to large ctenophores) and Gulf of California Sta. 1 and Gulf Stream Sta. 3 (both due to chaetognaths). ZM_B was significantly lower in the marine sites than freshwater, although there was no significant difference between NTL-UNDERC and ELA (Table 2, Fig. 7).

A multiple regression analysis was done between zooplankton taxa and stoichiometric parameters. Percent contribution of zooplankton taxonomic groupings to total biomass were regressed against seston C:N, C:P, and N:P, zooplankton N:P, total N:P, N:P imbalance, and N:P recycling ratio. Freshwater

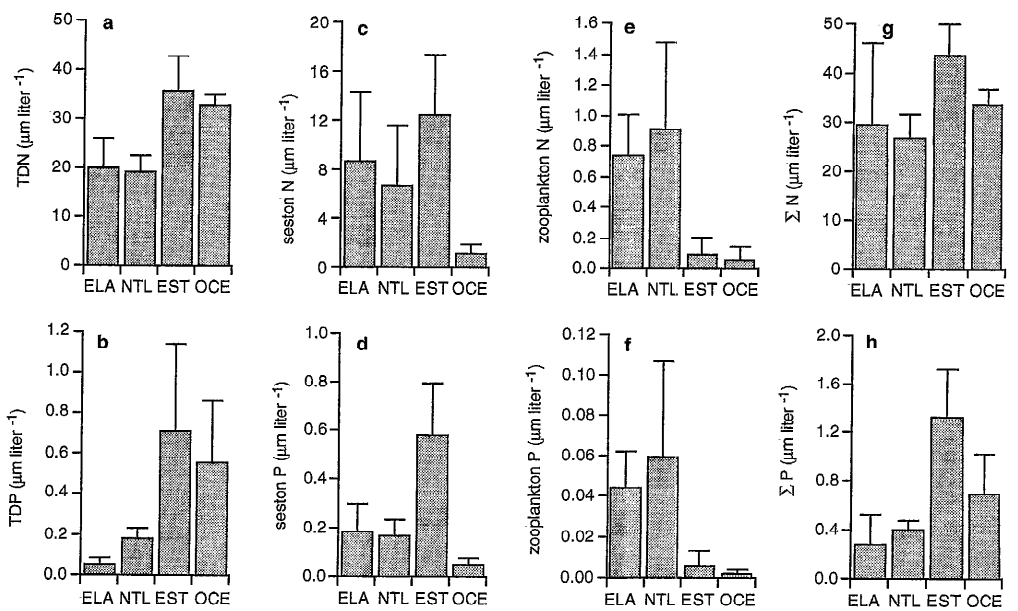

Fig. 3. Percent of element in particulate matter (seston and zooplankton combined) in the four freshwater and marine regions. Abbreviations and sample sizes as for Fig. 1.

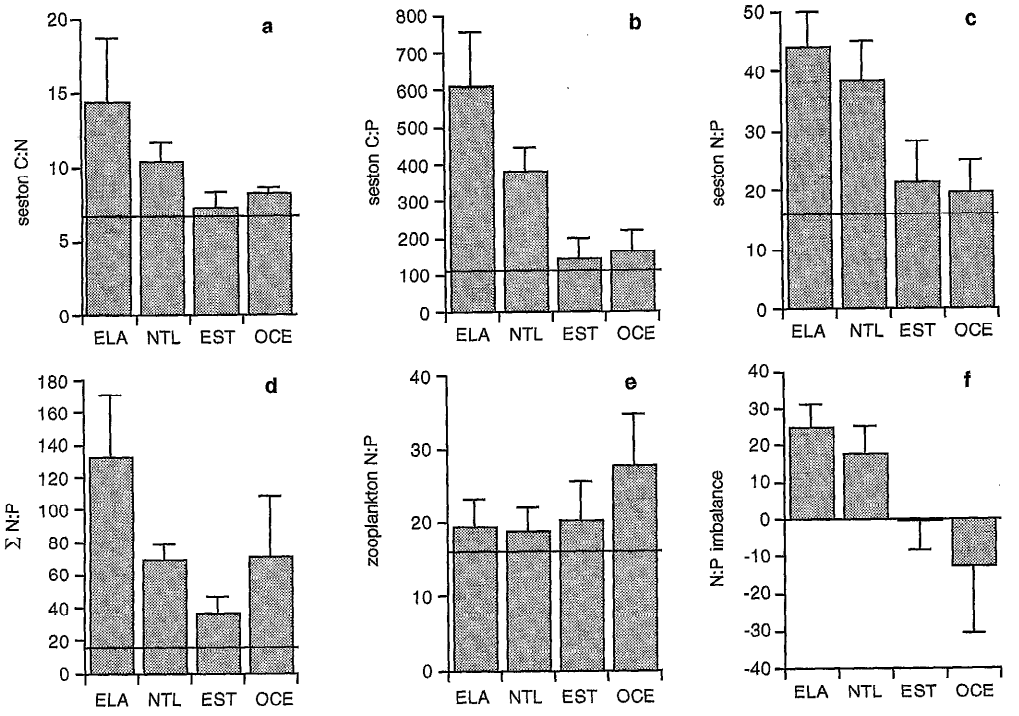

Fig. 4. Elemental ratios for seston C:N, seston C:P, seston N:P, total nutrients (=ΣN:P), zooplankton N:P, and N:P imbalance (seston N:P − zooplankton N:P). Abbreviations and sample sizes as for Fig. 1. Horizontal line denotes Redfield ratios, C:N = 6.6, N:P = 16, and C:P = 106.

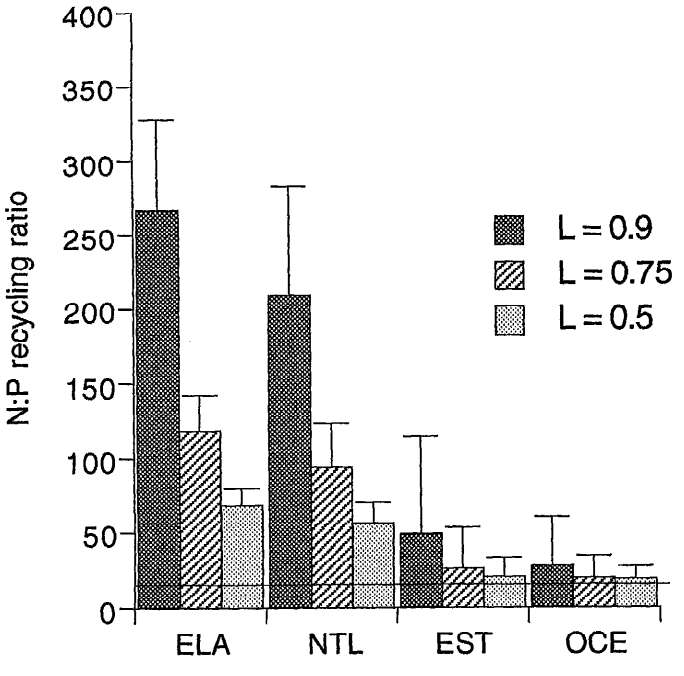

Fig. 5. Recycled N:P (calculated for accumulation efficiencies of 0.5, 0.75, and 0.9) for the four regions. Abbreviations and sample sizes as for Fig. 1. Horizontal line denotes Redfield ratio, N:P = 16.

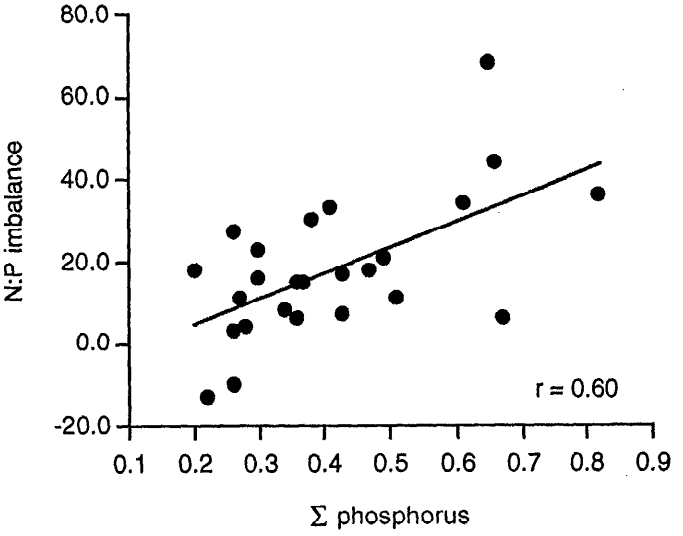

Fig. 6. N:P imbalance vs. total P (μm liter^{-1}, dissolved + seston + zooplankton) at freshwater sites. Line denotes linear-regression fit to the data.

Table 3. Zooplankton composition in percent contribution of taxa to total biomass. ZM_B refers to biomass-weighted size in μg ind.$^{-1}$.

Freshwater sites	Biomass (μg DW liter^{-1})	ZM_B (μg)	*Daphnia*	*Bosmina*	*Diaphano-soma*	*Holope-dium*	*Chydorus*	*Cerio-daphnia*	Calanoid copepods	Cyclopoid copepods
Big Muskellunge Lake	388	22.7	73.0	0.0	0.1	0.1	0.0	0.0	13.1	13.7
Allequash Lake	73	10.5	7.9	0.4	1.0	16.9	0.0	4.9	41.3	26.2
Sparkling Lake	93	8.8	2.7	1.1	0.5	0.0	0.2	0.0	41.0	54.4
Trout Lake 2	151	10.0	27.6	1.3	0.2	4.8	0.1	0.4	32.1	33.4
Blueberry lake	253	13.3	38.5	4.5	1.0	16.6	0.0	9.2	0.0	31.1
Crystal Lake	102	15.8	42.9	0.0	0.1	0.0	0.0	0.0	16.7	40.3
Mystery Lake	127	8.5	8.1	1.7	8.8	20.8	10.7	7.8	26.6	15.4
Spruce Lake	420	11.2	34.3	4.4	2.5	14.4	0.0	0.0	29.8	14.7
Firefly Lake 1	305	11.5	19.7	0.3	6.3	9.7	0.0	0.0	59.9	3.9
Peter Lake	18	7.4	4.4	2.3	0.0	0.0	0.0	0.0	10.1	82.6
Long Lake (west)	30	13.4	48.9	0.2	0.0	0.3	0.0	1.0	0.0	49.4
Long Lake (east) 1	20	8.5	61.2	11.0	0.0	0.0	0.0	20.2	0.0	7.5
Tender Bog	13	18.2	76.5	0.0	0.0	0.4	0.1	0.0	22.3	0.5
Long Lake (central)	221	22.8	87.7	0.0	0.2	0.4	0.0	0.4	3.6	7.7
Little Rock Lake (north)	271	7.5	35.6	17.7	18.4	1.4	0.0	0.0	2.9	23.0
Little Rock Lake (south)	56	16.0	2.0	0.3	7.3	52.0	0.0	0.0	20.5	17.7
Trout Bog	64	3.7	18.9	61.1	0.0	0.0	0.0	1.2	4.7	11.5
Firefly Lake 2	169	7.4	1.0	0.1	6.5	0.2	0.0	0.0	87.2	4.5
Little John Jr. Lake	21	8.5	0.3	0.0	58.4	2.5	0.0	0.0	32.9	5.9
Nebish Lake	101	33.7	0.0	0.1	1.5	74.5	0.0	0.0	16.6	7.2
Tuesday lake	46	8.4	4.9	1.8	3.5	0.0	0.0	0.0	0.5	89.0
Long Lake (east) 2	97	16.9	97.1	0.4	0.0	0.0	0.0	0.0	0.4	2.0
Pauto Lake	337	14.4	24.1	0.0	0.3	1.9	0.0	0.4	63.0	10.2
Trout Lake 3	49	8.5	5.8	0.2	8.8	3.6	0.3	0.3	37.2	43.5
Bug Lake	114	5.4	1.7	0.6	21.5	11.2	0.3	10.0	5.3	47.3
ELA Lake 109	187	10.8	3.3	0.2	0.0	49.4	0.1	0.0	32.1	14.8
ELA Lake 224	93	11.3	18.1	0.0	0.0	7.5	0.0	0.0	67.8	6.6
ELA Lake 110	238	10.2	0.0	0.0	0.1	0.0	0.0	0.0	60.4	39.5
ELA Lake 227	23	9.5	12.1	0.2	27.1	0.0	0.0	0.0	4.6	55.8
ELA Lake 261	160	8.5	11.3	0.3	13.3	0.0	0.0	0.0	35.0	40.2
ELA Lake 239	27	11.0	43.2	0.2	14.1	2.8	0.0	0.0	20.9	18.4
ELA Lake 305	112	9.6	5.6	0.0	0.2	6.0	0.0	0.0	34.6	53.6
ELA Lake 428	80	10.8	27.0	0.0	0.6	0.0	0.0	0.0	35.1	37.3
ELA Lake 240	53	9.7	14.4	0.0	1.2	3.9	0.0	4.0	61.8	14.6

taxa were analyzed in four groups and demonstrated a significant result for four stoichiometric parameters, with *Daphnia* spp. having a significant negative coefficient for seston C:P, seston N:P, N:P imbalance, and predicted N:P recycled, and calanoid copepods a significant positive coefficient for the same four parameters as well as total N:P (Table 5). Thus, at low seston N:P and C:P sites, *Daphnia* dominated zooplankton communities, with less N:P imbalance and lower recycling ratio. At high seston N:P and C:P, calanoids were more important and led to a greater N:P imbalance and higher recycling ratio. Marine taxa were analyzed in five groups and yielded significant regressions for total N:P and seston C:N. Both calanoid copepods and total nauplii (which includes all crustacean nauplii, with barnacle nauplii dominating the high biomass samples) were positively related to the total N:P ratio in the system. Salp and larvacean abundance was positively related to seston C:N, and calanoid copepods were negatively related to seston C:N.

Indices of nutrient deficiency—Lakes and coastal-oceanic sites differed significantly in the frequency and extent of P deficiency (Table 2, Fig. 8), with lakes being limited to a much greater degree than marine sites. P uptake occurred in 34 of 35 lake sites, with Trout Bog being the only exception. P uptake was common in the estuarine sites (10 of 11) but occurred in less than half of the coastal-oceanic sites (4 of 10) (Table 6). N debt was highly variable, particularly in planktivorous and trout-stocked lakes and in the coastal-oceanic sites. Overall, ammonia uptake was observed in 16 of 34 freshwater sites (3 of 9 at ELA and 13 of 25 at NTL-UNDERC) and in a similar percentage (10 of 21) of marine sites (6 of 11 estuarine and 4 of 10 coastal-oceanic). However, a higher carbon-specific uptake was observed in the coastal-oceanic sites. We also determined the chlorophyll-specific nutrient debt, and applied the ratios of N debt:Chl *a* and P debt:Chl *a* used by Healey and Hendzel (1980) as indicators of N and P deficiency [N debt:Chl $a > 0.15$ μm N (μg Chl a)$^{-1}$ and P debt:Chl $a > 0.075$ μm P (μg Chl a)$^{-1}$]. With these indicators, 2 of 11 coastal-oceanic sites were characterized as N deficient, while no estuarine or lake sites were N deficient. Conversely, 18 of 34 lake sites were P deficient (9 of 9 ELA lakes and 9 of 25 NTL lakes) and only 1 of 21 marine sites was P deficient (1 of 11 estuarine sites and no coastal-oceanic sites).

Table 4. Zooplankton composition in percent contribution of taxa to total biomass. ZM_B refers to biomass-weighted size in μg ind.$^{-1}$. Numbers in parentheses indicate ZM_B estimates when large carnivores are omitted: Stony Brook Harbor, ctenophores omitted; Gulf of California 1, chaetognaths; and Gulf Stream 3, *Corycaeus* spp. (cyclopoid). In other marine sites there was little difference in ZM_B estimates with and without carnivorous taxa.

Marine sites	Biomass (μg DW liter^{-1})	ZM_B (μg)	Calanoid copepods	Cyclopoid copepods	Harpacticoid copepods	Cladocerans	Ostracods	Nauplii	Other crustaceans	Chaetognaths	Larvaceans and salps	Ctenophores and medusae
Oyster Landing low tide	10.2	2.4	74.0	12.4	1.4	0.5	4.7	5.2	1.9	0.0	0.0	0.0
Oyster Landing high tide	0.8	1.9	61.1	7.8	2.1	0.0	4.1	16.1	8.7	0.0	0.0	0.2
Clam Bank low tide	7.1	2.8	31.6	19.6	2.5	0.8	21.1	22.1	0.0	1.6	0.0	0.8
Clam Bank high tide	3.0	1.8	63.2	20.4	7.5	0.0	2.3	5.8	0.5	0.4	0.0	0.0
Town Creek low tide	6.5	2.7	77.6	8.6	1.0	0.0	2.8	8.8	0.8	0.3	0.0	0.0
Town Creek high tide	9.6	2.8	70.1	20.7	3.3	0.0	1.5	1.6	1.1	1.4	0.0	0.4
Inlet Mouth	7.9	3.5	86.4	2.7	1.3	0.0	0.3	8.3	0.5	0.5	0.1	0.1
Damariscotta River	20.7	3.5	86.9	6.8	0.1	0.3	1.6	4.0	0.0	0.0	0.0	0.4
Damariscotta Mouth	68.5	7.3	86.0	9.5	0.0	2.6	1.3	0.4	0.0	0.0	0.0	0.0
Stony Brook Harbor	33.7	45.0(1.9)	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	99.6
Flax Pond, NY	1.2	1.7	15.1	68.4	5.9	0.0	7.3	1.3	0.4	0.0	0.0	1.6
Gulf of California 1	3.6	21.2(3.9)	21.2	12.7	18.4	10.0	0.0	0.1	2.8	34.6	0.2	0.0
Gulf of California 2	1.2	6.9	20.9	21.2	33.1	10.0	0.0	0.0	7.8	6.6	0.0	0.4
Gulf of California 3	4.9	4.3	64.2	9.0	6.0	8.8	0.0	0.1	5.4	4.0	2.6	0.0
South East Pacific 1	7.0	9.8	82.1	10.9	2.8	0.6	0.0	0.1	0.0	1.7	1.8	0.0
South East Pacific 2	8.6	4.9	80.7	16.7	1.1	0.4	0.0	0.0	0.2	0.0	0.9	0.0
South East Pacific 3	4.9	3.7	67.8	26.0	0.2	1.4	0.0	0.2	1.7	0.5	2.2	0.0
Gulf Stream 1	72.1	7.8	56.2	10.9	0.8	0.3	0.6	0.2	18.7	8.0	9.5	0.0
Gulf Stream 2	70.9	7.8	51.6	14.1	0.8	1.3	3.6	0.2	17.7	8.7	9.4	0.1
Gulf Stream 3	59.9	14.5(6.3)	22.5	55.4	1.8	1.0	1.7	0.1	7.9	7.0	4.9	0.6
Gulf Stream 4	267.0	3.4	28.6	27.7	1.5	26.2	0.0	0.4	16.3	11.8	1.6	0.4

Ammonium was released during about 50% of the incubations in both freshwater and marine sites, and size-fractionation experiments revealed that this increase was due entirely to the <1-μm seston size fraction. Ammonium production was especially high in east Long Lake in 1993 [0.16 μM N (μM C)$^{-1}$]. P uptake occurred consistently in both size fractions in lakes. N and P uptake were observed together in the same incubations about as often as P uptake alone (15 lakes exhibited both N and P uptake, and 18 lakes exhibited only P uptake; in marine sites, 6 exhibited N and P uptake, 7 only P uptake); however, N uptake in the absence of P uptake was less common, being observed in only one lake (Trout Bog) and four marine sites.

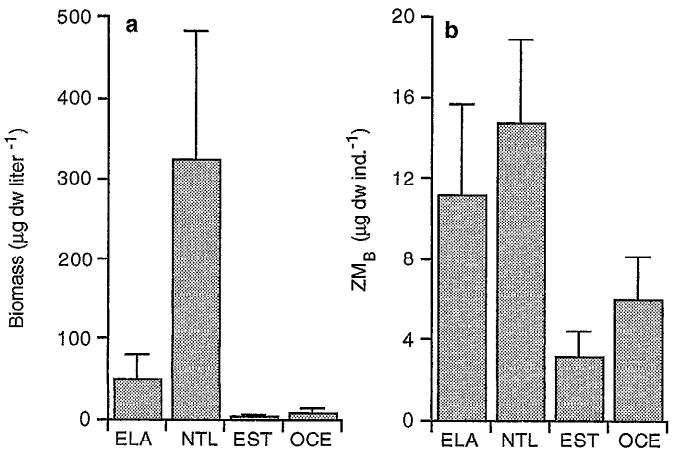

Fig. 7. [a.] Zooplankton biomass determined from replicate vertical metered net hauls. [b.] Biomass-weighted individual weight (ZM_B, μg DW ind.$^{-1}$) calculated from length–weight regressions. Abbreviations and sample sizes as for Fig. 1.

Bioassay responses to nutrient addition were quite limited. Strongest responses in freshwater sites were to combined N and P additions, where incubations showed a significant increase in Chl *a* at 11 of the 34 lake sites (Spruce, Mystery, Firefly, Bug, east Long and central Long, Tender Bog, ELA Lake 110, ELA Lake 239, and ELA Lake 240). Only 4 of 34 sites responded to N alone (Firefly, Bug, Tender Bog, ELA Lake 239), and 2 of 34 sites to P alone (Pauto, east Long). Marine sites showed little growth response to nutrient additions, except for the Gulf Stream stations, which showed a significant response to both N, P, and N + P additions. Due to differences in the light regime among sites during incubations, the magnitude of the responses cannot be compared among sites.

Discussion

We have previously documented general differences in elemental stoichiometry between marine and freshwater systems, in which imbalances in N:P between seston and zooplankton were positive (seston N:P > zooplankton N:P) in freshwater systems and negative in marine systems, as well as being of greater magnitude in freshwater systems (Elser and Hassett 1994). These results indicated that consumer-driven recycling ratios in freshwater systems would be 4–6 times higher than in marine systems. Our present results

Table 5. Results of multiple regression model of percent contribution to biomass by taxa vs. stoichiometric parameters. *P*-values for coefficients given in parentheses.

	R^2	*P*	Intercept	*Daphnia*	Non-daphnid cladocerans	Calanoid copepods	Cyclopoid copepods
Freshwater (4,29)							
Seston C:P	0.34	0.015	323	−46.7 (0.01)	5.27 (ns)	33.6 (0.03)	16.8 (ns)
Seston N:P	0.33	0.019	41.7	−4.28 (0.002)	0.235 (ns)	2.72 (0.02)	1.30 (ns)
Total N:P	0.60	0.001	55.4	−0.703 (ns)	−3.09 (0.006)	6.36 (0.02)	−0.423 (ns)
N:P imbalance	0.29	0.035	26.1	−4.44 (0.006)	0.088 (ns)	3.031 (0.02)	1.11 (ns)
N:P recycled	0.31	0.026	115	−18.8 (0.002)	2.54 (ns)	11.4 (0.02)	4.69 (ns)

	R^2	*P*	Intercept	Calanoid copepods	Cyclopoid copepods	Harpacticoid copepods	Total nauplii	Salps larvaceans
Marine (5,10)								
Total N:P	0.78	0.001	−148	48.0 (0.006)	−38.4 (0.001)	−17.7 (ns)	3.08 (0.05)	−1.35 (ns)

point to several other important distinctions in the stoichiometric relationships between marine and freshwater systems, as well as between lake districts (Canadian ELA lakes vs. the NTL of northern Wisconsin and Michigan) and marine habitats (estuarine vs. coastal-oceanic).

Comparisons between lake regions—The two lake districts were relatively similar for most parameters. However, the Canadian ELA lakes were relatively P-poor, resulting in a higher seston C:P and total N:P ratio than in the Wisconsin–Michigan lakes. The ELA lakes also had a relatively low zooplankton biomass. The multiple regression model indicates that *Daphnia* spp., which have low body N:P (Andersen and Hessen 1991), tend to occur in lakes with low seston N:P. Conversely, calanoid copepods, which have higher body N:P (Andersen and Hessen 1991), tend to occur in lakes with high seston N:P. If zooplankton were mediating seston N:P through nutrient recycling (Elser et al. 1988), we would predict that *Daphnia* and calanoid copepods would be driving lake seston toward high and low N:P, respectively, the opposite of what was observed. Zooplankton recycling therefore does not seem to be driving broadscale patterns in seston C:P and N:P ratios. Rather, the observations would suggest that the zooplankton community is likely to have an N:P ratio more similar to the seston N:P, which, together with the prevalence of seston C:P ratios above the incipient limiting ratio for zooplankton growth (Elser and Hassett 1994), argues for the importance of P- based food quality constraints on the zooplankton communities of lakes.

The question remains as to what is driving variation in seston C:P ratios in pelagic ecosystems. R. W. Sterner et al. (in press) propose a light–nutrient hypothesis whereby seston C:P is driven by the interaction between light intensity and nutrient (P) supply in the mixed layer. When light penetration is relatively deep compared to mixed-layer depth, P supply becomes limiting and high seston C:P results. Converse-

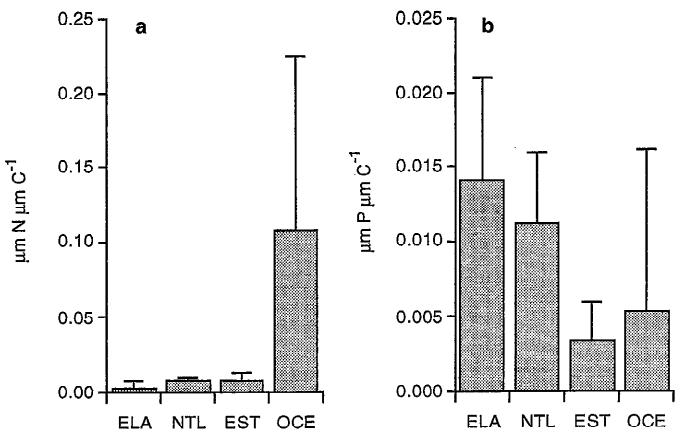

Fig. 8. N debt and P debt as measured by dark uptake of N (P) normalized to seston C. Only those sites in which nutrient uptake occurred are included. The number of such sites is given in Table 6.

Table 6. Frequency of responses in nutrient-debt experiments in different regions. + indicates nutrient uptake was observed; "deficient" indicates that uptake exceeded values of N debt:Chl a > 0.15 μm N (μg Chl a)$^{-1}$ and P debt:Chl a > 0.075 μm P (μg Chl a)$^{-1}$ used by Healey and Hendzel (1980) as indicators of phytoplankton nutrient deficiency.

		N		P	
Region	Total sites	+	Deficient	+	Deficient
ELA	9	3	0	9	9
NTL	25	13	0	24	9
EST	11	6	0	10	1
OCE	10	4	2	4	0

ly, if light penetration is shallow compared to mixed-layer depth, phytoplankton growth is light-limited and nutrient deficiency is weak, resulting in a lower seston C:P. To test this idea with out lake data, we calculated an index of the relative balance of light and nutrient supply in the following way. We calculated the mean light intensity in the mixed layer (I_m) by using the equation of Sterner (1990*a*) and by using data for light extinction and mixed-layer depth for dates closest to our sampling dates. As an index of nutrient supply we used the total phosphorus concentration. We found a strong correlation ($P < 0.001$, $r^2 = 0.45$) between seston C:P and I_m:TP. It seems that lakes of the Canadian Shield at ELA have higher seston C:P values than do lakes of northern Wisconsin (Fig. 4) because ELA lakes have a more imbalanced supply of light and nutrients for phytoplankton growth. Thus, mechanisms affecting light and nutrient supply in lakes appear to be an important factor in establishing the food quality of the seston and thus in imposing stoichiometric constraints on the zooplankton community.

Comparisons between estuaries and oceans—Both estuarine and coastal-oceanic sites were characterized by relatively low zooplankton biomass and small-bodied zooplankton communities compared to lakes, with little N or P in the zooplankton pool and low C:P and N:P ratios in the seston. Estuaries, however, had higher total N and P and a higher percentage of nutrients in the seston pool, similar to that of lakes. The estuarine sites were essentially in stoichiometric balance between seston and zooplankton, in contrast to the negative imbalance (seston N:P < zooplankton N:P) of coastal-oceanic sites and positive imbalance of lakes. Evidence of N deficiency was indicated at 2 of 11 coastal-oceanic sites, but no estuarine sites, based on the nutrient-debt criteria of Healey and Hendzel (1980). P deficiency was indicated in none of the coastal-oceanic sites and in 1 of 11 estuarine sites.

In both marine and freshwater systems, the total N:P (dissolved + seston + zooplankton) at all sites was greater than the Redfield ratio of 16:1. Due to the dominating contribution of dissolved N and P pools to total N:P ratio in coastal and oceanic marine systems, dissolved N:P is the primary determinant of total N:P. In deep-ocean and open-ocean waters, TDN:TDP ratios are typically near Redfield (Martin et al. 1987). At the US-JGOFS station in the oligotrophic North Pacific (22°45′N, 158°W), for instance, 22 vertical profiles yielded a consistent TDN:TDP of 17:1, with no significant difference between the shallow (0–200-m) samples and the total data base (0–4,500 m), although more variability was observed in surface waters (Karl et al. 1993). With minor contribution expected from seston and zooplankton, total N:P at the US-JGOFS station would be near the Redfield ratio, in contrast to the marine systems we sampled. For sites in which we have inorganic nitrogen (nitrate and ammonium) estimates (Gulf of California and North Inlet sites), it would seem that the bulk of TDN is organic (DON), typical of marine environments (Sharp 1983). Our measurements at North Inlet sites are in close agreement with values reported by Wolaver et al. (1984) for the same area during late summer (TDN ~25–40 μM, TDP ~0.4–0.8 μM, seston N ~12–15 μM, seston P ~1.0–1.2 μM, compared to our average values of TDN = 37, TDP = 0.4, seston N = 16, seston P = 0.8), so we do not think there is a systematic error in our TDN or TDP measurements. Sharp (1983) noted that DON:DOP ratios are typically higher in coastal than oceanic waters, which may explain the discrepancy between TDN:TDP values we observed and near-Redfield values observed by Karl et al. (1993) in oligotrophic ocean waters.

The largest pool for both N and P is the dissolved pool, and, as discussed above, oceanic total N:P values, in general may be less than what we measured in our primarily coastal and estuarine survey. Knauer et al. (1979) found that in coastal water under upwelling conditions, N:P of sinking particles was ~18 (about equivalent to seston N:P), but in open ocean and nonupwelling conditions N:P of settling particles is greater (~30). The near-Redfield N:P ratios in open-ocean and deep-ocean waters (Martin et al. 1987) implies a more efficient retention of phosphorus within surface waters of the open ocean or under nonupwelling conditions, consistent with observations of fast recycling of phosphorus relative to nitrogen in decomposing phytoplankton (Grill and Richards 1964). The negative N:P imbalance in the marine phytoplankton–zooplankton stoichiometry would tend to accentuate N limitation due to the relatively greater N demand of zooplankton compared to P (Elser and Hassett 1994). However, recycling by microzooplankton and bacteria could produce an opposing trend, due to low body N:P relative to seston (Skjøldal 1993). Bacterial N:P is a critical factor in determining the functional role of bacteria in nutrient cycling (Elser et al. 1995; Tezuka 1990). In the high total N:P systems we sampled, bacterial recycling would be expected to sequester P and release N, on balance, assuming the total N and P in the system are equally available. This may have been occurring in east Long Lake in 1993, where very high ammonia production was observed in the <1-μm seston size fraction (presumably representing bacterial recycling) as well as phosphate uptake in the same size fraction. The seston in east Long Lake had low C:N (4,6), high C:P (257), high N:P (56), and a positive response to P addition in the dilution bioassay, all indicating strong P limitation. In the marine (Gulf Stream) sites in which P uptake occurred in the nutrient debt experiments and where size fractionation was performed, it was the <1-μm fraction that was responsible for the uptake. Thus, in microbial food-web-dominated marine systems, stoichiometric relationships could accentuate phosphorus limitation, as seems to occur in the Mediterranean Sea (Thingstad and Rassoulzadegan 1995).

Hecky and Kilham (1988) made the point that evidence for N limitation in oceans is not as strong as that for P limitation in lakes, as the range of experimental scales in marine systems is more limited. Marine mesocosm-scale experiments that demonstrate N limitation (e.g. Oviatt et al. 1995) are essentially conducted under coastal-estuarine conditions and may involve very different stoichiometric constraints than corresponding open-ocean conditions. In light of the recent recognition of the potential for shifts between N and P limitation in the oligotrophic open ocean (Karl et al. 1995), the stoichiometric relationships involved in the microbial food web could be a significant factor in the transition.

Comparisons between lakes and oceans—Between-system differences (freshwater vs. marine) in both the concentrations and stoichiometry of N and P were more frequently observed than differences within systems (ELA vs. NTL, EST vs. OCE). A notable difference was that a much greater percentage of N and P was incorporated in seston and zooplankton pools in freshwater systems than in coastal-oceanic systems, with estuarine systems being intermediate. The difference was especially notable for zooplankton contribution, which was very small in marine sites.

In coastal and oceanic marine sites, vertical migration of zooplankton might lead to an underestimate of total mixed-layer zooplankton in our daytime sampling. For instance, at the BIOSTAT station in the eastern tropical Pacific (9°45′N, 93°45′W) there was a fourfold increase in biomass in the mixed layer at night (Sameoto 1986). However, even allowing for such an increase in zooplankton in the mixed layer, the contribution of the zooplankton pool to total phosphorus would be only ~1% for our southeast Pacific stations. It is therefore doubtful that zooplankton contribute significantly as a pool for N or P in our marine systems, whereas in some lakes 50% or more of total phosphorus resides in zooplankton. Also of note is that in all regions sampled (ELA, NTL, estuarine, and coastal-oceanic) at least twice as much P (as a fraction of total P in each system) was incorporated in particulates (seston + zooplankton) as was N.

Although our sampling range is necessarily limited in scope, these patterns are consistent with literature values covering a broader range. Lake seston N:P are generally greater than the Redfield ratio of 16:1, often far greater, over a broad range of lake systems (N:P 13–51, Hecky et al. 1993). N:P of lake zooplankton species has been found to vary over a similarly wide range (N:P 14–39; Andersen and Hessen 1991). In contrast, marine seston N:P has consistently been found to be near the Redfield ratio, varying over a much smaller range (e.g. LeBorgne 1982; Copin-Montegut and Copin-Montegut 1983; Karl et al. 1995). For instance, seston N:P in the eastern tropical Atlantic Ocean varied spatially across a range of 14–24 (LeBorgne 1982), and seston N:P in the North Pacific subtropical gyre shifted across a decadal time scale from 14 to 19 (Karl et al. 1995). Marine zooplankton N:P has consistently been found to be higher than Redfield (e.g. N:P = 21 for *Calanus finmarchicus* [Vinogradov 1953; Butler et al. 1969], 27 for copepods in the Sargasso Sea [Beers 1966], 24 for zooplankton of Long Island Sound [Harris and Riley 1956], and, in the Antarctic, 40 for copepods, 30–39 for salps, and 20–30 for *Eupahausia superba* [Ikeda and Mitchell 1982]). In an extensive field study by LeBorgne (1982), zooplankton N:P at 42 stations in the eastern tropical Atlantic Ocean varied across a range of 19–27, with an average of 24. Zooplankton N:P was greater than seston N:P at all 42 stations sampled. Thus, the general patterns we observe with respect to freshwater and marine stoichiometry are probably not affected by our limited sampling scheme, at least when considering temperate freshwater and marine systems. However, Ikeda and Mitchell's (1982) data for Antarctic zooplankton suggest that copepod-dominated water columns in Antarctic waters may, in fact, have a large stoichiometric imbalance, assuming seston N:P is near the Redfield ratio in the Antarctic.

Calculations of recycling ratios for different accumulation efficiencies *ae* indicate that varying zooplankton *ae* will have a much greater effect on lake nutrient recycling than on ocean recycling. Accumulation efficiencies can also vary markedly depending upon food source (e.g. Wang et al. [1996] found carbon *ae* between 70 and 94% depending upon phytoplankton food species). Furthermore, estimates of nutrient recycling ratios based on Sterner's (1990*b*) equations assume that both elements are accumulated by the consumer with equal efficiencies, which may not be a realistic assumption. Under the typical freshwater conditions of our study (seston N:P $\gg$ zooplankton N:P), much of the N ingested cannot be used if the consumer is to maintain homeostatic body N:P. P accumulation efficiency (P*ae*) should be maximized, particularly if zooplankton are P limited, but there would be little benefit from increasing N accumulation efficiency (N*ae*) except under circumstances of very low N*ae* (e.g. <0.3–0.4), because N would have to be excreted to maintain homeostatic N:P. Thus, we would expect any differences in *ae* to most likely lead to higher N:P recycled in lakes. Conversely, in marine systems (seston N:P < zooplankton N:P), there would be more benefit in maximizing N*ae*, although because marine systems are more stoichiometrically balanced, differences between N*ae* and P*ae* would be expected to be small. Thus, changes in zooplankton and phytoplankton community composition and differences in zooplankton N and P assimilation efficiencies both may have a more pronounced effect on recycling ratios in lakes than in oceans.

Our bottle incubation experiments, both N–P debt (*see also* Elser and Hassett 1994) and chlorophyll bioassay, tend to support the view that nutrient deficiency was more severe in the freshwater systems we studied than in the marine systems, as the frequency of both growth response and nutrient uptake was higher in the freshwater systems. Although our N–P debt data also indicate that our ocean sites were on average N deficient and lakes P deficient, the frequency of observations of deficiency was much greater in lakes. Stoichiometric data are consistent with this interpretation. Healey and Hendzel (1980) categorized phytoplankton nutrient deficiency based on the stoichiometry of C, N, P, and Chl *a*. In our study, lake sites at both ELA and NTL would be categorized as severely (N:P >22, C:P >258) or moderately (C:N 8.3–14.6, C:Chl *a* 4.2–8.3) nutrient deficient. Estuarine and coastal-oceanic sites would be categorized as either moderately deficient (C:P 129–258) or not deficient (N:P <22, C:N <8.3, C:Chl *a* <4.2). Nixon and Pilson (1983) concluded that marine systems tend to respond less strongly to N input than lakes do to P input, consistent with both the stoichiometry and nutrient-deficiency experiments in our study.

Smith (1984) and Hecky and Kilham (1988) both cautioned about extrapolating the results of bottle experiments, which isolate a portion of the ecosystem, to the whole ecosystem with its multitude of inputs. Bottle experiments only can demonstrate the potential for nutrient limitation at a larger scale (Hecky and Kilham 1988). Also, our chlorophyll bioassay experiments were incubated under ambient light, and light limitation could potentially be responsible for the infrequent growth response in these experiments. Thus, it is important to see the nutrient-deficiency experiments in light of the broader stoichi-

ometric relationships. The stoichiometric relationships previously discussed support the argument that lakes are more nutrient deficient than marine waters. Also, the high proportion of N, and particularly P, bound in particulate (seston + zooplankton) matter in lakes compared to oceans is consistent with a relatively greater degree of nutrient limitation, and especially limitation by P, in lakes. Similarly, the greater N:P imbalances between seston and zooplankton in the freshwater systems argue for a greater potential for zooplankton to alter nutrient recycling ratios in lakes than in the marine systems we sampled (Elser and Hassett 1994), although our results do not support zooplankton recycling as a mechanism for determining broad-scale patterns in N:P stoichiometry. These observations may help explain why phosphorus limitation of phytoplankton growth in lakes can be more readily demonstrated than growth limitation by N in the ocean (Hecky and Kilham 1988).

We have found that the quantity, relative amount, and ratio of N and P stored in major pelagic pools differ markedly for marine and freshwater ecosystems, as well as between oceanic and estuarine environments. The most notable features are the high proportion of P incorporated in particulate matter in lakes and the high proportion of dissolved N and P in oceanic systems. Estuaries appear to be intermediate between lakes and oceans, being more similar to the oceans stoichiometrically (similar seston and total N:P) and more similar to lakes in the amount of N and P in the different pools. The distribution of nutrient elements within particulate and dissolved pools represents a fundamental qualitative difference between freshwater and marine systems. The high C:N and C:P and the high proportion of N and P in particulate matter in freshwater compared to marine environments support the view that lakes are in general more nutrient deficient than oceans. Nutrient deficiency was most pronounced in lakes lacking large piscivores, i.e. in shallow planktivore-dominated lakes, trout-stocked lakes, and bogs.

Zooplankton recycling does not seem to be driving seston C:P and N:P ratios in our sampled lakes. However, P-based food quality effects may be an important constraint on the zooplankton community of these lakes (Elser and Hassett 1994). Multiple regression analysis indicates that low N:P zooplankton taxa (*Daphnia*) tend to be found in low seston N:P lakes, and high N:P zooplankton (copepods) in high seston N:P lakes, the opposite of what would be predicted if zooplankton stoichiometry were driving seston N:P ratios (see Elser et al. 1988; Urabe et al. 1995) but consistent with a food-quality effect. Such differences may reflect the scale of the studies—our broad survey of a relatively wide range of lakes vs. in-depth temporal studies at a single location. The frequent high C:P ratios observed in the lakes of the Canadian shield is a dominant factor in our study and leads to our interpretation of strong food-quality limitation of the zooplankton community. Within the context of the seasonal dynamics of a given lake, zooplankton recycling may be important (e.g. Elser et al. 1988; Urabe et al. 1995; Urabe 1993, 1995), and such recycling would be consistent with our observation of the high percentage of nutrient elements, particularly P, incorporated in zooplankton biomass in lakes. Finally, based on calculated N:P recycling ratios we previously concluded that zooplankton would tend to accentuate P limitation in lakes and N limitation in oceans (Elser and Hassett 1994). However, the potential exists for the microzooplankton grazers to exert an opposing effect in microbial food-web-dominated systems, tending to accentuate P limitation. Thus, elemental stoichiometry may impose important constraints on the functioning of food webs in different aquatic systems.

References

AMERICAN PUBLIC HEALTH ASSOCIATION. 1992. Standard methods for the examination of water and wastewater, 18th ed. APHA.

ANDERSEN, T., AND D. HESSEN. 1991. Carbon, nitrogen and phosphorus content of freshwater zooplankton. Limnol. Oceanogr. **36:** 807–814.

BEERS, J. R. 1966. Studies on the chemical composition of the major zooplankton groups in the Sargasso Sea off Bermuda. Limnol. Oceanogr. **11:** 520–528.

BUTLER, E. I., E. D. S. CORNER, AND S. M. MARSHALL. 1969. On the nutrition and metabolism of zooplankton. VI. Feeding efficiency of *Calanus* in terms of nitrogen and phosphorus. J. Mar. Biol. Assoc. U.K. **49:** 977–1001.

COLE, J. J., G. M. LOVETT, AND S. E. G. FINDLAY. 1991. Comparative analyses of ecosystems: Patterns, mechanisms, and theories. Springer.

COPIN-MONTEGUT, C., AND G. COPIN-MONTEGUT. 1983. Stoichiometry of carbon, nitrogen, and phosphorus in marine particulate matter. Deep-Sea Res. **30:** 31–46.

CURL, H. 1962. Standing crops of carbon, nitrogen, and phosphorus and transfer between trophic levels, in continental shelf waters south of New York. Rapp. P.-V. Reun. Cons. Int. Explor. Mer **153:** 183–189.

DAVIS, C. S. 1984. Predatory control of copepod seasonal cycles on Georges Bank. Mar. Biol. **82:** 31–40.

DOWNING, J. A. 1991. Comparing apples with oranges: Methods of ecosystem comparison, p. 24–45. *In* J. J. Cole et al. [eds.], Comparative analyses of ecosystems: Patterns, mechanisms, and theories. Springer.

ELSER, J. J., T. H. CHRZANOWSKI, R. W. STERNER, J. H. SCHAMPEL, AND D. K. FOSTER, 1995. Elemental ratios and the uptake and release of nutrients by phytoplankton and bacteria in three lakes of the Canadian shield. Microb. Ecol. **29:** 145–162.

———, AND R. P. HASSETT. 1994. A stoichiometric analysis of zooplankton–phytoplankton interactions in marine and freshwater systems. Nature **370:** 211–213.

———, M. ELSER, N. MACKAY, AND S. CARPENTER. 1988. Zooplankton-mediated transitions between N- and P-limited algal growth. Limnol. Oceanogr. **33:** 1–14.

GRILL, E. V., AND F. A. RICHARDS. 1964. Nutrient regeneration from phytoplankton decomposing in seawater. J. Mar. Res. **22:** 51–59.

HARRIS, E., AND G. A. RILEY. 1956. Oceanography of Long Island Sound, 1952–1959. VIII. Chemical composition of the plankton. Bull. Bingham Oceanogr. Collect. **15:** 315–323.

HEALEY, F. P., AND L. L. HENDZEL. 1980. Physiological indicators of nutrient deficiency in lake phytoplankton. Can. J. Fish. Aquat. Sci. **37:** 442–453.

HECKY, R. E., P. CAMBELL, AND L. L. HENDZEL. 1993. The stoichiometry of carbon, nitrogen, and phosphorus in particulate matter of lakes and oceans. Limnol. Oceanogr. **38:** 709–724.

HECKY, R., AND P. KILHAM. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. Limnol. Oceanogr. **33:** 796–822.

IKEDA, T., AND A. W. MITCHELL. 1982. Oxygen uptake, ammonia excretion and phosphate excretion by krill and other Antarctic

zooplankton in relation to their body size and chemical composition. Mar. Biol. **71:** 283–298.

KARL, D. M., AND OTHERS. 1995. Ecosystem changes in the North Pacific subtropical gyre attributed to the 1991–92 El Niño. Nature **373:** 230–234.

———, G. TIEN, J. DORE, AND C. D. WINN. 1993. Total dissolved nitrogen and phosphorus concentrations at US-JGOFS Station ALOHA: Redfield reconciliation. Mar. Chem. **41:** 203–208.

KNAUER, G. A., J. H. MARTIN, AND K. W. BRULAND. 1979. Fluxes of particulate carbon, nitrogen, and phosphorus in the upper water column of the northeast Pacific. Deep-Sea Res. **26:** 97–108.

LANDRY, M. R. 1978. Population dynamics and production of a planktonic marine copepod, *Acartia clausi,* in a small temperate lagoon on San Juan Island, Washington. Int. Rev. Gesamten. Hydrobiol. **63:** 77–119.

LEBORGNE, R. 1982. Zooplankton production in the eastern tropical Atlantic Ocean: Net growth efficiency and P:B in terms of carbon, nitrogen and phosphorus. Limnol. Oceanogr. **27:** 681–698.

LOTKA, A. J. 1924. Elements of physical biology. Williams and Wilkins.

MALLEY, D. F., S. G. LAWRENCE, M. A. MACIVER, AND W. J. FINDLEY. 1989. Range of variation in estimates of dry weight for planktonic crustacea and rotifera from temperate North American lakes. Can. Tech. Rep. Fish. Aquat. Sci. No. 1666. 49 p.

MARKER, A. F. H., E. A. NUSCH, H. RAI, AND B. RIEMANN. 1980. The measurement of photosynthetic pigments in freshwaters and standardization of methods: Conclusions and recommendations. Ergeb. Limnol. **14:** 91–106.

MARTIN, J. H., G. A. KNAUER, D. M. KARL, AND W. W. BROENKOW. 1987. VERTEX: Carbon cycling in the Northeast Pacific. Deep-Sea Res. **34:** 267–285.

MILLER, J. K. 1966. Biomass determinations of selected zooplankters found in the California Cooperative Oceanic Fisheries Investigations. Scripps Inst. Oceanogr. SIO Ref. 66–15. 16 p.

NIXON, S. W. 1988. Physical energy inputs and the comparative ecology of lake and marine ecosystems. Limnol. Oceanogr. **33:** 1005–1025.

———, AND M. E. Q. PILSON. 1983. Nitrogen in estuarine and coastal marine ecosystems, p. 565–648. *In* E. J. Carpenter and D. G. Capone [eds.], Nitrogen in the marine environment. Academic.

OMORI, M. 1969. Weight and chemical composition of some important oceanic zooplankton in the North Pacific Ocean. Mar. Biol. **3:** 4–10.

O'NEILL, R., D. DEANGELIS, J. PASTOR, B. JACKSON, AND W. POST. 1989. Multiple nutrient limitations in ecological models. Ecol. Model. **46:** 147–163.

OVIATT, C., AND OTHERS. 1995. An ecosystem level experiment on nutrient limitation in temperate coastal and marine environments. Mar. Ecol. Prog. Ser. **116:** 171–179.

PETERS, R. H., AND OTHERS. 1991. On the relevance of comparative ecology to the larger field of ecology, p. 46–63. *In* J. J. Cole et al. [eds.], Comparative analyses of ecosystems: Patterns, mechanisms, and theories. Springer.

RAHEL, F. J. 1984. Factors structuring fish assemblages along a bog lake successional gradient. Ecology **63:** 1276–1289.

REINERS, W. A. 1986. Complementary models for ecosystems. Am. Nat. **127:** 59–73.

ROOT, R. B. 1987. The challenge of increasing information and specialization. Bull. Ecol. Soc. Am. **68:** 538–543.

SABITINI, M., AND T. KIØRBOE. 1994. Egg production, growth and development of the cyclopoid copepod *Oithona similis.* J. Plankton Res. **16:** 1329–1351.

SAMEOTO, D. D. 1986. Influence of the biological and physical environment on the distribution of mesozooplankton and micronekton in the eastern tropical Pacific. Mar. Biol. **93:** 263–279.

SHARP, J. H. 1983. The distribution of inorganic nitrogen and dissolved and particulate organic nitrogen in the sea, p. 1–35. *In* E. J. Carpenter and D. G. Capone [eds.], Nitrogen in the marine environment. Academic.

SKJØLDAL, H. R. 1993. Eutrophication and algal growth in the North Sea, p. 445–478. *In* Symp. Mediterranean Seas 2000. Univ. Genoa.

SOLÓRZANO, L. 1969. Determination of ammonia in natural waters by the phenol–hypochlorite method. Limnol. Oceanogr. **14:** 799–801.

SMITH, S. V. 1984. Phosphorus versus nitrogen limitation in the marine environment. Limnol. Oceanogr. **29:** 1149–1160.

STERNER, R. W. 1990*a*. Lake morphometry and light in the surface layer. Can. J. Fish. Aquat. Sci. **47:** 687–692.

———. 1990*b*. The ratio of nitrogen to phosphorus resupplied by herbivores: Zooplankton and the algal competitive arena. Am. Nat. **136:** 209–229.

———, J. J. ELSER, E. J. FEE, S. J. GUILFORD, AND T. H. CHRZANOWSKI. 1997. The light:nutrient ratio in lakes: The balance of energy and materials affects ecosystem structure and process. Am. Nat. In press.

———, ———, AND D. HESSEN. 1992. Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. Biogeochemistry **17:** 49–67.

STRICKLAND, J., AND T. PARSONS. 1972. A practical handbook of sea-water analysis. Bull. Fish. Res. Bd. Can. 167.

TEZUKA, Y. 1990. Bacterial regeneration of ammonium and phosphate as affected by the carbon:nitrogen:phosphorus ratio of organic substrates. Microb. Ecol. **19:** 227–238.

THINGSTAD, T. F., AND F. RASSOULZADEGAN. 1995. Nutrient limitations, microbial food webs, and 'biological pumps': Suggested interactions in a P-limited Mediterranean. Mar. Ecol. Prog. Ser. **117:** 299–306.

TONN, W. M., AND J. J. MAGNUSON. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin Lakes. Ecology **63:** 1149–1166.

URABE, J. 1993. Coupling N to P cycling through grazers' activities: Food quality and nutrient release by zooplankton. Ecology **74:** 2337–2350.

———. 1995. Direct and indirect effects of zooplankton on seston stoichiometry. Ecoscience **2:** 286–296.

———, M. NAKANISHI, AND K. KAWABATA. 1995. Contribution of metazoan plankton to the cycling of nitrogen and phosphorus in Lake Biwa. Limnol. Oceanogr. **40:** 232–241.

VINOGRADOV, A. P. 1953. The elementary composition of marine organic matter. Mem. Sears Found. Mar. Res. 2. 647 p.

VITOUSEK, P. M. 1977. The regulation of element concentrations in mountain streams in the northeastern United States. Ecol. Monogr. **47:** 65–87.

VOLLENWEIDER, R. A. 1976. Advances in defining critical loading levels of phosphorus in lake eutrophication. Mem. Ist. Ital. Idrobiol. **33:** 53–83.

WANG, W.-X., J. R. REINFELDER, B.-G. LEE, AND N. S. FISHER. 1996. Assimilation and regeneration of trace elements by marine copepods. Limnol. Oceanogr. **41:** 70–81.

WOLAVER, T. G., W. JOHNSON, AND M. MAROZAS. 1984. Nitrogen and phosphorus concentrations within North Inlet, South Carolina—Speculation as to sources and sinks. Estuarine Coastal Shelf Sci. **19:** 243–255.

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