

by the alisphenoid)²². Moreover, the dental formula and the twinned entoconid and hypoconulid (present in all known marsupials) are perhaps the least ambiguous other synapomorphies that could diagnose marsupials, both fossil and recent, although we know that they are (respectively, possibly and certainly) homoplastic. □

Received 9 February; accepted 16 June 1994.

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ACKNOWLEDGEMENTS. I thank R. Suarez Soruco for his help in the preparation of the 1992 field season and R. Cespedes Paz and J. Jacay Huaraché who participated in the field expedition during which the type specimen of *Mayulestes ferox* was discovered. The research was supported by the Institut Français d'Etudes Andines. R. Emry, M. Novacek and J. Ostrom gave access to collection under their care. Valuable insights were given by R. Cifelli, R. Emry, M. Novacek, D. Sigogneau-Russell, F. Szalay and J. Wible. Illustrations are by M. Parrish (USNM, Washington) and photographs by D. Serrette (MNHN, Paris).

A stoichiometric analysis of the zooplankton–phytoplankton interaction in marine and freshwater ecosystems

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In the 35 years since A. C. Redfield's classic paper¹, the use of elemental ratios has become widespread in marine and freshwater phytoplankton studies^{2,3}. But nutrient ratios have only recently been studied elsewhere in pelagic ecosystems, such as the producer–consumer interface^{4,5}. Here we report the results of the first study, to our knowledge, of N:P ratios in pelagic producers and consumers (phytoplankton and zooplankton) in lacustrine and marine habitats. The N:P ratio of phytoplankton was higher in lakes than in marine sites; however, N:P ratios were higher in marine zooplankton than in freshwater zooplankton. The elemental imbalance of the phytoplankton–zooplankton interaction ($N:P_{\text{food}} - N:P_{\text{consumers}}$) in lakes was positive and exceeded the negative imbalance in marine sites; thus P-deficient food may limit zooplankton growth in lakes but not in oceans. Stoichiometric calculations⁶ indicated that consumer-driven nutrient recycling ratios in lakes may be 4–6 times higher than in marine systems. Consistent with this difference, phytoplankton P-limitation was more prevalent in lakes than in marine sites. Thus, the ecological stoichiometry of the zooplankton–phytoplankton interaction differs qualitatively in freshwater and marine ecosystems.

During the summers of 1992 and 1993, we sampled lakes of varying size, trophic state and food web structure in northern Wisconsin and Michigan (USA) and northwestern Ontario (Canada) as well as nearshore and offshore marine sites in the Atlantic and Pacific oceans (Table 1). At each site, we measured N:P ratios (N:P) in suspended particulate material that passed through an 83 µm mesh (seston, assumed to be dominated by phytoplankton) and in zooplankton (collected with a 153-µm mesh tow net) in the surface layers. We compared zooplankton N:P and phytoplankton N:P to determine if the nutrient stoichiometry of the producer–consumer interaction differs between

these ecosystem types, and thus, whether zooplankton in lakes and oceans face different food quality constraints and differ qualitatively in their N and P recycling. We also assessed N and P limitation of phytoplankton growth to determine if nutrient limitation patterns reflect the potential differential effects of zooplankton on N and P availability in lakes and oceans.

Freshwater and marine sites differed in the N:P of both seston and zooplankton. Lake seston had high N:P characteristic of P-limited growth⁷ whereas marine seston values were significantly lower ($P < 0.0001$; Fig. 1a) and similar to the Redfield ratio (16:1 by atoms¹). Unlike seston N:P, marine zooplankton N:P exceeded the N:P of freshwater zooplankton ($P = 0.054$; Fig. 1b). Although little data exist regarding species-specific N:P for marine or freshwater taxa, this difference in zooplankton N:P is consistent with what little is known about zooplankton N:P ratios. Marine zooplankton N:P encompassed values previously reported for various copepod species^{8,9}; freshwater N:P approached the low N:P of various cosmopolitan cladoceran taxa⁸, especially *Daphnia* (atomic N:P of 12–15⁸), a conspicuous member of the zooplankton in most of the study lakes. Differences in zooplankton size structure may also have contributed to the difference in zooplankton N:P in lakes and oceans. We measured zooplankton N:P in four size classes between 153 µm and 1,050 µm for a small subset of our sites. For both lacustrine and marine sites, large size-classes had lower N:P than small size-classes. Thus, zooplankton from lakes may have been more strongly skewed towards large animals than the marine zooplankton.

We characterized the stoichiometry of the phytoplankton–zooplankton interaction by calculating the elemental imbalance between producers and consumers for each site ($N:P_1 = N:P_{\text{seston}} - N:P_{\text{consumers}}$). In lakes, $N:P_1$ was positive and substantially exceeded the negative $N:P_1$ of marine sites ($P < 0.0001$; Fig. 1c). Seston N:P exceeded zooplankton N:P for 29 of the 30 lake observations, but for only 4 of the 14 marine samples. The elemental imbalances between producer and consumer demonstrated here apply only to the larger metazoan zooplankton captured with the 153-µm net. In many ecosystems, especially oligotrophic oceanic areas²², microconsumers are important grazers and might therefore contribute to the particulate matter collected in our seston fraction, especially in offshore marine sites. This potential contribution is, however, unlikely to alter the habitat difference in producer–consumer elemental imbalance as, based on our size fractionation studies, microconsumers are

TABLE 1 Sampling site summary

Lakes	No. of sites	TP (μM)*	TN (μM)†	Chl ($\mu\text{g l}^{-1}$)‡
Northern Lakes Long-Term Ecological Research Site (northern Wisconsin, USA)	18	0.15–0.63	13.4–65	2.35–58.94
University of Notre Dame Environmental Research Center (Upper Peninsula, Michigan, USA)	9	0.25–0.79	12.1–46.8	3.89–17.25
Experimental Lakes Area (northwestern Ontario, Canada)	9	0.057–1.06	15.9–83.8	0.57–22.4
Marine and Estuarine sites				
North Inlet Long-Term Ecological Research Site (South Carolina, USA)	3	0.37–0.92	37.5–56.0	22.5–43.8
Long Island Sound (Stony Brook Harbor, Flax Pond; New York, USA)	2	2.04–2.16	41.9–46.6	3.01–3.91
Damariscotta River Estuary (Maine, USA)	2	1.01–1.10	33.7–33.9	—
Gulf Stream, western Atlantic Ocean (4–40 km off Melbourne; Florida, USA)	4	0.18–0.43	35.0–41.9	0.71–1.01
Gulf of California (5–10 km off Puerto Penasco; Sonora, Mexico)	3	1.11–1.24	36.0–29.6	5.90–10.8
Southeast Pacific Ocean (26°31'277"–27°12'80"N/123°1'120"–121°4'117" W)	3	0.49–0.58	37.3–39.4	1.00–1.16

Locations, number of sites sampled in the vicinity of each location, limits of nutrient concentrations (TP, total P; TN, total N), and limits of phytoplankton biomass (as indicated by chlorophyll concentration) are given.

* TP is the sum of total dissolved P, determined colorimetrically after ultraviolet oxidation²⁰, and particulate P, determined by colorimetric analysis of P after persulphate oxidation²⁴ of material filtered onto precombusted glass-fibre filters (0.7 μm porosity).

† TN is the sum of total dissolved N, determined colorimetrically after ultraviolet oxidation²⁰, and particulate N, determined by elemental analysis of material filtered onto precombusted glass-fibre filters (0.7 μm porosity).

‡ Chlorophyll concentrations were determined fluorometrically²¹ using methanol extracts of material filtered on glass-fibre filters (0.7 μm porosity).

likely to have high N:P ratios. The potential disproportionate contribution of microconsumers to marine seston values would therefore only imply that actual marine imbalances are even more strongly negative than we measured.

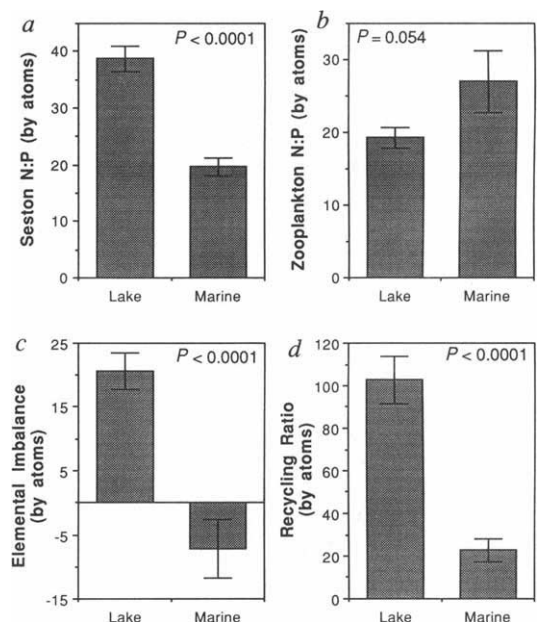
Strong differences in elemental ratios between producers and consumers affect both consumer individuals and the ecosystem. For individuals, mineral (especially P) limitation of zooplankton growth occurs when food has insufficient nutrient (P) content^{10–12}, although this possibility is controversial^{13–15}. Our results indicate that elementally based food quality constraints are stronger in fresh water where P-limited phytoplankton growth results in food potentially deficient in P, especially for taxa like *Daphnia* with high P demands⁸. We compared seston

C:P ratios in our study lakes to threshold values^{10–12} indicative of P-limitation of growth of *Bosmina* and *Daphnia* (common freshwater zooplankters; Fig. 2). C:P ratios exceeded even the most conservative thresholds in the majority of our study lakes. Thus, P-limitation of zooplankton growth may be ubiquitous in lakes. We know of no studies establishing P-limitation thresholds for marine zooplankton species; however, marine seston C:P was considerably lower than C:P in the lakes sampled (Fig. 2) and thus P-based food quality constraints appear unlikely. The weaker elemental imbalance in marine sites (Fig. 1c) also indicates that food quality constraints based on elemental content are unlikely for marine zooplankton.

At the ecosystem level, consumer–producer differences in N:P

FIG. 1 N:P ratios (by atoms) characterizing the zooplankton–phytoplankton interaction in lakes and marine sites. a, N:P ratio of suspended particulate matter (seston). b, N:P ratio of zooplankton. c, Elemental imbalance ($N:P_i = N:P_{\text{seston}} - N:P_{\text{consumers}}$) between phytoplankton and zooplankton. d, Estimated N:P ratio of zooplankton-recycled nutrients calculated using stoichiometric theory⁶ ($N:P_{\text{recycled}} = N:P_{\text{seston}}(1-L) - LN:P_{\text{consumers}}/(1-L)$ when $N:P_i > 0$; $N:P_{\text{recycled}} = N:P_{\text{seston}}(1-L)/(1-LN:P_{\text{consumers}}/N:P_{\text{consumers}})$ when $N:P_i < 0$. L , Maximum accumulation efficiency). In this case, L was set at 0.75, a somewhat conservative value given data indicating that zooplankton feeding on P-deficient food reduce P-release to values approaching zero (that is, $L \approx 1.0$)¹². Error bars indicate ± 1 s.e. Data were first examined for normality and then log-transformed when necessary to stabilize the variance (seston N:P, zooplankton N:P, recycling N:P). For all variables except N:P_i, variances were uniform for the two groups. Means for lake and marine sampling sites were compared using a standard t-test or a t-test assuming unequal variances (N:P_i only). P values given reflect the results of these t-tests.

METHODS. Lake and marine seston values from each study site used in calculating these overall means were the mean of duplicate collections from the surface mixed layer at each sampling station. Particulate matter (pre-screened through 83- μm mesh to remove most larger zooplankton) was collected onto pre-combusted (24 h at 450 °C) glass-fibre filters (0.7 μm porosity) and analysed for P content by colorimetric means after persulphate oxidation²⁰, or for C and N using a Perkin-Elmer Model 2400 CHN analyser. Zooplankton data represent means from duplicate vertical tows made with a metered tow net constructed of 153- μm mesh. In lakes and shallow marine sites, tows were made from 0.5 m above the bottom to the surface. For deeper marine sites, tows encompassing the entire surface mixed layer were taken. 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 glass fibre filters. Filters with animals were dried (60 °C), reweighed, and analysed for P or N with the same methods used for seston. N:P ratio for zooplankton was then calculated for each duplicate net tow based on %P and %N per unit dry weight. The mean of these duplicates for each sampling site was used in calculating the overall means shown.

can affect the relative rates of nutrient recycling by zooplankton⁵. Metazoan zooplankton regulate their N and P content at fixed ratios^{8,12}. Thus, when consuming food with an N:P higher than their body N:P, animals will retain P and differentially recycle N. The converse occurs when animal N:P exceeds food N:P. Reflecting the mass balance of these processes, the N:P of potential zooplankton recycling can be calculated from food N:P and zooplankton N:P⁶. Recycling N:P was significantly ($P < 0.0001$) and substantially (4–6 times) higher for lakes than for marine sites (Fig. 1d). High N:P recycling ratios in lakes were reflected in assays of the relative degree of N and P limitation of phytoplankton (measurements of N and P uptake in the dark⁷): lake phytoplankton were significantly more P-deficient (relative to N) than marine phytoplankton (Mann-Whitney U-test, $P < 0.05$). This association of recycling N:P and phytoplankton nutritional status raises the issue of cause and effect. Whole-ecosystem and enclosure experiments in lakes have shown that shifts in the zooplankton community can change the element (N versus P) primarily limiting phytoplankton growth¹⁶. The correspondence between relative N versus P limitation and the stoichiometry of the zooplankton–phytoplankton interaction in marine and freshwater ecosystems is consistent with the suggestion that zooplankton recycling can qualitatively alter the relative availability of N and P. However, our results do not demonstrate that differences in phytoplankton nutrient limitation were caused by differential nutrient recycling but do indicate that the effect of zooplankton on N and P availability differed qualitatively in the marine and freshwater habitats sampled. In lakes, zooplankton nutrient recycling further accentuates P limitation of phytoplankton whereas in marine systems, zooplankton recycling of N and P is less disproportionate but may amplify N limitation.

Although Redfield's stoichiometric approach has provided insights into the coupling of biogeochemical cycles in the sea¹, ecological stoichiometry is still in its infancy¹⁷. However, increasing data demonstrate that studies of multiple elements can provide new insights into the processes affecting behavioural patterns, population regulation, and community interactions in

a variety of study organisms, from mammals¹⁸ to microorganisms¹⁹. In our study, analyses of the ratios of biologically important elements (C, N, P) in functionally dominant food web components lead us to conclude that the producer–consumer interaction differs qualitatively in marine and freshwater pelagic ecosystems. This difference probably results in contrasting dynamics of food quality and nutrient recycling at the zooplankton–phytoplankton interface in lakes and oceans. □

Received 3 February; accepted 3 June 1994.

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ACKNOWLEDGEMENTS. We thank the members of the Stoichiometry Research Team for much of the sampling and analyses necessary for this paper, especially B. Cardinale, J. Schampel and L. B. Stabler. This study was made possible by the cooperation and assistance of the captain and crew of the R. V. *Sprout* (Scripps Inst. of Oceanography), captain Charles Hatch of Indianland, Florida, and the staffs of the Experimental Lakes Area (Canada), the Northern Lakes and North Inlet LTER sites, the University of Notre Dame Environmental Research Center, the Darling Marine Center (University of Maine), the Marine Science Research Center (SUNY-Stony Brook), and the Center for the Ecology of Deserts and Oceans (Puerto Peñasco, Mexico). J. Collins, D. Schindler and R. Sterner commented on the manuscript. This work was supported by a US NSF grant to J.J.E.

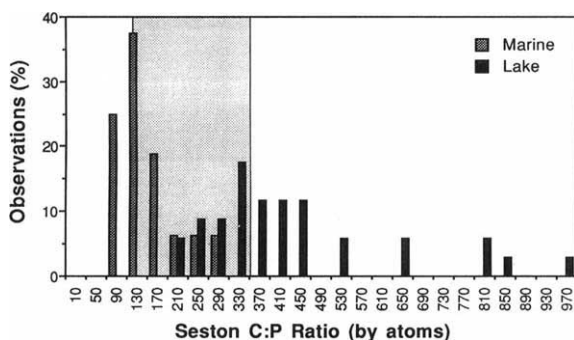


FIG. 2 Relative frequency of seston C:P ratios (by atoms) indicative of P-based food quality for zooplankton in lakes and marine sites. The boxed area indicates the range of values of recently published^{10–12} food C:P ratios indicative of a transition from C (energy)-limitation of zooplankton growth to limitation by P-content for two common freshwater zooplankton taxa (*Bosmina* sp. and *Daphnia* sp.). Values higher than this range indicate a strong potential for the occurrence of P-based food quality constraints on growth of these species. The majority of lakes sampled had seston C:P values higher than this range. High C:P ratios potentially reflect contributions of allochthonous detritus (high in C relative to P) rather than phytoplankton composition; we evaluated this possibility by calculating the C concentration of phytoplankton from directly measured chlorophyll concentrations using a C:chl ratio characteristic of P-limited phytoplankton (200:1 by mass⁷). These calculations indicated that chlorophyll-containing particles accounted for an average of 90% of the particulate C collected on filters. This indicates that allochthonous organic matter did not substantially interfere with our estimates of phytoplankton C:P.

The asexual ploidy cycle and the origin of sex

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SEX involves syngamy (gamete fusion), which doubles the amount of DNA in a cell, and meiosis¹, which halves it. The result is a 'ploidy cycle' of alternating diploid and haploid phases. Asexual reproduction does not require changes of ploidy, and yet asexual forms may have ploidy cycles. Here I show that such cycles lessen the mutation load, compared with permanent diploidy or polyploidy, and are thus likely to evolve in cases where it is always advantageous to have more than one copy of the genome per cell. The asexual ploidy cycle could have facilitated the origin of sex, by providing a means of orderly genetic reduction available immediately after the origin of syngamy.

The ploidy of some asexual forms may increase by endomitosis (replication not followed by cell division) and decrease by reduction (cell division not preceded by replication). This can cause variation of either the number of copies of the genome per nucleus (a ploidy cycle *sensu stricto*), of the number of nuclei per cell (a karyonic cycle), or both. Strict alternation of endomitosis and reduction leads to a haplo-diploid cycle, while successive endomitoses followed by reductions lead to complex cycles with polyploid phases. Mitoses may occur at some or all levels of ploidy^{2–4}.