

GRAZING AND ZOOPLANKTON PRODUCTION AS KEY CONTROLS OF PHYTOPLANKTON PRODUCTION IN THE OPEN OCEAN

By Karl Banse

THANKS TO NASA's Coastal Zone Color Scanner (CZCS, 1978–1986), nearly ocean-wide coverage of the distribution of phytoplankton pigment in the upper part of the euphotic zone and, in effect, in the mixed layer of the open ocean, is now available. This coverage includes seasonality and interannual variability. The CZCS observations confirm that the physics of the ocean provide the backbone of the geographic and temporal patterns of pigment distribution and, by inference, of primary production rate. For example, phytoplankton concentrations and production are enhanced where upwelling or seasonal overturn of the water column replenishes nutrient concentrations in the mixed layer, whereas the timing of this enhancement may be controlled by upwelling, seasonal overturn, or the mixed layer becoming shallower than the critical depth.

I propose that the next task is to understand the cause of the phytoplankton concentrations and to be able to predict them and the temporal rate of change of concentrations on the scale of several days to seasons. I will show that this major challenge for biological oceanography cannot be addressed without a vastly improved understanding of the zooplankton. Understanding the animals is of intrinsic interest, which is also true for phytoplankton. However, the task of predicting phytoplankton concentrations and their rates of change also may be considered as a subset of the challenge of anticipating the effect of climate change on, e.g., the geographic and temporal (seasonal) distribution of the sign of the CO₂ gradient between atmosphere and sea via the connection between phytoplankton concentration and photosynthesis, or on plankton community composition and its feedback to the atmosphere from changes in the distributions of DMS producers.

K. Banse, School of Oceanography, WB-10, University of Washington, Seattle, WA 98195, USA.

Phytoplankton Concentrations and Seasonality

Regions Without Marked Phytoplankton Seasonality

In much of the open ocean, the seasonal change of phytoplankton pigment and, by implication, of biomass is small. Figure 1 juxtaposes monthly medians of CZCS-derived pigment of a cool-temperate area (Fig. 1a; see Frost, 1991, for regional background), an equatorial area (Fig. 1b; see Barber and Chavez, 1991), and a subtropical area (Fig. 1c; see Venrick *et al.*, 1987). The first two areas are persistently nutrient-rich, the last is persistently nutrient-depleted. Patterns similar to those in Fig. 1a prevail in the subantarctic water ring (Banse, unpub. observations) that encompasses about 1/6 of the ocean area; patterns similar to those in Fig. 1c prevail in all subtropical central gyres that I estimate comprise close to 1/3 of the ocean area (cf. Banse and English, 1994).

Figure 1a shows that a marked seasonal cycle of incident light in the year-round presence of nutrients, as observed at ~50°N, does not necessarily lead to clear seasonality of phytoplankton, e.g., to spring and fall blooms of several mg m⁻³ of pigment that supposedly are typical for temperate latitudes. (The 2 values > 1 mg m⁻³ occur during a season when inaccurate values were recorded by the CZCS in 1980, Banse and English, 1994). At the subtropical site (Fig. 1c), the trend to seasonality is caused by enhanced vertical mixing and nutrient supply during the cool season. Further, comparison of Figure 1, b and c indicates that drastically different nutrient (N, P) concentrations have little effect on pigment levels; the same small effect holds for the rate of nutrient supply from below the thermocline at the two sites. The low pigment levels in situations rich in N and P as in Figure 1, a and b are not likely to be caused by lack of iron. In or near these areas, phytoplankton enclosed in the control flasks (no iron added) of the recent iron bioassays (mostly by Martin *et al.*, 1991) doubled to quadrupled in biomass over a few days (Martin *et al.*, 1991 for the eastern tropical Pacific; see Banse, 1991a, for the southern

I propose that the next task is to understand the cause of the phytoplankton concentrations and to be able to predict them and the temporal rate of change of concentrations on the scale of several days to seasons.

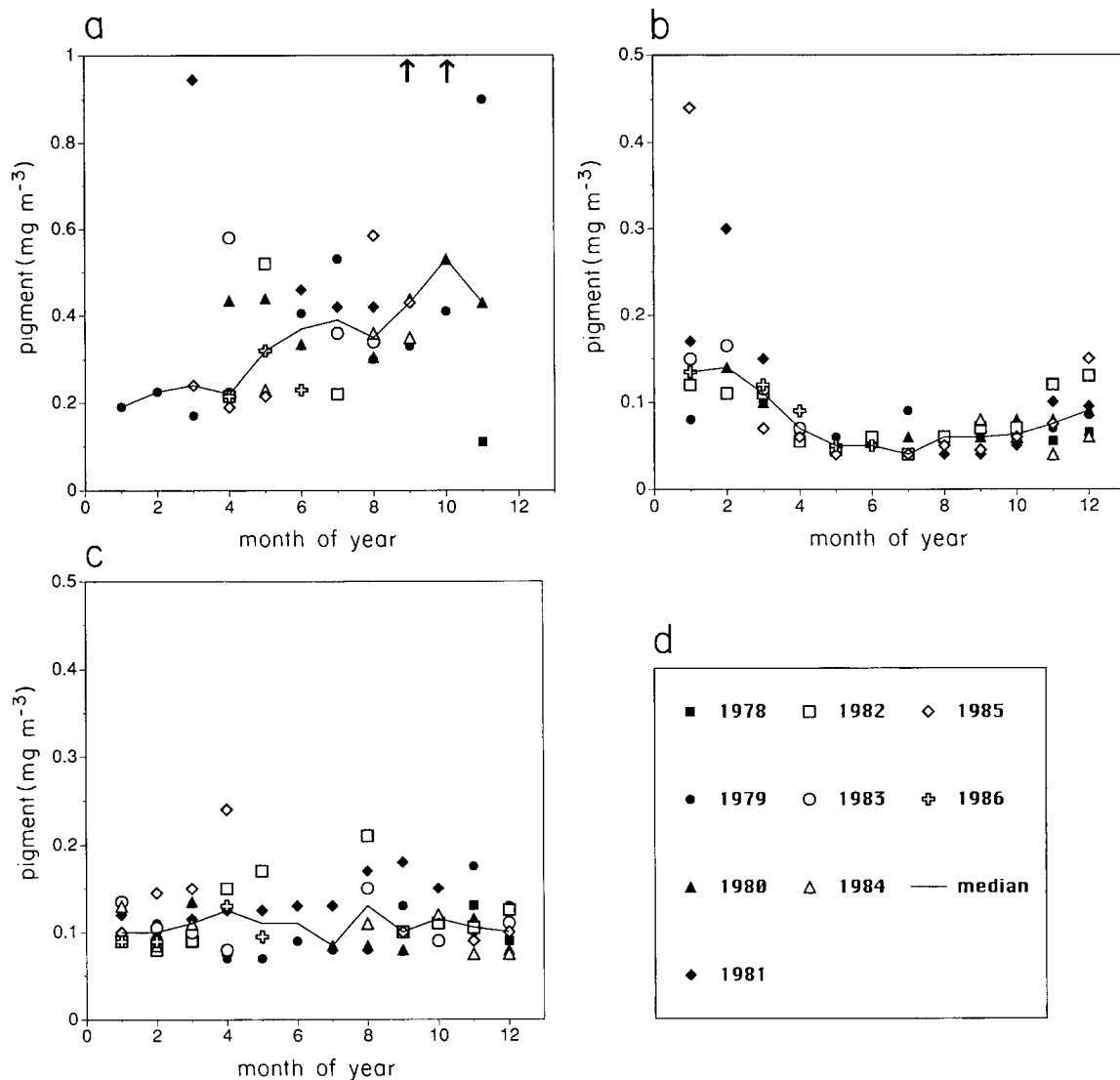


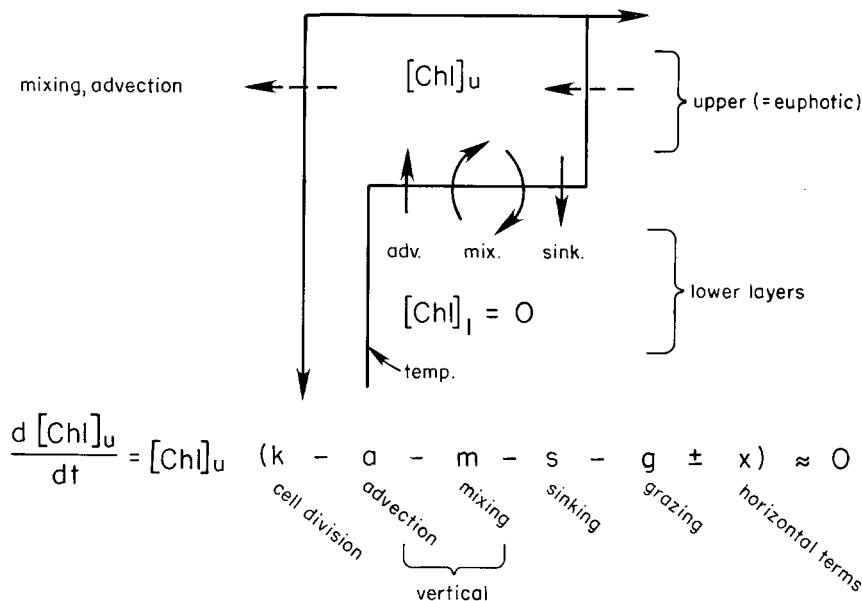
Fig. 1: Monthly medians of CZCS-derived pigment in three oceanic domains for 9 years. Medians for each month are connected by lines. The areas are approximately parallelograms with the coordinates of the southwestern, southeastern, and northeastern corners indicated. (a) Subarctic Pacific south of Gulf of Alaska, 45°N, 155°W; 45°N, 138°W; 50°N, 144°W (the last coordinates approximately those of the former Ocean Weather Station PAPA; note reduced scale of ordinate and omitted values [arrows at top margin], 1.16 mg m⁻³ for Sept. 1983 and 1.71 for Oct. 1981). (b) Eastern equatorial Pacific, 6°S, 124°W; 6°S, 97°W; 4°N, 97°W. (c) Central North Pacific around CLIMAX area, 25°N, 160°; 25°N, 144°W; 30°N, 148°W. (d) Symbols for years. (see Banse and English, 1994, for methods).

... the rate of change of phytoplankton concentration is principally understandable as the balance between the rates of cell division and mortality.

Gulf of Alaska and Antarctic sites), despite demonstrated adsorption of iron to the container walls.

As to the understanding of the rate of temporal change of pigment, only in the last few years have accurate growth rates of bulk phytoplankton become available, which permit us to draw up a balance sheet (Fig. 2; see Banse, 1992, for sources supporting the following discussion). In the geographic domains identified (Fig. 2, bottom part), horizontal gradients of pigment are slight, especially in the zonal direction. Also, considering the time change at a fixed station over a few days or

more, horizontal advection will average out the effect of patchiness of pigment. Thus the horizontal terms in the equation in Figure 2 can be neglected. Further, Figure 1 shows that the percentage daily change of pigment due to seasonality, if any, is very small so that $d[\text{chl}]/dt$ in Figure 2 can be set to zero. Then, the measured rates of cell division k are balanced by the three vertical terms and mortality, g . Since each of the vertical terms is known to be equivalent to a few percent per day, the rate of change of phytoplankton concentration is principally understandable as the balance between the rates of cell division and mortality.



| | k | a | m | s | g |
|-------------------------------|----------------|-------|-------|-------|-------|
| SUBANTARCTIC (Summer) | 0.25 (0.5)* | 0.04 | 0.05? | ≤0.02 | 0.15? |
| SUBARCTIC ("Papa", Summer) | 0.5 (0.8)* | <0.01 | ~0.03 | 0.01 | ~0.45 |
| SUBTROPICAL GYRE | 1.2 (1.7)* | <0.01 | <0.01 | ≤0.01 | ~1.2 |
| EQUATORIAL UPWELLING | 1.0 (1.4)* | 0.04 | 0.02 | 0.01 | ~0.9 |

*max. instant. growth rate

Fig. 2: The temporal balance of rates of algal growth and loss in the mixed layer at 4 representative sites of the open sea. The equation, based on the model above, compares the instantaneous rates of growth (k) and loss (a, m, s, g, x , all as d^{-1}) for bulk phytoplankton in the euphotic zone (= mixed layer), which is assumed to overlie phytoplankton-free water. The maximal instantaneous rates for the respective temperatures also are given, mostly representing diatoms at replete nutrients and light, with varying daylengths taken into account. To obtain division rates (d^{-1}), divide by 0.69; the doubling times (d) are the inverse of the division rates (from Banse, 1992, with permission of Plenum Press).

In normal, near-steady state situations with high algal division rates, as in the domains of Figure 2, cell mortality mainly is caused by grazing. Most of the grazing is due to small, unicellular animals (protozoans) with division rates that are potentially similar (given sufficient food) to those of the phytoplankton or even higher, so that the animals quickly can adjust the grazing pressure to an enhanced food supply and the underlying phytoplankton production rate. The only other source of mortality for the phytoplankton might be from lysis of cell contents by viruses, so far little studied. I suggest, however, that this mortality, at least for the larger algal species, is normally very low, since so rarely does one see empty, unbroken di-

atom cells when counting phytoplankton under the microscope. Even these cells might have died from grazing by heterotrophic dinoflagellates with digestion outside the cell body, i.e., without breakage of the prey (cf. Jacobson and Anderson, 1986).

Note regarding the grazing term in Figure 2, that g (d^{-1}) equals the fraction of water (liter/liter) that is being cleared of particles per day. With divisions approaching $2 d^{-1}$ (3rd line of Fig. 2), more than 1 liter/liter has to be strained of phytoplankton per day. At the same time, other particles will be removed, so that the optics of the water, i.e., the particle concentrations, also are difficult to understand without studying the role of the grazers.

... cell mortality
mainly is caused by
grazing.

. . . the temperate
North Atlantic . . .
with its common
spring blooms, is the
“oddball” among the
temperate oceans.

Regions With Marked Phytoplankton Seasonality
Relatively few oceanographers work in the areas discussed so far; the majority either investigate plankton on continental shelves, characterized by regular seasonal phytoplankton blooms, or in the temperate North Atlantic which, with its common spring blooms, is the “oddball” among the temperate oceans. How important is grazing in these much-studied areas?

Figure 3, based on papers by D.H. Cushing and colleagues, illustrates the fate of a phytoplankton spring bloom in a zooplankton patch in the North Sea, of a diameter of ~50 km or larger (only cells larger than several micrometers were

counted). The design of the study eliminated the horizontal advection, which is so troublesome for time series at fixed stations, and diminished the effect of horizontal eddy diffusion, the daily losses from the plankton patch being estimated as well below 10%. The principal bloom ended although nutrients were replete (Fig. 3) and algal division rates continued to increase due to increasing day length and, perhaps, rising temperature. Presumably, the bloom terminated because the animal population, nourished by the phytoplankton production, grew over the many weeks of study and also made g time-dependent such that g exceeded k toward the end of April [Fig. 3, top; the rate of loss was inferred to be due primarily to grazing (Cushing and Vucetic, 1963)]. Prior to Cruise 6, when the algal mean peak concentration of $0.9 \text{ mm}^3 \text{ l}^{-1}$ was reached, $3.6 \text{ mm}^3 \text{ l}^{-1}$ of algal cells had been produced, and $2.7 \text{ mm}^3 \text{ l}^{-1}$ had been lost. Plant production proceeded at a high rate for another cruise (Fig. 3, cumulative production curve), although the sign of population change had become negative.

In the patch, phytoplankton production continued until (and presumably past) the end of the observations, as seen from the gradual decline of nutrients through May but, judging from the low cell volume, it must have been due to cells that were too small to be counted. Also note that instantaneous rates of loss of $\sim 2 \text{ d}^{-1}$ (Fig. 3, top, around 10 May 1954) indicate that losses other than grazing mortality became important, as otherwise, each liter had passed twice per day through animal appendages, which is too high. Either an unaccounted-for major source of loss appeared like cell aggregation and massive sinking or enhanced large horizontal diffusion, or the uncertainty in mapping the patch combined with low cell numbers led to the drastic change of mean cell volume per cruise (for inferred massive sinking elsewhere in the North Sea, see Fransz and Gieskes, 1984). In summary, the temporal change of algal concentrations in the patch was heavily affected by grazing, and especially the reversal of sign of change after Cruise 6 was caused by grazing outrunning the algal division rate.

Spring blooms of phytoplankton in other regions may be terminated by nutrient exhaustion (i.e., k decreases greatly, while the loss terms persist) and, thus, are governed by bottom-up control (i.e., resource-mediated control, where hydrography \rightarrow nutrients \rightarrow algal division rate; see Fransz *et al.*, 1991, p. 132). However, grazing plays a large role even in such situations, as shown by the large fraction of plant production supported by ammonium during the bloom period, ratios of new/total production of <0.5 being common (e.g., Ducklow and Harris, 1993, for the open North Atlantic). These ratios are often calculated from the rates of uptake of nitrate/[ammonium + nitrate]. The ammonium is generated by grazers and their

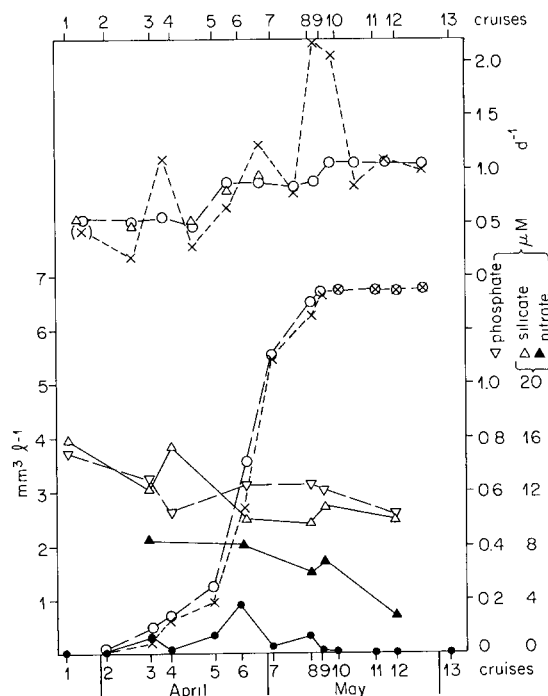


Fig. 3: Dynamics of phytoplankton cell volumes (cruise means) in a spring bloom in the North Sea, plotted vs months (mean dates) and cruise numbers. During 1954, a patch of the copepod *Calanus finmarchicus* drifted along the English northeast coast and was mapped 12 times under the direction of D.H. Cushing. **Top part,** instantaneous rates of algal growth (\circ , Δ , by independent methods, Cushing, 1963) and mortality (x ; scales for both on right-hand ordinate). **Bottom part,** concentrations of nutrients (symbols on right ordinate, from Cushing and Nicholson, 1963) and algae (\bullet ; left ordinate, from Cushing and Vucetic, 1963), and cumulative algal production (\circ) and mortality (x ; scale for both on left ordinate). The last three variables were calculated as in Cushing (1975, p. 9), but using intervals between cruises from Cushing and Vucetic (1963, Table 1). D.H. Cushing (personal communication, 1984) notes errors in this respect in Cushing (1975, Fig. 1a, top and Table 3).

predators directly or by bacteria from the by-products of grazing and animal growth.

Conclusions

Figures 1 and 3 offer persuasive evidence that the modelers, beginning with G.A. Riley, were right after all, i.e., that phytoplankton dynamics cannot be understood from measuring only concentrations and photosynthesis and converting the latter to division rates. Riley (1946) offered the first quantitative model of a seasonal cycle of phytoplankton but for decades had few followers (see Banse, 1992). While this conclusion, now backed by empirical evidence referred to above, is reasonably clear with respect to the rate of change of biomass, the principal determinant of the phytoplankton concentration is less obvious. In a model for an equilibrium situation that simulates a foodweb like that of the equatorial Pacific (Frost and Franzen, 1992), the equation for the phytoplankton biomass (Frost and Franzen, 1992, Eq. 7) does not contain any plant-physiological parameter; instead, it is dominated by the feeding threshold of the grazers, i.e., the food concentration at which the animals stop feeding because they cannot meet their expenses in food-collecting, as it were. In the model, the abundance of phytoplankton is clearly under top-down control, i.e., limited by the mortality exerted by the trophic level above it. For all variables the model can only achieve similarity with the field observations (DIN, pigment, k) after adding two levels of carnivores (Table 1). This illustrates that modeling the grazing mortality of phytoplankton and the ensuing animal production will be inadequate when the construct contains only phytoplankton and its grazers (the "herbivores" of current models; see also Steele and Henderson, 1992, about closing problems in plankton models).

In regard to more realistic modeling of food webs, i.e., to going beyond the trophic-level con-

cept as in Table 1, we are short on explicit theory, not only for marine and freshwater systems, but also for ecology in general. The behavior of models as in Table 1 is altered considerably, for example, when more than one species is present on a trophic level (e.g., 2 herbivores; see Pimm, 1992).

Future Challenges

At present, comprehensive programs directed at phytoplankton-related issues measure the grazing rate because it is broadly recognized as an important term. The empirically determined rate then is used in modeling. The challenge for future research, as mentioned above, is to predict the rate. Toward this end, better modeling and an enormous accumulation of data on natural history and rate coefficients will be needed.

Development of Foodweb Theory

Among the unresolved issues regarding animal-phytoplankton relations is a satisfactory treatment of size-dependence of processes in foodwebs, aside from the well-documented physiological aspects of size dependence. For example, invertebrates feed size-selectively because most small animals can neither swallow large prey intact nor nibble on it, and most large animals are inefficient in straining small food particles out of a mixed food assemblage. Also, medium-sized species feeding on phytoplankton (herbivores) will retain small herbivores by straining, together with phytoplankton of the same size and, worse, swallow small carnivores that may be small by nature, such as protozoans, or young specimens that as adults may prey on the same herbivores. Thus, large populations of invertebrate planktonic true herbivores occur only in lectures, textbooks, and models. In addition to size selectivity, there may be selection by food quality or kind, such that some protozoans may feed on one kind of phytoplankton.

Further, the shift in the size composition of the phytoplankton resulting from size-selective mortality will change the algal bulk division rate because it depends on average cell size. (Note that algal physiology depends on cell size, while grazing mortality and sinking losses depend on entity size, i.e., the cell with its spines, or the size of the colony.) Moreover, not only may the phytoplankton size composition change with time, but the mean size of the grazer assemblage also is time-dependent because the metazoans among them increase their numbers by laying eggs that hatch specimens with small mouth openings instead of dividing into two cells as most protozoans do. The grazers, in turn, are subject to time-dependent predation that likewise tends to be size-selective. Note that some predators while young may mostly consume phytoplankton, for reasons of size or taste. Because of all these permutations, which follow rules tied to the species and only sometimes to higher taxonomic categories, it matters which species are

... better modeling
and an enormous
accumulation of data
on natural history and
rate coefficients will
be needed.

... algal physiology
depends on cell size,
while grazing
mortality and sinking
losses depend on
entity size, ...

Table 1

Steady-state concentrations and phytoplankton instantaneous growth rates (all rounded) in a model simulating a chemostat with progressively added trophic levels

| Category | DIN μM | Chlorophyll μg l ⁻¹ | k d ⁻¹ | Herbivore μM N | Carnivores | |
|------------|-----------|-----------------------------------|----------------------|-------------------|------------|------------|
| | | | | | 1° μM N | 2° μM N |
| Phytopl. | 0.001 | 16 | 0.03 | — | — | — |
| Herbivore | 0.4 | 0.2 | 1.3 | 2.2 | — | — |
| 1° carniv. | 0.002 | 10 | 0.07 | 0.2 | 1.0 | — |
| 2° carniv. | 0.3 | 0.4 | 1.3 | 0.6 | 0.2 | 0.4 |

(Calculations by B.W. Frost, using model by Frost and Franzen, 1992.) DIN, dissolved inorganic nitrogen; k, algal instantaneous growth rate; 1° and 2° carnivores, animals feeding on "herbivores" and 1° carnivores, respectively. Dilution rate 0.033 d⁻¹, simulating an upwelling rate of 1 m d⁻¹ into a mixed layer of 30 m depth; inorganic nitrogen concentration in the inflow (simulating the upwelling water), 10 μM; algal maximal k, 1.4 d⁻¹; 1 μg chlorophyll = 0.63 μmol N, i.e., carbon-to-chlorophyll ratio, 50 by weight.

dominant at a particular place and time. Lampert *et al.* (1993) have progressively incorporated some of these realities into examples of models for freshwater plankton.

Considering these aspects, it may not come as a surprise that the trophic-level concept exemplified by Table 1, so useful for pedagogic purposes and utilized by Frost and Franzen (1992) toward this end, is disliked by biologists. The assignment of species or developmental stages to a trophic level at and especially above the herbivores is ambiguous, because of the role of size and taste in feeding, so that a rigorous test of such a model above the phytoplankton level is deemed impossible (e.g., Murdoch 1966); the construct is based on nonmeasurable entities. Therefore, more realistic models, incorporating rather narrowly defined functional types (see below) or even the dominant species, must be devised if prediction of grazing rates is the goal. However, presuming that at some future date we have a well-known initial state of an area and a very advanced, realistic biological model with sufficient data on rates, how predictable in principle is such a system for longer periods, e.g., a season or 10 years? Today, we lack any really useful theory to answer this question, and skepticism abounds. Yet, without theory as a guide, it may be difficult to design an efficient and timely program of accumulating the biological information needed for modeling the feedback by the marine biota to climate change.

Regional Scope of the Problem of Timely Prediction

What do we want to know in the short and long run for predicting phytoplankton concentrations and their rates of change? In the near future, during programs like Joint Global Ocean Flux Study (JGOFS), when investigating the interaction between phytoplankton and zooplankton, including the mechanisms that generate vertical flux of particles, and testing associated models, it would be most helpful to be able to predict at least qualitatively the following: will an open-ocean cruise, which always has to be scheduled well in advance, encounter primarily dinoflagellates or diatoms in an upwelling study off Baja California (e.g., Walsh *et al.*, 1974; Estrada and Blasco, 1979), or a cool-temperate versus warm-temperate zooplankton assemblage in the North Atlantic (e.g., Glover, 1961), or salps and euphausiids instead of other grazers in the eastern equatorial Pacific (e.g., Murray *et al.*, 1989)? The first two examples refer to cases where hydrographic processes preceding the cruise seeded the entire region of interest. In the last example, the cause might have been the same but, since only individual stations seem to have been affected, a flexible station schedule, with the biota determining the choice of stations, might have helped. In all three cases, prediction is not possible at present, except for an empirical assess-

ment by a pre-expedition, but it seems to be feasible in principle.

In the far future, 50–100 years from now, for reasons of intellectual curiosity if nothing else, we would wish to understand the abundance and the rates of change with season (or longer time scales) of at least the dominant plankton species in the major biogeographic zones of the oceans, as we currently recognize major habitats on land. Hopefully, this will be feasible in principle. The basis would be the understanding of interactions of populations with each other and with the abiotic environment that in turn would be based on knowledge of the biology of these species (e.g., Smetacek and Pollehne, 1986). Note that the biogeography within each ocean beyond the continental shelves (i.e., beyond the complicated neritic zone) is related to climate (e.g., tropics vs. northern-hemisphere warm-temperate zone); among oceans, it is also related to the history of the oceans and, hence, the biogeographic difference is not predictable from present environmental variables. Each biogeographic province harbors its own set of species, although the life forms (functional types) are similar or nearly identical.

Probably at a much earlier time, it will become imperative to be able to anticipate the effect of climate change on the biota. The rest of this paper is predicated on the premises that 1) only limited time remains for us (2 decades?) until firm answers are needed for political decisions about global warming, and 2) the marine pelagic biota are profoundly involved in climate change via the air-sea gradients of CO₂, DMS, N₂O, etc. (see the controversy of Broecker 1991 vs. Banse 1991b). Premise (2) must be tested by modeling with data, which are currently being collected, before profound changes in our mode of working on phytoplankton-zooplankton relations (see below) are made. For example, how important are the organisms in the Subantarctic water ring that contributes about 1/10 of the ocean surface and is believed to partake significantly in the exchange of CO₂ between the atmosphere and the ocean as a whole? To my mind, the marked drawdown of CO₂ during fall in the Pacific and Atlantic sectors of the ring (Tans *et al.*, 1990; Murphy *et al.*, 1991) proves that during this season at least, biological processes are more important for the surface water than physically mediated ones (e.g., from temperature changes or vertical water motions).

To set the stage for biological studies at the level of dominant species, suppose that two decades from now it can be predicted that an expected climate change will in fact shift the average positions of the polar and subtropical fronts in the southern hemisphere by a certain distance. Between the two fronts, will that lead to a wholesale latitudinal move of the plankton community with the composition as we know it now, so that there will merely be a broader or

What do we want to know in the short and long run for predicting phytoplankton concentrations and their rates of change?

narrower expanse of DMS production of the same flux per unit surface as today, with the same feedback to climate via cloud formation (see Taylor *et al.*, 1992, for North Atlantic biogeographic shifts)? I suspect, instead—and especially for the broad biological boundary zones adjoining the hydrographic fronts—that selective change of dominant species will occur. How will we learn enough by year 2014 to address with useful accuracy the issue of changing geographic and seasonal DMS production, which is determined only by some phytoplankton species?

Although the question of zooplankton production as key control of phytoplankton production, as formulated here, is of a global nature, in my view it cannot be answered globally within two decades but first must be tackled regionally. For the global answer to be based on dominant species, far too many life histories and rate processes would have to be studied after taxonomic revisions of very many genera had been undertaken for many biogeographic provinces. (Note that only the correct name opens the door to the literature on the particular species!) As a substitute, it might be possible to develop at this time near-global, general plankton production models, aiming at climatic zones (e.g., “offshore subtropical sea”), that contain general submodels for functional types, e.g., for “a small, slowly growing, nonmigratory crustacean omnivore” like the copepod *Oithona* or “a medium-sized, fast-growing, nonmigratory crustacean suspension feeder” like the copepod *Paracalanus* and their interactions with standardized phytoplankton (see Vinogradov *et al.*, 1976, for early work in this direction). The actual fleshing out of such skeletons, by finding and entering the coefficients for the particular dominant species, should be attempted only in the very few best-known regions of the world’s ocean. I suppose that within two decades, decisive, integrated success along the lines sketched here can be expected only for the North Sea, including the western approaches to Great Britain and the Baltic, the northern Black Sea, the eastern seaboard of the United States and Canada (actually, 2 biogeographic provinces), the northeastern cool-temperate Pacific, and perhaps the northwestern Mediterranean and the Sea of Japan. For other regions, too little basic biological information is at hand to make a start for addressing the entire system on the basis of dominant species in about two decades. Even for the named areas, the quandary is that processes effecting climate change in the context treated here principally operate in open sea regions while much of the available natural history and experimental laboratory work has been concerned with the inhabitants of the coastal biogeographic provinces, many of which do not live in the open sea.

Directing the Collection of Biological Information

Investigating zooplankton population dynamics is one of the central goals of the current Global Ocean Ecosystems dynamics (GLOBEC) program that principally aims at understanding the abundance, variations in abundance, and production of animal populations in the sea. This task also involves an understanding of the food consumption by animals. However, I believe it unlikely that the extension of GLOBEC’s efforts to the feedback of 1) grazing to the size composition and concentration of phytoplankton, and 2) animal population dynamics to mass fluxes of, e.g., O₂, CO₂, or organic matter and the associated elements, will be achieved during GLOBEC’s life time. Because of our presently inadequate theoretical understanding, the current Joint Global Ocean Flux Study (JGOFS) program also cannot address these fluxes in the manner proposed here, but must proceed on an empirical basis by using, e.g., the measured grazing mortality. Global Ocean Euphotic Zone Study (GOEZO) is being planned under International Geosphere-Biosphere Programme (IGBP) for the late 1990s and beyond and is expected to tie together, and expand upon, results of the JGOFS, World Ocean Circulation Experiment (WOCE), and GLOBEC programs. GOEZO also will be in dire need of a predictive capability for zooplankton dynamics, e.g., regarding the coupling of temporal changes of the dominant populations of phytoplankton and zooplankton (and bacteria).

How to gather the biological data on the dominant species within two decades? In my opinion, even in the relatively well-studied regions mentioned above we face a research problem of a size that requires a large, concerted, and maintained effort well beyond what we are accustomed to in marine biology. In this effort, guided focusing of effort and maintenance of continuity should be the major new features of research administration. The intellectual guidance would come from continued contact between modelers and experimentalists, while the maintenance of continuity of effort and funding is an institutional task. Unless guided in some form, but without stifling individual initiative, work on taxonomy and natural history are bottomless pits in the temporal sense. Also, measuring the rates of feeding, respiration, growth, etc., for one dominant species after another will not be particularly stimulating and therefore will require unusual discipline by the investigators and funding agencies. I do not believe that leaving the solution to chance, i.e., to individuals or transient groups pursuing “their own thing”, will yield the results by the time that accurate predictions of the ocean’s role in, and the response to, climate change have to be in hand.

. . . we face a research problem of a size that requires a large, concerted, and maintained effort well beyond what we are accustomed to in marine biology.

Acknowledgements

This paper is an elaboration of a lecture with the same title at the Third Scientific Meeting of The Oceanography Society in Seattle, WA, in April 1993. The preparation of the manuscript was partly supported by the Office of Naval Research grant N00014-93-1-0064 and National Aeronautics and Space Administration grant NAGW-3606. Two anonymous reviewers and D.P. Henry suggested improvements to the text. University of Washington Contribution No. 1991.

References

- Banase, K., 1991a: Rates of phytoplankton cell division in the field and in iron enrichment experiments. *Limnol. Oceanogr.*, **36**, 1886–1898.
- , 1991b: False advertising in the greenhouse? *Global Biogeochem. Cycles*, **5**, 305–307.
- , 1992: Grazing, the temporal changes of phytoplankton concentrations, and the microbial loop in the open sea. In: *Primary Productivity and Biogeochemical Cycles in the Sea*, P. Falkowski and A.D. Woodhead, eds., Plenum Press, New York, 409–440.
- and D.C. English, 1994: Seasonality of CZCS phytoplankton pigment in the offshore oceans. *J. Geophys. Res.*, **99C**, 7323–7345.
- Barber, R.T. and F.P. Chavez, 1991: Regulation of primary productivity rate in the equatorial Pacific. *Limnol. Oceanogr.*, **36**, 1803–1815.
- Broecker, W.S., 1991: Keeping global change honest. *Global Biogeochem. Cycles*, **5**, 191–192.
- Cushing, D.H., 1963: Studies on a *Calanus* patch. II. The estimation of algal productive rates. *J. Mar. Biol. Assoc. U.K.*, **43**, 339–347.
- , 1975: *Marine Ecology and Fisheries*. Cambridge University Press, Cambridge, MA, 278 pp.
- and H.F. Nicholson, 1963: Studies on a *Calanus* patch. IV. Nutrient salts off the north-east coast of England in the spring of 1954. *J. Mar. Biol. Assoc. U.K.*, **43**, 373–386.
- and T. Vucetic, 1963: Studies on a *Calanus* patch. III. The quantity of food eaten by *Calanus finmarchicus*. *J. Mar. Biol. Assoc. U.K.*, **43**, 349–371.
- Ducklow, H.W. and R.P. Harris, 1993: Introduction to the JGOFS North Atlantic Bloom Experiment. *Deep-Sea Res. II*, **40**, 1–8.
- Estrada, M. and D. Blasco, 1979: Two phases of the phytoplankton community in the Baja California upwelling system. *Limnol. Oceanogr.*, **24**, 1065–1080.
- Fransz, H.G. and W.W.C. Gieskes, 1984: The unbalance of phytoplankton and copepods in the North Sea. *Rapp. P.-V. Réun. Cons. Int. Explor. Mer*, **183**, 218–225.
- Fransz, H.G., J.P. Mommaerts and G. Radach, 1991: Ecological modelling of the North Sea. *Neth. J. Sea Res.*, **28**, 67–140.
- Frost, B.W., 1991: The role of grazing in nutrient-rich areas of the open sea. *Limnol. Oceanogr.*, **36**, 1616–1630.
- and N. Franzen, 1992: Grazing and iron limitation in the control of phytoplankton stock and nutrient concentration: a chemostat analogue of the Pacific equatorial upwelling zone. *Mar. Ecol. Prog. Ser.*, **83**, 291–303.
- Glover, R.S., 1961: Biogeographic boundaries: the shapes of distributions. In: *Oceanography*, M. Sears, ed., Publ. 67, Am. Ass. Adv. Sci., Washington, D.C., 201–228.
- Jacobson, D.M. and D.M. Anderson, 1986: Thecate heterotrophic dinoflagellates: feeding behavior and mechanisms. *J. Phycol.*, **22**, 249–258.
- Lampert, W., W. Gabriel and K.O. Rotthaupt, 1993: Ecophysiological models: a tool for understanding interactions in freshwater communities? *Verh. Dtsch. Zool. Ges.*, **85.2**, 95–110.
- Martin, J.H., R.M. Gordon and S.E. Fitzwater, 1991: The case for iron. *Limnol. Oceanogr.*, **36**, 1793–1802.
- Murdoch, W.W., 1966: Community structure, population control, and competition—a critique. *Am. Nat.*, **100**, 219–226.
- Murphy, P.P., R.A. Feely, R.H. Gammon, D.E. Harrison, K.C. Kelly and L.S. Waterman, 1991: Assessment of the air-sea exchange of CO₂ in the South Pacific during austral autumn. *J. Geophys. Res.*, **96C**, 20455–20465.
- Murray, J.W., J.N. Downs, S. Strom, C.-L. Wei and H.W. Jannasch, 1989: Nutrient assimilation, export production and ²³⁴Th scavenging in the eastern equatorial Pacific. *Deep-Sea Res.*, **36**, 1471–1489.
- Pimm, S.L., 1992: Frog ponds and ocean iron. *Nature*, **360**, 298–299.
- Riley, G.A., 1946: Factors controlling phytoplankton populations on Georges Bank. *J. Mar. Res.*, **6**, 54–73.
- Smetacek, V. and F. Pollehne, 1986: Nutrient recycling in pelagic systems: a reappraisal of the conceptual framework. *Ophelia*, **26**, 401–428.
- Steele, J.H. and E.W. Henderson, 1992: The role of predation in plankton models. *J. Plankton Res.*, **14**, 157–172.
- Tans, P.P., I.Y. Fung and T. Takahashi, 1990: Observational constraints on the global atmospheric CO₂ budget. *Science*, **247**, 1431–1438.
- Taylor, A.H., J.M. Colebrook, J.A. Stephens and N.G. Baker, 1992: Latitudinal displacement of the Gulf Stream and the abundance of plankton in the North-East Atlantic. *J. Mar. Biol. Ass. U.K.*, **72**, 919–921.
- Venrick, E.L., J.A. McGowan, D.R. Cayan and T.L. Hayward, 1987: Climate and chlorophyll a: long-term trends in the central North Pacific Ocean. *Science*, **238**, 70–72.
- Vinogradov, M.Ye., E.A. Shushkina and I.N. Kukina, 1976: Functional characteristics of a planktonic community in an equatorial upwelling region. *Oceanology*, **16**, 67–76 (transl. from *Okeanologiya*, **16**, 1976).
- Walsh, J.J., J.C. Kelley, T.E. Whitledge and J.J. MacIsaac, 1974: Spin-up of the Baja California upwelling system. *Limnol. Oceanogr.*, **19**, 553–572. □