

On the possible causes of the seasonal phytoplankton blooms along the southwest coast of India

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Data collected off the southwest coast of India at the onset of the 1987 southwest monsoon season suggest that the commonly observed high concentrations of chlorophyll and rates of photosynthesis of the season may not be due to greatly enhanced chlorophyll-specific (normalized) photosynthetic rates of the bulk phytoplankton. Instead it is proposed that the seasonally increased nutrient supply primarily increases the growth rate of the otherwise more diffusion-limited large-celled species, which then can materially increase in numbers, since they are poorly controlled by grazers. If so, the principal role of the high nutrient concentrations would be to permit the build-up of a large algal biomass and pigment concentrations that, coupled with moderate normalized photosynthetic rates, yield the observed high production rates per m^3 and m^2 of the upwelling season.

The authors wish to speculate on the causes of the large concentrations of phytoplankton (blooms) that are a regular feature of the southwest monsoon season along the southwest coast of India¹. At the outset it is observed that the reason for the build-up of phytoplankton biomass may not be a greatly enhanced rate of cell division of the bulk phytoplankton caused by the nutrients supplied by the coastal upwelling of the season, as commonly believed, but instead may represent, especially among the large-celled algae, a new balance between the rates of cell division and grazing mortality. Much of the argument may be traced back to at least Malone², but additional evidence is supplied herein.

Materials and Methods

This paper elaborates on observations³ of chlorophyll and primary production between 17 June and 10 July 1987 during the *ORV Sagar Kanya* cruise 33. Papers on the physical oceanography of the cruise⁴ and on the zooplankton collected by a 200 μm mesh net⁵ are also at hand. The data for nitrate concentrations (determined by M.D. Rajagopal by reduction with cadmium and partially used in ref. 3) were provided by the Indian National

Oceanographic Data Centre (INODC) in Goa, as were hydrographic observations. The present authors add to the previously published methods for the phytoplankton studies during the cruise³ that Whatman glass fiber filters GF/C covered with $MgCO_3$ were used for pigment determination. Thus, the retention can be expected to be similar to that of the 0.45 μm Millipore filters employed for the 24 h ¹⁴C uptake (photosynthesis) simulated *in situ* measurements. These were started during the day or night, depending on the ship's schedule. The 60% level of irradiance, between 2 and 5 m depth, herein is assumed to have been near the light saturation level of photosynthesis.

Results

On the eight sections of the cruise^{3,4} (cf. Fig. 1), marked upsloping of the pycnocline and, in part, near-shore upwelling to the surface were present. The top of the pycno- and oxyclines rose from ≥ 50 m depth offshore to approximately 20 (30) m at the shelf stations with biological observations (< 10 m at sts. 3 and 4 [see Fig. 1a for locations]; surface temperatures were lowered from about 29°C elsewhere in the region to 27 and 28°C, respectively), while at the same time the vertical

gradients of density and oxygen concentrations greatly sharpened (ref. 4 and original data from INODC). Column chlorophyll concentration and photosynthesis (both to the 1 % irradiance level, situated between 12 m [21 m without st. 4] and 39 m depth) were high in a belt essentially extending over the Indian shelf and continental slope (Fig. 1 a, b). Very high values were measured on the shelf at approximately 8° and 9°N (sts. 3 and 4). The extension beyond the continental slope of the enriched area along the southernmost section was perhaps related to the shear and mixing in the strong east-setting current (ref. 4, Fig. 12). Elevated levels of chlorophyll and carbon uptake also occurred offshore at 72°E, 9° and 12°N, but no reason is apparent.

On the shelf, nitrate was undetectable at the surface and at 10 m (next sampling depth for nutrients), except for surface values of 0.2 μM at sts. 3 and 26 and of 0.1 μM at st. 13 (13°N). Measurable concentrations of nitrate + nitrite at the bottom of the euphotic zone also were encountered at only a few places (Fig. 1 a, b; judging from the hydrography at the shelf station at 10° 30'N, the analytical result of undetectable nitrate at the 1 % irradiance level is almost certainly erroneous). With or without this questionable station, presence or absence of nitrate at the bottom of the euphotic zone does not predict the level of column pigment or photosynthesis (Fig. 1 a, b). However, nitrate

largely undetectable in the mixed layer by the conventional method of analysis does not mean that it was not available at all⁶⁻⁸. Moreover, in coastal waters off southern California⁹ and in the open western and central equatorial Pacific¹⁰, where primary production also was primarily driven by ammonium, total production (based on nitrate + ammonium) was related to the nitrate gradient below the mixed layer⁹ and the nitrate concentration at 60 m depth¹⁰, respectively, i.e., was related to the upward transport of nitrate. It is assumed that a similar mild nutrient flux, which does not yield nitrate concentrations detectable in the upper layers by the conventional analytical method, is the basis for the direct relation in the present data between hydrography, i.e., upsloping and sharpened pycno- and oxyclines (hence, steepened nutriclines), and column pigment concentration and photosynthesis. Obviously, most of the observed production must have been based on regenerated nitrogen, i.e., principally ammonium.

The stations with photosynthetic rates $> 100 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ had markedly higher column pigment concentrations than those with rates $< 100 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ (Table 1). Also, the near-surface pigment concentrations at the stations with $> 100 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ were eight times higher (four times without sts. 3 and 4) than in the other group. In contrast, the rates of pigment-normalized carbon uptake at the 100 % and 60 % irradiance levels [i.e.,

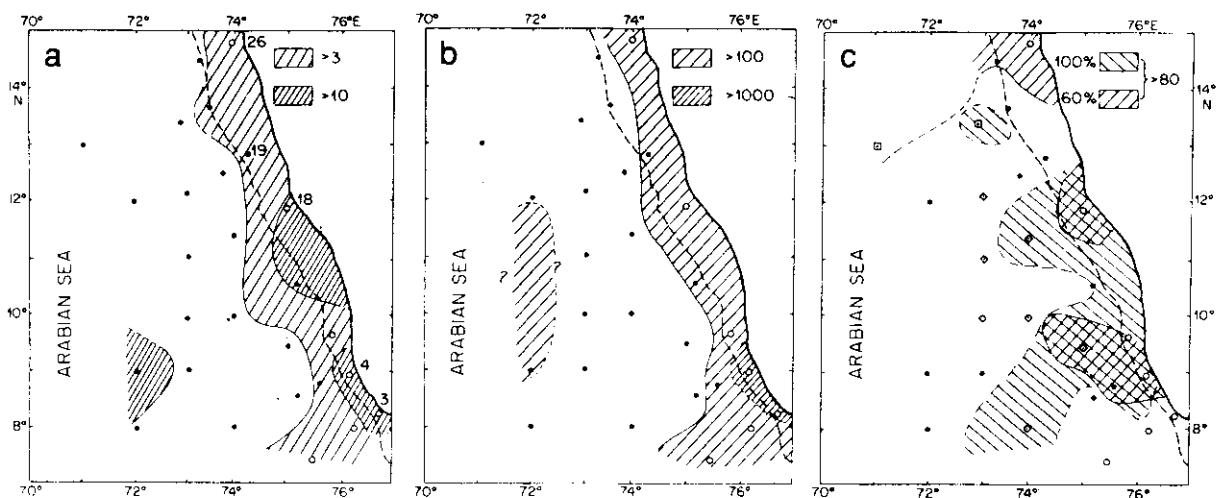


Fig. 1— Station location and distribution of properties (dashed line following the coast, 180 m isobath). (a) column chlorophyll concentration ($\text{mg} \cdot \text{m}^{-2}$) to the 1 % irradiance level, with 5 stations designated by their numbers. (b) column photosynthetic rate ($\text{mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) to the 1 % irradiance level. (c) photosynthetic rate divided by chlorophyll for the 100 % and 60 % irradiance levels [$\text{mg C} \cdot \text{m}^{-3} (\text{mg chl} \cdot \text{m}^{-3} \cdot \text{d})^{-1}$]. (Dots, station locations. Open circles, nitrate concentration in lower photic zone $\geq 0.9 \mu\text{M}$; squares, chlorophyll $\leq 0.05 \text{ mg} \cdot \text{m}^{-3}$ at 100 % or 60 % irradiance levels; diamonds, chlorophyll $\leq 0.05 \text{ mg} \cdot \text{m}^{-3}$ at 100 % and 60 % irradiance levels.)

mg C (mg chlorophyll . d)⁻¹; "assimilation numbers"], used as a proxy for the growth rates [units, C (C . d)⁻¹] do not differ significantly between the two groups of stations; the stations with > 100 mg . m⁻² . d⁻¹ do not even tend uniformly toward higher rates. (The median values for the groups with > 100 and < 100 mg C m⁻² . d⁻¹ are 63 and 46, and 62 and 53 mg C [mg chlor . d]⁻¹, respectively, for the 100 % and 60 % irradiance levels). This lack of clear differences in normalized rates between the two groups of stations reflects the geographic distribution of these rates (Fig. 1 c), which does not coincide with the pattern of near-surface pigment and only partly resembles that of near-surface photosynthesis (not shown; see also the large differences between sts. 3 and 4, Table 1).

In Fig. 1 c stations are designated where the chlorophyll concentrations at the two upper depths were so low that the unavoidable analytical variability might have introduced large percentage errors in the normalized rates. The location of these stations, however, suggests that such errors, if they occurred, had not affected the basic differences in patterns between Fig. 1 a and b *versus* Fig. 1 c.

As with column pigment and photosynthesis in these observations, nitrate concentrations at the bottom of the euphotic zone do not predict the physiological performance, as expressed by the normalized photosynthetic rates, in the layers above. The reason presumably is that, owing to the rapid recycling of nitrogen, the division rates of phytoplankton tend to be rather high relative to the physiological maximum also in oligotrophic (nutrient-poor) water. This has emerged elsewhere during the last 5-10 years from measurements with the chlorophyll-labeling and the dilution

techniques¹¹ (for the Arabian Sea, see ref. 12). Moreover, in these new data from other seas, presence of nitrate does not lead to cell division rates of the bulk phytoplankton that are drastically higher than in truly oligotrophic waters.

Development of the hypothesis

What may be the reason(s) for the high rates of photosynthesis on the Indian shelf, especially at sts. 3 and 4? Proximally, of course, these rates are the product of the pigment-normalized rates times the pigment concentrations, but why are the latter so high in spite of only a near-average normalized rate at st. 3 (Table 1)? Toward the explanation, first note the clear tendency, recorded elsewhere¹³⁻¹⁵, of larger algal cells to contribute a higher percentage of the phytoplankton biomass at sites with high pigment concentrations or photosynthesis. In the equatorial Atlantic, the small size fraction (< 3 µm) did not exceed concentrations of approximately 0.5 mg m⁻³ chlorophyll, regardless of the total pigment content (ref. 13, Fig. 2). A similar trend was observed in the Arabian Sea (fraction > 5 µm, Table 1 in ref. 14; also fraction > 20 µm, Table 1 in ref. 15). For the shelf off the Indian southwest coast, the observations off Calicut¹ also show the enormous seasonal increase of net phytoplankton (Table 1 in ref. 1; 1 Harvey Pigment Unit ca. 0.3 mg chlorophyll). These data, however, are not quite suitable for testing the present hypothesis (see below), because the division between net- and nanoplankton at that time could only be effected by a mesh size of 80-85 µm (No. 16 bolting silk). Nowadays for shelf waters, a separation at 15 - 20 mm (20 µm in ref. 2) would be preferable.

Secondly, as hinted first by Malone², the underlying reason for the relative increase of the

Table 1—Means (standard deviations) of data

	> 100 mg C.m ⁻² .d ⁻¹		< 100 mg C.m ⁻² .d ⁻¹	St. 3	St. 4
	All sts.	Without Sts. 3, 4			
Number of Observations	11	9			
1. Column pigment (mg chl.m ⁻²)	11.7 (4.2)	6.0 (1.1)	2.2 (0.1)	46	28
2. Column photosynth. (mg C.m ⁻² .d ⁻¹)	434 (192)	171 (23)	66 (5)	1260	1970
3. Normalized photosynth. at 100 % irradiance level [mg C (mg chl.d) ⁻¹]	74 (15)	74 (18)	81 (22)	42	103
4. As in (3) for 60% level	76 (17)	68 (17)	55 (7)	44	176

large fraction when chlorophyll levels increase owing to nutrient addition, is likely to be the continued grazing pressure exerted by the protozoans on the small fraction. Protozoans can keep up even with increased division rates of their prey because of their small size and short generation time, but cannot handle large algal cells effectively enough. By and large, the bigger cells can only be consumed by the bigger animals (metazoans), which, on account of their larger size, have longer generation times than their prey. Thus, once division rates of the larger size fraction of phytoplankton are even mildly enhanced, there will be a temporary lag period until the new food for the metazoans has been converted into eggs, and the offspring have grown to a sufficient size to emulate the parents (about 2 weeks in the tropics?). Note that the effect of enhanced nutrient concentrations on cell division rates can be expected to be more marked for the large-sized species (normally of low abundance in oligotrophic seas) than for small cells, since the former are more subject to diffusion limitation than the bulk (small) phytoplankton (e.g., ref. 16). With exponential growth reigning among phytoplankton, even a small difference between algal division and mortality rates can result in a large accumulation of biomass in 2 weeks, provided nutrients sufficient for this buildup are at hand.

Thus, the hypothesis for explaining the 1987 data illustrated in Fig. 1 a is as follows: (a) the enhanced nutrient supply from upsloping of deep water onto the shelf and, partially, upwelling to the surface increased only the division rates of the relatively few larger, nutrient-limited cells, but not of the bulk, small-celled phytoplankton that divided at relatively high rates like elsewhere in oligotrophic waters; (b) the zooplankton grazing was unable to keep pace with the growth of these larger cells; and (c) sufficient nutrients were available to support an enhanced biomass of phytoplankton on the shelf. The support for (c) is self-evident from Fig. 1 a. There is no observational evidence regarding (a) in the data, except that the bulk assimilation numbers do not differ systematically between shelf and offshore waters (cf. Fig. 1 c). Recall, though, that a proxy [units, $C(\text{chl} \cdot \text{d}^{-1})$] is used here for the growth (division) rates [units, $C(C \cdot \text{d})^{-1}$]. If enhanced nutrient supply had increased division rates of an entire nutrient-deficient assemblage, the bulk carbon-to-chlorophyll (C/chl) ratio would have

declined (e.g., as in ref. 17) and probably resulted in only a small shift, if any, of the proxy, i.e., the bulk phytoplankton assimilation number. The hypothesis is based on the assumption that the high bulk phytoplankton division rates observed elsewhere in oligotrophic waters¹¹ pertain also on the Indian shelf. Estimating the role of grazing (b) requires a lengthy exposition.

Estimates of grazing impact by mesozooplankton

To state the result of estimating the possible grazing impact by the larger zooplankton on the phytoplankton during the cruise at the outset, the calculated clearing rates were entirely inadequate to control phytoplankton growth on 5 shelf stations with little net-collected zooplankton and on 3 out of 4 stations with high chlorophyll that was accompanied by high zooplankton concentrations. For the fourth station [our st. 19; named st. 25 in ref. 5], the daily clearing rates probably also were inadequate, as estimated in the following.

The number of adult copepods were by far the highest at st. 19 among the 4 stations with high chlorophyll and elevated zooplankton numbers (sts. 4, 18, 19, and 26; cf. Figs. 1 and 4 in ref. 5). The concentrations per m^3 of those copepod species, which contributed the highest numbers of adults and/or biomass, were 143 *Eucalanus pileatus*, 86 *Canthocalanus pauper*, 307 *Acrocalanus* sp., and 100 *Paracalanus* sp. (numbers refer mostly to adults; species arranged by decreasing body size). In addition, the 28 specimens of the salp *Thalia democratica* were important.

Clearing rates of copepods depend on food concentrations and particle size. Multiplying the average chlorophyll concentration of $0.3 \mu\text{m} \cdot \text{l}^{-1}$ at st. 19 by an estimated carbon-to-chlorophyll ratio of 50 (ref. 18) yields a phytoplankton carbon content of approximately $15 \text{ mg C} \cdot \text{l}^{-1}$. If all of this had been suitable as food for the copepods, adult females of the largest species, *Eucalanus pileatus*, would clear about $0.5 \text{ l} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$ at 20°C ; the concentration-dependence of the rate was determined off the U.S. southeast coast¹⁹, but the species is circum-tropical/subtropical. Since we are concerned with the large algal species, which made up only a part of the phytoplankton, up to $0.7 \text{ l} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$ might be swept clear (ref. 19, Fig. 2). The smallest species among the dominant copepods was *Paracalanus* sp. Adult females of *P. parvus*, a

widely-distributed member of the genus, from off the U.S. southeast coast, cleared about $0.15 \text{ l} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$ of a $12 \mu\text{m}$ diameter diatom at 20°C (ref. 19, Fig. 2). Adult females of the same species from the U.S. west coast cleared maximally $0.25 \text{ l} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$ at $17\text{-}18^\circ\text{C}$ for very large particles ($44 \mu\text{m}$ equivalent radius)²⁰, a rate approximately applicable to the food concentration at issue (Figs. 2 and 10, ref. 20; herein, the rate for the largest particles is chosen for estimating the grazing impact on the large cells in a bloom).

Using $0.7 \text{ l} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$ for the two larger species and $0.25 \text{ l} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$ for the two smaller species and multiplying with the specimen numbers yields a total clearance of $262 \text{ l} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$ at 20°C . To account for the water temperature of the station (ca. 29°C); Eq. 4 of Ikeda²¹ for respiration was applied to an animal of 10 mg dry weight, somewhat (twice?) higher than the smallest species of concern. The equation predicts an increase of the respiratory rate by 2.6 times over that at 20°C , but the factor would be smaller for the larger species. Assuming that respiration is a good proxy for the clearing rate, $680 \text{ l} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$ might have been cleared by the copepods. This figure is likely to be on the high side, not only because of the mentioned lower temperature coefficient for the larger animals, but also because the specimens from the higher temperatures of the Arabian Sea probably have smaller body sizes than the experimental material in ref. 21, resulting in lower clearing rates. Further, males of *Eucalanus* and *Paracalanus* have reduced mouth parts; to the extent that some males must have been present, the use of total adult specimen numbers as herein is inappropriate. Finally, the highest rates, applicable to very large algal cells at low concentrations, were chosen, again leading to estimates on the high side.

The clearing rate of the salp species (in this collection, ca. 7 mm long), studied at the Australian northeast coast at $30\text{-}32^\circ\text{C}$ with large solitary specimens ($8\text{-}10 \text{ mm}$ length)²², was about $0.7 \text{ l} \cdot \text{animal}^{-1} \cdot \text{d}^{-1}$ (probably an underestimate²³), adding another $20 \text{ l} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$. The other net-collected suspension feeders that may figure importantly for large phytoplankton are euphausiids. Their average concentrations on the shelf for the entire cruise⁵ were approximately 9 m^{-3} (including carnivorous species) so that they are neglected.

Thus, the total volume estimated to be swept clear by the dominant species at st. 19 corresponds to $700 \text{ l} \cdot \text{m}^{-3} \cdot \text{d}^{-1} = 700 \text{ ml} \cdot \text{l}^{-1} \cdot \text{d}^{-1}$. The same calculation, however, for sts. 4, 18, and 26 (from zooplankton numbers on the adjoining sts. 6, 21, and 34, respectively⁵) yields $130, 130,$ and $75 \text{ ml} \cdot \text{l}^{-1} \cdot \text{d}^{-1}$, respectively. The rates would be even lower for the other shelf stations.

These clearing rates compare with the likely growth rate of the phytoplankton as follows. The bulk phytoplankton may have divided approximately 1.5 times per day (estimated rates for the 25 and 50 % light depths in samples from the Arabian Sea in October/November 1963 for a C/chl ratio of 50 (ref. 18). The mean rate is the same for 22 new worldwide field observations at ample irradiance in water $\geq 27^\circ\text{C}$ (Fig. 2 in ref. 11) with a range of $0.7\text{-}3.3 \text{ d}^{-1}$; the mean is 1.4 d^{-1} for the 19 oligotrophic stations in the figures, with a range of $0.7\text{-}2.9 \text{ d}^{-1}$. Note that all these determinations were of the bulk division rates; the 1963 data from the Arabian Sea certainly would have contained large cells, but the majority of samples in the worldwide set probably were dominated by very small, non-diatom phytoplankton (so-called picophytoplankton). Since, however, medium-sized diatoms (of concern here) divide about as fast as the much smaller members of other classes of phytoplankton²⁴, the use of the bulk value seems reasonable.

The instantaneous division rate (k) corresponding to 1.5 div. d^{-1} is 1.04 d^{-1} (from $1.5 \times \ln 2$). Assuming continuous cell division and grazing mortality of phytoplankton during 24 h and considering the case of no change of phytoplankton concentrations with time, the instantaneous grazing mortality (m) is also 1.04 d^{-1} , i.e., $d[\text{chl}]/dt = [\text{chl}](k - m) = 0$. Under these assumptions, the grazers need to clear $1040 \text{ ml} \cdot \text{l}^{-1} \cdot \text{d}^{-1}$ of cells. If the grazers filtered less, the concentrations of phytoplankton (or large cells) would increase and reach bloom proportions provided enough nutrients supporting the biomass increase are made available.

Thus, the estimated clearing rates for sts. 4, 18, and 26, let alone those for the other shelf stations with even fewer zooplankters, are totally inadequate for coping with phytoplankton dividing at an instantaneous rate of 1.04 d^{-1} , or even of 0.69 d^{-1} (i.e., dividing once a day), even though the named

stations were those with higher than average concentrations of metazoans. In consequence, large phytoplankton cells could have multiplied with little grazing loss. A similar lack of control of the larger phytoplankton by copepods was reported for a temperate spring bloom²⁵. In the present data, only the estimated clearing rate of $700 \text{ ml} \cdot \text{l}^{-1} \cdot \text{d}^{-1}$ for st. 19, likely to be on the high side, as indicated, may be regarded as rather close to the about $1000 \text{ ml} \cdot \text{l}^{-1} \cdot \text{d}^{-1}$ needed to balance a phytoplankton bulk division rate equivalent to $1.5 \text{ div} \cdot \text{d}^{-1}$. Note that the zooplankton data for the cruise⁵ concerned only adults, while at least a number of copepodite stages would have been able to handle medium-sized ("bloom") algae, albeit at much smaller clearing rates than the adults because of much smaller body size; they would need to be included in future attempts along similar lines. Consider, however, that a difference between instantaneous rates of phytoplankton growth and mortality ($k - m$) of only 0.1 d^{-1} over only 10 d would increase a chlorophyll concentration 2.7 times, which is exactly the ratio between the observed means for the stations offshore and on the shelf in Table 1. Thus, the arguments rest principally on 3 out of 4 stations with high phytoplankton accompanied by relatively high zooplankton concentrations, as well as on 5 other shelf stations with high phytoplankton but low zooplankton concentrations.

Future tests of the hypothesis

To recapitulate, it is suggested for this cruise that hydrographically-caused supply of nutrients enhanced the bulk division rates of the phytoplankton on the shelf only slightly, if any, but affected critically those of the large-celled species which, then, could outpace their grazers. The principal role of the upwelling would have been to supply sufficient nutrients to permit the build-up of phytoplankton biomass. With active upsloping and upwelling near sts. 3 and 4, the build-up was especially marked.

The tests for the hypothesis, which should be undertaken at more than one site, might be as follows: (a) prior to the upwelling season (or, less comfortably, offshore during the season), measure the growth rate (or the pigment-normalized photosynthesis) of the large size fraction (e.g., $> 15 - 20 \mu\text{m}$) of phytoplankton on several stations in oligotrophic water, without and with an addition of

nutrients (by using deep water), and with the larger grazers ($>50 - 100 \mu\text{m}$ in length) removed; while the grazers have to be strained beforehand, the size fractionating is best done after incubation; to avoid diel effects on the photosynthetic efficiency, experiments should be started at the same time of day²⁶; (b) in upwelled water, measure the rates of division and mortality of the small phytoplankton by the dilution method^{8,27}; (c) on the same stations used in [b], estimate the grazing pressure exerted by the larger zooplankton by applying rates from the literature multiplied by the observed concentrations in the euphotic zone, or (better) by determining the rates for the dominant species²⁸. The present paper amply demonstrates the uncertainties incurred when using literature values for (c), but then, the approach is faster and easier than performing experiments. Also, note for (a) that determining the growth rate would be more convincing than relying on the pigment-normalized photosynthesis (assimilation number), as stated. The results of such tests would be of broad interest, applicable far beyond the southwest coast of India.

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