

ECOLOGICAL PROCESSES IN THE SUBARCTIC PACIFIC: IRON LIMITATION CANNOT BE THE WHOLE STORY

By Charles B. Miller, Bruce W. Frost, Beatrice Booth, Patricia A. Wheeler, Michael R. Landry, and Nicholas Welschmeyer

STRETCHING ACROSS the Pacific between 45°N and the coast of Alaska (Fig. 1) is an oceanic region referred to as subarctic. It is part of a broader oceanic region in which major phytoplankton nutrients (nitrate, phosphate, and silicate) apparently are never depleted from the surface layer. Persistently high nutrient concentrations are found along the entire eastern edge of the Pacific with westward extensions in the subarctic and along the equator and with eastward extensions through Drake Passage and then around the globe south of 35°S (Reid, 1962). Ecological relationships vary dramatically along this nutrient-replete belt, and assembly of a complete comparative ecology for all of its distinctive parts has only begun.

Martin (1990; 1991, this issue) has opened a new chapter in this analysis by suggesting that limited availability of soluble iron may be a common factor preventing major nutrient depletion throughout the nutrient-replete belt. The initial observations leading to this suggestion (Martin and Fitzwater, 1988; Martin *et al.*, 1989) were made in the subarctic Pacific, which immediately stimulated our interest as workers in the subarctic Pacific Ecosystem Research (SUPER) Program. Although the testing of Martin's hypothesis is still in an early phase (Banse, 1990; Martin *et al.*, 1990), it is an attractive idea. It is one of several candidate explanations for the dominance of subarctic Pacific phytoplankton by cells of very small size. Given a flora composed of small cells, most other observations on subarctic Pacific ecology fit into a sensible, logical scheme. Perhaps similar schemes can be found for other sectors of the high-nutrient belt. Iron limitation, if it proves impor-

tant, can be only one facet of full understanding for pelagic ecosystem processes.

The Subarctic Pacific Habitat

The subarctic Pacific shares a feature with river estuaries. Its upper layer is diluted with freshwater (Fig. 2), which stabilizes the water column and prevents rapid vertical exchange through the halocline at 100–200 m. It differs in this from the subarctic North Atlantic, where small vertical density differences poise the water column for convective mixing with small changes in surface properties. The Pacific retains its freshened surface because it is colder on average, which lessens evaporation. It is colder because it has smaller input of subtropical water from the south. Warren (1983), in a simple analysis, attributes this to the lack of a cold northern basin (an equivalent to the Norwegian Sea) and a difference in the patterns of surface wind. The fundamental cause is not the velocity of the winds, which is sufficient to produce strong winter storm activity (cover photo, this issue), but that the pattern of wind-stress curl (from cross-wind gradients and turning of the large-scale wind) changes sign farther south in the eastern North Pacific than in the eastern North Atlantic.

Lack of deep winter mixing in the subarctic Pacific prevents seasonal elevation of surface nutrients to concentrations matching those of the subhalocline layers, which is $\sim 45 \mu\text{M}$ in nitrate. Breakdown of seasonal thermal stratification in late winter allows mixing of the surface layer with the zone between the seasonal thermocline (~ 35 m) and the halocline. This intermediate layer receives about $300 \text{ mmol NO}_3 \text{ m}^{-2} \text{ yr}^{-1}$, according to estimates of vertical advection and diffusion in the halocline (Miller and others, unpublished data). Thus, the productive surface layer receives nutrient intermittently, mostly in February and March, reaching concentrations as great as $17 \mu\text{M NO}_3$ by spring but with considerable interannual variation. Phytoplankton uptake from April to October reduces that by $< 10 \mu\text{M}$, occasionally to

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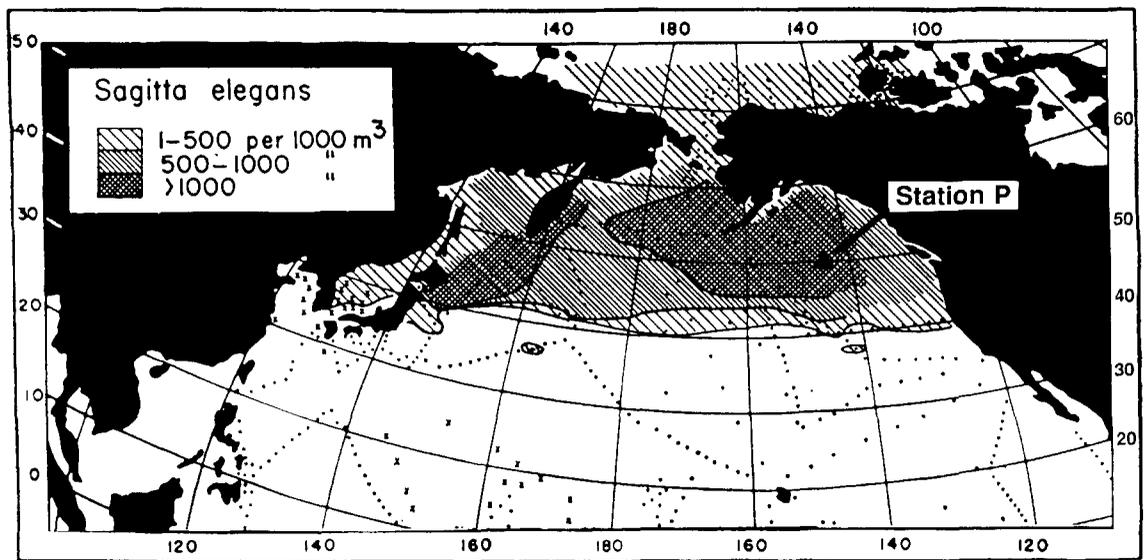


Fig. 1: Delineation of the subarctic region of the North Pacific Ocean by the distribution of *Sagitta elegans*, a chaetognath (after Bieri, 1959). The subarctic Pacific is both a hydrographic feature and a biogeographic province. Station P in the southern Gulf of Alaska was formerly occupied by Canadian weatherships and was the site of most of the SUPER Program studies.

6 or 7 μM (Fig. 8B). Constrained deep mixing also prevents flushing of the euphotic zone with large volumes of phytoplankton-free deep water so that phytoplankton stocks can remain high throughout the winter (Fig. 3). In the subarctic North Atlantic, the few winter observations available suggest that phytoplankton stock measured as chlorophyll-a (Chl-a) concentration is reduced to $<0.1 \text{ mg Chl-a m}^{-3}$ (Parsons and Lalli, 1988).

Subarctic Pacific Ecology

Absence of seasonal phytoplankton blooms is an ecologic signature of the subarctic Pacific. This was amply demonstrated by many years of data (Fig. 3) collected from Canadian weatherships on patrol at Ocean Station P (50°N, 145°W). Not only do plant stocks stay constant through the winter, they stay roughly constant all year long. This has had several explanations, all involving a dynamic balance between phytoplankton growth rates, which vary seasonally, and zooplankton grazing rates, which therefore must also change seasonally. One explanation involves peculiarities of the larger zooplankton. The dominant net-captured zooplankton in the euphotic zone are the large copepods *Neocalanus plumchrus* and *Neocalanus flemingeri*. These zooplankton spawn yolky eggs at depth in winter without feeding (Miller and Clemons, 1988), supplying early copepodites to the surface layers in advance of the spring increase in phytoplankton production rates. Heinrich (1957, 1962) first suggested that the increased grazing capacity of these copepods as they grow through the spring allows them to keep pace with increasing plant growth, thus imposing "balance" on the phytoplankton stock. Heinrich con-

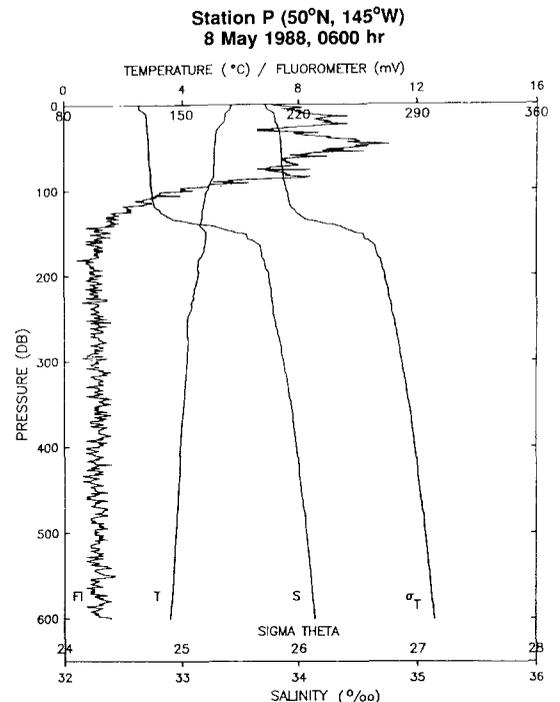


Fig. 2: Salinity (S), temperature (T), density (σ_T), and stimulated fluorescence (F) profiles from Ocean Station P in the Gulf of Alaska, May 1988. The halocline from 110–170 m constrains mixing between the surface and deep layers. The fluorometer output (arbitrary millivolt units) shows that phytoplankton are strongly restricted to the surface layer.

trasted this with the North Atlantic case where the dominant macrozooplankter is *Calanus finmarchicus*, a copepod that only reproduces sig-

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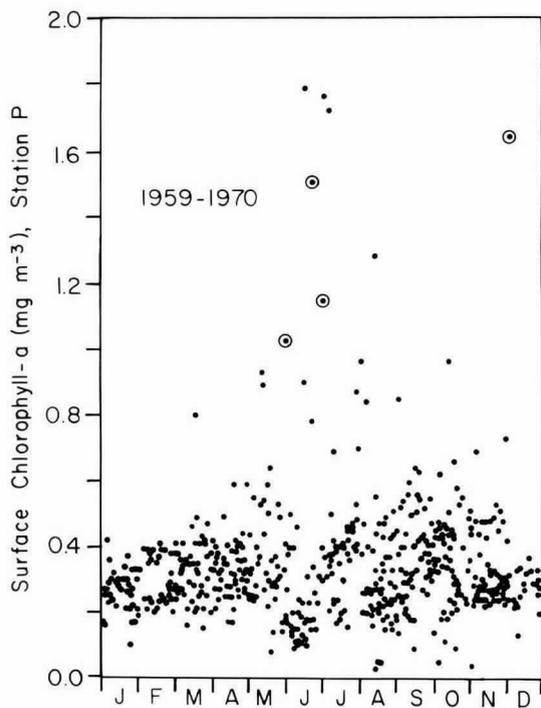


Fig. 3: Cumulative chlorophyll-a data from Ocean Station P. Scale extends only to 2.0 mg m^{-3} . Four circled points are all the values over 1.0 mg m^{-3} from 1970-1976.

nificantly when food is abundant in surface layers (Smith, 1990). This creates a lag between phytoplankton growth and grazer response, which allows spring blooms and nutrient depletion. Heinrich characterized this system as “unbalanced.”

The SUPER Program has tested that explanation (Miller and SUPER Group, 1988), showing that the spring stock of large copepods is not large enough, given the rate at which they feed and the rate of phytoplankton growth, to sustain balance. In fact, *Neocalanus* spp. appear not to be primarily herbivorous because there is not enough plant material in their guts at any time (Dagg and Walser, 1987) to sustain their respiration and observed growth (Miller and Nielsen, 1988).

Elimination of the life history-based “major grazer hypothesis” led us to consider microzooplankton, specifically heterotrophic protists, as the most likely source of grazing control of phytoplankton stocks. On our first expeditions, Booth and Horner (unpublished data) observed large numbers of very small ($\sim 5 \mu\text{m}$) heterotrophic flagellates, substantial numbers of aloricotic oligotrichous ciliates, and some larger ($\sim 40 \mu\text{m}$) mixotrophic ciliates including *Laboea* sp. Such microheterotrophs are capable of population increase at higher rates, up to five doublings per day (Banse, 1982; Fenchel, 1982; Goldman and Caron, 1985), than phytoplankton, which are limited to about two doublings per day. This is because they can feed around the clock, which photoau-

totrophs cannot do, and because their prey organisms handle all small-molecule syntheses, saving them costly chemical work. Thus, with their population-increase rates responding to phytoplankton abundance, they can rapidly catch up to any rise in phytoplankton stock above a feeding threshold level.

Pelagic microheterotrophs are mostly very small, certainly smaller than the larger forms among the phytoplankton. Many species of diatoms and dinoflagellates exceed $50 \mu\text{m}$, and (ignoring giants such as the tropical *Ethmodiscus rex*) $200\text{-}\mu\text{m}$ cells are common and much larger than microheterotrophs. Thus, grazing control of phytoplankton stock by microheterotrophs depends upon dominance of the flora by very small species. Larger phytoplankton must be controlled by other processes. In the subarctic Pacific, it is typical for $>90\%$ of phytoplankton biomass to be in cells $< 10 \mu\text{m}$ diameter (Booth, 1988) (Fig. 4). Larger phytoplankton are present (Clemons and Miller, 1984), but they are only a small proportion of the flora. The mechanism for their control is not clear, but Martin *et al.*'s (1989) experiment with iron addition suggests that iron limitation may slow their growth enough to allow control by macrozooplankton grazers. Selection for small size by a limiting trace metal has been explained in detail by Morel *et al.* (1991, this issue). Dominance of small phytoplankton results in a food web (Fig. 5) with one or several trophic steps involving small grazers, which are in turn the main food of particle-feeding macrozooplankton. Because microheterotrophs can switch to a bacterial diet, a microbial loop (dissolved organic matter to bacteria to microheterotrophs) may stabilize trophic relationships in the system, keeping small

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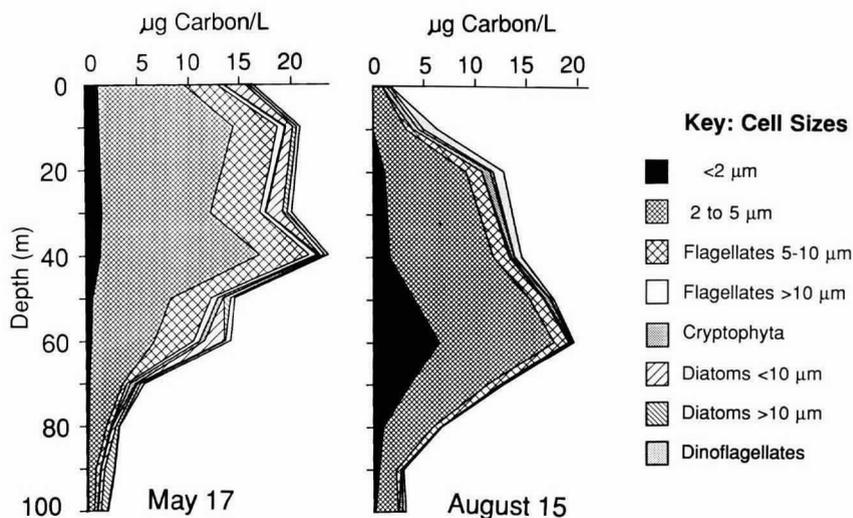


Fig. 4: Vertical and size distribution data for phytoplankton at Ocean Station P in two seasons of 1984. Most cells $< 2 \mu\text{m}$ were *Synechococcus* spp. Most phytoplankton biomass is in cells $< 10 \mu\text{m}$ diameter. Redrawn from Booth (1988).

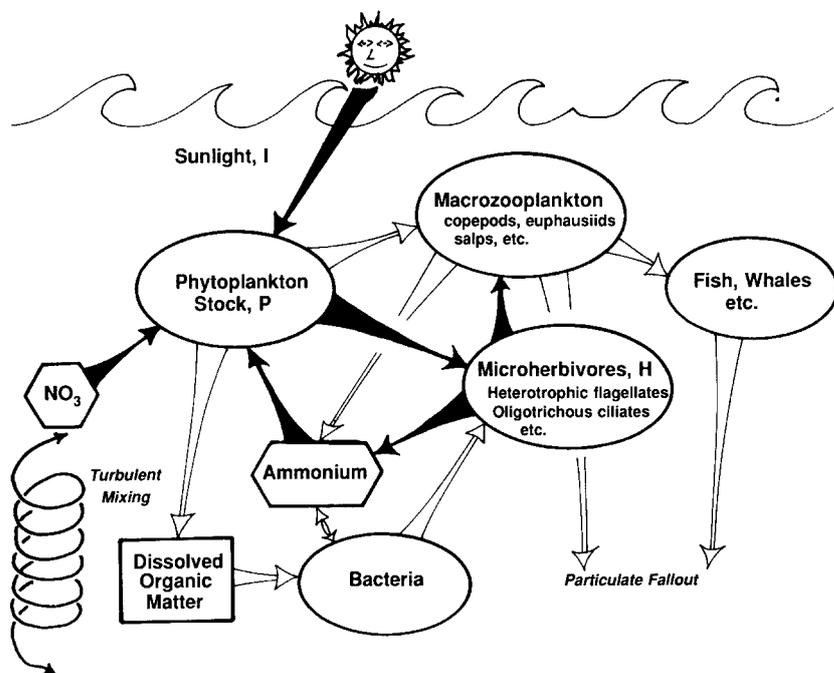


Fig. 5: Diagram of principal food web connections in the subarctic Pacific. Transfers of energy (and matter) are represented by arrows. Solid black arrows are transfers explicitly represented in the SUPER synthesis model. Open arrows represent other transfers that stabilize the system (i.e., herbivory by macrozooplankton and the microbial loop) or return matter to outside the system (i.e., particulate fallout). Some transfers, such as contributions of fish to ammonium, have been left out to simplify the diagram.

grazers present and active when phytoplankton are reduced for any reason.

The subarctic Atlantic may differ from the Pacific in two respects that lead to imbalance. First, iron limitation, if it operates, should be much less severe due to the generally closer proximity to land (but, see iron-flux data shown by Donaghay *et al.*, 1991, this issue). Second, deep-winter mixing should clear the system of microheterotrophs as well as phytoplankton. It is possible that re-establishing the microheterotroph stock and its interaction with the phytoplankton requires time, with this lag allowing a phytoplankton bloom. It is more likely that the macrozooplankton have no dependable food source at the surface for their

Table 1

Relative contributions of micro- and macrograzers to removal of chlorophyll from the mixed layer in the Gulf of Alaska. The chlorophyll-budget technique is explained in the text and in Welschmeyer and Lorenzen (1985).

| Expedition | Date | Number | Mean (of N budget estimates) contributions to grazing | |
|------------|----------------|---------|---|-------|
| | | | Micro | Macro |
| SUPER-3 | June 1987 | (N = 4) | 83% | 17% |
| SUPER-4 | September 1987 | (N = 4) | 93% | 7% |
| SUPER-5 | May 1988 | (N = 4) | 70% | 30% |
| SUPER-6 | August 1988 | (N = 1) | 82% | 18% |

young (equivalent to the persistent microheterotroph stock of the Pacific), so they cannot reproduce before the phytoplankton stock rebuilds in spring. Their absence during this season allows a bloom of large cells, despite their greater sensitivity to iron limitation. Heinrich's hypothesis is revived here in a modified form.

We term this understanding of production dynamics in the subarctic Pacific and of its distinction from the North Atlantic the "mixing and micrograzer hypothesis." Several aspects of it were tested on expeditions of the SUPER Program. We used phytoplankton pigment budgets (Welschmeyer and Lorenzen, 1985) to determine the relative impacts of microheterotroph and macrozooplankton grazing on phytoplankton stocks. Pigment budgets are possible because a fraction of the breakdown products of chlorophyll survive digestion in most animals. For large grazers, these "phaeopigments" appear in fecal matter large enough to sink out of the water column. For microheterotrophs, the fecal matter remains dispersed in the euphotic zone where it is subject to photodegradation by a reaction of known quantum efficiency. Thus, large-grazer impact should be proportional to the sinking flux of phaeopigments measured by sediment traps, whereas small-grazer impact is proportional to net near-surface phaeopigment increase plus phaeopigment destruction (quantum flux \times phaeopigment concentration \times photodegradation efficiency). Relative comparisons of these two sources of grazing (Table 1) show that microheterotrophs account for at least four-fifths of chlorophyll conversion, and thus, of total grazing. That agrees with the hypothesis.

For microheterotroph grazing to sustain balance, feeding rates on phytoplankton should be consistently of the same absolute magnitude as phytoplankton growth rates. Expressed as an equation, phytoplankton stock, P , should change with time according to $dP/dt = (\mu - g)P$, where μ is the growth rate and g is the overall grazing rate (both in units of days^{-1}). When there is balance, $(1/P)(dP/dt) = 0 = \mu - g$, so that $\mu \approx g$. To examine the relation of μ to g , we applied Landry and Hassett's (1982) dilution technique, which provides estimates of both growth and grazing. Filtered seawater is added to incubations of near-surface seawater in varying amounts. Dilution produces increase in apparent per capita phytoplankton growth because microheterotroph grazing is reduced by increased spacing of both grazers and plant prey. Plots of apparent μ versus dilution fraction ($0 = \text{infinite dilution}$; $1 = \text{no dilution}$) give the grazing-free μ as Y -intercept and $-g$ as slope. In the Gulf of Alaska in spring, μ and $-g$ alternated in dominance (Fig. 6), which is consonant with the sorts of variations in phytoplankton stock that were observed from day to day (Fig. 7).

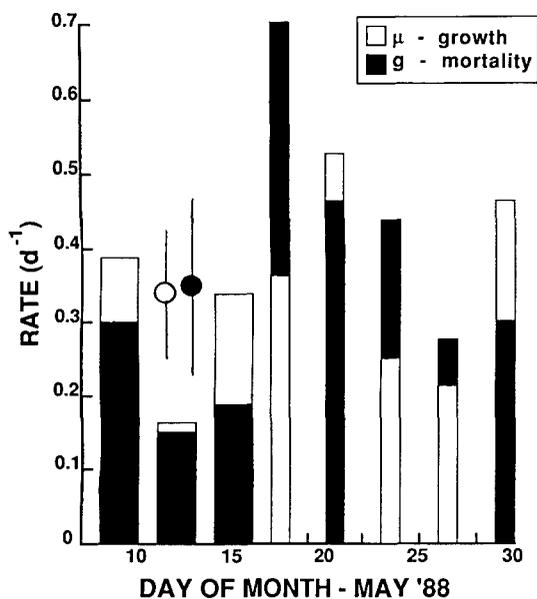


Fig. 6: Estimates of phytoplankton community growth and microzooplankton grazing rates from dilution experiments conducted during cruises to the Gulf of Alaska in May, 1988. Samples were collected from the surface mixed layer (~10 m) and incubated on shipboard for 1 or 2 days under ambient temperature and light (shaded) conditions. Analyses based on chlorophyll *a*. Histograms indicate results of individual experiments. Circles indicate cruise-mean growth and grazing estimates (with 95% confidence limits).

In summary, once the phytoplankton are forced consistently to small cell size, a balanced system can develop in which stocks oscillate within relatively narrow limits because they are controlled by unicellular grazers with even higher population growth potential. It remains to show why such a system would always leave an excess of major nutrients. We term our explanation "the SUPER synthesis."

The SUPER Synthesis

Microheterotrophs are small, so they produce suspended fecal matter and, on short rations, they should die rapidly and decompose without sinking. Thus, their constituents should be recycled efficiently and their nitrogen recycled primarily as ammonium. Sufficient dissolved ammonium suppresses uptake of nitrate, which must be reduced before incorporation. Ammonium is available for immediate incorporation in proteins, and in some phytoplankton it directly interferes with the activity of nitrate reductase (Dortch, 1990). We have shown this suppression specifically for the subarctic Pacific by $^{15}\text{NO}_3$ -uptake experiments (Wheeler and Kokkinakis, 1990). Phosphate is rapidly recycled too, although it doesn't have an associated redox change to aid in tracing the effect. Location of most nutrient recycling in the surface layer explains the persistence of substantial major

nutrient levels throughout the year. Recycling holds the net annual nitrate use to $\sim 6 \mu\text{M}$ in the upper 50 meters.

We represent this SUPER synthesis of the ecological relationships with a systems model based on that of Frost (1987). A simplified schematic food web (solid arrows in Fig. 5) is the basis of the model, which considers the following state variables.

Phytoplankton Stock,

P – mg organic carbon m^{-3} ;

$$dP/dt = f_1(I, P) - f_2(H, P),$$

where I is solar illumination

Phytoplankton Chlorophyll,

Ch – mg Chl-*a* m^{-3} ,

$$Ch = (\text{seasonal constant}) \times P$$

Micrograzer Stock,

H – mg organic carbon m^{-3} ,

$$dH/dt = f_3(P) - f_4(H)$$

Nitrate concentration – μ -moles liter $^{-1}$

Ammonium concentration – μ -moles liter $^{-1}$

$$d([\text{NO}_3] + [\text{NH}_4])/dt$$

$$= f_1(I, P), \text{NH}_4 \text{ preferred}$$

Chlorophyll is used only for ready comparison to historical chlorophyll values, and it is derived from the phytoplankton stock by a carbon/chlorophyll ratio. Similarly, nitrate and ammonium taken up by phytoplankton or transferred to micrograzers are converted to organic carbon by a simple carbon/nitrogen ratio.

The physical habitat of the model is specified in terms of available photosynthetically active ra-

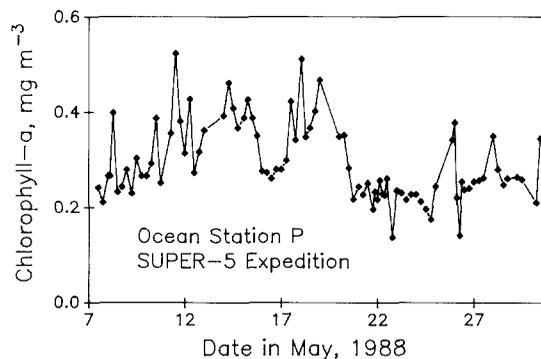


Fig. 7: Variability in mixed-layer chlorophyll-*a* concentration in the Gulf of Alaska during May 1988. Some variability is small-scale spatial difference; some is larger-scale temporal change. There are larger longer-term changes as well. The variation compares well to that shown by the process model.

Location of most nutrient recycling in the surface layer explains the persistence of substantial major nutrient levels . . .

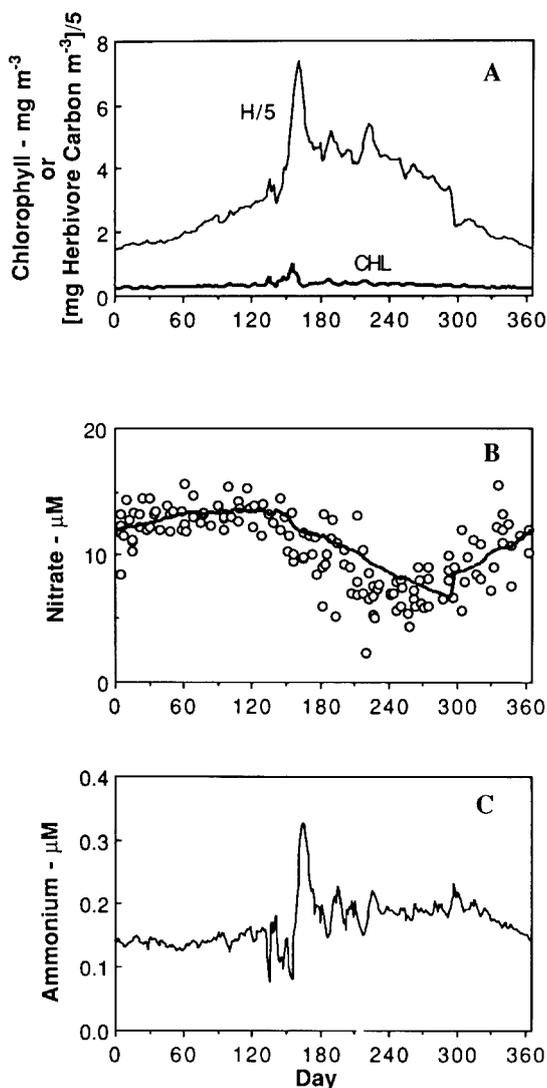


Fig. 8: Output of the ecosystem model of subarctic Pacific production processes. The model succeeds in several respects. 1) The total seasonal production (not shown) is approximately correct. 2) Chlorophyll-a (A) is held in the range observed in the field and the short-term variability of chlorophyll is realistic, driven by variability in insolation. 3) Nitrate (B; circles are Ocean Station P data from the weathership program; Parslow, 1981) utilization over the year is approximately as observed in the Gulf of Alaska. 4) Microzooplankton (A) increase and vary through the spring and summer when phytoplankton production is high and are not greatly reduced in winter.

diation (PAR) and a seasonally variable vertical-mixing regime. The model uses daily time steps, so daily integrals of actual illumination data gathered by the weatherships are used to model the seasonal and short-term variability of PAR. Vertical structure of the water column is represented as three layers: a rapidly mixing upper layer, a stratified intermediate layer extending to 120 m depth, and the permanent halocline. Exchange

through the middle layer is represented as turbulent, Fickian, diffusion, whose eddy diffusivity was varied seasonally ($0.1 \text{ cm}^2 \text{ sec}^{-1}$ in summer, higher in late autumn through spring). Diffusivities were fitted to give reasonable property profiles at all times and to bring nitrate concentration back to the starting value at the end of the year. As done by Frost (1987), micrograzers are given a functional response (the relation between the per capita rate of ingestion of phytoplankton and the size of the phytoplankton stock) resembling that of tintinnids (Heinbokel, 1978). That is, mass-specific ingestion at saturating phytoplankton availability was set at one body weight per day. An hyperbolic approach to this asymptote represented ingestion above a threshold phytoplankton stock of 5 mgC m^{-3} . Growth efficiency was set conservatively at 30% (Caron and Goldman, 1990) and mortality was made a hyperbolic function of micrograzer stock size.

Growth of phytoplankton in the model is set (or "limited") by either PAR or by nitrogen availability. However, because the parameters represent the subarctic Pacific, nitrogen-limitation never becomes important. Effectively, water-column production is controlled by light and plant standing stock, with stock established by growth and grazing. The relationship of photosynthesis to PAR in the model has a very steep slope, $\alpha = 5.0 \text{ (mg carbon [mg Chl-a]}^{-1} \text{ m}^{-3}) / (\text{Einstein m}^{-2})$. In situ primary productivity estimates made on SUPER cruises demonstrated this capacity of the small dominant flora for dramatic response to relatively low illumination. This must be conditioned on both ecological and evolutionary time scales by the strong day-to-day variability of PAR in the region.

Inorganic nitrogen is modeled as two components equivalent to nitrate and ammonium, somewhat as done independently by Fasham *et*

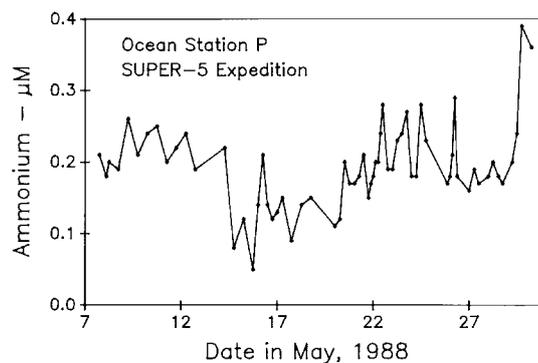


Fig. 9: Variability in mixed-layer ammonium concentration in the Gulf of Alaska during May 1988. Some variability is small-scale spatial difference; some is larger-scale temporal change. Diel variation is evident (Wheeler *et al.*, 1989), and there are larger longer-term changes as well.

... capacity of the small dominant flora for dramatic response to relatively low illumination.

al. (1990). Nitrate uptake was modeled as a function of photosynthetic activity limited by available light but reduced according to the amount of ammonium in the system (Fig. 8). When ammonium is available, uptake of ammonium replaces nitrate uptake, with the total nitrogen uptake set by the PAR-limited photosynthetic rate. The results of the model are daily time-series of the state variables.

The output of this ecosystem model reproduces the seasonal (Fig. 8) and (just as important) short-term variabilities of phytoplankton stock (Fig. 7), nitrate and ammonium (Fig. 9) in the oceanic subarctic Pacific. Key results from SUPER field work are represented by the model. First, photosynthetic rates are principally limited by the available illumination. Even though growth of some rare large cells may be limited by iron availability, the dominant stock of small cells probably is not iron limited. Phytoplankton grow at the highest rates that the relatively cold temperatures and moderate illumination allow (Booth *et al.*, 1988). Second, available nitrate (also phosphate) is not used in the course of the year because nitrogen as ammonium is efficiently recycled in the euphotic zone by the microheterotrophic grazing community.

Conclusion

All of the SUPER synthesis is consonant with Martin's (1991, this issue) suggestion that oceanic regions persistently rich in major nutrients are in some sense iron limited. Something sustains the dominance of very small phytoplankton in the subarctic Pacific. It could very well be the greater susceptibility of larger phytoplankton to iron limitation. Martin *et al.* (1989) showed that added iron shifts the dominant flora to larger cell sizes,

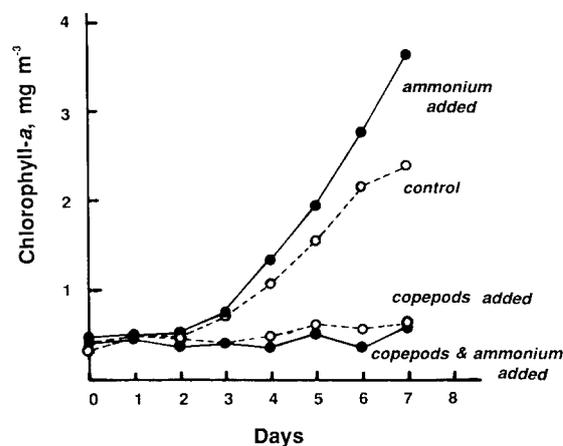


Fig. 10: Comparison of time courses for chlorophyll-*a* as a measure of phytoplankton stock in 60-liter containers with and without one fifth copepodite of *Neocalanus plumchirus* (large grazing copepod) per liter. Both treatments replicated with and without added ammonium. Redrawn from Landry and Lehner-Fournier (1988).

particularly large diatoms. They also showed that iron had no immediate effect on the photosynthetic rates of the usual flora. If differential susceptibility of large and small phytoplankton to micronutrient limitation is involved, it must be backed by some grazing on large cells by macrozooplankton. Large cells are present, and their stocks could not be sustained without positive growth rates. Those must be balanced by some population loss. Landry and Lehner-Fournier (1988) have shown (Fig. 10) that at copepod densities somewhat above those observed in the field, growth of large phytoplankton can be balanced by their grazing, despite almost certain alleviation of iron limitation by inadvertent contamination. Precise quantification of all the important interactions remains on our agenda.

Acknowledgements

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