

From carbon flux to regime shift

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ABSTRACT

The basic assumption in biological oceanography – and in GLOBEC – is that physical forcing at a wide range of space and time scales determines most of the dynamics of marine populations. This has been very productive and provides the global context for GLOBEC and other programmes. How far can it take us in the future; and, alternatively, what role is played by community interactions?

Key words: carbon, flux, regime, shift

INTRODUCTION

Physical oceanography is a relatively young science. It is exactly 50 years since Henry Stommel (1948) gave the first satisfactory explanation for the Gulf Stream. It is only 25 years since satellites revealed the mesoscale landscape of the ocean surface.

Marine biology is very much older, with its roots in the classics. But the emergence of biological oceanography is quite recent and, I believe, results from the realization that the close connections between biology and physics in the ocean define the evolutionary and ecological processes as well as the similarities in observed distributions. Thus the underlying assumption in this field – and the dominant theme in GLOBEC – is that the patterns in marine populations can be explained primarily in terms of physical processes at a wide range of space and time scales.

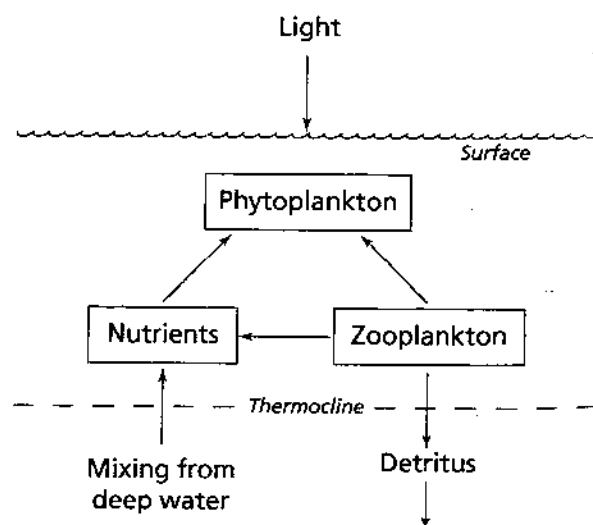
In this paper I shall review, selectively, progress in determining and using these physical–biological linkages. I shall explore the question of whether this assumption is not only a necessary but also a sufficient basis for further advances.

THE FLUX APPROACH

The development of methods to measure standing stock and flux rates of carbon and essential nutrients, plus measures of photosynthetic pigments, gave the impetus to representation of ocean biogeochemistry by simple nutrient–phytoplankton–zooplankton or N/P/Z models (Fig. 1). When one expanded version (Fasham *et al.*, 1990) was combined with a relatively simple model of the Atlantic circulation, it was possible to simulate the basic productivity of an ocean basin and compare the output, as chlorophyll, with remotely sensed ocean colour (Fig. 2; Sarmiento *et al.*, 1993).

There are broad similarities in Fig. 2 between simulation and observation for features such as the Sargasso Sea. Some of the quantitative inaccuracies undoubtedly reflect the simplifications in the biology, but a large part of the lack of fit, particularly in the tropics, can be attributed to the physical model (Hofmann and Lascara, 1998). This is because wind-driven circulation models match the horizontal movements whereas the N/P/Z models are driven primarily by vertical processes. The longer-term resolution of this mismatch requires inclusion of the

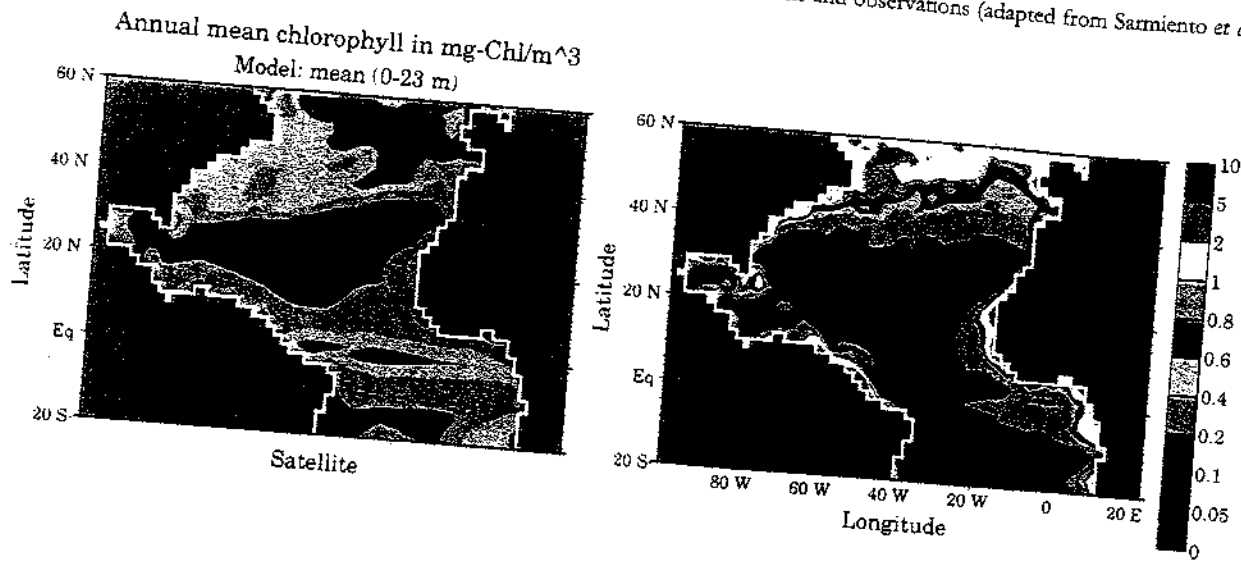
Figure 1. The simplest N/P/Z conceptual model.



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Figure 2. Comparison of annual mean chlorophyll in mg m^{-3} from simulations and observations (adapted from Sarmiento *et al.*, 1993).



thermohaline circulation – the great conveyor belt (Broecker, 1991).

The next test of the N/P/Z approach, Fig. 1, was in the equatorial Pacific, where it was apparent that the HNLC (high nitrate, low chlorophyll) areas did not fit easily into the Atlantic patterns. Two explanations emerged: iron limitation and microzooplankton grazing. However, the main outcome was the commission of real ocean experiments, IRONEX I and II (Coale *et al.*, 1996). The major conclusion was that iron was a limiting nutrient, but the interesting and relevant aspects were the striking changes in community structure induced by the nutrient enrichment. In consequence, Fig. 1 needs to be modified, not only at the nutrient box, but also for the grazing–detritus link.

The representation of the microbial loop by Azam *et al.* (1983) adapted by Cushing (1989), Fig. 3, was intended to represent changes across broad ocean regimes, from coastal upwelling to central gyres. But IRONEX and other work (Goldman, 1988) indicate that this scenario can also apply to short-lived events and to small spatial scales such as eddy uplift of the thermocline (McGillicuddy and Robinson, 1997).

These results have two implications: (1) measures of primary production are not related linearly to flux rates; and (2) the rates of flux out of the euphotic zone – the biological pump (Longhurst and Harrison, 1988) – depend largely on the role of copepods as ‘gatekeepers’ for the vertical transfer of particulate material. (Note that, in Fig. 3, compared with Fig. 1, fish have replaced detritus as the destination.) Thus variations in mesoplankton may be more sen-

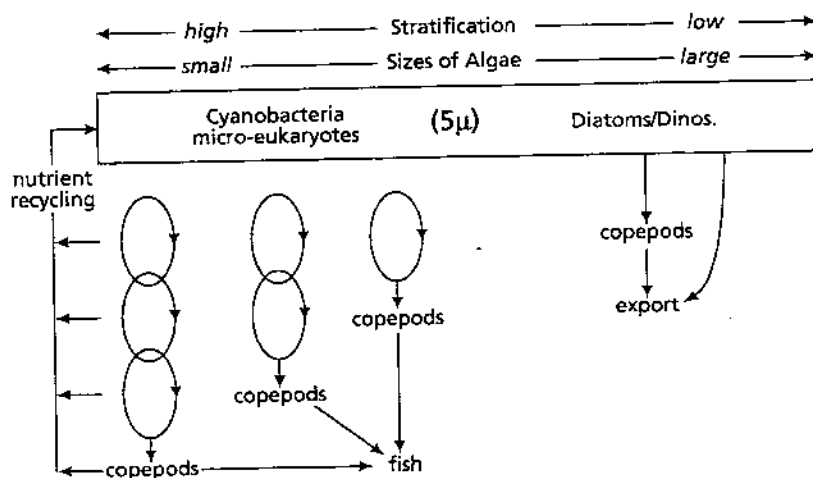
sitive indicators of change than, say, variations in chlorophyll. As an example, the very marked changes in plankton abundance in the north-east Pacific between the 1960s and 1980s (Brodeur and Ware, 1992) may be the best indication of the response to decadal changes in ocean circulation (Polovina *et al.*, 1995), and may have consequences for higher trophic levels.

These elaborations on the simple N/P/Z system result in some basic ecological questions. What are the processes, both physical and biological, determining the abundance of the mesoplankton; and what are the effects of changes in abundance on higher trophic levels? These are GLOBEC questions.

POPULATION DYNAMICS

Calanus finmarchicus is not only one of the most abundant animals in the sea, but also one of the most studied (Marshall and Orr, 1955), in part because of its presumed importance as fish food. Its pan-Atlantic distribution was well known, as was its need to overwinter in deep water. Marshall and Orr recognized that, in the northern North Sea, ‘its numbers are largely dependent on immigration from the North Atlantic’ (Marshall and Orr, 1955, p.104). It has been fascinating to watch the evolution of this approach in both the Gulf of Maine and the North Sea. The driving force has been the application of regional models of circulation, which have been used to demonstrate the 3-D connections between deep overwintering areas and spring populations. These illustrate

Figure 3. Shifts in ecosystem structure in stratified waters, illustrating the increasing carnivory of copepods with increasing oligotrophy (adapted from Azam *et al.*, 1983 and Cushing, 1989).



the technical advances in linking physics and biology and, especially, the conceptual consequences. It would appear likely that *Calanus* found in the North Sea or on Georges Bank are terminal cohorts dependent, in the long term, on open-ocean stocks; and therefore on ocean currents.

The Continuous Plankton Recorder (CPR) data show the pan-Atlantic distribution of *Calanus finmarchicus* and Fromentin and Planque (1996) have demonstrated correspondences between its oceanic abundance and the North Atlantic Oscillation. Subsequent questions concern the relationships between this oceanic variability and, say, recruitment to the cod stocks that lie around the peripheries of these oceanic distributions. How far are the climatic connections direct and how far do they depend on ecological intermediaries such as *Calanus*? These questions exemplify the range of issues raised: from individual life-history strategies to fish stock recruitment, and from local mixing rates to global circulation.

The same general types of question arise in the very different context of Antarctic krill. It would appear that the relation between deep and shelf habitats is important; that the location of overwintering stocks is critical; that there may be 'terminal' stocks around south Georgia; and, especially, that 3-D coupled models are essential to the integration of all these aspects (Eileen Hofmann, Old Dominion University, Norfolk, USA, pers. comm.).

The level of research engagement required to study the physical control of the life cycles of individual species – *Calanus*, krill or cod – presents extensive operational complications and demands on funding. This may be adequate for insight into the average

annual cycles and the year-to-year fluctuations in recruitment. But beyond this, lie issues of the role of community dynamics in longer-term variability. How far are changes in community structure the response to large-scale environmental trends?

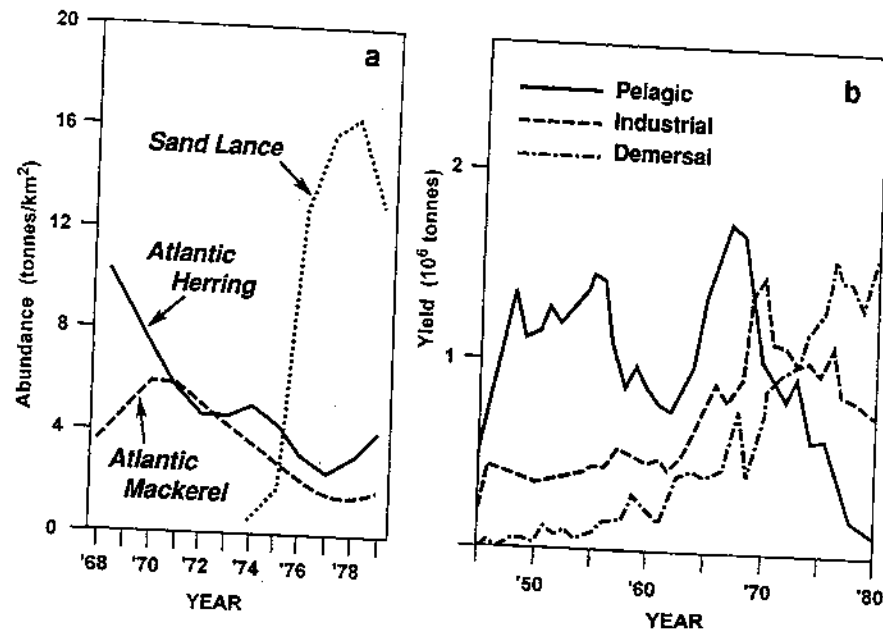
REGIME SHIFTS

The best historical data on responses of community structure to environmental trends come from fisheries (Cushing, 1982). Many of the examples derive from catches of pelagic stocks such as sardine and anchovy (Hunter and Alheit, 1995), which exhibit great swings in abundance. Other cases relate to switches in abundance between traditional species, herring and mackerel, and the smaller pelagics such as sand eel, which form the basis for 'industrial' fisheries (Fig. 4a). Finally, and more controversially (Cushing, 1983), there are the apparent inverse changes in pelagic and demersal stocks in the North Sea (Fig. 4b), and possibly on Georges Bank.

The historically earlier examples reflect natural fluctuations, whereas the latter ones (Fig. 4) are a consequence of gross overfishing. Yet realistic, but quite different, energy flow patterns fit the 1960s and the 1980s (Jones, 1984); and overall diversity does not change significantly (Solow, 1994; Greenstreet and Hall, 1996). The very varied patterns in these switches, and in many others (Caddy and Gulland, 1983), raise two further questions: are there regime shifts; and are there top-down effects of these shifts in the plankton?

The phrase 'regime shift' implies a coherent response, at the community level, to external stresses. In

Figure 4. Changes in (a) New England and (b) North Sea fisheries (adapted from Sherman *et al.*, 1981 and Bailey and Steele, 1992).



principle, we require an ecological mechanism to prevent random walks to extinction of individual populations. In practice, density dependence is very difficult to detect (Strong, 1986), especially if it occurs as punctuated equilibrium with decadal time scales.

Top-down or 'cascade' sequences are described for fresh water (Carpenter *et al.*, 1985), where changes in abundance of fish lead to changes in size structure and species composition of the plankton. The massive perturbations in marine fish stocks might be expected to have impacts on their food supplies, yet I do not know of any cases where this has been demonstrated in the sea. An important factor may be the significant and possibly dominant role of gelatinous carnivores in the oceans (Mills, 1995).

All these aspects, affecting community structure at different trophic levels, can complicate investigations of the dynamics of single populations. However, they may be central to understanding longer-term change in marine systems – one of the aims of GLOBEC. The step from the description of particular states of a system to explanation of changes in that system is a crucial transition.

UNDERSTANDING CHANGE

The various 'global' programmes with biogeochemical content have packaged the scientific questions in a way that has been effective in the deployment of re-

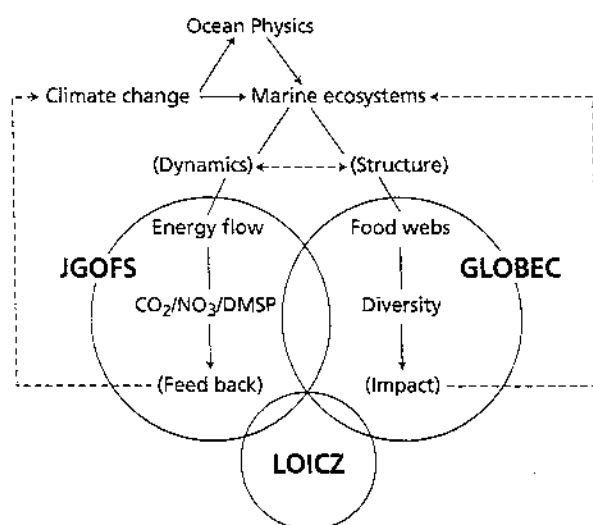
sources (Fig. 5). But there has also been a division into ocean sectors and to societal problems:

Programme	Sector	Problem
JGOFS	Open ocean	Global warming
GLOBEC	Shelf seas	Fisheries
LOICZ	Coasts	Pollution

The main achievements of these programmes, and of the World Ocean Circulation Experiment (WOCE), have been in discovering and describing the processes underlying particular physical, chemical, and biological regimes. The unfinished parts in all of their mission statements concern our ability to understand the dynamics, and predict the consequences, of longer-term change.

This is the challenge that faces all the proposals that are emerging in the second wave of global programmes. Thus WOCE is being replaced by Climate Variability and Predictability (CLIVAR), which is explicitly aimed at variability on (1) seasonal to interannual and (2) decadal to centennial scales. CLIVAR focuses on the coupled ocean-atmosphere system, taking the Tropical Ocean and Global Atmosphere Programme (TOGA) as its starting point. The separation of scales is more than merely a convenience. It determines the character of the work. The short-term scale allows prospective

Figure 5. Links between major global ocean programmes: JGOFS (Joint Global Ocean Flux Study), GLOBEC (Global Ecosystem Dynamics) and LOICZ (Land–Ocean Interactions in the Coastal Zone).



testing, whereas the long-term scale will rely on palaeo-oceanographic data.

Similarly, successors to JGOFS, such as SOLAS (Surface Ocean Lower Atmosphere Study) are likely to focus on air–sea exchanges in the context of possible decreases in vertical mixing and advection. Thus, there is not merely a new emphasis on change, but a shift in the physical and trophic positioning of these programmes. The new pattern will not map onto the old – not in ocean regions, nor in trophic structure, nor in logistics.

Where does this put an emerging international GLOBEC? What ocean sectors should be the focus? What trophic levels, and what space and time scales? These are questions for the implementation planners in terms of what is technically – and fiscally – feasible. I will only suggest some of the alternatives.

The *Calanus* story described earlier, and corresponding work in the Pacific (Parsons and Lal, 1988), indicates the need to consider the open ocean as the starting point for major shelf populations. At the same time, the role of the mesoplankton as gatekeepers of vertical transport has been neglected in flux studies. Thus the overlap between JGOFS and GLOBEC in Fig. 5 may be a significant component of both systems, especially in the open ocean.

At the other end of the GLOBEC spectrum is the interest in the environmental basis of fish stock recruitment and its variability. The simplest assumption is that interannual fluctuations in recruitment are determined primarily by physical processes. This would define a separate path in Fig. 5 from ocean currents to annual recruits. On the other hand, if abundance of any stock is bounded by the total available energy flow, then the community structure must play a role and the concept of regime shifts could apply.

These are not alternative assumptions. They are complementary when considered in the context of the third issue – time scales (Table 1). The seasonal-to-interannual and the decadal-to-centennial scales of variability defined by CLIVAR are a useful division. These scales could define the shift in emphasis from a single species to a multispecies approach, both for research and for management (Steele, 1998).

The different scales also imply differing approaches. The longer time frame demands the application of retrospective analyses to the testing of models. Gross overfishing worldwide provides us with a good number of drastically perturbed systems for comparative study. Ironically the major gaps occur in descriptions of humanly unperturbed systems that would define 'natural' variability.

Finally, the long-term perspective requires these various strands of GLOBEC – copepods and cod, physics and fishing – to be intertwined. That is

Table 1. Time scales for various processes relevant to GLOBEC.

Process	Time scale (years)		
	1.0	10	100
Space scale	Regional	Ocean basin	Global
Physics	El Niño prediction	N. Atlantic Oscillation	Thermohaline circulation
Biology	Stock recruitment	Regime shifts	
Data	Predictive	Retrospective	
Models	Single species	Community/ecosystem	

the Grand Challenge for the implementation planners.

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