

C:N:P Ratios of Benthic Marine Plants

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## C:N:P ratios of benthic marine plants<sup>1</sup>

**Abstract**—The median C:N:P atomic ratio of benthic marine macroalgae and seagrasses is about 550:30:1. Benthic plants are much more depleted in P and less in N, relative to C, than phytoplankton. The amount of nutrients required to support a particular level of net production is much lower for benthic marine plants than it is for phytoplankton.

A unifying concept in biological oceanography is commonly expressed in terms of the "Redfield ratio." As widely discussed (e.g. Redfield et al. 1963), the average carbon : nitrogen : phosphorus (C:N:P) atomic ratio of organisms in the sea is 106:16:1. This ratio is based on extensive analyses of marine plankton. A corollary to this standard compositional ratio of marine organisms is the observation that the net uptake and release of nutrients through biochemical processes in the sea

also tend toward this same ratio. The inorganic N:P ratio of deep ocean water is about 16:1, apparently as a result of the decomposition of organic materials to an inorganic nutrient end product. The inorganic C content of deep ocean water does not fit the Redfield ratio, because C is far more abundant in seawater (relative to the Redfield ratio) than either N or P.

Deviations of phytoplankton composition from the Redfield ratio are often used to infer the nutrient limiting the growth of these plants. Phytoplankton deprived of P during growth typically have N:P ratios >30:1, while phytoplankton deprived of N during growth have N:P ratios <10:1. C:N ratios and C:P ratios are similarly dependent on growth conditions. Goldman et al. (1979) reasoned that phytoplankton with a composition near the Redfield ratio are growing at their maximum rates.

There is some discussion about the most appropriate value for the average

<sup>1</sup>Hawaii Institute of Marine Biology Contribution 636.

phytoplankton C:N:P ratio. For example, data given by Parsons et al. (1961) and the discussion of Ryther and Dunstan (1971) suggest that the "ideal" N:P ratio of phytoplankton may be about 70:10:1, rather than 106:16:1. Despite such minor discrepancies, the Redfield ratio approximates plankton composition and is useful for comparison with other biological materials in the sea.

We document here that benthic macroalgae and seagrasses deviate markedly from the Redfield ratio in their C, N, and P composition and suggest that this deviation is ecologically significant.

This research was undertaken while both of us were at the University of Hawaii. Analytical methods used were developed by J. Szyper and T. Walsh. T. Walsh and G. Akiyama did the analyses. We thank the several individuals who supplied samples from around the world: C. Agegian, D. Bay, K. and E. Chave, I. Cooke, C. Crossland, M. Foster, L. Murray, S. Nixon, and M. Pichon. Ideas on the nutritional significance of benthic plant composition have particularly benefited from discussion with D. Karl and J. McLachlan. We thank R. Johannes for criticism of the manuscript.

Plants were collected; most epiphytic material was removed; the plants were rinsed quickly with freshwater, air-dried, oven-dried at 60°C, and then ground to a fine powder. Total C and N were measured on two aliquots of the sample with a Hewlett-Packard 185B CHN analyzer. One aliquot was burned at 500°C before analysis to oxidize all organic carbon, and the organic carbon content of the sample was calculated by difference between total carbon (organic C plus  $\text{CaCO}_3\text{-C}$ ) and the  $\text{CaCO}_3\text{-C}$  in the preburned sample (see Hirota and Szyper 1975). Total phosphorus was determined by digesting preweighed, finely ground material in boiling 7 N sulfuric acid. The solution was brought to a concentration of 0.5% (by wt) potassium persulfate in water and boiled again. Samples were then diluted with distilled water and analyzed for reactive phosphate using a single-solution molyb-

date, ascorbic acid reagent on a Technicon II autoanalyzer.

Some of the data presented here are extracted from the literature. The relevant literature data are surprisingly limited. The existence of CHN analyzers makes C:N ratios easily obtainable, hence widely available; however, much less information is available for P. Published data sets which include both N and P tend not to include C; some do include other elements (especially S, K, Mg, Ca, Na, Cl). For two such data sets (algae: Johnston 1971; seagrass: Birch 1975) we estimated the percent C to be the percent C in carbohydrate (about 40%) minus the summed weight percentages of the other elements. The average percent C estimated by this procedure was 27% of the dry weight. Because the C:N:P ratio of organic material is more sensitive to N and P than to C, the small difference between this estimated C percent and our measured C percent does not greatly influence the C:N:P ratio. We have therefore used this estimated organic C value in the absence of direct C data for comparison between our data and the literature data, and we have restricted our use of published data to tabulations which include both N and P.

The C, N, and P composition of benthic marine plants analyzed by us and others is presented in Table 1. Our data, as % C, C:N ratios, C:P ratios, and N:P ratios, are summarized in Fig. 1. The mean C:N:P ratio of 92 benthic plant samples from five phyla and nine locations worldwide (our data) is about 700:35:1; the median ratio is about 550:30:1. Both the mean and the median are well above the phytoplankton ratio (Redfield) of 106:16:1, with few individual analyses of benthic plants as low as the Redfield ratio. The mean ratio for 26 literature values is 430:17:1. The wide range in C:N:P ratios is probably caused by differences in environmental conditioning. Because the plants were collected from nine different locations at different seasons, they surely had large differences in their nutrient, light, temperature, and water motion precon-

Table 1. Percent of plant dry weight and atomic C:N:P ratios in marine macroalgae and seagrass.

Taxon	Plant part	Phylum*	Locality	% C†	C:N:P‡	References§
<i>Acanthophora spicifera</i>		R	Hawaii	33	555:38:1	
<i>A. spicifera</i>		R	N. Queensland	29	1,093:62:1	
<i>Alaria crassifolia</i>		P	Japan	—	143:16:1	Johnston 1971
<i>Amphibolis griffithii</i>	leaves	S	W. Australia	38	535:20:1	
<i>A. griffithii</i>	stems	S	W. Australia	39	982:27:1	
<i>Amphiroa foliacea</i>		R	N. Queensland	21	295:16:1	
<i>Asparagopsis</i> sp.		R	Enewetak	22	495:47:1	
<i>Boodlea</i> sp.		Ch	Enewetak	25	605:71:1	
<i>Boodlea</i> sp.		Ch	Enewetak	17	371:33:1	
<i>Calothrix</i> sp.		Cy	Enewetak	18	466:46:1	
<i>Calothrix</i> sp.		Cy	Enewetak	17	429:52:1	
<i>Cladophora</i> sp.		Ch	Enewetak	18	265:38:1	
<i>Cladostephus spongiosus</i>		R	Corsica	33	1,927:70:1	
<i>Codium</i> sp.		Ch	Rhode Island	20	251:31:1	
<i>Codium arabicum</i>		Ch	Hawaii	22	468:24:1	
<i>Codium bursa</i>		Ch	Corsica	18	971:74:1	
<i>Colpomenia sinuosa</i>		P	N. Queensland	24	437:18:1	
<i>Cymodocea nodosa</i>	leaves	S	Corsica	38	408:15:1	
<i>Cymodocea serrulata</i>	leaves	S	N. Queensland	38	638:18:1	
<i>C. serrulata</i>	leaves	S	N. Queensland	—	410:19:1	Birch 1975
<i>C. serrulata</i>	rhizomes	S	N. Queensland	—	872:13:1	Birch 1975
<i>Cystoseria balearica</i>		P	Corsica	37	995:54:1	
<i>Cystoseria fimbriata</i>		P	Corsica	34	1,896:68:1	
<i>Cystoseria spinosa</i>		P	Corsica	43	589:61:1	
<i>Cystoseria stricta</i>		P	Corsica	40	1,124:65:1	
<i>Cystoseria trinodis</i>		P	N. Queensland	34	933:35:1	
<i>Dictyosphaeria cavernosa</i>		Ch	Hawaii	15	623:31:1	
<i>Dictyosphaeria versluysii</i>		Ch	N. Queensland	22	478:20:1	
<i>Dictyota acutiloba</i>		P	Hawaii	37	744:35:1	
<i>Dictyota pardalis</i>		P	N. Queensland	41	1,201:58:1	
<i>Dictyota sandvicenvis</i>		P	Hawaii	47	951:53:1	
<i>Ecklonia radiata</i>		P	W. Australia	36	364:14:1	
<i>Enhalus acoroides</i>	leaves	S	N. Queensland	—	317:16:1	Birch 1975
<i>E. acoroides</i>	rhizomes	S	N. Queensland	—	410: 5:1	Birch 1975
<i>E. acoroides</i>	leaves	S	N. Queensland	37	444:18:1	
<i>E. acoroides</i>	leaves	S	Palau	41	1,000:48:1	
<i>E. acoroides</i>	rhizomes	S	Palau	37	659:16:1	
<i>Enteromorpha flexuosa</i>		Ch	N. Queensland	15	362:16:1	
<i>Galaxaura rugosa</i>		R	Hawaii	28	545:31:1	
<i>Gracilaria</i> sp.		R	Hawaii	21	315:16:1	
<i>Gracilaria verrucosa</i>		R	Japan	—	291:43:1	Johnston 1971
<i>Gracilaria</i> sp.		R	Virginia	38	819:29:1	
<i>Halimeda</i> sp.		Ch	Enewetak	30	872:42:1	
<i>Halimeda discoidea</i>		Ch	Hawaii	33	499:47:1	
<i>Halimeda opuntia</i>		Ch	N. Queensland	48	488:33:1	
<i>Halimeda tuna</i>		Ch	Corsica	34	501:67:1	
<i>Halodule univervis</i>	leaves	S	N. Queensland	—	465:13:1	Birch 1975
<i>H. univervis</i>	rhizomes	S	N. Queensland	—	388:14:1	Birch 1975
<i>H. univervis</i>	leaves	S	N. Queensland	36	623:18:1	
<i>Halophila decipiens</i>		S	N. Queensland	—	268:11:1	Birch 1975
<i>Halophila hawaiiiana</i>		S	Hawaii	29	447:18:1	
<i>Halophila ovalis</i>		S	W. Australia	29	388:13:1	
<i>H. ovalis</i>		S	N. Queensland	—	465: 9:1	Birch 1975
<i>Halophila ovata</i>		R	N. Queensland	—	698: 9:1	Birch 1975
<i>Halophila spinulosa</i>		S	N. Queensland	—	465:10:1	Birch 1975
<i>H. spinulosa</i>		S	N. Queensland	29	256:11:1	
<i>Heterochordia abietina</i>		P	Japan	—	139:17:1	Johnston 1971
<i>Hydroclathrus clathratus</i>		P	Hawaii	33	400:20:1	
<i>H. clathratus</i>		P	N. Queensland	21	300:18:1	
<i>Hypnea valentiae</i>		R	N. Queensland	24	612:31:1	
<i>Iridaea cordata</i>		R	California	30	388:22:1	
<i>Kjellmaniella crassifolia</i>		P	Japan	—	239:13:1	Johnston 1971
<i>Laminaria angustata</i>		P	Japan	—	279:12:1	Johnston 1971
<i>Laminaria japonica</i>		P	Japan	—	183: 9:1	Johnston 1971
<i>Laminaria religiosa</i>		P	Japan	—	384:25:1	Johnston 1971
<i>Laminaria dentiger</i>	stipe/blades	P	California	29	390:18:1	
<i>Laurencia</i> sp.		R	N. Queensland	27	1,274:66:1	

Table 1. Continued.

Taxon	Plant part	Phylum*	Locality	% C†	C:N:P‡	References§
<i>Laurencia</i> sp.		R	Hawaii	33	571:62:1	
<i>Lyngbia majuscula</i>		Cy	Enewetak	23	302:38:1	
<i>L. majuscula</i>		Cy	Hawaii	45	377:40:1	
<i>Macrocystis pyrifera</i>	blades	P	California	29	222:11:1	
<i>Monostroma latissimum</i>		C	Japan	—	1,316:58:1	Johnston 1971
<i>Nereocystis luetkeana</i>	blades	P	California	24	176:18:1	
<i>Padina japonica</i>		P	Hawaii	29	594:22:1	
<i>Padina tenuis</i>		P	N. Queensland	29	584:24:1	
<i>Padina</i> sp.		P	Hawaii	31	566:29:1	
<i>Padina</i> sp.		P	Corsica	33	1,271:76:1	
<i>Peyssonelia</i>		R	Corsica	31	744:59:1	
<i>Phyllospadix scouleri</i>	leaves	S	California	37	509:24:1	
<i>Porphyra yezoensis</i>		R	Japan	—	137:23:1	Johnston 1971
<i>Posidonia oceanica</i>	leaves	S	Corsica	36	956:39:1	
<i>P. oceanica</i>	roots	S	Corsica	39	3,550:61:1	
<i>P. oceanica</i>	rhizomes	S	Corsica	38	1,749:40:1	
<i>Posidonia ostenfeldia</i>	leaves	S	W. Australia	38	1,070:29:1	
<i>P. ostenfeldia</i>	roots/rhizomes	S	W. Australia	37	1,297:24:1	
<i>Posidonia sinuosa</i>	leaves	S	W. Australia	29	512:16:1	
<i>P. sinuosa</i>	roots	S	W. Australia	35	809:18:1	
<i>Polysiphonia</i>		Ch	Rhode Island	24	186:27:1	
<i>Ruppia maritima</i>	leaves	S	Virginia	29	457:29:1	
<i>Sargassum</i> sp.		P	Hawaii	30	1,031:20:1	
<i>Sargassum</i> sp.		P	Hawaii	21	765:20:1	
<i>Sargassum</i> sp.		P	N. Queensland	30	1,106:38:1	
<i>Sargassum</i> sp.		P	N. Queensland	32	687:38:1	
<i>Sargassum</i> sp.		P	N. Queensland	32	770:31:1	
<i>Sargassum</i> sp.		P	W. Australia	42	537:22:1	
<i>Schizothrix</i> sp.		Cy	Enewetak	18	554:21:1	
<i>Schizothrix</i> sp.		Cy	Enewetak	19	501:33:1	
<i>Schizothrix</i> sp.		Cy	Hawaii	26	398:33:1	
<i>Sphaerococcus coronopifolius</i>		R	Corsica	37	1,625:182:1	
<i>Spyridia</i> sp.		R	Virginia	20	240:31:1	
<i>Stypopodium</i>		P	Hawaii	37	847:35:1	
<i>Syringodium isoetifolium</i>	leaves	S	N. Queensland	—	332:13:1	Birch 1975
<i>S. isoetifolium</i>	rhizomes	S	N. Queensland	—	775:10:1	Birch 1975
<i>Thalassia hemprichii</i>	leaves	S	N. Queensland	33	599:27:1	
<i>Thalassia testudinum</i>	leaves	S	Barbados	—	445:32:1	Patriquin 1972
<i>T. testudinum</i>	rhizomes	S	Barbados	—	601:20:1	Patriquin 1972
<i>Turbinaria ornata</i>		P	Hawaii	30	1,090:20:1	
<i>T. ornata</i>		P	N. Queensland	36	925:22:1	
<i>Udotea petiolata</i>		Ch	Corsica	29	527:78:1	
<i>Ulva</i> sp.		Ch	Rhode Island	35	336:35:1	
<i>Ulva reticulata</i>		Ch	Hawaii	32	1,051:80:1	
<i>Undaria pinnatifida</i>		P	Japan	—	307:18:1	Johnston 1971
<i>Zostera capricorni</i>	leaves	S	N. Queensland	—	349:17:1	Birch 1975
<i>Z. capricorni</i>	rhizomes	S	N. Queensland	—	465: 8:1	Birch 1975
<i>Z. capricorni</i>	leaves	S	N. Queensland	32	302: 9:1	
<i>Zostera marina</i>	leaves	S	California	39	274:38:1	
<i>Z. marina</i>	leaves	S	Rhode Island	34	481:27:1	
<i>Z. marina</i>	leaves	S	Virginia	42	584:41:1	

\* Spermatophyta—S; Phaeophyta—P; Rhodophyta—R; Chlorophyta—Ch; Cyanophyta—Cy.

† Figured on a CaCO<sub>3</sub>-free basis: % organic C/[100 - (% inorganic × 12/100)] × 100. Not directly available except for our data.

‡ Value of C figured at 27% for data sources other than our own.

§ Values from our laboratory unless noted otherwise.

ditioning; all these factors are likely to influence the composition of the organisms.

The only significant difference we find in the C:N:P ratios is between samples collected from relatively low nutrient regimes (Corsica, Hawaii, Enewetak,

Northern Queensland, Western Australia, Palau) and those collected from high nutrient regimes (California, Virginia, Rhode Island). The plants from low nutrient environments show significantly higher C:N and C:P ratios than those from high nutrient regimes. The large environ-

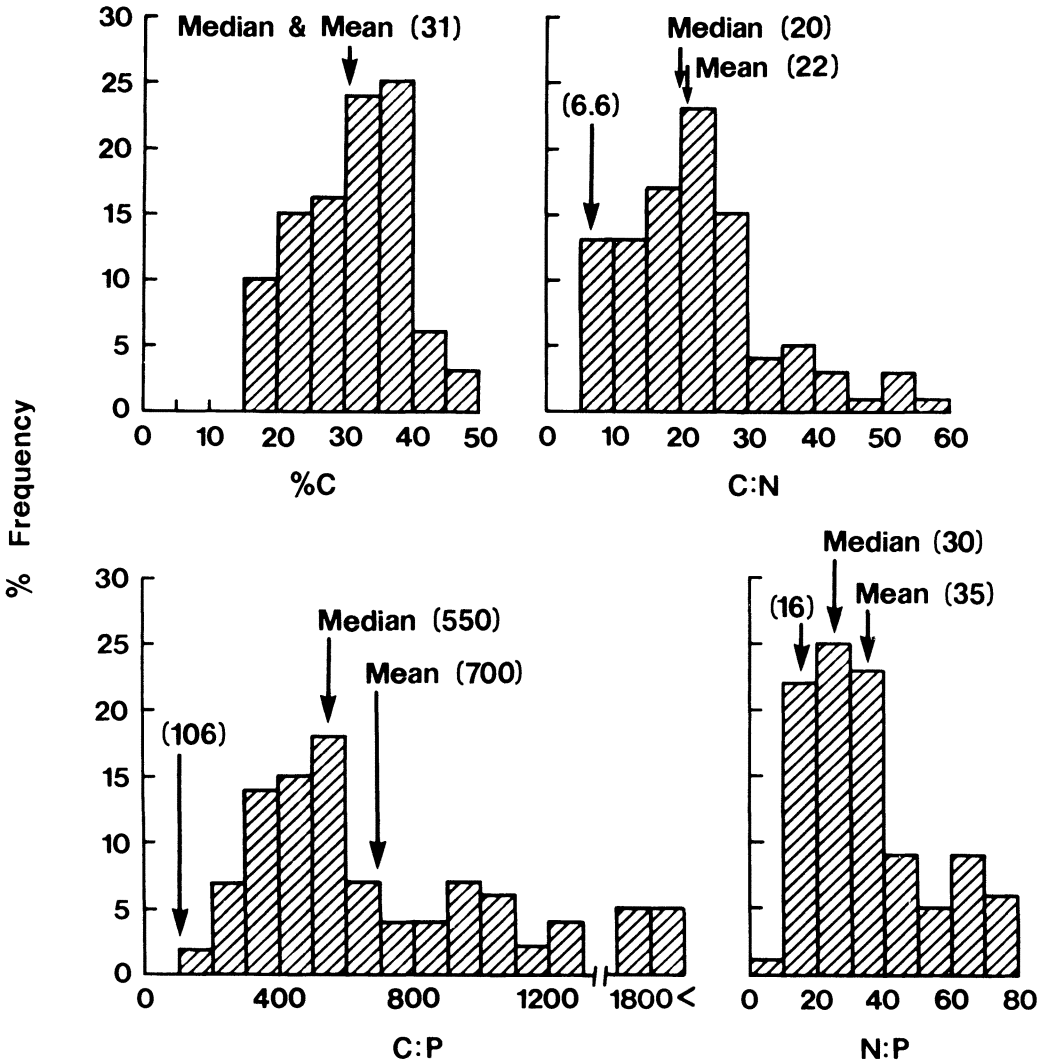


Fig. 1. Percent frequency vs. percent C of plant dry weight, C:N, C:P, and N:P ratios for marine plants listed in Table 1. Mean and median ratios based on our data are shown for comparison with Redfield ratios (unlabeled, in parentheses).

mental variation in C:N:P ratios masks any taxonomic differences that might exist, although taxonomic differences in C:N ratios have been reported previously (Niell 1976).

Fenchel and Jørgensen (1977) stated that the C:N ratio of benthic plants ranges from 10:1 to 70:1 and that the C:P ratio is about 200:1. The C:N ratios of our data agree well with the range reported by

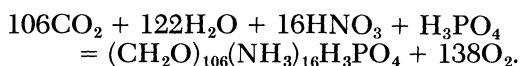
them, but our C:P ratios are well above their estimate. The median C:N ratio of our data is three times the Redfield C:N ratio, while the median C:P ratio is five times the Redfield ratio.

The average C:N:P ratio that we have found in benthic plants would suggest to those who study phytoplankton that these plants have a low specific growth rate and are limited for P. The nutrient half-satu-

ration constants for macrophytes are usually well above ambient nutrient concentrations (e.g. Steffensen 1976; Topinka 1978; De Boer et al. 1978), so the specific growth rates of these plants are quite low. Data from Gerloff and Krombholz (1966) indicate that freshwater plants in a highly fertile lake had a mean N:P ratio of 15:1, while the mean N:P ratio of plants in a relatively infertile lake was 30:1. Various workers have observed that the C:N ratio of benthic plants decreases with increased dissolved inorganic nitrogen concentration (e.g. Lapointe et al. 1976; Jackson 1977; Hansiak 1979; Lapointe and Tenore 1981). Presumably, the varying C:N ratios are a response to nitrogen storage and indicate possible nitrogen limitation of specific growth rate. Our observation that plants in low nutrient regimes have high C:N:P ratios is consistent with the interpretation that these high ratios indicate limitation of specific growth rate by nutrient concentration. The lowest C:N ratios reported, for plants growing at very elevated nitrogen levels, seem to approach the Redfield C:N ratio as a limit instead of showing a central tendency toward this ratio.

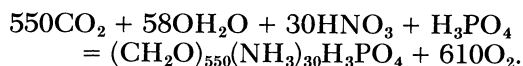
Another interpretation of the high C:N:P ratios in benthic plants is the accepted belief that these plants have a large amount of structural carbon. The ash-free dry weight of plankton averages 50% protein, 35% carbohydrate, and 10% lipid (Parsons et al. 1961, 1977). We estimate, from the standard conversion factor ( $6.25 \times$  nitrogen wt = protein wt), that the average protein content of the benthic plants is about 15% of the ash-free dry weight. Since the lipid content of macroalgae is generally <5% (Schmidt 1969; also suggested by our P data), about 80% of the ash-free dry weight of the benthic plants is carbohydrate. This dominance by carbohydrate is consistent with the notion that these plants have a large amount of structural carbon. Despite uncertainties in understanding the physiological significance of the high C:N:P ratios in the benthic plants, some ecologically significant points emerge.

The Redfield ratio has been used to express the net chemical reaction for phytoplankton metabolism or nutrient regeneration from plankton detritus. The mass balance of carbon and nutrient reactions through the particulate organic matter in the oceans has been expressed by the following equation (Richards 1965; Stumm and Morgan 1970):



The equation would need slight modification if a somewhat different phytoplankton C:N:P ratio were used or if ammonia rather than nitrate were the primary source of nitrogen. These modifications would not greatly alter the mass balance, and the equation provides a useful overview of net metabolism based upon plankton in the ocean.

No equivalent equation has been suggested for metabolism based upon benthic plants or materials derived from benthic plants. For heuristic purposes, one might style a generalized mass-balance equation for benthic systems after the median C:N:P ratio we observe:



Obviously a more appropriate equation can and should be formulated for any particular study.

The stoichiometry of this equation differs markedly from the stoichiometry inferred from the Redfield ratio. For example, net community production of organic carbon can be estimated by using the net depletion of any particular nutrient and scaling it to C (Odum 1971). Atkinson (1981) used P depletion in water which flowed across two alga-dominated communities and the C:P ratio of benthic algae in those communities (about 500:1) to estimate the net organic production of the communities. Estimates of net production based on depletion of P matched the net community production as independently measured by  $\text{CO}_2$  and  $\text{O}_2$  flux.

Direct application of the Redfield C:P ratio for scaling P to C in those communities would have underestimated the net production by about 80%.

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