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Biol. Ocean. Processes
Chapter 10
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NITROGEN CYCLE, NUTRIENT LIMITATION & CHEMOSTATS

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References

ON MICHAELIS-MENTEN KINETICS AND 'STEADY-STATE' KINETICS

Burmaster, D. E. 1979. The continuous culture of phytoplankton: mathematical equivalence among three steady-state models. Amer. Natur. *113*: 123-139. *[Caperon's Monod-style and* ***Droop's (1968)*** *cell quotient models are equivalent]*

Button, D. K. 1985. Kinetics of nutrient-limited transport and growth of microorganisms. Micorbiol. Rev. *49*: 270-297. *[An excellent in-depth review of the kinetic data derived from chemostats for bacteria and algae and the methods used to get the estimates. Button provides estimates for the kinetic constants for most nutrients, some reduced organic compounds (for heterotrophs), vitamins and light.]*

Button, D. K. 1986. Affinity of organisms for substrate. Limnol. Oceanogr. *31*: 453-456. *[Definitions of the meanings of `affinity' are discussed in kinetic terms.]*

Caperon, J. and J. Meyer. 1972a. Nitrogen-limited growth of marine phytoplankton - I. Changes in population characteristics with steady-state growth rate. Deep-Sea Research *19*: 601-618. *[A classic study, which used the the Monod formulation of the cell quota model (introduced earlier by* ***Fuhs (1969)*** *for P limitation:*

$$\mu = \frac{\mu_{\max} S}{K_s + S}.] \ \{5\}$$

Caperon, J. and J. Meyer. 1972b. Nitrogen-limited growth of marine phytoplankton - II. Uptake kinetics and their role in nutrient limited growth of phytoplankton. Deep-Sea Research *19:* 619-632. *[The uptake parameters measured by tracking the disappearance of N pulses to chemostats]*

Droop, M. R. 1968. Vitamin B_{12} and marine ecology. IV. The kinetics of uptake, growth, and inhibition in *Monochrysis lutheri*. J. mar. biol. Ass. U.K. *48*: 689-733. *[The classic paper that introduced the Droop equation for modeling the relationship between μ and the internal cell quotient q:*

$$\frac{\mu}{\mu'_{\max}} = 1 - \left(\frac{k_q}{Q}\right).]$$

Droop, M. R. 1973. Nutrient limitation in Osmotrophic Protista. American Zoologist *13*: 209-214. *[This is a very readable introduction to the major concepts. Most of the material is handled better in Droop (1983)]*

Droop, M. R. 1974. The nutrient status of algal cells in continuous culture. J. mar. Biol. Ass. U.K. *54*: 825-855. *[In a clever interpretation of chemostat experiments, Droop concludes that the specific growth rate is controlled by one nutrient at a time. He rejects the multiplicative nutrient limitation model in favor of Liebig's law of the minimum.* ***Rhee (1978)*** *performed similar experiments testing N & P limitation, again concluding that only 1 nutrient at a time controls growth]*

Droop, M. R. 1983. 25 years of algal growth kinetics. Bot. Mar. *26*: 99-112.

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Eppley, R. W. and E. H. Renger. 1974. Nitrogen assimilation of an oceanic diatom in nitrogen limited continuous culture. J. Phycology *10:* 15-23.

Goldman, J. C. 1980. Physiological processes, nutrient availability, and the concept of relative growth rate in marine phytoplankton ecology. Pp. 179-194 *in* P. G. Falkowski, *ed.*, Primary productivity in the sea. Plenum Press, New York. *[Phytoplankton attain Redfield ratios only when relative growth rate approaches 1]*

Goldman, J. 1986. On phytoplankton growth rates and particulate C:N:P ratios at low light. Limnol. Oceanogr. *31*: 1358-1363. *[C:N:P ratios=f(μ), but are not greatly affected by light]*

Goldman, J. C. and P. M. Glibert. 1983. Kinetics of inorganic nitrogen uptake by phytoplankton. Pp. 233-274 *in* E. J. Carpenter and D. Capone, *eds*., Nitrogen in the Marine Environment. Academic Press, New York.

Rhee, G.-Yull. 1973. A continuous culture study of phosphate uptake, growth rate and polyphosphate in *Scenedesmus* sp. J. Phycol. *9*: 495-506.

Rhee, G.-Yull. 1974. Phosphate uptake under nitrate limitation by *Scenedesmus* sp. and its ecological implications. J. Phycol. *10*: 470-475.

Rhee, G.-Yull. 1978. Effects of N/P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake: a study of dual nutrient limitation. Limnol. Oceanogr. *23*: 10-25. *[Like Droop (1974), Rhee rejects muliplicative nutrient limitation models in favor of Liebig's law of the minimum: one nutrient at a time controls growth rate]*

Rhee, G.-Yull. 1980. Continuous culture in phytoplankton ecology. Pp. 151-203. *in* M. R. Droop and H. W. Jannasch, eds., Advances in Aquatic Microbiology, Vol. 2, Academic Press, New York.

Rhee, G.-Yull, I. J. Gotham, and S. W. Chisholm. 1981. Use of cyclostat cultures to study phytoplankton ecology. Pp. 159-186 *in* P. C. Calcott, ed., Continuous culture of cells. CRC Press, Cleveland Ohio.

Shuter, B. J. 1978. Size dependence of phosphorous and nitrogen subsistence quotas in unicellular microorganisms. Limnol. Oceanogr. *23*: 1248-1255. *[The Droop equation is fit to 45 data sets. k_q increases allometrically with cell volume and carbon content, but the later exponent is almost 1.0.]*

Sommer, U. 1986. Phytoplankton competition along a gradient of dilution rates. Oecologia *68*: 503-506. *[Sommer analyzes changes in species composition at different growth rates. Tilman's R* model is tested, but the test is not rigorous since k_s is difficult to estimate. With Si addition, Synedra acus dominated at all but the highest dilution rate. Synedra is never a dominant in Lake Constance, from which the inoculum was taken.]*

Sommer, U. 1988. The species composition of Antarctic phytoplankton interpreted in terms of Tilman's competition theory. Oecologia *77*: 464-467. *[Tilman's theory (and some postulates) predicts that species should be distributed according to ambient ratios of N:P, N:Si, and N:light. Sommer tests this hypothesis and finds some relationships indicating competition.]*

LIEBIG'S LAW & GENERAL NUTRIENT LIMITATION

Arrigo, K. R. 2005. Marine microorganisms and global nutrient cycles. Nature *437*: 349-355. *[A brief review of new work on Redfield ratios, Liebig's law, dual nutrient limitation, and anammox]{}*

De Baar, H. J. W. 1994. von Liebig's law of the minimum and plankton ecology. Prog. Oceanogr. *33*: 347-386. *[Contains a review of Liebig's original law, Brandt's inappropriate use of it, and the modern role of Fe-limitation in phytoplankton ecology]*

Howarth, R. W. 1988. Nutrient limitation of net primary production in marine ecosystems. Ann. Rev. Ecol. Syst. *19*: 89-110. [See outline above]

Mills, E. L. 1989. Biological Oceanography: An early history. Cornell University Press, Ithaca NY and London. *[Mills reviews the work of the Kiel School, Plymouth Biological Laboratory and Riley. These groups laid the foundation for the study of phytoplankton ecology, especially the cause of the vernal phytoplankton bloom.* ***See full outline above****]*{**4**, **7**, **12**, **23**}

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton *[Reviews and updates his influential theory of resource limitation, including definitions of resource types.]*

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Phytoplankton & N

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Balch, W. M. 1985. Differences between dinoflagellates and diatoms in the uptake of ^{36}Cl-ClO$_3$, an analogue of NO$_3$. Pp 121-124 in Anderson, White and Baden, eds, Toxic dinoflagellates. Elsevier. *[Chlorate is used as a nitrate analogue since there are no radioactive isotopes of N available for oceanographers. Dinoflagellates don't take up chlorate, even though they do take up nitrate. Chlorate uptake related to the ability to store nitrate.]*

Balch, W. M. 1987. Studies of nitrate transport by marine phytoplankton using ^{36}Cl-ClO$_3^-$ as a transport analogue. I. Physiological findings. J. Phycol. *23*: 107-118. *[Pulse-chase experiments are use to document the kinetics of nitrate and chlorate transport. Dinoflagellates did not take up chlorate.]*

Balch, W. M., E. Garside, and E. H. Renger. 1987. Studies of nitrate transport by marine phytoplankton using ^{36}Cl-ClO$_3^-$ as a transport analogue - II. Field observations. Deep-Sea Res. *34*: 221-236. *[Observations on chlorate uptake on the California coast and Gulf of Maine]*

Banse, K. 1974. On the interpretation of data for the carbon-to-nitrogen ratio of phytoplankton. Limnol. Oceanogr. *19*: 695-699.

Blackburn, T. H. and J. Sorensen, editors. 1988. Nitrogen cycling in coastal marine environments. Wiley.

Bratbak, G. and T. F. Thingstad. 1985. Phytoplankton-bacteria interactions: an apparent paradox? Analysis of a model system with competition and amensalism. Mar. Ecol. Prog. Ser. *25*: 23-30. *[Nutrient limitation leads to increased phytoplankton DOM release which stimulates bacterial growth which leads to higher bacterial nutrient uptake which leads to more nutrient limitation. Hey, wait a minute...something doesn't work here]*

Carpenter, E. J. and K. Romans. 1991. Major role of the cyanobacterium Trichodesmium in nutrient cycling in the North Atlantic Ocean. Science *254*: 1356-1358.

Chalup, M. S. and E. A. Laws. 1990. A test of the assumptions and predictions of recent microalgal growth models with the marine phytoplankter *Pavlova lutheri*. Limnol. Oceanogr. *35*: 583-596.

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Codispoti, L. A. 1989. Phosphorous vs. Nitrogen limitation of new and export production. Pp. 377-394 in Berger, ed. Production of the Oceans.

Collos, Y. and G. Slawyk. 1983. Ammonium and nitrate in the tropical and equatorial Atlantic: relations with the primary nitrite maximum. Marine Biology Letters 4: 295-308. *[Only some of the profiles are related to ammonium oxidation; some are due to nitrite excretion (up to 90% on nitrate uptake in some cases)]*

Collos, Y. and G. Slawyk. 1984. ^{13}C and ^{15}N uptake by marine phytoplankton. III. Interactions in euphotic zone profiles of stratified oceanic areas. Mar. Ecol. Prog. Ser. *19*: 223-234. *[In some species and profiles, pulsed addition of N of all forms reduces C uptake. This is particularly true for* NO$_3^-$*, where 7-fold reductions in carbon uptake are observed. At the nitracline, the pattern is reversed with enhanced carbon uptake with added nitrogen.]*

DiTullio, G. R. and E. A. Laws. 1986. Diel periodicity of nitrogen and carbon assimilation in five species of marine phytoplankton: accuracy of methodology for predicting N-assimilation rates and N/C composition ratios. Mar. Ecol. Prog. Ser. *32*: 123-132. *[Estimates of the percentage of* ^{14}C *incorporated into protein after 24 h (12L:12D) can provide estimates of the relative rates of C and N assimilation and hence relative growth rates]*

Dugdale, R. C. and J. J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnol. Oceanogr. *12*: 196-206. *[The classic paper describing the terms new and regenerated production]*

Dugdale, R. C. and F. P. Wilkerson. 1986. The use of ^{15}N to measure nitrogen uptake in eutrophic oceans: experimental considerations. Limnol. Oceanogr. *31*: 673-689.

Dugdale, R. C., F. P. Wilkerson, R. T. Barber, and F. P. Chavez. 1992. Estimating new production in the equatorial Pacific Ocean at 150º W. J. Geophys. Res. *97*: 681-686.

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Falkowski, P. G. 1983. Enzymology of nitrogen assimilation. Pp. 839-868 *in* E. J. Carpenter, and D. G. Capone, eds. Nitrogen in the marine environment. Academic Press, New York.

Fanning, K. A. 1989. Influence of atmospheric pollution on nutrient limitation in the ocean. Nature *339*: 460-463. *[Atmospheric N input may produce P limitation in the N. Atlantic]*

Flynn, K. J. 1991. Algal carbon-nitrogen metabolism: a biochemical basis for modelling the interactions between nitrate and ammonium uptake. J. Plankton Res. *13*: 373-387. *[Model predicts simultaneous incorporation of* NO_3^- *and* NH_4^+ *at ambient N concentrations]*

French, D. P., M. J. Furnas, and T. J. Smayda. 1983. Diel changes in nitrite concentration in the chlorophyll maximum in the Gulf of Mexico. Deep-Sea Res. *30*: 707-722.

Garfield, P. C, T. T. Packard, G. E. Friedrich, and L. A. Codispoti. 1983. A subsurface particle maximum layer and enhanced microbial activity in the secondary nitrite maximum of the northeastern tropical Pacific Ocean. J. Mar. Res. *41*: 747-768.

Garside, C. 1982. A chemiluminescent technique for the determination of nanomolar concentrations of nitrate and nitrite in seawater. Marine Chemistry *11*: 159-167. *[Can detect* NO_3^- *concentrations in the nanomolar range. Glover et al. (1989) apply the technique to great effect]*

Glibert, P. M. and J. J. McCarthy. 1984. Uptake and assimilation of ammonium and nitrate by phytoplankton: indices of nutritional status for natural assemblages. J. Plankton Res. *6*: 677-697.

Glover, H. E., B. B. Prezelin, L. Campbell, M. Wyman, and C. Garside. 1988. A nitrate dependent *Synechococcus* bloom in surface Sargasso sea water. Nature *331*: 161-163. *[As discussed by Platt et al. (1989), intermittent* NO_3^- *pulses and blooms may reconcile short-term incubation results with bulk measurements of primary production.]*

Goldman, J. C. and P. M. Glibert. 1983. Kinetics of nitrogen uptake by phytoplankton. Pp. 233-274 *in* E. J. Carpenter and D. Capone, eds., Nitrogen in the marine environment. Academic Press. *[A nice review]*

Granelli, E. and K. Sundback. 1985. The response of planktonic and microbenthic algal assemblages to nutrient enrichment in shallow coastal waters, southwest Sweden. J. exp. Mar. Biol. Ecol. *85*: 253-268.

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Harrison, W. G. 1980. Nutrient regeneration and primary production in the sea. Pp. 433-460 *in* P.G. Falkowski, ed., Primary Productivity in the Sea. Plenum Press, New York.

Harrison, W. G., T. Platt, and M. R. Lewis. 1987. *f* ratio and its relationship to ambient nitrate concentrations in coastal waters. J. Plankton Res. *9*: 235-248.

Harrison, W. G. and L. J. E. Wood. 1988. Inorganic nitrogen uptake by marine picoplankton: evidence for size partitioning. Limnol. Oceanogr. *33*: 468-475. *[Picoplankton preferentially take up* NH_4^+*]*

Hayward, T. L. 1987. The nutrient distribution and primary production in the central N. Pacific. Deep-Sea Res. *34*: 1593-1627.

Hecky, R. E. 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* (4, part 2): 796-822. *[Evidence in favor of marine N limitation reviewed and found somewhat wanting. Freshwater systems are generally P limited. RKR ratio justified]*

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Jørgensen, B. B. and J. Sorensen. 1985. Seasonal cycles of O_2, NO_3^-, and SO_4^{-2} reduction in estuarine sediments. The significance of an NO_3^- reduction maximum in spring. Mar. Ecol. Prog. Ser. *24*: 65-74.

Kamykowski, D. 1987. A preliminary biophysical model of the relationship between temperature and plant nutrients in the upper ocean. Deep-Sea Res. *34*: 1067-1079. *[The latitudinal gradient in* NO_3^- *is modeled. There is a distinct S-N latitudinal asymmetry, with nitrogen enrichment in the Southern ocean]*

Kamykowski, D. and S-J. Zentara. 1985. Nitrate and silicic acid in the world ocean: patterns and processes. Mar. Ecol. Prog. Ser. *26*: 47-59. *[Regression analyses are used to analyze the intercepts of N vs. Si plots using 217 GEOSECS and 11,576 NODC stations. In the Southern ocean, both N and Si remain high year-round. Fig. 12 indicates that the relative amount of new production can be crudely assessed from the intercept of* NO_3^- *vs silicate. If new production is not particularly important, then the intercepts will fall on the silicic acid part of the curve. Silicic acid positive intercepts occur throughout the Pacific and Atlantic, and south of 60° S. Nitrate excess occurs North of the Antarctic divergence]*

Kamykowski, D. and S.-J. Zentara. 1986. Predicting plant nutrient concentrations from temperature and σ-t in the upper kilometer of the world ocean. Deep-Sea Res. *33*: 89-105. *[NODC data used to map global nitrate, temp. and* σ_t *distributions]*

Kanda, J., E. A. Laws, T. Saino, and A. Hattori. 1987. An evaluation of the isotope dilution effect from conventional data sets of ^{15}N uptake experiments. J. Plankton Res. *9*: 79-90.

Kiefer, D. A. and J. N. Kremer. 1981. Origins of vertical patterns of phytoplankton and nutrients in the temperate, open ocean: a stratigraphic hypothesis. Deep-Sea Res. *28*: 1087-1105.

Koike, I, O. Holm-Hansen, and D. C. Briggs. 1986. Inorganic nitrogen metabolism by Antarctic phytoplankton with special reference to ammonia cycling. Mar. Ecol. Prog. Ser. *30*: 105-116. *[Confirms Malone's hypothesis that small cells use* NH_4^+*; large cells use* NO_3^-*]*

Laws, E. A. 1983. Man's impact on the marine nitrogen cycle. Pp. 459-485 *in* E. J. Carpenter and D. G. Capone, eds., Nitrogen in the Marine Environment. Academic Press, New York. *[A simple model, based on the expected new production from Eppley and Peterson (1972) is applied to anoxia in the New York bight, and eutrophication of a coastal Hawaiian Bay]*

Lipschultz, F. S., S. C. Wofsy, and L. E. Fox. 1986. Nitrogen metabolism in the eutrophic Delaware River Ecosystem. Limnol. Oceanogr. *31*: 701-716.

Malone, T. C. 1980. Size-fractionated primary productivity of marine phytoplankton. Brookhaven Symp. Biol. *31*: 301-319. *[Large phytoplankton (e.g., diatoms take up* NO_3^-*); small phytoplankton utilize regenerated production]*

Martinez, R., T. T. Packard, and D. Blasco. 1987. Light effects and diel variations of nitrate reductase activity in phytoplankton from the northwest African upwelling region. Deep-Sea Res. *34*: 741-753. *[NR activity is higher in the light and can be modeled with a hyperbolic function {like a P vs. I curve}. Typical light values were 10 nM* NO_3^- *(µg chl a hr)*$^{-1}$*).]*

McCarthy, J. J. 1980. Nitrogen. Pp. 191-233 *in* I. Morris, ed., The physiological ecology of phytoplankton. University of California Press, Berkeley.

McCarthy, J. J. and E. J. Carpenter. 1983. Nitrogen cycling in the near-surface waters of the open ocean. Pp. 487-512 *in* E. J. Carpenter and D. G. Capone, eds., Nitrogen in the Marine Environment. Academic Press, New York.

McCarthy, J. J. and J. C. Nevins. 1986a. Sources of nitrogen for primary production in warm-core rings 79-I and 81-D. Limnol. Oceanogr. *31*: 690-700.

McCarthy, J. J. and J. C. Nevins. 1986b. Utilization of nitrogen and phosphorous by primary producers in warm-core ring 82-B following deep convection mixing. Deep-Sea Res. *33*: 1773-1788. *[As the warm core ring decelerates,* NO_3^- *vertical flux increases.]*

Nixon, S. W. 1987. Chesapeake Bay nutrient budgets - a reassessment. Biogeochemistry *4*: 77-90. *[Recent studies estimated that most of the nutrients released into Chesapeake Bay were being trapped there; Nixon disagrees and estimates that only 3-6% of N and 11-17% of P are trapped. 'Nixon's work has major implications for the management of eutrophication by reduction of nutrient inputs in that eutrophication can be alleviated more readily if his rates are true.]*

Nixon, S. W. and M. E. Pilson. 1983. Nitrogen in estuarine and coastal marine ecosystems. Pp. 565-648 *in* E. J. Carpenter and D. G. Capone, *eds*. Nitrogen in the Marine Environment. Academic press *[Recycling of N in estuaries is very important. Sewage input accounts for >50% of N in Long Island Sound, New York, Raritan Bay and San Francisco Bay.]*

Paerl, H. W. 1989. Physiological ecology and regulation of N_2 fixation in natural waters. Adv. Microb. Ecol. *11*: 305-344.

Pahlow, M, U. Riebesell, and D. A. Wolf-Gladrow. 1997. Impact of cell shape and chain formation on the nutrient acquisition by marine diatoms. Limnol. Oceanogr. *42*: 1660-1672. *[Diffusion models applied to uptake of nutrients in turbulent water]*

Pennock, J. R. 1987. Temporal and spatial variability in phytoplankton ammonium and nitrate uptake in the Delaware Bay. Est. Coastal and Shelf Sci. *24*: 841-857.

Probyn, T. A. and S. J. Painting. 1985. Nitrogen uptake by size-fractionated phytoplankton populations in Antarctic surface waters. Limnol. Oceanogr. *30*: 1327-1332. *[*NO_3^- *makes up 96% of the N pool, but on average regenerated production accounted for 62% for the nanoplankton and 75% for the picoplankton]*

Redfield, A. C., B. H. Ketchum, and F. A. Richards. 1963. The influence of organisms on the composition of sea-water. Pp. 26-77 in M. N. Hill (ed.) The Sea, Vol. 2. Interscience, New York. *[The Redfield ratio, originally proposed by Redfield in the 30's, of* $C:N:P \approx 106:16:1$ *is described]*

Ryther, J. H. and W. M. Dunstan. 1971. Nitrogen, phosphorous, and eutrophication in the coastal marine environment. Science *171*: 1008-1013. *[Phytoplankton added to New York bight seawater increase in biomass with Nitrogen spikes, not Phosphorus spikes]*

Schuller, K. A., W. C. Plaxton, and D. H. Turpin. 1990. Regulation of C_3 phosphoenolpyruvate carboxylase from the green alga *Selenastrum minutum*. Properties associated with replenishment of TCA cycle intermediates during amino acid biosynthesis. Plant Physiol. *93*: 1303-1311.

Sciandra, A, J. Gostan, Y. Collos, C. Descolas-Gros, C. Leboulanger, V. Martin-Jézéquesl, M. Denis, D. Lefèvre, C. Copin-Montégut, and B. Avril. 1997. Growth-compensating phenomena in continuous cultures of Dunaliella tertiolecta limited simultaneously by light and nitrate. Limnol. Oceanogr. *42*: 1325-1399. *[Cultures growing with limiting & non-limiting light and switched. Cell size and other physiological traits affected more strongly by N limitation than light]*

Smetacek, V. and F. Pollehne. 1986. Nutrient cycling in pelagic systems: a reappraisal of the conceptual framework. Ophelia *26*: 401-428. *[An odd collection of natural history observations. Diatom slime production can lead to high sedimentation rates. New and regenerating N systems are discussed]*

Smith, S. V. 1984. Phosphorous versus nitrogen limitation in the marine environment. Limnol. Oceanogr. *29*: 1149-1160.

Sugimara, Y. and Y. Suzuki. 1988. A high-temperature catalytic oxidation method for non-volatile dissolved organic carbon in seawater by direct injection of a liquid sample. Marine Chemistry 24: 105-131. *[Very high rates of DOC and DON, which may lead to a reevaluation of new nitrogen fluxes in marine waters.]*

Sterner, R. W. and J. J. Elsner. 2002. Ecological stoichiometry. The biology of elements from molecules to the biosphere. Princeton University Press, Princeton NJ. 439 pp. *[Contains a thorough treatment of the history of Redfield ratios and Goldman's theory of the relation between Redfield ratios and phytoplankton relative growth rate]* {?}

Takahashi, T., W. S. Broecker, and S. Langer. 1985. Redfield ratio based on chemical data from isopycnal surfaces. J. Geophys. Res. *90*: 6907-6924. *[The Redfield ratio of* $P:N:C:O_2$ *is 1:16:106:138, their new ratio is 1:16:122(±18):172]*

Vanlerberghe, G. S, K. A. Schuller, R. G. Smith, R. Feil, W. C. Plaxton and D. H. Turpin. 1990. Relationship between NH_4^+ assimilation rate and *in vivo* phosphoenolpyruvate carboxylase activity. Plant Physiol. *94*: 284-290. *[PEPC plays a key anaplerotic function.* NH_4^+ *assimilation requires carbon skeletons from TCA cycle intermediates. These TCA components are replaced by the carboxylation of PEP to OAA by PEPC.]*

Wheeler, P. A. and D. L. Kirchman. 1986. Utilization of inorganic and organic nitrogen by bacteria in marine systems. Limnol. Oceanogr. *31*: 998-1009. *[A significant portion of the ammonium uptake may be due to heterotrophic bacteria. Confirmed by Lipshultz* et al. *for the Eastern Tropical Pacific]*

Genetics of nitrogen metabolism

Alan, A. E., M. G. Booth, M. E. Frischer, P. G. Verity, J. P. Zehr, and S. Zani. 2001. Diversity and detection of nitrate assimilation genes in marine bacteria. Appl. Env. Microbiol. 67: 5343-5348. *[PCR approach used to create a library of NAS {nitrate assimilation} genes for marine bacteria. Using these gene probes, they isolated and sequenced NAS genes from three oceanic regimes. Several different NAS genes are abundant and widespread.]*

PHOSPHORUS

Benitez-Nelson, C. and D. M. Karl. 2002. Phosphorus cycling in the North Pacific subtropical gyre using cosmogenic ^{32}P and ^{33}P. Limnol. Oceanogr. 47: 762-770. [?].

Fuhs, G. W. 1969. Phosphorus content and rate of growth in the diatoms Cyclotella nana and Thalassiosira fluviatilis. J. Phycology *5*: 312-321. *[Demonstrates with marine phytoplankton that P-limited chemostat cultures show a Michaelis-Menten relation between µ and the internal phosphorus pool.] {**5**, **20**}*

Perry, M. J. 1972. Alkaline phosphatase activity in subtropical central North Pacific waters using a sensitive fluorometric method. Marine Biology *15*: 113-119.

Perry, M. J. 1976. Phosphate utilization by an oceanic diatom in phosphorous-limited chemostat culture in the oligotrophic waters of the central North Pacific. Limnol. Oceanogr. *21*: 88-107. *[Only a few gyre samples had detectable alkaline phosphatase activity]*

Sañudo-Wilhelmy et al. 2001. Phosphorus limitation of nitrogen fixation by *Trichodesmium* in the central Atlantic Ocean. Nature 411: 66-69.

Wu, J., W. Sunda, E. A. Boyle, and D. M. Karl. 2000. Phosphorus depletion in the western North Atlantic Ocean. Science 289: 759-762.*[The Sargasso Sea receives more iron-laden dust than the N. Pacific gyre. Nitrogen fixing bacteria are often Fe limited and fix sufficient N in the Sargasso sea to make P the limiting nutrient.] [?]*

ON 'PULSED' OR 'PATCHY' NUTRIENT ADDITIONS, NON-STEADY-STATE KINETICS AND THE ZOOPLANKTON MICROPATCH HYPOTHESIS

Comment

Goldman *et al.* (1979) introduced the argument that phytoplankton in nature are growing at nearly maximal relative growth rates and might be utilizing short-lived patches of nutrients (NH_4^+), excreted by macrozooplankton. **Jackson (1980)** and **Williams and Muir (1981)** argued from physical laws that such patches would be too short-lived to constitute a major nutrient source for phytoplankton. Lehman and Scavia (**1982a**, **b**, **1984**) found that freshwater phytoplankton could indeed take up patches of phosphorous in culture. **Currie (1984a)** asked whether the high cell and patch densities used by Lehman and Scavia could be found in nature. As summarized in Mann and Lazier's (1991) text, the conclusion is no. Phytoplankton can utilize patches of excreted nutrients from zooplankton, but the densities of phytoplankton and patches are too low to make this process important in nature.

Jackson (1987) shows that chemical patches will not persist around phytoplankton cells < 5 µm. Cells smaller than this could not be detected chemically by either bacteria or macrozooplankton.

Alldredge, A. L. and Y. Cohen. 1987. Can microscale chemical patches persist in the sea? Microelectrode study of marine snow, fecal pellets. Science *235*: 689-691.

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COMPETITION FOR NUTRIENTS & PARADOX OF THE PLANKTON

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Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton *[Reviews and updates his influential theory of resource limitation, including definitions of resource types.]*

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Tilman D (1989) Discussion: population dynamics and species interactions.Pp. 89-100 in Roughgarden J, May RM and Levin S (eds.) Perspectives in Ecological Theory. Princeton University Press, Princeton

Venrick E L (1990) Phytoplankton in an oligotrophic ocean: species structure and interannual variability. Ecology 71: 1547-1563 *[Contains an excellent discussion of species diversity and stability in the oligotrophic Pacific and difficulties in resolving the paradox of the plankton]*

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Web Resources

Table 1. Nutrient limitation resources on the web

URL	Site	Description
http://www.anammox.com/	Anammox online resource	
http://www.mpi-bremen.de/en/Anammox_Bacteria_produce_Nitrogen_Gas_in_Oceans_Snackbar.html	Max Planck Institute	Press release about **Kuypers et al. (2005)**
http://www.ozestuaries.org/indicators/Def_denitrification.html	Denitrification	Denitrification in coastal systems.

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