Ecological dynamics in the subarctic Pacific, a possibly iron-limited ecosystem

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Abstract

   It has been suggested that production in offshore waters of the subarctic Pacific is limited by availability of dissolved Fe. Although that is not yet adequately established, the functional consequences of the limitation (if it exists) can be characterized from the results of the SUbarctic Pacific Ecosystem Research (SUPER) program. Fe limitation, or something like it, establishes a phytoplankton community dominated by very small cells. These plants are not limited by Fe availability. Rather, their production is limited by their stock and available illumination. Stock is set by microzooplankton grazers with rapid population growth rates and, thus, rapid response to increases in phytoplankton abundance. Micrograzers provide efficient recycling of nitrogen as NH_4, and the ready availability of NH_4 sharply limits the annual utilization of NO_3. Persistently high NO_3 concentrations result. Other possibly Fe-limited, oceanic ecosystems with persistently high, near-surface nutrients require similar, detailed analysis of ecosystem function.

   Three regions of the oceans far from land continuously retain high levels of the major phytoplankton nutrients required for formation of structural cell constituents: NO_3, PO_4, and SiO_4. These regions are the eastern tropical Pacific, part of the Southern Ocean, and the subarctic Pacific. Other oceanic areas are either continuously or seasonally depleted in major nutrients. The nutrient-rich regions are geographically separate and distinctive. The equator bisects the eastern tropical Pacific, whereas the Southern Ocean

and subarctic Pacific are both at high latitude and strongly seasonal. In ecological detail the two high-latitude regions differ considerably. Therefore, there has been no tendency until recently to see these three oceanic ecosystems as examples of any single phenomenon. For each there was a separate explanation of persistently high nutrients.

   Recently this has changed. Martin (1990) has suggested that the persistence of substantial concentrations of major nutrients
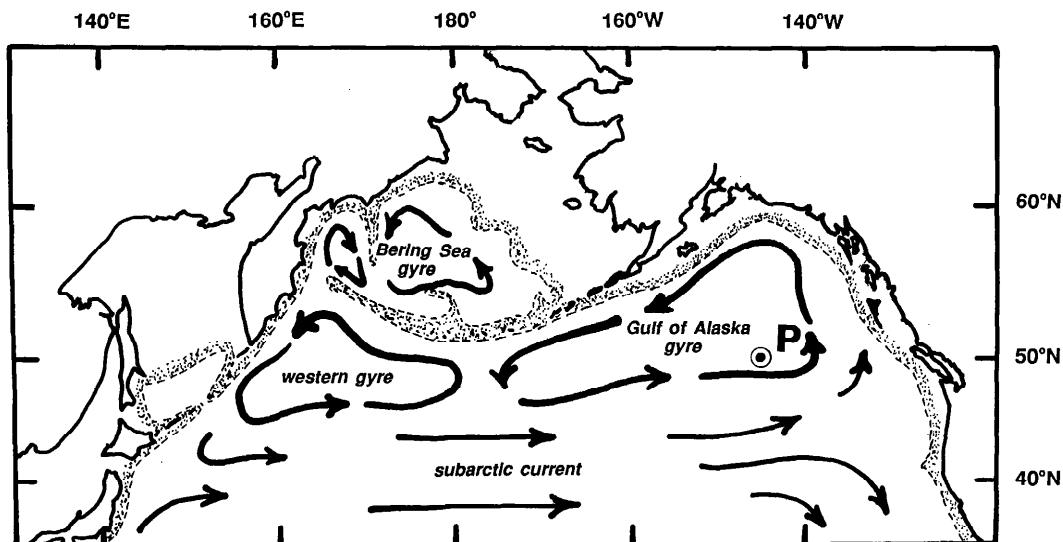
Fig. 1. Map of the North Pacific Ocean delineating several distinctive sectors of the subarctic region.

in all three regions results from limitation of phytoplankton production by very low levels of available Fe. Fe is not part of structural cell constituents. Rather, its flexible oxidation states and its capacity (when suitably coupled in proteins) for labile bonding to oxygen make it an important part of many enzymes (nitrate reductase and cytochromes among others) and oxygen transport pigments. It serves as a catalyst, or micronutrient, in the growth of phytoplankton. Other elements, such as Zn, Cu, and Mo, are also important as micronutrients, but they are more soluble than Fe in weakly basic solutions such as seawater. Fe is relatively insoluble, and thus is removed from the water column by particle scavenging processes. As Duce (1986) has made clear, Fe must primarily be supplied via the atmosphere. Because it is fundamentally different from the major nutrients and from most other micronutrients, Fe limitation makes an interesting candidate explanation for persistently nutrient-rich oceanic regions.

An experiment (Martin and Fitzwater 1988; Martin et al. 1989) in the Gulf of Alaska, a major part of the subarctic Pacific (Fig. 1), was the observational basis for Martin's suggestion. Martin and his coworkers observed that samples of seawater collected with special, clean techniques ex-

hibited different levels of phytoplankton stock accumulation after 4 or 5 d, depending on the level of added Fe. The reports made clear that the phytoplankton developing in the enriched treatments were large cells, mostly diatoms of species relatively rare in the water column.

Partly because the site of Martin's experiment was the subarctic Pacific, his initial report excited much interest among workers studying production processes in that region, particularly among participants in the SUbarctic Pacific Ecosystem Research (or SUPER) program of which we are part. Prolonged incubations had been done in the region for many years (McAllister et al. 1960), and some were done by the SUPER group. The usual result was development of large plant stocks after 4 or 5 d, and a standard explanation had arisen that sequestering samples in incubation bottles removed the grazers of larger phytoplankton, which then accumulated. Much of the SUPER program was aimed at evaluating the roles of grazers in setting phytoplankton stock size and in controlling annual nutrient consumption so that NO_3, PO_4, and SiO_4 could persist. However, nobody before Martin et al. had attempted to prevent small accidental Fe additions to incubated samples. So, Fe contamination may partially explain ear-
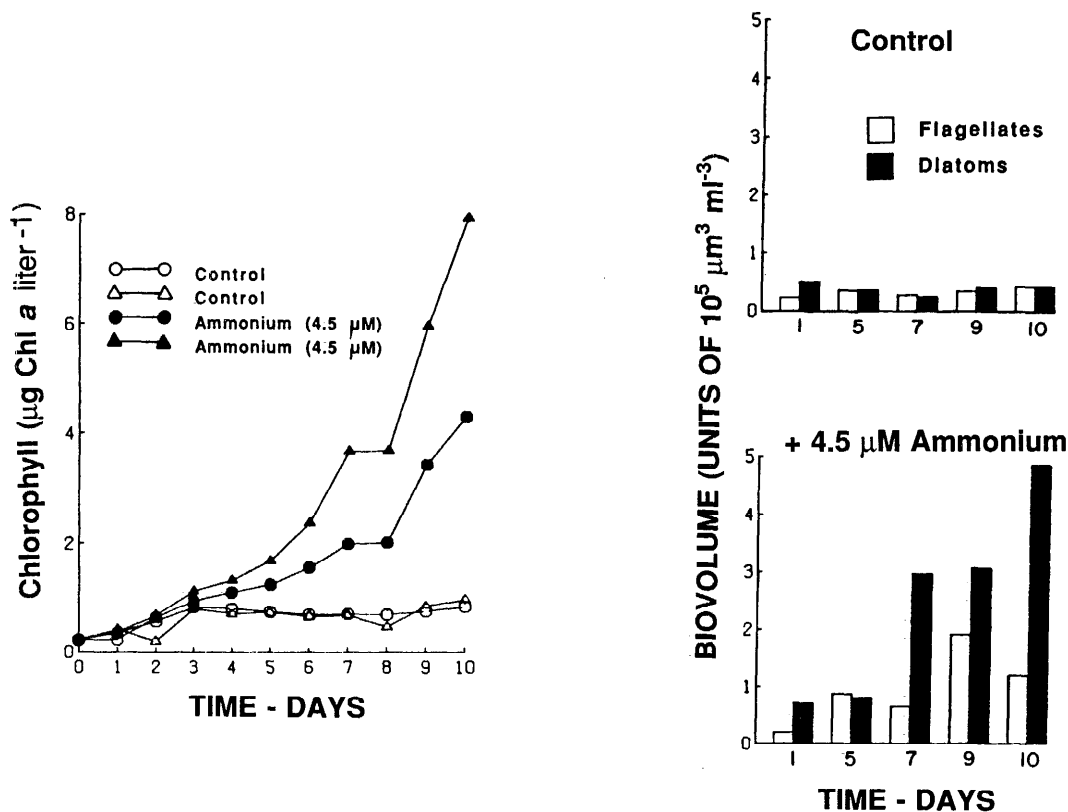
Fig. 2. Effect of NH_4 addition on phytoplankton abundance, measured as Chl a (left) and on composition of the phytoplankton community (right) in rotating, 60-liter microcosms filled with seawater from the mixed layer. Experiment was at 50°N, 145°W, 3–13 August 1984. Microcosms were on deck in a water-cooled incubator illuminated by natural sunlight.

lier incubation experiments, although some change in grazing is always incurred in establishing an incubation.

We had been puzzled in August 1984 by a result (Landry and Lehner-Fournier in press) (Fig. 2) resembling that of Martin et al. (1989). On that occasion, incubations of subsurface water with added NH_3 eventually showed large stock increases, mostly diatoms, while control incubations showed only slight increases. If Fe is important, this difference in growth might be explained as a result of Fe contamination introduced only with the NH_3 addition or by Fe limitation of larger phytoplankton that is stringent enough to prevent function of nitrate reductase, but not of other, more vital, Fe-requiring enzymes (Rueter and Ades 1987). In the latter case, NH_4 addition would alleviate Fe limitation.

Some of the fieldwork of the SUPER program was done after Martin's suggestion was published. We attempted with some success to repeat his experiment (Horness in prep.). We measured Fe levels in some incubation containers and found that we were not able with our crude system for clean work to keep accidental Fe additions to <3 nM. However, there were differences among our lowest and highest addition levels in the direction of Martin's result. Moreover, our results paralleled Martin's (and earlier) results in that the stock built up after 4–5 d was mostly large diatoms. We found no substantial increases in smaller flora—stocks of which could have been controlled by micrograzers included in the incubations. None of our results contradicted Martin's. Nevertheless, his notion rests on a very small observational base (Banse 1990; Martin et

al. 1990). Considerably more direct work is needed on the role of trace metals in the subarctic Pacific and other, persistently nutrient-rich, oceanic ecosystems.

The work of the SUPER program produced a picture of ecosystem function in the subarctic Pacific which stands whether Fe is limiting to production of some component of the phytoplankton. If Fe is limiting, then the details of ecosystem dynamics in the face of that limitation are very important. All the nutrient-rich oceanic ecosystems have healthy ecological functions and substantial productivity at all trophic levels, including large fisheries. Although recognizing and testing Fe limitation is valuable, that testing is only part of evaluating their systems ecology. We will review our start on this necessary analysis that SUPER provided for the subarctic Pacific. Similar work is needed to address the Southern Ocean and the eastern tropical Pacific and to readdress the subarctic Pacific. The latter is far from fully understood.

The classical subarctic Pacific problem

The SUPER project set out in 1980 to examine a classical explanation for the persistence of major nutrients in the subarctic Pacific. Along with persistence of nutrients, the region has long been recognized for lacking the substantial phytoplankton blooms that might be expected to grow on the continuously high major nutrients (always ≥ 6 μM NO_3, ≥ 0.2 μM PO_4, ≥ 14 μM SiO_4). This lack of phytoplankton blooms was well documented by long-term sampling from the weather ships of the Canadian Coast Guard which patrolled at Ocean Weather Station P from the 1950s until 1981. Throughout that period (Fig. 3), there was never a phytoplankton bloom reaching 2 mg Chl a m^{-3}; the vast majority of observations in all seasons fell between 0.3 and 0.4, which contrasts with the subarctic North Atlantic, where even the most remote oceanic sites have phytoplankton blooms in excess of 1 mg Chl a m^{-3} every year (Parsons and Lalli 1988) and where major nutrient levels drop to the detection limits of standard chemical methods (Bainbridge 1981).

The classical explanation, suggested by Heinrich (1957) and Beklemishev (1957),
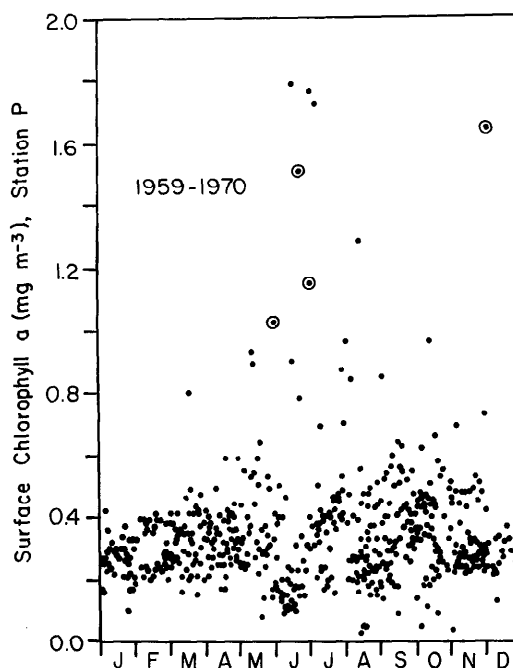

Fig. 3. Cumulative Chl a data from Station P over 10 yr. Scale extends only to 2.0 mg m^{-3}. Four circled points are all the values >1.0 m gm^{-3} from 1970 to 1976.

was biological. The subarctic zones of the two oceans have different copepod grazers with different life history patterns. *Calanus finmarchicus*, the dominant grazer in the North Atlantic, only produces eggs when the females obtain abundant food near the sea surface during a vernal bloom. This introduces a lag in development of the new generation of copepodite-stage grazers, a lag which allows the bloom to occur. Larger *Neocalanus* species in the North Pacific reproduce in winter at depths below 400 m using large oil reserves, rather than currently ingested food (Miller and Clemons 1988). The yolky eggs produced allow the young to develop to actively feeding stages prior to acceleration of phytoplankton growth in spring, and thus they might control phytoplankton stocks and prevent blooms. Cushing (1959) referred to these different modes of grazer control of phytoplankton stocks as "unbalanced" (Atlantic) and "balanced" (Pacific) ecosystems.

The SUPER group's initial work (Miller et al. 1988) was a test of this notion, which

Table 1. Compilation of phytoplankton growth rates from four SUPER expeditions to the Gulf of Alaska. Each estimate is the mean of three to seven, 24-h, in situ profiles. Detailed methods are given by Booth et al. (1988). Comparison to Sargasso Sea results by identical methods is taken from Welschmeyer (1991).

Cruise		No. profiles	Mean primary production (mg C m^{-2} d^{-1})
SUPER-1	May 84	3	415
SUPER-2	Aug 84	4	444
SUPER-3	Jun 87	7	868
SUPER-4	Sep/Oct 87	5	664
SUPER-5	May 88	7	546
SUPER-6	Aug 88	7	578
Range			240–1,300
Sargasso Sea	Jan, Mar, Jul 88	13	251
Range			100–400

we termed the major grazer hypothesis. We based our test on the requirement that grazing capacity be consistently greater than the capacity of the phytoplankton stock to increase. Multiple comparisons were made in spring and late summer between primary productivity and the "installed" grazing capacity of large copepods, euphausiids, and salps available to limit the increase of the phytoplankton stock. Our results were, first, that phytoplankton growth rates were in fact substantial (Table 1). A comparison to the Sargasso Sea, where major nutrients are typically depleted but illumination is consistently greater, has been made by Welschmeyer (1991). That comparison is included in Table 1, showing that subarctic Pacific productivity is 2–3 times greater. According to all measures we have made in the subarctic Pacific, the phytoplankton never show any sign of nutrient limitation. As argued in detail by Booth et al. (1988) for our 1984 data, we consistently find the phytoplankton growing as fast as temperature and available light allow. The small dominant phytoplankton are capable of rapid growth— growth always seen in our productivity experiments. Work by Martin et al. (1989) agrees with this. Their 24-h primary productivity measures by the same ^{14}C technique we use show no effect from Fe addition. The cells dominant at any given time in this possibly "Fe-limited system" are not Fe limited. They show no short-term response to added Fe.

Second, to our surprise, available grazing capacity was never close to that needed to match the growth rates of the phytoplankton. Moreover, we observed during the spring period that, while the large *Neocalanus* copepodites were growing actively (Miller and Nielsen 1988), they were not eating enough phytoplankton to support their respiration (Dagg and Walser 1987). Consumption of phytoplankton was quantified by measures of phytoplankton pigments in the copepod guts, a method that would not show animal food in the copepod diet. The solution to this double dilemma seemed to be that phytoplankton must be grazed primarily by much smaller, previously unnoticed microzooplankton, probably mostly protozoans, which must be the principal diet of the large copepods (Fig. 4).

The subarctic Pacific problem recast

Once we recognized that microzooplankton are a substantial trophic strand in the subarctic food web, the entire system looked different. Our recognition of the importance of protozoa occurred just as they were recognized by oceanographers everywhere as major trophic links in pelagic habitats of all latitudes, both neritic and oceanic. Therefore, our work seemed less unique and original that it might have, but such confluences are not unusual. Perhaps the recurrence of microzooplankton in oceanographic discourse during the 1980s made the solution of the subarctic problem obvious. Protozoa are capable of considerably higher growth rates than phytoplankton, rates of 5 doublings d^{-1} or more (Banse 1982; Fenchel 1982; Goldman and Caron 1985). As het-
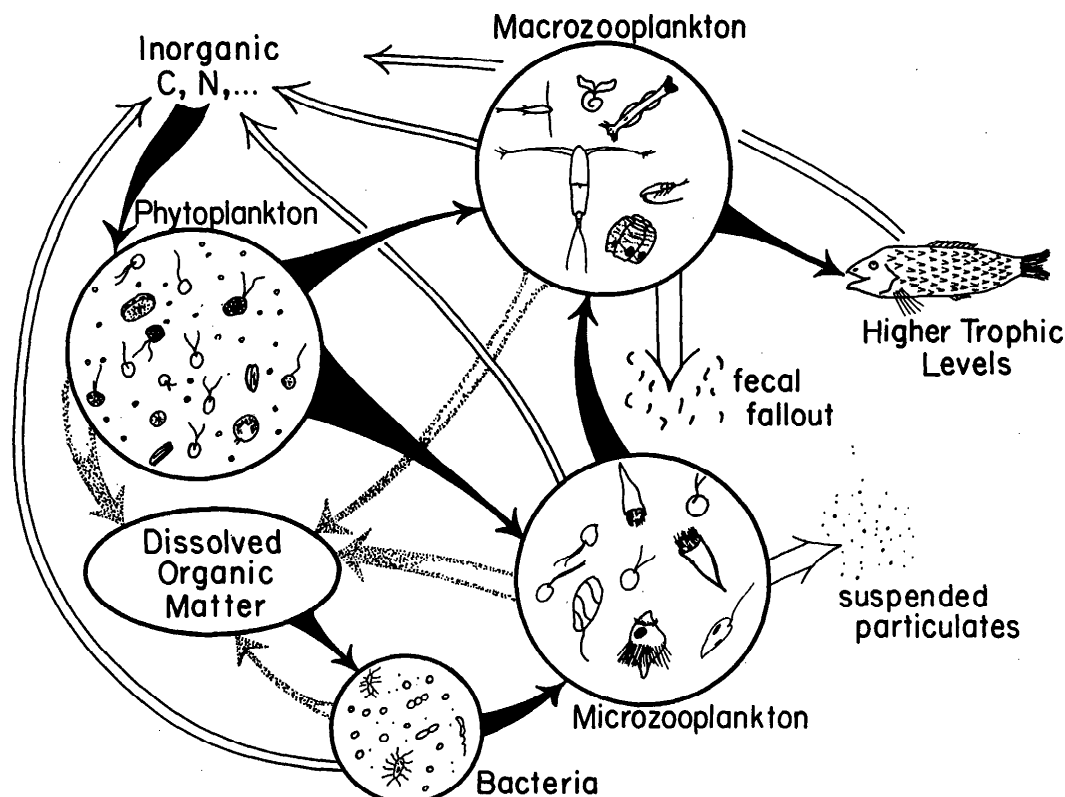
Fig. 4. Diagram of principal food-web connections in the subarctic Pacific. Black arrows—consumption; white arrows—regeneration processes; stippled arrows—transfers to dissolved organic pool.

erotrophs they can grow faster than photoautotrophs for two reasons: they can obtain new nutrition around the clock, while phytoplankton can add new photosynthate only in daylight; they are saved the energetic expense of synthesizing basic biological molecules, receiving ready-made amino acids, sugars, and fatty acids. Because they can grow faster given enough food, protozoan stocks can always overtake and suppress incipient blooms of small phytoplankton.

With life history differences in large zooplankton displaced as the distinctive, controlling difference between balanced and unbalanced pelagic systems, we needed a new explanation of the difference in production cycles between the subarctic sectors of the Pacific and the Atlantic. Returning to the list of major differences, we noted that the North Atlantic not only had a vernal bloom that left nutrients depleted, but winter mixing in that ocean region reduced

the phytoplankton stocks to practically nil. In the North Pacific there was little reduction of phytoplankton stocks throughout the winter.

The obvious physical difference corresponding to this biological one is that the subarctic Atlantic mixes to great depths every winter—to at least 250 m (Levitus 1982; Glover and Brewer 1988). Upper layers of the subarctic Pacific, in contrast, are stabilized by low salinity surface water (Fig. 5), and winter mixing (despite lots of storm activity) reaches only to the upper levels of the permanent halocline at ~100 m. We hypothesized that the lesser extent of vertical mixing allows the phytoplankton to sustain their stock in the euphotic zone throughout the winter season. The reduced illumination surely slows their growth, but stocks are not much reduced. Because mixing is insufficient to sweep away the phytoplankton, it must also fail to sweep away

Station P (50°N, 145°W)
8 May 1988, 0600

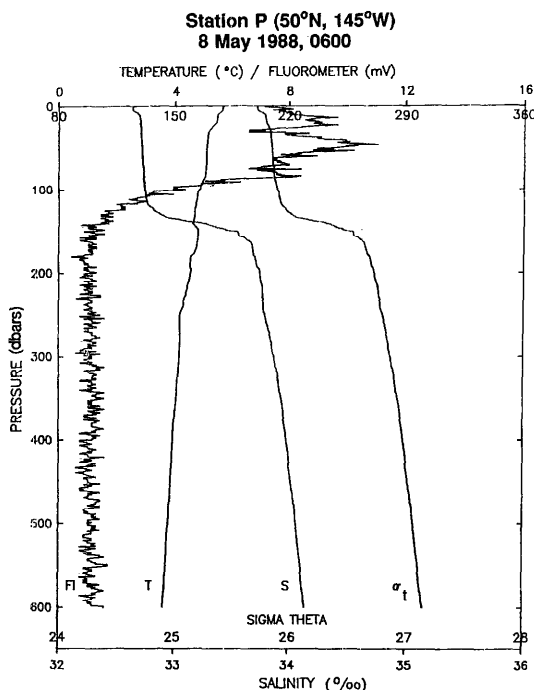TEMPERATURE (°C) / FLUOROMETER (mV)

Fig. 5. CTD profile from Station P. Note low-salinity (low density) layer above the permanent halocline from 110 to 170 m. Fluorometer output (arbitrary mV scale) shows the vertical distribution of phytoplankton.

Station P   NO₃⁻ (μg-atoms liter⁻¹)

Fig. 6. Annual variation in upper-layer NO_3 concentration at Ocean Station P. Redrawn from Anderson et al. 1977.

the microzooplankton that depend on them. Thus, in the subarctic Pacific the microzooplankton stocks can remain substantial all year and never lose control of the phytoplankton. We called this scheme the mixing and micrograzer hypothesis.

The mixing and micrograzer hypothesis has another part. Micrograzers are limited to eating rather small phytoplankton, those ≲10-μm diameter. Thus, something else must control stocks of the larger phytoplankton. Large phytoplankton are always relatively rare in the subarctic Pacific (Booth 1988), but they are consistently present. They even exhibit periods of strong stock increase, if not actual blooms (Clemons and Miller 1984). Our guess was that the larger grazers, while clearly insufficient in numbers and individual grazing capacity to control the small phytoplankton, might attain high enough search or filtration rates to control the rare, larger phytoplankton. We have not achieved a satisfactory test of this to date.
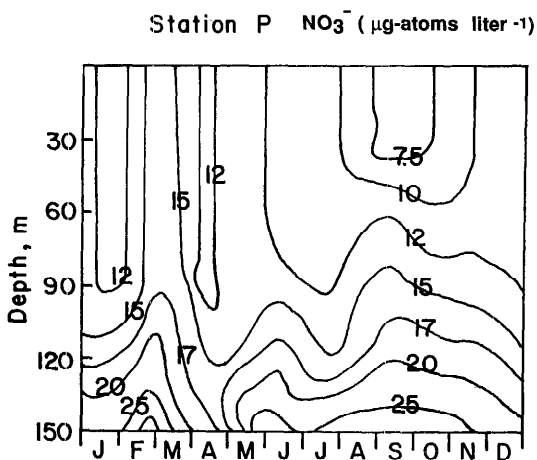
Martin's notion of Fe limitation is a very interesting alternative. Clearly the small, dominant flora are not Fe limited. However, larger plants may grow only very slowly at the same concentrations of available Fe (Hudson and Morel 1990). Relative reduction in surface area of large cells may, or may not, be the difference between large and small cells. Cytoplasm of large cells is often spread over an interior vacuole and thus has a surprisingly large surface in contact with the medium. Nevertheless, the postulated (Martin et al. 1989) effect of sharply limited Fe is to select the flora active in the ecosystem, strongly favoring plants, which apparently are mostly small, with high affinity for Fe. A small flora favors the growth of micrograzers. Reduced growth of large phytoplankton may facilitate control of their stocks by macrozooplankton.

The mixing constraint — Because constrained vertical mixing appears to be a key to subarctic Pacific ecology, it needs quantification and explanation. Quantification of mixing is critical to understanding the nutrient supply from depth. Estimated rates of upward flux can be compared to the annual cycle of NO_3 concentration (Fig. 6) to obtain a rough supply and consumption budget. Surface-layer NO_3 is maximum in March at the end of the most active winter mixing. March–October reduction of surface-layer NO_3 is on the order of 10 μM (Anderson et al. 1969, 1977; Parslow 1981). May–August
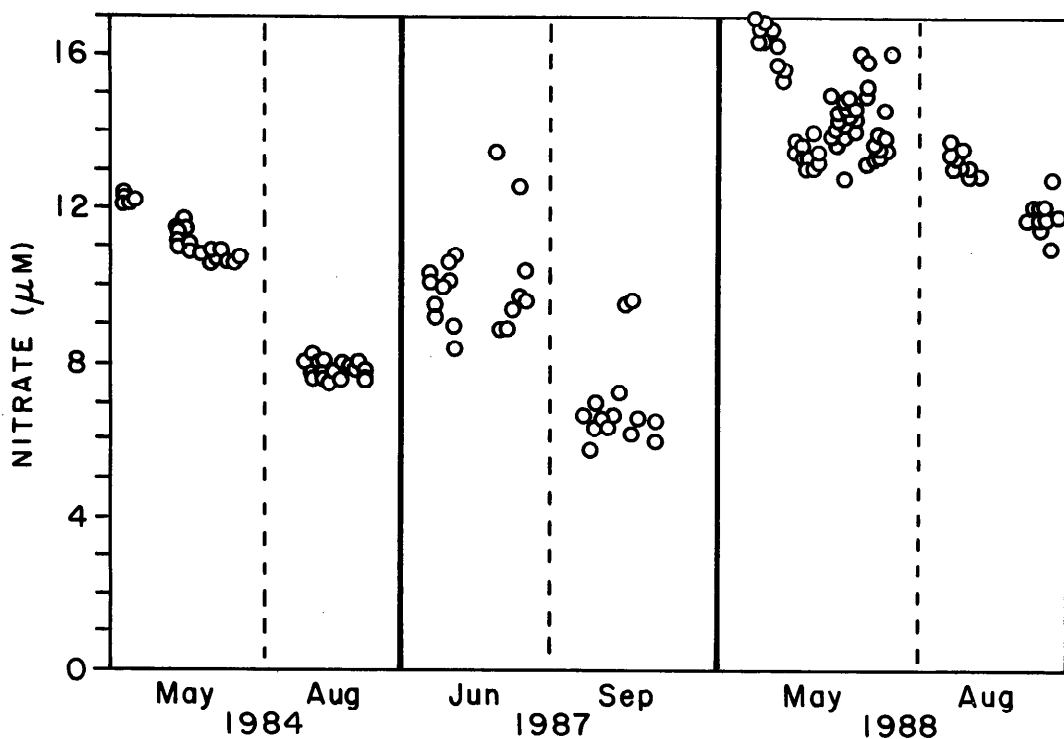
Fig. 7. Interannual variation in NO_3 concentration as seen during three spring and summer cruises.

and June–September cruise pairs found 4-month reductions for this season of highest productivity on the order of 6 μM (Fig. 7) (Wheeler and Kokkinakis 1990).

A May NO_3 profile (Fig. 8) suggests by its form that an advective-diffusive process supplies NO_3 from below the halocline to the consuming layer above. Vertical advection, as well as diffusion, must operate because estimates for near-surface Ekman pumping velocities from wind-stress curl information (Fofonoff and Dodson 1963; Royer and Emery 1981; Talley 1985) are positive upward and of the order 0.05–0.1 m d^{-1}. Moreover, the eastern subarctic is known to export surface water to the southeast (Reid 1973). The vertical diffusivity for mass within the halocline has been estimated (T. Powell pers. comm.) from density-based, Thorpe-scale determinations of the effect of turbulent overturns (Osborn 1980; Dillon 1982). Further, using Tabata's (1989) compilation of water properties at Station P for the years 1956–1981 (especially σ_t from his figure 2) and Powell's microstructure estimate for vertical diffusivity (K

≈ 1 cm^2 s^{-1}, Table 2), we arrive at an estimate for w, the vertical advective velocity, of ~1–2 × 10^{-5} cm s^{-1}. The calculation is identical to the "abyssal recipes" prescription of Munk (1966) for w/K. Gammon et al. (1982) have also developed estimates of
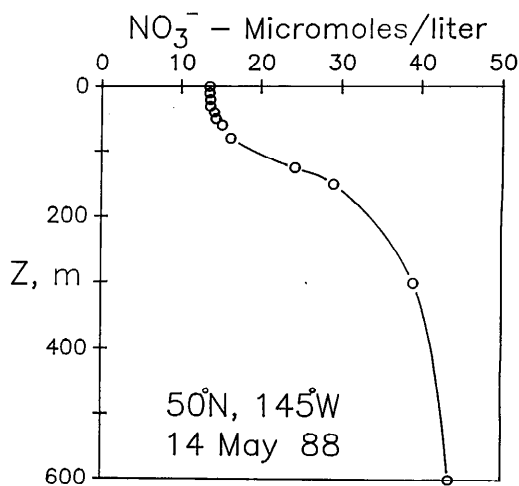

Fig. 8. May NO_3 profile from Station P (SUPER data; P. A. Wheeler unpubl.).

Table 2. Estimated rates of vertical transfer of NO_3 through the halocline to the euphotic zone in the eastern subarctic Pacific.

Advective flux = vertical velocity × NO_3 concentration		
Velocity estimates ($\times 10^{-5}$ cm s^{-1}):		
Ekman pumping	10*	Royer and Emery 1981
	5.6	Fofonoff and Dodson 1963
	5	Talley 1985
CFM distribution	4.3–4.7	Gammon et al. 1982
σ_t/μ-structure	1–2	Tabata 1989/T. Powell pers. comm.
NO_3^- concentration:		
30–45 μM		SUPER data, Fig. 8 (P. A. Wheeler)
Taking "medians" $w = 5 \times 10^{-5}$ cm s^{-1} and $[NO_3] = 37$ μM,		
Flux ≈ 1.6 mmol m^{-2} d^{-1}		
Diffusive flux $= K_z \, \partial[NO_3]/\partial z$		
Diffusivity, K_z, estimates:		
CFM distribution	1.2–1.3 cm^2 s^{-1}	Gammon et al. 1982
μ-structure/Thorpe scales	0.6–0.8	Powell pers. comm.
Taking $K_z = 1$ cm^2 s^{-1} and $\partial[NO_3]/\partial z = 0.07$ μM m^{-1},		SUPER Data
Flux ≈ 0.6 mmol m^{-2} d^{-1}		
Total flux ≈ 2.2 mmol m^{-2} d^{-1}		

* Royer and Emery (1981, figure 12) show a median wind-stress curl of 70×10^{-10} dyn cm^{-3}. This velocity is calculated from $W_e = (\rho f)^{-1}(\partial Y_s/\partial x - \partial X_s/\partial y) = (\rho f)^{-1}$ (wind-stress curl), a steady state approximation for Ekman pumping velocity, W_e.

vertical diffusion and advection in the subarctic Pacific from a model of chlorofluoromethane dispersion in the halocline. The vertical diffusivities and advective velocities of Gammon et al. and Powell are of the same magnitude (Table 2). Combining these estimates suggests an annual mean NO_3 flux of nearly 2 mmol m^{-2} d^{-1} through the halocline.

An approximate nitrate budget for the layer above the halocline might be written

net rate of change
= + upward flux into layer
− (losses to consumers, export, etc.).

The net change observed in the upper 80 m during the 4-month spans of spring–summer SUPER expeditions was 12.2 mg N m^{-2} d^{-1} ≈ -0.9 mmol m^{-2} d^{-1}. Total upward flux is ≈ 2.2 mmol m^{-2} d^{-1} (Table 2), so net loss to export and accumulated biomass must be ~ 3.1 mmol m^{-2} d^{-1}. Although none of the estimates are very precise, they are all of the same magnitude and agree with other aspects of the nitrogen budget (Wheeler in prep.; Emerson et al. 1991). More exact budgets will require extremely large data sets, particularly to determine total NO_3 utilization in the euphotic zone. The seasonal phase difference between supply (occurring mostly in the late winter) and utilization (maximum in spring to autumn) implies that data must be detailed year-round.

Mixing is restricted to the upper 100 m or so in the subarctic Pacific by the steep halocline between 100 and 150 m (Fig. 5). Keffer (1985), using potential vorticity arguments, demonstrated that no water from below ~ 125 m in the Gulf of Alaska reaches the surface without substantial modification above the halocline of T-S characteristics. Indeed, the low salinity of the surface layer—an essentially estuarine feature—defines the region (Dodimead et al. 1963), and it obviously results from the balance among rainfall, evaporation, coastal freshwater supply, surface layer export, and vertical mixing. Obtaining the terms for evaluating this balance is less obvious. Rough estimates by Warren (1983) show that the primary difference between subarctic sectors of the Atlantic and Pacific is that Pacific evaporation rates are much lower. These lower rates are caused by the lower temperature of the Pacific, particularly summer temperature. Lower temperatures, in turn, are caused by the lesser influx of subtropical water, which partly results from the lack of an open northern basin in the Pacific comparable to the Norwegian Sea; Arctic cooling drives a vertical component of circulation in the Atlantic that allows subtropical water (and thus heat) transport farther poleward. In part, it results from the distribution of wind-stress curl, which shifts in sign along 45°N in the North Pacific, whereas it shifts

in sign over the Atlantic along a line from Newfoundland (46°N) to Ireland (53°N). Warren (1983, p. 339, citing I. M. Held) suggests that the Pacific pattern of wind stress may derive from "the relative positions of the Himalayas and Rockies, which tend through orographic deflections to fix the positions of the large-scale troughs and ridges in the planetary wave system of the westerlies." Thus, the ecological character of the subarctic Pacific may derive, through a long causal chain, from the detailed layout of the planetary surface.

Testing the mixing and micrograzer hypothesis—A simple test derives from the expectation that small grazers must be removing more of the phytoplankton stock than large grazers. Large grazers produce large, rapidly sinking fecal matter, whereas protozoans produce much smaller, dispersed fecal matter, which remains suspended for long periods. Both sorts of feces contain pheopigments. Grazing by large animals can be estimated using sediment traps to estimate the flux of large, pheopigment-containing particles exiting the upper water column. Grazing by protozoans can be estimated by comparing the existing stock of pheopigments dispersed in the upper water column with their expected rate of decrease through photodegradation. The requirements of this latter measurement are accurate pheopigment determinations and accurate measures of photon flux for the upper water column. Given these measures, the pheopigment production rate is estimated from an input(grazing)-output(photodegradation) model. Combination of the macro- and micrograzing estimates was proposed as a "grazing budget" technique by Welschmeyer and Lorenzen (1985). Budget estimates of this type were generated repeatedly as part of SUPER, consistently showing (Table 3) micrograzing in the subarctic Pacific greater than macrograzing by a factor of 5–10. Clearly, the principal grazers of phytoplankton in the subarctic Pacific are microzooplankton, protozoans, and very small metazoans. That is in agreement with the mixing and micrograzer hypothesis.

To be a viable explanation for the constancy of phytoplankton stocks in the subarctic Pacific, the mixing and micrograzer hypothesis should pass the same test that

Table 3. 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 by Welschmeyer and Lorenzen (1985).

Expedition		N	Mean (of N budget estimates) contributions to grazing (%)	
			Micro	Macro
SUPER-3	Jun 87	4	83	17
SUPER-4	Sep 87	4	93	7
SUPER-5	May 88	4	70	30
SUPER-6	Aug 88	1	82	18

caused us to discard the major grazer hypothesis—the installed grazing capacity of the microzooplankton must equal or exceed the growth rate of the phytoplankton. The required measurement of microzooplankton grazing rate is not so straightforward as for larger zooplankton. However, some approaches to the problem have provided reasonable results, particularly dilution experiments (Landry and Hassett 1982). The dilution approach assumes that both the growth rates of individual plant cells and the capacity of individual micrograzers to process volumes of seawater to find plant cells remain relatively constant for plant cell concentrations less than and up to ambient levels. According to this model, when seawater containing the community of phytoplankton and micrograzers is diluted, per capita growth rate of the phytoplankton should remain unchanged. However, the total rate of grazing by microzooplankton should be reduced. By diluting samples to varying levels with filtered water and then incubating, the observed, per capita rate of increase of the phytoplankton is greatest in the most diluted sample (with reduced grazing) and decreases linearly for less diluted samples containing more grazers. When these "observed growth rates" are plotted against the grazer dilution factor (the fractional density of grazers in the treatment), the grazing rate in undiluted seawater can be estimated as the slope of the resulting relationship, and the true growth rate of the phytoplankton (i.e. growth with zero grazing) can be estimated as the Y-axis intercept.

This approach was applied in the Gulf of Alaska with some success. Microzooplank-
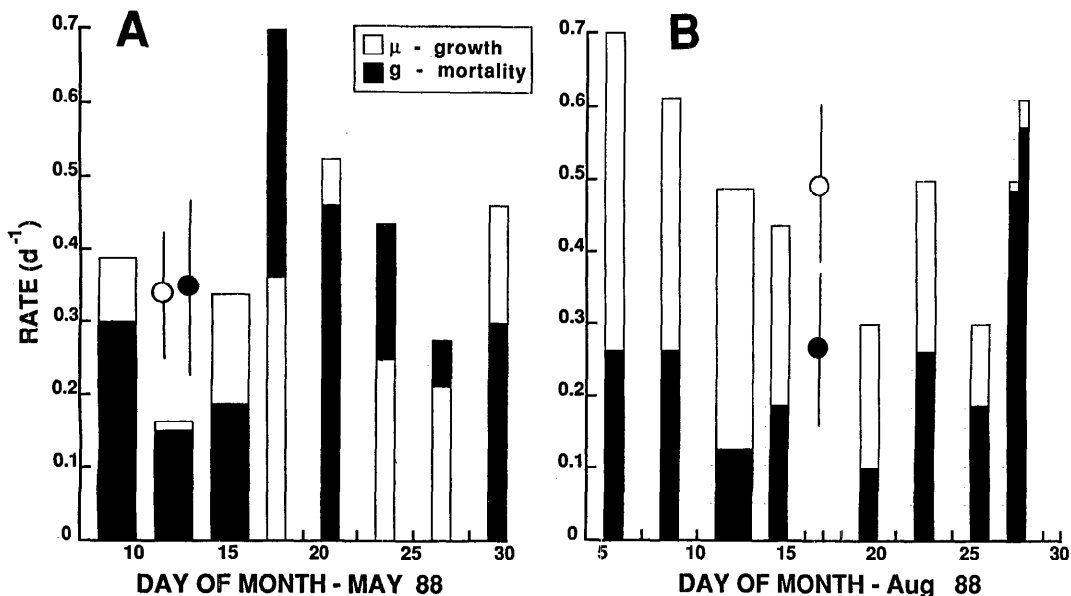
Fig. 9. Estimates of phytoplankton community growth and microzooplankton grazing rates from dilution experiments conducted during cruises to the Gulf of Alaska in May and August 1988. Samples were collected from the surface mixed layer ($\sim$10 m) and incubated on board for 1 or 2 d under ambient temperature and light (black) conditions. Analyses based on Chl a; histograms indicate results of individual experiments; circles indicate cruise-mean growth and grazing estimates (with 95% C.L.).

ton grazing and phytoplankton growth were generally not in balance at any given point in time. Phytoplankton growth exceeded grazing in some individual experiments, but sometimes grazing exceeded growth. For May 1988 (Fig. 9A), grazing more or less balanced growth on average, as predicted. In August 1988 (Fig. 9B), however, microzooplankton grazing only accounted for about half of the estimated phytoplankton growth. In fact, the stocks of small phytoplankton cells grew appreciably from the beginning to the end of our cruise in August 1988, by a factor of $\sim$3. This increase did not produce stocks at bloom levels, and the grazing rate was overtaking phytoplankton growth when we left. Although our evaluation remains incomplete, it is certain that microzooplankton grazing is generally the major loss term for phytoplankton in the subarctic Pacific. Dominant floral components are controlled by micrograzers, but in a dynamic and variable fashion.

Although the flora of the oceanic subarctic Pacific is predominantly constituted of small or nanophytoplankton, there is always a stock of larger phytoplankton, par-

ticularly diatoms (Clemons and Miller 1984). It is these cells that serve as the inocula for eventual domination of enriched, incubated samples by large phytoplankton (Martin et al. 1989). Fe limitation may be holding these large cells in check, but they must have positive rates of increase in the field — increase that must ultimately be controlled by grazers, in this case the larger zooplankton. We do not have the full quantitative evaluation of this that we would like. However, Landry and Lehner-Fournier (1988) reported an incubation experiment which shows that this can be the control mechanism for larger phytoplankton. They incubated 60-liter carboys of water from the Gulf of Alaska with and without 60 added fifth copepodites of *N. plumchrus*. They also controlled for the effects of copepod excretion by comparing containers with and without addition of 4.5 μM NH_4^+. At this density, probably 4–5 times the field population density (Miller and Nielsen 1988), the copepods held the phytoplankton stock constant (Fig. 10) for a week while the controls grew to chlorophyll levels comparable to those observed by Martin et al. (1989).

The stock which developed in the controls was mostly 7–10-μm diatoms (Landry and Lehner-Fournier 1988)—not huge but much larger than the water-column flora. We assume that Fe limitation was alleviated by contamination in this experiment, in contrast to the controls of the experiment shown in Fig. 2. New experiments with more realistic copepod densities were done in later SUPER fieldwork, but the results are not ready to report. Fe limitation cannot be the only factor controlling subarctic Pacific ecodynamics. The effects of low Fe availability must be reinforced by grazing on large cells.

All of our field observations are in accord with the mixing and micrograzer hypothesis. However, an important aspect of that scheme is left completely untested. It is necessary to examine the relationship between phytoplankton stocks and their protozoan grazers during the winter season. Are the plant-grazer relationships still much the same at winter temperatures and light levels as in spring and summer? We would expect rates to be much lower, but the phytoplankton should be growing and micrograzers should be keeping the phytoplankton stocks in check. The subarctic Pacific is a ferocious stretch of ocean in winter, and we are letting the problem wait until a very large, winter-capable ship is available.

The SUPER synthesis

The SUPER expeditions also produced data suggesting how the system carries on primary production at high rates in spring and summer, yet does not use up its nitrogen. Our explanation is that a system dominated by micrograzers is efficient at recycling nutrients for renewed uptake by phytoplankton. As noted above, micrograzers produce fecal matter that is finely divided and does not sink. Moreover, they do not themselves migrate out of the euphotic zone, removing their incorporated nutrients. Nitrogen that they (and macrograzers, for that matter) return to the system is returned as NH_4, which is favored over NO_3 for uptake by phytoplankton because it need not be reduced before incorporation. Available NH_4 suppresses NO_3 uptake by the phytoplankton (Wheeler and Kokkinakis 1990). Suppression of NO_3 uptake (Fig. 11)

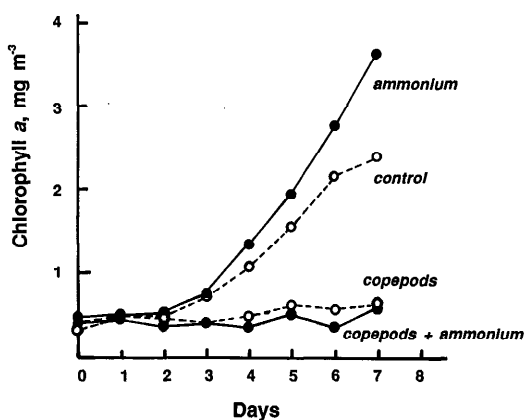
Fig. 10. Comparison of time-courses of Chl a as a measure of phytoplankton stock in 60-liter containers with and without one CV *Neocalanus plumchrus* (large grazing copepod) per liter. Both treatments replicated with and without added NH_4. (Redrawn from Landry and Lehner-Fournier 1988.)

occurs at very low levels in the subarctic Pacific. NH_4 concentration varies widely from day to day in both the spring and late summer seasons in the Gulf of Alaska (Fig. 12). Thus, NO_3 uptake must be switched off and again switched on at a fairly high frequency. Over the year as a whole, efficient recycling of N as NH_4 holds the annual total NO_3 use to ~10 μM throughout the upper mixed layer (Fig. 6). Resupply by mixing through the halocline in winter, as discussed above, returns about this much, but with strong year-to-year variations (Fig. 7). This brings up an interesting feature of the system. The residual NO_3 stock at the end of the summer season of fastest phytoplankton growth is a buffer against winters with less than usual storm activity and mixing. If this buffer NO_3 were ever fully utilized, the system might have insufficient NO_3 in the following spring–summer period.

We call this explanation of the persistence of major phytoplankton nutrients in the subarctic Pacific the SUPER synthesis. This overall understanding of the ecological relationships is represented by a systems model developed by Frost. Its salient features and conclusions are included separately (Frost 1991). The output of this ecosystem model strikingly reproduces the seasonal and (just as important) short-term variabilities of phytoplankton stock and of
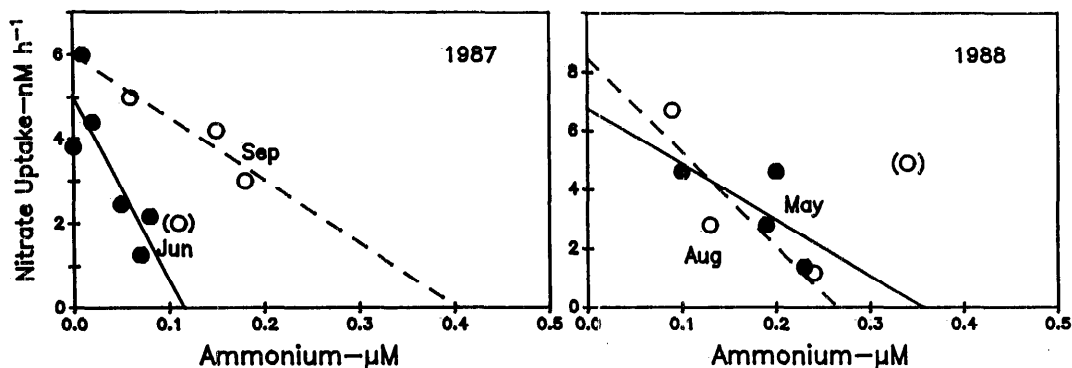
Fig. 11. Relationship between midincubation NH_4 concentration and NO_3 uptake by phytoplankton during short-term incubations. Points in parentheses not included in regressions. NO_3 uptake is suppressed by NH_4 concentrations frequently seen in the field. (Redrawn from Wheeler and Kokkinakis 1990.)

both NO_3 and NH_4 in the oceanic subarctic Pacific. The key conclusions from SUPER fieldwork that are represented by the model are that photosynthetic rates are principally limited by the available illumination, that available NO_3 (also PO_4) is not used in the course of the year because N as NH_4 is efficiently recycled in the euphotic zone by the protozoan grazing community, and that within a range usually below 0.5 mg Chl a m^{-3} there is high-frequency variation in phytoplankton stock (Fig. 12) that is driven by day-to-day changes in illumination and is inverse to variation in NH_4 concentration.

None of this is to say that Fe limitation does not occur. We believe that if Fe limitation exists, its effect is to set the character of the phytoplankton component of the community. The results of Martin et al. (1989) show exactly that: added Fe shifts the dominant flora to larger cell sizes, particularly large diatoms. In the field, Fe limitation, or something like it, forces the flora toward very small cell sizes. That, in turn, enables controlling grazing by very small herbivores, principally protozoans.

Large-scale Fe additions

What would be the effect of large-scale Fe additions to surface waters in the subarctic Pacific? Assume for a moment that Fe limitation is an established fact. Then imagine a storm wafting in enough Fe to totally alleviate any Fe limitation on growth of larger phytoplankton cells. The large cells would

suddenly begin to grow very rapidly. Particularly in late summer or autumn, when the *Neocalanus* species are in their resting phase deep in the water, there would be no rapid response of large grazers. The burgeoning stock of large phytoplankton would simply use all the N in the euphotic zone,
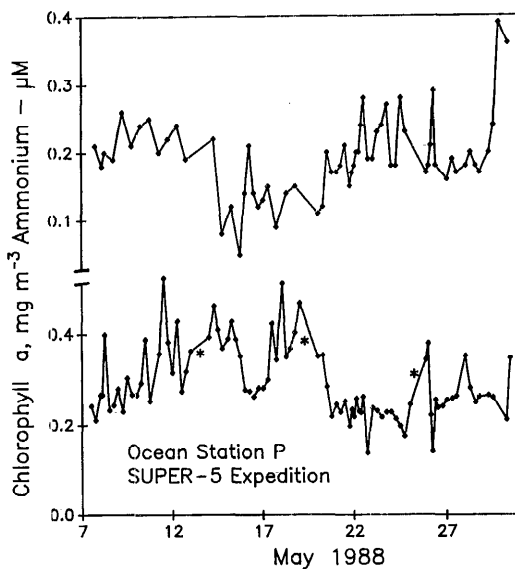

Fig. 12. Variability in mixed-layer NH_4 and chlorophyll concentrations in the Gulf of Alaska, May 1988. Asterisks mark 1-d work breaks on the expedition. Some variability is small-scale spatial difference, some is larger scale temporal change, and there are larger, longer term changes as well. Diel variation of NH_4 content is evident (Wheeler et al. 1989). The variation compares well to that shown by Frost's (1991) process model.

reducing the NO_3 buffer (usually ≥ 6 μM) to zero. At that point the system would become N limited, not Fe/light/micrograzer limited. After a few further cell divisions by the large phytoplankton, decreasing their relative content by favoring lipid and carbohydrate components over proteins, they would become senescent and sink from the upper water. This is a recurring, annual phenomenon in the oceanic North Atlantic (Smetacek 1985); it would happen in the Pacific, too.

At this stage the entire relationship among the usual phytoplankton and grazer communities, and of each to the physical-chemical habitat, would already be altered beyond recognition. Nitrogen to sustain the small phytoplankton stock would be gone. Micrograzers, upon whose continuous presence we think the character of the ecosystem depends, would radically decline. The reverberation along the food web would damage populations of copepods, euphausiids, pteropods, and the fish stocks that depend on them as food. Not only would there be an immediate change in the character of the ecosystem, it might very well not recover in the following growing season. Our nutrient data (Fig. 7) suggest that the system does not mix to equal depths in all winters. While we don't have much good, continuous nutrient data, the early spring, near-surface NO_3 concentration appears to be less in some years than in others. We have found NO_3 as high as 17 μM in some years and as low as 12 μM in others. Some of the difference derives from the times of our sampling in spring. However, the level of depletion we have observed by late summer has the same implication. About 10 μM is used over the summer, leaving surprisingly variable residuals in August or September. A winter of weak mixing following immediately after our imaginary "Fe storm" could leave the system with almost no fixed N for an entire growing season.

For this reason, the subarctic Pacific could not be a feasible site for an industrial-scale Fe fertilization project with the goal of reducing atmospheric CO_2. Moreover, it is simply calculated, using optimistic assumptions, that complete utilization of the NO_3 above the halocline throughout the subarctic Pacific region would reduce atmospheric CO_2 by only a trivial amount relative to anthropogenic inputs. If there is hope for such a scheme, it must reside in the Southern Ocean, where upward transport is more continuous and is not seasonally uncoupled from the spring–summer period of rapid phytoplankton growth. We look forward to similar evaluations of the environmental consequences of Fe fertilization in the other nutrient-rich, oceanic regions.

The subarctic Pacific is an excellent site for a modestly scaled field test of Martin's suggestion that Fe limitation explains persistently nutrient-rich, oceanic regions. The experiment will be difficult and failures will be encountered. Perhaps it is not even possible, and careful design and review are required. An appropriate scale will be large enough to prevent diffusive disappearance over the 10–20 d for initial system response—probably 20 km². The addition patch can be traced and diffusion determined with standard tracers such as chlorofluorocarbons, sulfur hexafluoride, or rhodamine. If a test by direct addition of Fe to the ocean is possible, it would lift the objections to container experiments. Incubations in containers inevitably change many variables beside Fe availability (Venrick et al. 1977). Direct Fe fertilization of a patch of ocean would address the limitation issue at the scale of the fully functional ecosystem, rather than just the effects of Fe addition on accidentally selected fractions.

Conclusion

Short supply of available Fe is a reasonable candidate explanation for the limitation of major nutrient utilization in the oceanic subarctic Pacific. We tentatively propose that Fe availability (or something similar) selects a flora dominated by small cells. That allows dominance of herbivory by protozoa. Protozoa efficiently recycle nitrogen as NH_3, which strongly constrains the annual utilization of NO_3, leaving the system persistently rich in major nutrients.

All oceanic ecosystems need to be understood at this level of mechanistic detail. Studies stimulated by the current interest in Fe limitation of ocean productivity should

seek to provide detailed analyses of ecological dynamics.

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