

# Chapter 1



## Biogeochemical Provinces: Towards a JGOFS Synthesis

Hugh W. Ducklow

'The ocean is a desert with the life underground,  
and the perfect disguise up above.'

*America, A Horse With No Name, 1972*

Most people are intuitively familiar with the existence of recognizable, bounded units of landscape with characteristic climatic regimes, land cover and animal populations – the basis of the ecosystem concept in ecology. Theophrastus (ca. 320 B.C.) documented this recognition in his 'Inquiry into Plants' and it is implicit much later in the writings of Thoreau, G. P. Marsh and others who by the mid-19<sup>th</sup> century already lamented the loss of the North American primeval forests (Cronon 1983). Thus we recognize particular terrestrial ecosystems: grasslands, savannas, deserts, temperate and tropical forests, polar tundra and so on. What about the ocean? To the uneducated eye of the non-sailor, the surface of nearly three quarters of the planet is largely homogeneous, with minor differences in surface roughness and color. The featureless nature of the ocean's upper surface is especially conspicuous offshore, away from the gradients in color resulting from terrestrial sources of organic matter and resuspended sediments found in shallow waters. Do distinct marine provinces or ecosystems analogous to the familiar terrestrial biomes exist? Many (but not all) oceanographers agree that they do, and there have been many schemes to distinguish and classify them, but there is little agreement on how many should be identified and their spatial scale. Yet most of us would agree that there are distinctive, large scale ocean regimes which also support characteristic flora and fauna, and exist in the familiar climatic regions of the planet.

In this chapter I address the question of biogeochemical provinces in the ocean. JGOFS embodied the ocean biogeochemistry paradigm, that is, the idea that ocean is an organized system of physically-driven, biologically-controlled chemical cycles which regulate the planetary climate over large spatial and temporal scales. Much of the JGOFS program over the past decade has been structured around intensive studies in particular geographic locations chosen because they exemplify different aspects of the ocean biogeochemical system (SCOR 1990 and see the many special volumes of Deep-Sea Research, Part II). Thus at this point it is important to look critically at the question of whether such locations are distinctive, and whether a province-based approach was a good way to study ocean carbon fluxes and

the controls acting on them. An alternative to the province approach is the continuum model in which the ocean is viewed (and modeled) as a continuously varying biogeochemical system, structured and differentiated by the responses of organisms to regional changes in stratification, vertical mixing and advection (e.g., Sarmiento et al. 1993). Here I review how we can characterize different ocean regions using biogeochemical criteria. I am less concerned with whether biogeochemical provinces have some ultimate reality (the strong province model) or arise as emergent properties from a continuum of physical drivers and biological responses. I start by reviewing some previous attempts and schemes to partition the ocean into distinctive provinces or regions. Then I review some recent observations on primary production, bacterial activity, and the net production of dissolved organic carbon (DOC) in various ocean provinces studied by JGOFS and allied programs. These observations will serve as an introduction to JGOFS for non-JGOFS readers (and some JGOFS readers too): where we worked and what we found. Other authors in this volume examine some of these same questions in much greater detail. Finally I conclude with some thoughts on where this approach might lead in the coming decade of ocean science.

### 1.1 Plankton Community Structure and Distribution

Whether or not one believes in partitioning the ocean into discrete provinces or domains, it seems beyond debate that the ocean climate determines the composition and size of the regional-scale phytoplankton community, which in turn influences the structure of the plankton system in a given area. Cullen et al. (2002) review the modern theory of plankton community dynamics, based on Margalef's (1978) scheme of how turbulence and nutrient availability select phytoplankton life forms. They conclude:

We infer from such observations that it is the characteristic physical oceanography of each region that primarily determines the functional composition and seasonal biomass of the pelagic ecosystem from plants to predators. This 'bottom-up' control of



the ecosystem is, of course, mediated by the time-dependent supply of inorganic nutrients to the euphotic zone. Consequently, 'top-down' modulation of ecosystem structure by herbivory and predation must be considered a subsidiary process. In this, the pelagic biomes resemble terrestrial biomes. A simple combination of geology, latitude, altitude, exposure and rainfall determines the characteristic vegetation of any site ashore. Though terrestrial herbivores undoubtedly modulate the final expression of forest or tundra, neither elephants nor reindeer determine which vegetation type shall develop. It can be argued that a similarly parsimonious set of factors determines the distribution of pelagic biomes, each with its characteristic type of plant growth. For the open ocean, these factors are simply those required by Sverdrup (1953) to control illumination and the vertical stratification of the water column; they may be reduced to latitude, regional winds, cloud cover and the flux (if any) of low-salinity surface water. From these factors may be deduced sufficient information to predict the seasonality and kind of phytoplankton production. Over continental shelves we must also know water depth and tidal range. Copepods and whales do not determine which groups of plants shall flourish: like the phytoplankton, they are themselves expressions of the regional physical oceanographic regime (Cullen et al. 2002, pp. 8–9).

This theory provides the mechanistic foundation for the existence of ocean provinces. Cullen et al. (2002) also make the important point that not all limiting nutrients are supplied from below by turbulent mixing processes. In particular iron is supplied to wide areas of the surface ocean principally by aeolian deposition, and elemental nitrogen ( $N_2$ ) is fixed by diazotrophs like *Trichodesmium* and other cyanobacteria. Thus not all departures from the equilibrium, background state dominated by picoplankton are initiated by turbulence. It is also important to understand that multiple nutrient colimitation seems to regulate interbasin differences in plankton community structure and N vs. P limitation (Wu et al. 2000). Before proceeding, I review briefly our current understanding of plankton community structure in the context of geographic variability in ocean climate and physical forcing.

In general open ocean photosynthesis is dominated by picoplankton (diameter 0.2–2  $\mu\text{m}$ ; Sieburth et al. 1978) and nanoplankton (diameter 2–20  $\mu\text{m}$ ), with as much as 90% of the active primary producers small enough to pass through 2  $\mu\text{m}$  pore-sized filters (Li et al. 1982). These microbial phytoplankton exhibit little variability in time and space (Malone 1980; Banse 1992) because their iron requirements are relatively low and they are preyed on by small grazers, principally heterotrophic nanoflagellates (HNAN) which have growth rates as fast or faster than their prey (Landry et al. 1997; Strom et al. 2000). Population outbreaks of the smallest primary producers are held in check by the rapid functional responses of their predators. Coexisting with, and supporting, oceanic primary producers through its role in nutrient regeneration is a complex assemblage of viruses, bacterioplankton and protozoans, all in the 0.02–20  $\mu\text{m}$  size range (Azam et al. 1983; Ducklow and Carlson 1992; Sherr and Sherr 2000; Fuhrman 2000). Larger phytoplankton (e.g., diatoms and dinoflagellates) contribute the major source of variability in plankton biomass and

production (Malone 1980) during population outbreaks occurring over a range of scales from small, sporadic local miniblooms stimulated by event-scale processes (Walsh 1976) to the basin scale spring bloom covering the North Atlantic (Ducklow and Harris 1993), seen conspicuously in ocean color imagery. It is against, or underlying, this pattern of bloom and decline of larger-celled organisms at various scales that the background, small-celled plankton system persists, sustained by nutrient recycling and held in check by intense grazing pressure.

Until 1977, the very existence of the dominant oceanic cyanobacterial primary producers was unknown (Johnson and Sieburth 1979; Waterbury et al. 1979; Chisholm et al. 1988), and even today the taxonomic affinities of many major groups are just now being identified by new molecular genomic tools (Giovannoni and Rappe 2000). The large operational grouping generically known as 'bacteria' typifies the problem and presents a good case in point. 'Bacteria' include the oxygenic, photosynthetic cyanobacteria (both *Synechococcus* spp. and prochlorophytes), the heterotrophic 'true' *Bacteria* and the *Archaea*, newly recognized as a separate major domain of life (Giovannoni and Rappe 2000). The cyanobacteria also include the major oceanic nitrogen-fixing organism, *Trichodesmium* which is becoming dominant in a new regime or successional stage developing in the North Central Pacific Gyre (Letelier and Karl 1996, 1998; Cullen et al. 2002; but see also Wu et al. 2000). Within the heterotrophic bacteria, most of the major groups still cannot be cultivated and studied in the laboratory, so the identities and occurrence of the unculturable majority are known only from molecular probes (Giovannoni and Rappe 2000). The specific roles of these organisms and of the *Archaea* are almost completely unknown. This situation is especially pointed for the mesopelagic depths below the euphotic zone (ca 200–1000 m) where *Archaea* might predominate numerically (Karner et al. 2001). Even among the grazers, identity and role identification are not well understood, because a possibly large portion of the HNAN are mixotrophic, combining both photosynthetic and grazing trophic functions (Caron 2000).

In the open sea approximately 90% of the total net primary production (NPP) is supported by regenerated nutrients, of which the great majority is produced by the small grazers and heterotrophic bacteria (Harrison 1980). Bacterial productivity may average 20% of the NPP (Cole et al. 1988; Ducklow and Carlson 1992; Ducklow 1999) and is sustained by a flux of dissolved organic matter (DOM) arising from phytoplankton exudation, grazer feeding and metabolism, viral attack and particle decomposition (Nagata 2000; Williams 2000). Since the bacterial conversion efficiency is low (10–30%; del Giorgio and Cole 1998, 2000), the DOM flux fueling bacterial metabolism approaches the magnitude of the NPP



(Pomeroy 1974; Williams 1981, 1984). Our ignorance of microbial identity is mirrored in a similar lack of knowledge about the composition of the DOM pool, a complicated mixture of monomers, polymers and condensed heterocyclic compounds of which less than 10% is chemically identified (Benner et al. 1992). Besides serving as the sole quantitatively important agents of DOM oxidation and as important nutrient remineralizers, bacteria are an important alternative food source for HNAN, and thus a stabilizing factor in the nanoplankton foodweb (Strom et al. 2000). A large portion of oceanic respiration is bacterial, or derived from bacterial processes, and a large portion of ocean metabolism is driven by fluxes of dissolved matter. All these issues are not trivial and are intimately related to our understanding of ocean ecology and biogeography. We cannot move beyond the current simple PZND models of plankton dynamics toward more detailed, adaptive model ecosystems without a better appreciation of the identity and functional roles of these major plankton groups.

## 1.2 Partitioning the Oceans

Most schemes to partition the ocean into a system of bounded regions have been based on physical climate and circulation or have been biogeographic, based on the occurrence of distinctive species assemblages (e.g., van der Spoel and Heyman 1983). Longhurst (1998) pioneered a more encompassing ecological scheme, to which I return below. In his book, 'Ecological Geography of the Sea,' Longhurst (1998) reviews previous partitioning schemes in some detail. The following summary is taken largely from Longhurst's review.

Most later efforts, including Longhurst's, can be traced to Dietrich (1963), who distinguished seven ma-

jor regions on the basis of global winds and the underlying current systems. Thus Bailey (1998), who erected a detailed 'ecosystem geography' of the continents based on climate, geomorphology, vegetation cover and local meteorology, also mapped out a series of oceanic ecoregions in the sea. Bailey's marine ecoregions, however, bear little similarity to the richness of ecological differentiation of his land classification. Banse (1987) and Barber (1988) took more comprehensive approaches by integrating physical and ecological processes to distinguish both larger and smaller scale partitioning. Banse (1987) showed that three previously defined hydrographic areas in the NW Arabian Sea also possessed distinctive seasonality in surface chlorophyll *a*, providing a foreshadowing of several later syntheses of the Coastal Zone Color Scanner (CZCS) imagery of ocean color (e.g., Platt and Sathyendranath 1988; Banse and English 1993; Longhurst et al. 1995). Barber (1988) considered the reality of ocean basin ecosystems, eventually distinguishing six (Table 1.1). Barber (1988, p. 171) recalled Odum's (1969) definition of an ecosystem "... as the unit of biological organization interacting with the physical environment such that the flow of energy and mass leads to a *characteristic trophic structure and material cycles*," (my emphasis) which elegantly ties together ecological and biogeochemical dynamics. Barber also argued that during ENSO events, much of the tropical and subtropical Pacific becomes a unified large scale ecosystem, blurring the distinctions evident during non-ENSO conditions. This is important: ecosystem or province boundaries in the sea are literally and figuratively fluid in time and space. The lines shown on maps are inescapable if we want to map regions on a solid medium, but those lines belie the fluidity of the actual boundaries.

The concept of a new biogeographical segmentation of the sea was proposed by Platt and Sathyendranath

Table 1.1. Typology and description of ocean basin ecosystems (after Barber 1988)

Ecosystem	Stratification		New nutrients <sup>a</sup>		Primary productivity <sup>c</sup> per unit area	Process regulating productivity <sup>d</sup>
	Strength	Duration	Level <sup>b</sup>	Source		
Coastal upwelling	Patchy	Continuous	High	Advection	Medium to high	Space
Low latitude gyre	Strong	Permanent	Low	Mixing	Low to medium	Nutrient supply
Equatorial upwelling	Strong	Permanent	High	Advection	Medium	Physical processes and grazing
Subarctic gyre	Strong	Seasonal	High	Mixing	Medium (low in winter)	Grazing (summer); mixing/light (winter)
Southern Ocean	Weak	Seasonal	Very high	Mixing	High (low in winter)	Mixing (summer); light (winter)
Eastern boundary current	Medium	Permanent	Medium	Advection	Medium	Grazing and nutrient supply

<sup>a</sup> New nutrients *sensu* Dugdale and Goering (1967).

<sup>b</sup> Relative to phytoplankton uptake characteristics (*high*: concentration always saturating uptake rate; *low*: concentrating always rate limiting; *medium*: varies between high-low).

<sup>c</sup> *Low*: <0.1 g C m<sup>-2</sup> d<sup>-1</sup>; *medium*: ≈ 0.5 g C m<sup>-2</sup> d<sup>-1</sup>; *high*: >1 g C m<sup>-2</sup> d<sup>-1</sup>.

<sup>d</sup> Regulation may refer to rate or yield limitation (*sensu* Caperton 1975).



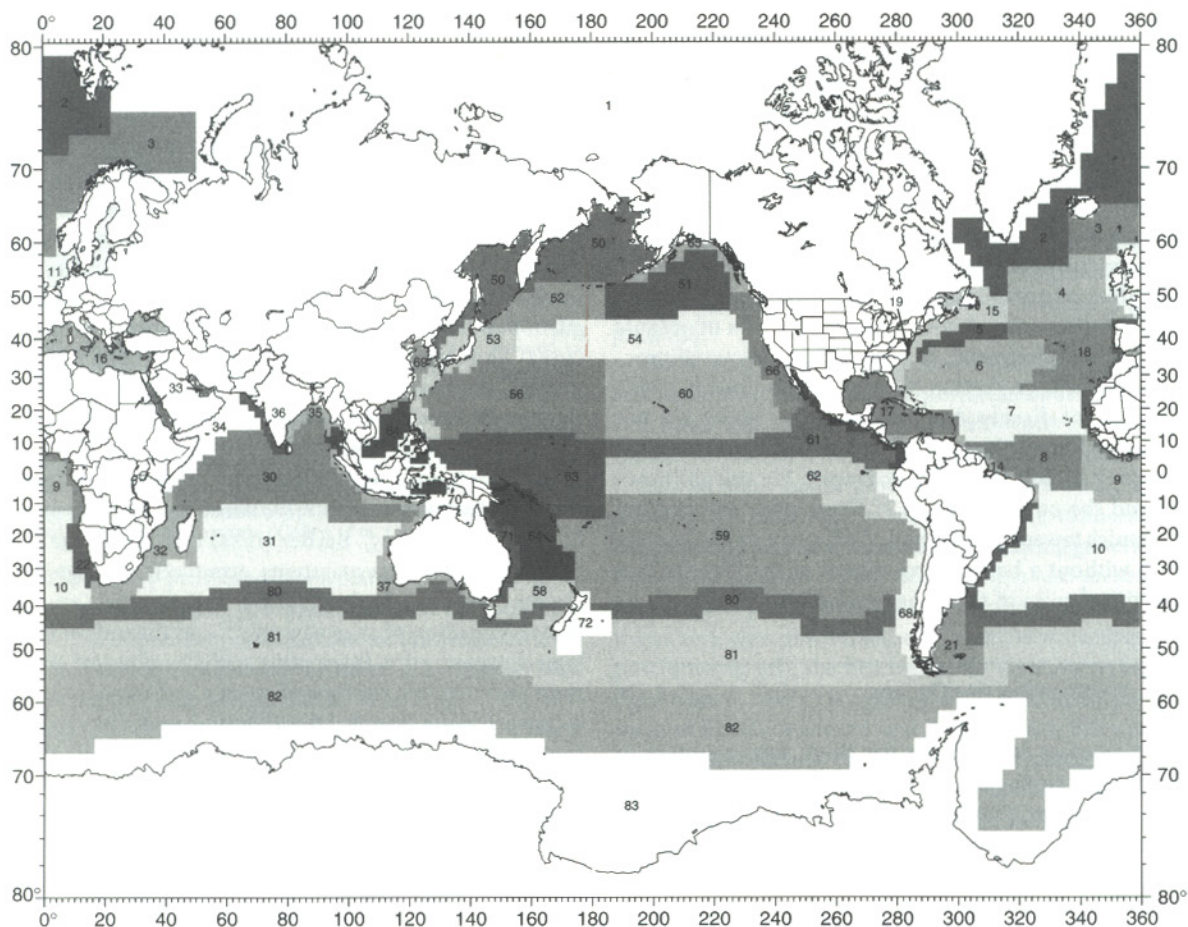


Fig. 1.1. Longhurst's 'Ecological Geography of the Sea'. This map is available from: <http://www.mar.dfo-mpo.gc.ca/science/ocean/BedfordBasin/Papers/Longhurst1998/Provinces/>, and described in detail in Longhurst (1998) although in this slightly newer version, some of the provinces have been subdivided and a few new ones have been added. A table identifying the provinces is also available at the website, and those studied in JGOFS are listed in Table 1.3

(1988). Later, possibly reflecting the influence of JGOFS on their thinking, they were apparently the first to use the term 'biogeochemical province' (Platt et al. 1991). Longhurst and colleagues (Longhurst 1995, 1998; Longhurst et al. 1995; Platt and Sathyendranath 1999) exploited the global, near-synoptic CZCS data sets on regional and basin-global scale, seasonally-resolved distributions of surface ocean pigments, along with extensive data on the vertical structure of chlorophyll *a* and photosynthesis-irradiance (P-I) relationships to produce a new ecological geography of the sea. Longhurst's scheme (Fig. 1.1) borrows from Dietrich (1963) and verifies with his own analysis of global hydrography a global ocean system with four principal *domains* (Longhurst 1995) or *biomes* (Longhurst 1998) which are the major climate regimes in which the provinces are based (Table 1.2). In the rest of this chapter I use the more generic term domain when referring to the four major divisions of the ocean shown in Table 1.2, to avoid the more strictly ecological connotation of biome. I use the term province

Table 1.2. Four primary domains or biomes in the ocean (after Longhurst 1998)

Domain	Definition
Polar	Where the mixed layer is constrained by a surface brackish layer formed each spring in the marginal ice zone (>60° latitude)
Westerlies	Where the mixed layer depth is forced largely by local winds and irradiance (ca. 30°–60° latitude).
Trades	Where the mixed layer depth is forced by geostrophic adjustment on a basin scale to often-distant wind forcing (ca. 30° N to 30° S latitude).
Coastal	Where diverse coastal processes (e.g., tidal mixing, estuarine runoff) force mixed layer depth (all latitudes).

in the same sense as Longhurst, to denote the regional-scale divisions of the domains within each ocean basin (Table 1.3). Platt and Sathyendranath (1988, 1999) systematically analyzed P-I data and argue that P-I parameters are distributed discontinuously, and assume that prov-

**Table 1.3.** JGOFS studies in ocean biogeochemical provinces. Province names and locations from Longhurst (1998) and <http://www.mar.dfo-mpo.gc.ca/science/ocean/BedfordBasin/Papers/Longhurst1998/Provinces/>

Year	Province/domain <sup>a</sup> and map number <sup>b</sup>	Study	Nations	Reference
<b>Atlantic Ocean</b>				
1986–1997	Mediterranean Sea (MEDI)/W (16)	DYFAMED	France	Copin-Montegut (2000)
1988–1992	NE. Atlantic Shelves (NECS)/C (11) Mediterranean (MEDI)/W (16)	FRONTAL, ECOMARGE	France	Monaco et al. (1999)
1988–1989	N. Atlantic Subtropical Gyral – E (NASE)/W (18)	MEDATLANTE	France	Savenkoff et al. (1993)
1988–present	N. Atlantic Subtropical Gyral – W (NASW)/W (6)	BATS	USA	Karl and Michaels (1996)
1989–present	Atlantic Arctic (ARCT)/P (2) Atlantic Subarctic (SARC)/P (3) N. Atlantic Drift (NADR)/W (4) N. Atlantic Subtropical Gyral – E (NASE)/W (18)	NABE/BOFS, German JGOFS	USA, UK, Netherlands, Germany, Canada	Ducklow and Harris (1993) Harris et al. (1997) Harrison et al. (1993)
1990–1996	Atlantic Arctic (ARCT)/P (2) Atlantic Subarctic (SARC)/P (3)	Nordic Seas	Norway	Chierici et al. (1997)
1991–1992	N. Atlantic Subtropical Gyral – E (NASE) (18)	EUMELI	France	Morel (1996)
1991–1992	Canary Coastal (CNRY) (12)	EUMELI	France	Morel (1996)
1992–1994	NW Atlantic Shelves (NWCS)/C (15)	Gulf of St. Lawrence	Canada	Roy and Sundby (2000)
1992–1996	Benguela Current Coastal (BENG)/C (22)	Benguela Ecology Program (BEP)	S. Africa	Jarre-Teichmann et al. (1998)
<b>Pacific Ocean</b>				
1988–present	N. Pacific Tropical Gyre (NPTG)/T (60)	HOT	USA	Karl and Michaels (1996)
1989–present	Kuroshio Current (KURO)/W (53)	KEEP	China-Taipei	Wong et al. (2000)
1992	N. Pacific Tropical Gyre (NPTG)/T (60) N. Pacific Equatorial Countercurrent (PNEC)/T (61) Pacific Equatorial Divergence (PEQD)/T (62) S. Pacific Subtropical Gyre (SPSG)/W (59)	EQPAC	USA	Murray et al. (1994)
1992–1998	Pacific Subarctic Gyres – East (PSAG-E)/W (51) Alaskan Downwelling Coastal (ALSK)/C (65) California Downwelling Coastal (CCAL)/C (66)	Canadian NE Pacific JGOFS NPPS	Canada	Boyd et al. (1999)
1993–present	China Sea Coastal (CHIN)/C (69)	China JGOFS	China-Beijing	Hu and Tsunogai (1999)
1994	W. Pacific Warm Pool (WARM)/T (63) Pacific Equatorial Divergence (PEQD)/T (62)	EPOPE/FLUPAC	France	
1990–present	N. Pacific Epicontinental (BERS)/P (50) Pacific Subarctic Gyres – West (PSAG-W)/W (52) Kuroshio Current (KURO)/W (53)	Japan-JGOFS	Japan	Tsunogai (1997)
<b>Indian Ocean</b>				
1994–1997	Indian Monsoon Gyres (MONS)/T (30) NW Arabian Upwelling (ARAB)/C (34) W. India Coastal (INDW)/C (36) Red Sea / Persian Gulf (REDS)/C (33)	Arabian Sea	Germany, India, Netherlands, Pakistan, UK, USA	Lal (1994) Smith (1998) Burkill (1999) Pfannkuche and Lochte (2001)
<b>Southern Ocean</b>				
1993–1995	S. Subtropical Convergence (SSTC)/W (80) Subantarctic (SANT)/W (81) Antarctic (ANTA)/P (82)	ANTARES	France	Gaillard and Tréguer (1997) LeFevre and Treguer
1990–1995	Subantarctic (SANT)/W (81)	KERFIX	France	Pondaven et al. (2000)
1992	Subantarctic (SANT)/W (81) Antarctic (ANTA)/P (82) Austral Polar (APLR)/P (83)	BOFS/STERNA	UK	Turner et al. (1995)
1992	Subantarctic (SANT)/W (81) Antarctic (ANTA)/P (82)	POLARSTERN ANT X/6	Germany, Belgium, France, Netherlands, UK	Smetacek et al. (1997)
1996–1998	Subantarctic (SANT)/W (81) Antarctic (ANTA)/P (82) Austral Polar (APLR)/P (83)	AESOPS	USA	Smith et al. (2000)
1999	Antarctic (ANTA)/P (82)	SOIRE	New Zealand	Boyd and Law (2000)

<sup>a</sup> Principal domains: P: Polar; W: Westerlies; T: Trade Winds; C: coastal (after Longhurst 1998).<sup>b</sup> Numbers refer to provinces shown in Fig. 1.1.



ince boundaries delineate regions within which the parameters are predictable. Provinces then provide a systematic means of using remotely sensed data to recover global estimates of primary and new production (Longhurst et al. 1995) or to parameterize large-scale models. Below, as a way to flesh out the province concept and introduce the JGOFS field program, I compare Longhurst's (1998) regional (province-based) estimates of primary production with in situ observations based on new  $^{14}\text{C}$  measurements made during NABE and other recent research cruises.

### 1.3 Primary Production in Ocean Domains and Provinces

Primary production (PP) of organic matter by phytoplankton forms the foundation of life in the sea (Falkowski and Raven 1997; Falkowski et al. (2003, this volume) and also formed the basis of Longhurst's partitioning scheme. Since the  $^{14}\text{C}$  method was one of the most widely performed core measurements of a rate process in JGOFS, the PP data set is useful for looking at differences among the domains and provinces. The following summary is preliminary but provides one of the first such syntheses of the recent observations. All these data were obtained from bottle incubations (on-deck or in situ) using  $^{14}\text{C}$ -labelled bicarbonate and following trace-metal-free clean techniques as specified in the JGOFS Core Measurement Protocols (Knap et al. 1996). I obtained the data starting from the International JGOFS Data Management Homepage (<http://ads.smr.uib.no/jgoifs/inventory/index.htm>) and following links where available. In some cases data were provided by individual investigators. Each graph shows

the PP observations integrated to the base of the euphotic zone (depth of 0.1–1% of surface irradiance,  $I_0$ ) and plotted against the day of the year. Observations are composited from different years in some cases. I also plotted the domain-averaged PP derived by Longhurst (1998) from the global CZCS data, which I obtained on Excel spreadsheets from [www.mar.dfo-mpo.gc.ca/science/ocean/BedfordBasin/Papers/Longhurst1998/Provinces/](http://www.mar.dfo-mpo.gc.ca/science/ocean/BedfordBasin/Papers/Longhurst1998/Provinces/), for comparison. The comparison is discussed further below.

Sathyendranath et al. (1995) concluded from their analysis of chlorophyll *a* profiles and photosynthetic parameters in 19 provinces of the North Atlantic that the most fundamental distinction among provinces was between the coastal and ocean domains. That distinction is exemplified by comparison of the adjacent coastal (ARAB) and trade winds (MONS) provinces in the Arabian Sea studied in great detail during the international Arabian Sea expeditions in JGOFS (Fig. 1.2). The new JGOFS observations support Longhurst's (1998) estimates of primary productivity approaching  $4 \text{ g C m}^{-2} \text{ d}^{-1}$  during the Southwest Monsoon, driven by intense coastal upwelling and abundant inputs of iron-containing dust from the Arabian Peninsula (Tindale and Pease 1999). With the exception of a few individual measurements in the Antarctic, these are the highest PP observations recorded in JGOFS. Observations from three separate expeditions (Germany, The Netherlands and UK) all suggest that primary production responds to the onset of the monsoon more rapidly than the CZCS-based estimates from Longhurst's (1998) synthesis, with values ranging from  $1\text{--}3 \text{ g C m}^{-2} \text{ d}^{-1}$  by mid-May. In contrast, PP reached about  $2 \text{ g C m}^{-2} \text{ d}^{-1}$  during June–August in the offshore Indian Monsoons (MONS) Province.

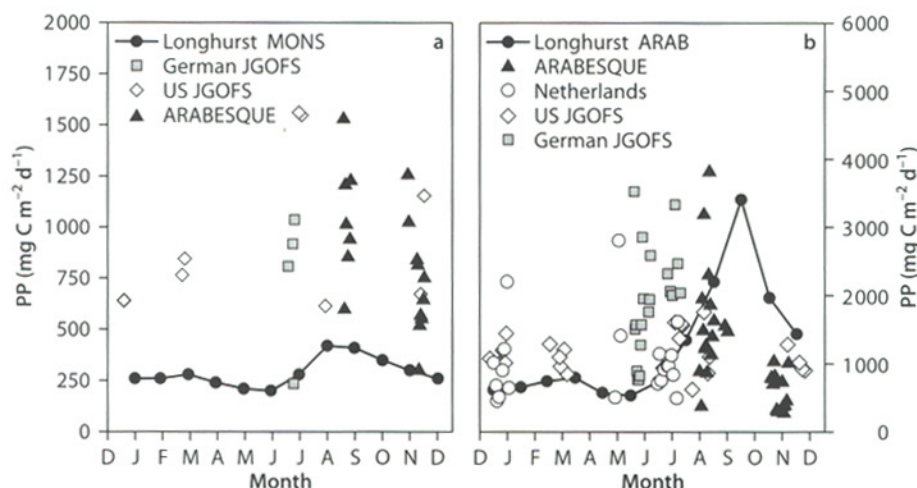


Fig. 1.2. Primary production in the Arabian Sea. **a** Indian Monsoon Gyres Province (Trade Winds Domain) with observations from the UK ARABESQUE (triangles), US (diamonds) and German JGOFS (squares) JGOFS cruises. **b** NW Arabian Upwelling Gyre Province (Coastal Domain; note change in Y-axis scale) with data from the UK ARABESQUE (triangles), Netherlands (circles), US (diamonds) and German JGOFS (squares) cruises. The domain-averaged annual cycles of PP derived by Longhurst (1998) are shown for the MONS (a) and ARAB (b) provinces for comparison (lines with symbols). Observational data were obtained from published reports and JGOFS databases (see text)



However there was little seasonality apparent in the oceanic province, with no clear distinction between the NE and SW Monsoons (Fig. 1.2b). Also striking is the contrast between Longhurst's (1998) estimate of PP in the MONS region and the new observations. The underestimates might be due in part to interference of dust and aerosols; and could also be an artifact of concentrated sampling in the NW part of the MONS Province which is more geographically extensive, extending throughout the northern Indian Ocean (Fig. 1.1).

Clearly the most intensively studied region by JGOFS has been the Trade Winds Domain, especially the equatorial region and tropical gyre of the N Pacific and subtropical gyre of the western Atlantic. Data from the Hawaii Ocean Time-series (HOT) and Bermuda Atlantic Time-series Study (BATS) stations are shown in Fig. 1.3. Over 100 trace-metal-free, in situ  $^{14}\text{C}$  determinations of PP have been accomplished at each station. The physical regimes at the two sites are not comparable: HOT is a true low-latitude tropical gyre regime which is permanently stratified with sporadic mixing events (Karl and Lukas 1996; Karl 1999) whereas BATS is on the western edge of the N Atlantic subtropical gyre, and is influenced by the high eddy kinetic energy regime of the adjacent Gulf Stream. BATS experiences large interannual variability in vernal deep mixing from <100 to >400 m (Michaels and Knap 1996), and periodic nutrient enrichment during the passage of mesoscale eddies (McGillicuddy et al. 1998). Nonetheless, PP in the two areas is comparable, except during January–April, the period of the spring bloom at BATS. The two areas have similar annual mean PP (BATS,  $459 \pm 216 \text{ mg C m}^{-2} \text{ d}^{-1}$ ; HOT,  $478 \pm 147 \text{ mg C m}^{-2} \text{ d}^{-1}$ ). The seasonal cycle in PP at HOT (Fig. 1.3a) is a consequence of enhanced growth

under peak summer irradiance (Winn et al. 1995; Karl et al. 1996). The new, high-quality in situ data from HOT surpass the estimates derived from CZCS by Longhurst (1998) by a factor of 2–4, suggesting global estimates of PP in the tropical gyres may require substantial upward revision (see below). The estimates are more consistent at BATS, especially if one takes into account the proximity of the BATS station to the Gulf Stream Province (GFST shown for comparison in Fig. 1.3b). PP observations in the French EUMELI Program (Fig. 1.3b) do not suggest much difference between the eastern and western gyres in the Atlantic, a conclusion also reached for PP by Harrison et al. (2001).

The Pacific Ocean has been intensively studied in JGOFS and by several other programs (Fig. 1.4). Extensive Canadian observations by C. S. Wong (Institute of Ocean Sciences, Sidney, BC; data not shown here) make Station P in the subarctic North Pacific among the most heavily sampled oceanic sites. Station P was among the first oceanic regimes where PP was measured with trace-metal-clean technique (Welschmeyer et al. 1993), and these early 'modern' estimates have now been corroborated by the Canadian JGOFS Program (Boyd and Harrison 1999; both data sets depicted in Fig. 1.4b). Although there is considerable (3-fold, presumably interannual) variability in the observations, the data are consistent with a broad summertime peak in PP, as modeled by Frost (1987), somewhat in contrast to the late-spring peak derived by Longhurst (1998) for the east and west gyres (*dashed lines* in Fig. 1.4b). The few early data now available for the eastern Pacific subarctic gyre from the Japanese time series station KNOT suggest lower PP, which is surprising since the region is closer to sources of iron-containing dust from Asia.

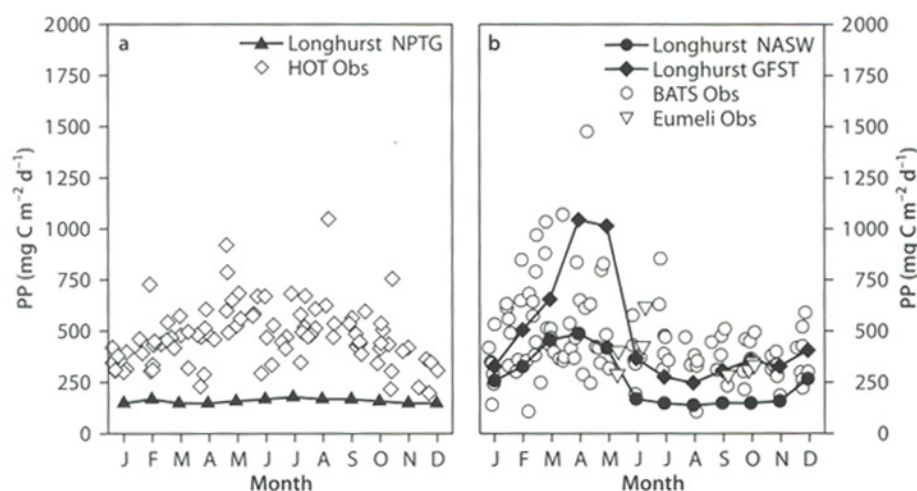


Fig. 1.3. Primary production in the Trade Winds Domain at the JGOFS Hawaii Ocean Time Series (a HOT, 1990–1998), the Bermuda Atlantic Time Series (b BATS, 1990–1998) and EUMELI Oligotrophic stations (1991–1992; *inverse triangles*, b). The domain-averaged annual cycles of PP derived by Longhurst (1998) for the North Pacific Tropical Gyres Province (a), North Atlantic Subtropical Gyre – West (b) and Gulf Stream (b) are shown for comparison (*lines with symbols*). Observational data were obtained from the JGOFS database (see text). The Hawaii and Bermuda data sets represent the most intensive oceanic primary production observations available ( $n = 91$  and  $105$  for HOT and BATS respectively).

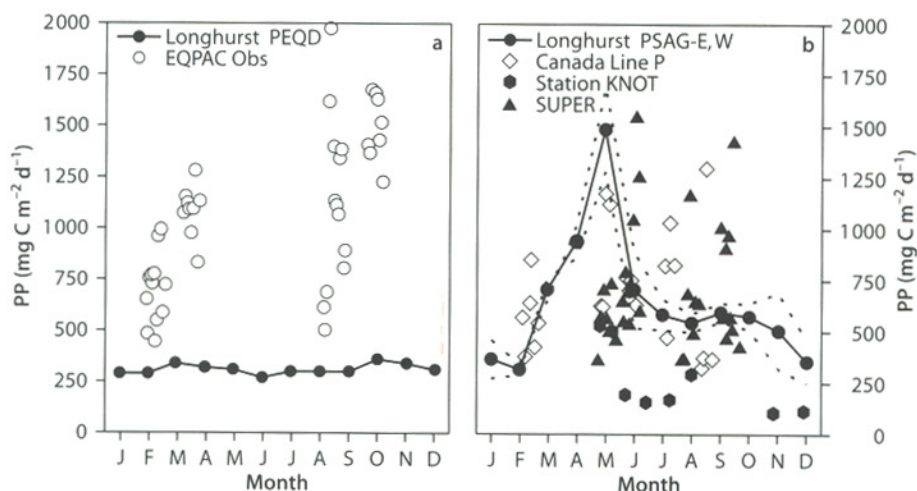


Fig. 1.4. Primary production in the Pacific Ocean. **a** Pacific Equatorial Divergence Province (Trade Winds Domain) with observations within  $1^\circ$  of the equator at  $140^\circ$  W Longitude (US EqPac, open circles). **b** Pacific Subarctic Gyre Province (Westerlies Domain) with data from the US SUPER (triangles) and Canadian JGOFS (open diamonds) programs and the Japanese KNOT Time Series (closed octagons). The domain-averaged annual cycles of PP derived by Longhurst (1998) are shown for the east and west PSAG Provinces for comparison (lines with symbols and dashed lines). Observational data were obtained from published reports and from Y. Nojiri (see text for details on data acquisition and processing)

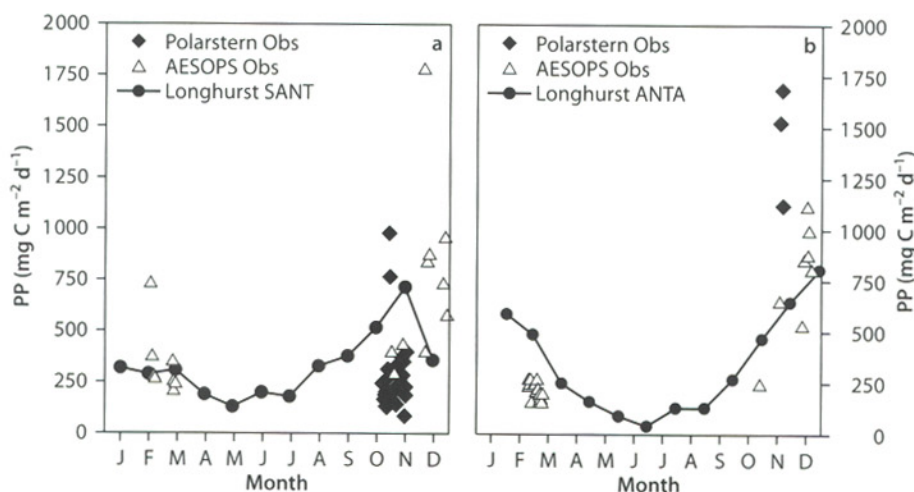


Fig. 1.5. Primary production in the Southern Ocean. **a** Subantarctic Water Ring Province (Westerlies Domain) with observations from the South Atlantic (German POLARSTERN, diamonds) and South Pacific (US AESOPS, open triangles). **b** Antarctic Province (Polar Domain) with data from Atlantic and Pacific Oceans as in (a). The domain-averaged annual cycles of PP derived by Longhurst (1998) are shown for these two provinces for comparison (lines with symbols). Observational data were obtained from JGOFS databases (see text). Note the lack of observations during the Austral Winter (April–September)

The US JGOFS Equatorial Pacific process study (EQPAC) revealed unexpectedly high PP in the central equatorial Pacific, with values  $500\text{--}2000\text{ g C m}^{-2}\text{ d}^{-1}$  (mean  $95\text{ mmol m}^{-2}\text{ d}^{-1}$ ) which exceeded the older 'climatological' data from the region by a factor of about 1.3 (Barber et al. 1996). PP was slightly higher in August–October 1992 during a relaxation of El Niño conditions (Murray et al. 1994), perhaps triggered by the passage of a tropical instability wave (Archer et al. 1997). The EQPAC PP observations are also startlingly higher than Longhurst's (1998) estimates, for reasons not entirely understood. The contrast is especially striking for

the February–April period when the 1991–1992 El Niño was near its peak and PP might have been expected to be reduced from the 'normal' condition.

Another important JGOFS contribution is the great expansion of carbon system measurements in the Southern Ocean. PP was measured by the US and German JGOFS expeditions to the south Pacific and Atlantic, respectively (Fig. 1.5a,b) and by the UK STERNA cruise to the Bellingshausen Sea. The available observations suggest austral spring blooms equal in magnitude to PP observed elsewhere ( $\geq 1000\text{ g C m}^{-2}\text{ d}^{-1}$ ), in spite of low temperature, deep mixing and severe iron depletion. This area



has also been studied in detail by the New Zealand Southern Ocean Iron Enrichment Experiment (SOIREE). Figure 1.5 points out the need for wintertime measurements, a key shortcoming of many studies in the Polar and West-erlies Domains (cf. also Fig. 1.4b). Extensive PP observations have also been made by US AESOPS at the high-latitude study area in the Ross Sea (Smith et al. 2000).

### 1.3.1 Adding up Global PP Observations

Longhurst et al. (1995) showed the utility of a province-based partitioning of marine primary production for making estimates of the total global PP. Here I utilize the new JGOFS data to provide a preliminary updating of Longhurst et al.'s (1995) estimate of oceanic PP. The Coastal Domain is excluded because so few data were available for my analysis, especially considering the heterogeneity of the Coastal Domain. PP values shown in Table 1.4 were taken from Longhurst et al. (1995) and from the data compilations shown in Fig. 1.2–1.5 and a few other source regions (see Table 1.3). The observations were simply averaged without any time weighting to yield regional, annual means for the better-studied provinces. The areal estimates ( $\text{g C m}^{-2} \text{d}^{-1}$ ) were multiplied by Longhurst's province areas to give new annual totals ( $\text{Gt C yr}^{-1}$ ) for each province. Primarily because of the greatly increased PP estimates for the Trade Winds provinces (shaded values in Table 1.4) these few JGOFS estimates alone yield a new global total (excluding the Coastal Domain) of ca  $45 \text{ Gt C yr}^{-1}$ . This value is about equal to the global totals derived by Field et al. (1998) and Laws et al. (2000), but should be viewed with reservation since the areal coverage is patchy and the productive coastal zones are excluded. The greatly increased PP estimates in the three Trade Winds provinces, which if true, might require upward revision in other, similar but still unstudied area (e.g., South Pacific), seem very worthy of careful scrutiny. It is also important to remember that the Longhurst et al. (1995) estimates were based on CZCS imagery and presuppose that there exist data on photosynthetic parameters for each region. When information is lacking, or sparse, educated guesses were made to fill in the global picture. Divergences between observations and estimations are more a reflection of paucity of data rather than a weakness of the idea of a partition (T. Platt, pers. comm.).

## 1.4 Bacterial Production and DOC Flux

JGOFS caused a tremendous expansion in understanding of microheterotrophic processes fueled by dissolved organic matter flux. This is surprising since the Program was initially conceived as emphasizing  $\text{CO}_2$  exchange, vertical flux of particles and remote sensing. But in or-

der to interpret and model integrating, system-level fluxes like export and  $\text{CO}_2$  exchange, or large-scale pigment distributions, clearer insight into trophodynamic processes was required (e.g., Eppley and Ducklow 1986; SCOR 1990). Among the great successes of JGOFS was a new high precision assay for the concentration of dissolved organic carbon (DOC) in seawater (Sharp et al. 1993; Hedges and Farrington 1993). This assay was initially developed by Sugimura and Suzuki (1988), and subsequently corrected and improved by Benner and Strom (1993), following a series of JGOFS-sponsored workshops and 'bake-offs' during which different DOC analytical instruments and methods were compared and intercalibrated. The perfection of a reliable assay for DOC led to an unprecedented view of the distribution and dynamics of DOC, which we can now begin to place into a global scale, geographical context. DOC is produced seasonally in the upper ocean with greater buildup in the tropics and subtropics, and lower accumulations at higher latitudes (Kumar et al. 1990; Carlson and Ducklow 1995, 1996; Kähler et al. 1997; Carlson et al. 1998). It appears that net DOC production is minimal below the Antarctic Polar Frontal Zone (Hansell and Carlson 1998b). The small seasonal build-up of DOC in the Ross Sea is entirely consumed by bacteria (or perhaps also oxidized by UV radiation – see Moran and Zepp 2000 for a review) by the end of the growing season in April (Carlson et al. 2000). It is not known if the same is true in the North Polar Domain (Arctic Ocean), where terrestrial DOC from the high freshwater input (Tomczak and Godfrey 1994) potentially obscures the marine signal and fuels exceptionally high bacterial activity (Rich et al. 1998). At this time, we can generalize a global pattern at the level of the four great biogeochemical domains, but cannot yet distinguish differences at the basin scale or province level. A global pattern in DOC distribution is also observed in the deep ocean, where DOC concentrations reflect the thermohaline conveyor belt circulation. The highest concentrations of deep ocean DOC are in the North Atlantic, whereas the lowest concentrations are in the deep North Pacific, at the opposite end of the conveyor belt (Hansell and Carlson 1998a). This large scale pattern is the result of interaction between geographically-focused inputs of DOC at sites of mode water and deepwater formation and slow bacterial decomposition. Thus fresh DOC is supplied in North Atlantic Deep Water, and slowly decays during its transit through the deep sea. The origin of the DOC in NADW is not yet clear: it may be produced locally, or it might be transported from lower latitudes in the surface circulation. There is abundant net production of semilabile DOC in the tropics and subtropics which survives bacterial decomposition over seasonal time scales so it can be exported horizontally off the equator (Archer et al. 1997; Hansell et al. 1997; Peltzer and Hayward 1996), or vertically during late win-



**Table 1.4.** Global partitioning of oceanic primary production (after Longhurst et al. 1995). Note that coastal provinces are not included. New in situ estimates from JGOFS and other studies are included for several well-studied provinces, and a new province-averaged annual PP has been extrapolated (see text). The three shaded boxes indicated regions for which a large change in the original estimate impacted the new global total

Domain	Province	Original estimation		JGOFS	
		(g C m <sup>-2</sup> d <sup>-1</sup> )	(Gt C yr <sup>-1</sup> )	(g C m <sup>-2</sup> d <sup>-1</sup> )	(Gt C yr <sup>-1</sup> )
Polar	BPLR	1770	1.07		1.07
Polar	ARCT	1330	1.02		1.02
Polar	SARC	830	0.7		0.70
Polar	BERS	990	1.41		1.41
Polar	ANTA	450	1.47		1.47
Polar	APLR	1090	0.77	1204	0.85
Westerlies	NADR	660	0.84		0.84
Westerlies	GFST	490	0.2		0.20
Westerlies	NASW	260	0.55	459	0.97
Westerlies	MEDI	590	0.67		0.67
Westerlies	NASE	330	0.54		0.54
Westerlies	PSAE	550	0.64	704	0.82
Westerlies	PSAW	720	0.77		0.77
Westerlies	KURO	530	0.72	489	0.66
Westerlies	NPPF	470	0.52		0.52
Westerlies	NPSE	300	0.76		0.76
Westerlies	NPSW	300	0.43		0.43
Westerlies	OCAL	320	0.28		0.28
Westerlies	TASM	450	0.27		0.27
Westerlies	SPSG	240	3.23		3.23
Westerlies	SSTC	370	2.29		2.29
Westerlies	SANT	330	3.63	393	4.32
Trades	NATR	290	0.88		0.88
Trades	WTRA	360	0.7		0.70
Trades	ETRA	430	0.84		0.84
Trades	SATL	210	1.33		1.33
Trades	CARB	520	0.85		0.85
Trades	MONS	290	1.49	876	4.50
Trades	ISSG	190	1.37		1.37
Trades	NPTG	160	1.24	478	3.70
Trades	PNEC	290	0.87		0.87
Trades	PEQD	310	1.17	1083	4.09
2Trades	WARM	220	1.38		1.38
Trades	ARCH	270	0.88		0.88
Total			35.78		45.48

ter overturning (Copin-Montegut and Avril 1993; Carlson et al. 1994). Export of DOC appears to account for about 20% of the total export production globally (Hansell and Carlson 1998b).

The principal sink for DOC is bacterial metabolism, assisted by photochemical breakdown (Anderson and Williams 1999; Ducklow 2000). PP estimates may have increased during JGOFS but estimates of bacterial pro-

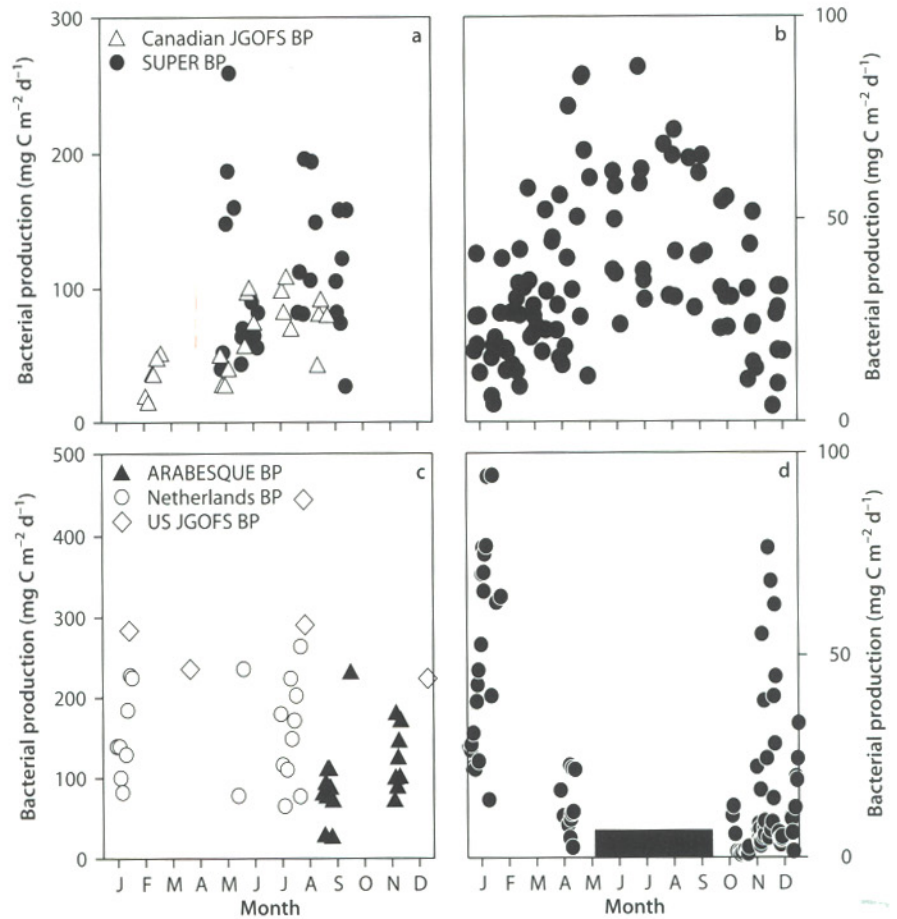
duction (BP), the rate at which bacteria convert DOC and inorganic nutrients into biomass, have declined. Earlier estimates of BP (which included very few oceanic measurements) indicated the BP was 20–30% of PP measured approximately simultaneously (Cole et al. 1988; Ducklow and Carlson 1992). Williams (2000) notes that many of the earlier estimates now seem unrealistic in light of a more comprehensive understanding of DOC



Fig. 1.6.

Bacterial production in well-studied ocean domains.

**a** Pacific Subarctic Gyres Province, with data from Project SUPER (circles) and Canadian JGOFS (triangles). **b** North Atlantic Subtropical Gyres – West Province (data from BATS); **c** Arabian Upwelling Province, with data from UK ARABESQUE (triangles), US (diamonds) and Netherlands (circles) JGOFS programs; and **d** the Austral Polar Province, with data from the US AESOPS program in the Ross Sea. Note that Y-axis scales differ from plot to plot



flux and bacterial conversion efficiencies. Once thought to be 50% or higher, the bacterial growth efficiency (BGE) on DOC is now estimated to be about 15–30% (del Giorgio and Cole 1998). A simple example shows the impossibility of  $BP = 0.3$  times  $PP$  and  $BGE = 0.15$ : since  $BGE$  is  $BP$  divided by  $BP$  plus respiration, the respiration in this example is 1.7 times  $PP$ ! This situation might occur when bacteria utilize accumulated products of a bloom (Ducklow et al. 1993; Azam et al. 1994) but cannot occur in the quasi-steady state ecosystems of the oceanic gyres and other Trade Winds provinces.

In fact recently synthesized JGOFS data do suggest  $BP$  is closer to 10% of  $PP$ . Figure 1.6 shows  $BP$  observations in four well-studied provinces. Strong seasonal cycles are apparent in the subarctic North Pacific (Fig. 1.6a; Kirchman et al. 1993; Sherry et al. 1999), at the BATS station (Fig. 1.6b; Carlson et al. 1996) and in the Ross Sea, Antarctica (Fig. 1.6d; Ducklow et al. 2001). In the Ross Sea,  $BP$  has an amplitude of almost 100-fold, with values increasing from about  $1 \text{ mg C m}^{-2} \text{ d}^{-1}$  in late October to almost 100 in mid-January. However the mean  $PP$  is very high and the annual average  $BP$  is just  $24 \text{ mg C m}^{-2} \text{ d}^{-1}$ , lowest among the provinces studied, so  $BP/PP$  in the Antarctic Polar Province is just 2% (Table 1.5). As suggested above, the low  $BP$  is possibly due

Table 1.5. Bacterial and primary production rates in several ocean provinces

Province	PP <sup>a</sup>	BP <sup>a</sup>	BP/PP	Eff <sup>b</sup>	Carbon utilized/PP <sup>c</sup>
ARAB	1479	163	0.11	0.17	0.65
MONS	998	166	0.17	0.17	0.98
PSAG	647	86	0.13	0.27	0.49
PEQD	1185	111	0.09	0.15	0.60
NASW	459	37	0.08	0.15	0.54
APLR	1234	24	0.02	0.15	0.13

<sup>a</sup> Primary and bacterial production in the euphotic zone ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ).

<sup>b</sup> Bacterial growth (conversion) efficiency measured in the same studies.

<sup>c</sup> Bacterial carbon utilization is  $BP/\text{Eff}$ .

to a lack of net DOC production in Polar Domains. Interestingly  $BP/PP$  is very high (17%) in the Indian Ocean Monsoon Province (MONS, Table 1.5; Wiebinga et al. 1997; Pomroy and Joint 1999; Ducklow et al. 2001) where offshore transport of DOC produced during coastal upwelling in the southwest monsoon might subsidize offshore  $BP$ .  $BP$  in the coastal Arabian Upwelling Province (ARAB; Fig. 1.4c) is equally high (Table 1.5) but the



high PP renders the fraction BP/PP somewhat lower. In general these new observations indicate BP/PP in the range 8–13%, outside the Polar Domain and away from coastal influence. Nonetheless, the relatively low growth efficiencies necessitate a large flux of organic matter through bacterial compartments – bacterial carbon demand averages about 50% of PP in these provinces. At this point we can distinguish large-scale contrasts between domains, with high BP/PP in the coastal provinces, possibly subsidized by terrestrial inputs, low values in the Antarctic Polar Domain, and intermediate values in the Westerlies and Trade Winds Domains which cover a large area of the global ocean.

### 1.5 A Provincial Outlook

In this chapter I have tried to use a province – based partitioning of the oceans to look at some biogeochemical processes studied in JGOFS, and show how our views of ocean carbon cycling might be changing. A large part of JGOFS emphasized intensive process studies in various ocean regimes or provinces. Most of the data shown here, for example, came from studies which were concentrated at a few individual stations or in relatively small areas within individual provinces. Examples include the HOT and BATS stations, a multinational set of observations of the spring phytoplankton bloom in the North Atlantic near 47° N, 20° W, the spring and fall time series in EQPAC and extended observations at Station P in the North Pacific. In other locations, traditional transect studies were employed, for example the NABE cruises along 20° W, the Arabian Sea expeditions and several national studies in the Southern Ocean. It remains difficult and expensive to carry out process-related studies over geographically-extended areas, although lines or arrays of sediment trap moorings were deployed in the N Atlantic, central Pacific, Arabian Sea and Southern Ocean. Intensive, but geographically concentrated process studies, moorings and time series provide the means to characterize a manifold of processes within a province, but we still need to know if the observations made at local scales are characteristic of larger areas. This problem has been attacked in the BATS program with a series of regional validation cruises (Michaels and Knap 1996). Establishing ecological continuity within provinces is in fact the acid test of the province concept – are relevant ecological and biogeochemical properties and processes consistently distributed within provinces? In most cases we still don't know. Harrison et al. (2001) examined a range of hydrographic properties, and biological rate processes during two cruises across three provinces in the North Atlantic. They found that some properties and rates differed significantly among provinces and seasons (e.g., regenerated production and bacterial production), whereas others

did not, and some seemed to be continuously distributed along environmental gradients (e.g., primary production, new production and chlorophyll standing stocks along cross-Atlantic gradients of nitracline depth). They noted that meridional variability could have influenced their observations. Further transects and/or wider area coverage are required to test the province concept. Longhurst's pioneering work provided a valuable and provocative template for synthesis of JGOFS observations, but it was based almost entirely on knowledge of regional physical oceanography and remotely-sensed chlorophyll from the CZCS. Re-analysis with the much higher resolving power and more complete temporal coverage of the SeaWiFS sensors will help to refine Longhurst's work. Still, it is critical to recognize that for the foreseeable future, chlorophyll and some additional optical properties will remain the only biogeochemical properties we can observe at the global scale with relevant temporal and spatial resolution. New kinds of observational strategies and models are still needed to extend our knowledge of ocean biogeochemistry to the global scale. But most of all, we need new ideas to exploit fully the rich harvest of observations made in JGOFS. Some are found in this volume and others will come out of the JGOFS Synthesis, of which this book is just a first step.

### Acknowledgements

Preparation of this chapter was supported by NSF Grant OCE 9819581. I am grateful to the following individuals who contributed data and answered questions: Nelson Sherry, Joachim Herrmann, Wolfgang Koeve, Glen Harrison, Bill Li, Beatriz Balino, Craig Carlson, Dennis Hansell, Dave Kirchman and Dave Karl.

### References

- Anderson TR, Williams PJ leB (1999) A one-dimensional model of DOC cycling in the water column incorporating combined biological-photochemical decomposition. *Global Biogeochem Cy* 13:337–349
- Archer D, Peltzer ET, Kirchman DL (1997a) A timescale for dissolved organic carbon production in equatorial Pacific surface waters. *Global Biogeochem Cy* 11:435–452
- Archer D, Aiken J, Balch W, Barber R, Dunne J, Flament P, Gardner W, Garside C, Goyet C, Johnson E, Kirchman D, McPhaden M, Newton J, Peltzer E, Welling L, White J, Yoder J (1997b) A meeting place of great ocean currents: Shipboard observations of a convergent front at 2° N in the Pacific. *Deep-Sea Res Pt II* 44:1827–1849
- Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. *Mar Ecol Prog Ser* 10:257–263
- Azam F, Steward GF, Smith DC, Ducklow HW (1994) Significance of bacteria in the carbon fluxes of the Arabian Sea. *P Indian As-Earth* 103:341–351
- Bailey RG (1998) Ecoregions: the ecosystem geography of the oceans and continents. Springer-Verlag, New York, 176 pp



- Banase K (1987) Seasonality of phytoplankton chlorophyll *a* in the central and northern Arabian Sea. *Deep-Sea Res Pt I* 34:713–723
- Banase K (1992) Grazing, temporal changes of phytoplankton concentrations and the microbial loop in the open sea. In: Falkowski P (ed) *Primary productivity and biogeochemical cycles in the sea*. Plenum, New York, pp 409–440
- Banase K, English DC (1993) Revision of satellite-based phytoplankton pigment data from the Arabian Sea during the Northeast Monsoon. *Marine Research* 2:83–103
- Barber RT (1988) Ocean basin ecosystems. In: Alberts J, Pomeroy LR (eds) *Concepts of ecosystem ecology: a comparative view*. Springer-Verlag, New York, pp 171–193
- Barber RT, Sanderson MP, Lindley ST, Chai F, Newton J, Trees CC, Foley DG, Chavez FP (1996) Primary productivity and its regulation in the equatorial Pacific during and following the 1991–1992 El Niño. *Deep-Sea Res Pt II* 43:933–969
- Benner R, Strom S (1993) A critical evaluation of the analytical blank associated with DOC measurements by high-temperature catalytic oxidation. *Mar Chem* 41:153–60
- Benner R, Pakulski JD, McCarthy M, Hedges JJ, Hatcher PG (1992) Bulk chemical characteristics of dissolved organic matter in the ocean. *Science* 255:1561–1564
- Boyd PW, Harrison PJ (1999) Phytoplankton dynamics in the NE subarctic Pacific. *Deep-Sea Res Pt II* 46:2405–2432
- Boyd PW, Law CS (2000) The Southern Ocean Iron Release Experiment (SOIREE) – introduction and summary. *Deep-Sea Res Pt II* 48:2425–2438
- Boyd PW, Harrison PJ, Johnson BD (1999) The Joint Global Ocean Flux Study (Canada) in the NE subarctic Pacific. *Deep-Sea Res Pt II* 46:2345–2350
- Burkill PH (1999) ARABESQUE: An overview. *Deep-Sea Res Pt II* 46:529–547
- Caperon J (1975) A trophic level ecosystem model analysis of the plankton community in a shallow-water subtropical estuarine embayment. In: Cronin LE (ed) *Estuarine research, vol. 1. chemistry, biology and the estuarine system*. Academic Press, New York, pp 691–709
- Carlson CA, Ducklow HW (1995) Dissolved organic carbon in the upper ocean of the central equatorial Pacific Ocean, 1992: Daily and finescale vertical variations. *Deep-Sea Res Pt II* 42:639–56
- Carlson CA, Ducklow HW (1996) Growth of bacterioplankton and consumption of dissolved organic carbon in the Sargasso Sea. *Aquat Microb Ecol* 10:69–85
- Carlson CA, Michaels AM, Ducklow HW (1994) Annual flux of dissolved organic carbon from the euphotic zone in the northwestern Sargasso Sea. *Nature* 371:405–408
- Carlson CA, Ducklow HW, Sleeter TD (1996) Stocks and dynamics of bacterioplankton in the northwestern Sargasso Sea. *Deep-Sea Res Pt II* 43:491–516
- Carlson CA, Ducklow HW, Smith WO, Hansell DA (1998) Carbon dynamics during spring blooms in the Ross Sea polynya and the Sargasso Sea: Contrasts in dissolved and particulate organic carbon partitioning. *Limnol Oceanogr* 43:375–386
- Carlson CA, Hansell DA, Peltzer ET, Smith WO Jr. (2000) Stocks and dynamics of dissolved and particulate organic matter in the southern Ross Sea, Antarctica. *Deep-Sea Res Pt II* 47:3201–3226
- Caron DA (2000) Symbiosis and mixotrophy among pelagic microorganisms. In: Kirchman D (ed) *Microbial ecology of the oceans*. John Wiley & Sons, New York, pp 495–524
- Chierici M, Drange H, Andersen LG, Johannessen T (1997) Inorganic carbon fluxes through the boundaries of the Greenland Sea Basin based on in situ observations and water. *J Marine Syst* 22:295–309
- Chisholm SW, Olson RJ, Zettler ER, Goericke R, Waterbury JB, Welschmeyer NA (1988) A novel free-living prochlorophyte abundant in the oceanic euphotic zone. *Nature* 334:340–343
- Cole JJ, Pace ML, Findlay S (1988) Bacterial production in fresh and saltwater ecosystems: a cross-system overview. *Mar Ecol Prog Ser* 43:1–10
- Copin-Montegut C (2000) Consumption and production on scales of a few days of inorganic carbon, nitrate and oxygen by the planktonic community: results of continuous measurements at the Dyfamed Station in the northwestern Mediterranean Sea (May 1995). *Deep-Sea Res Pt I* 47:447–477
- Copin-Montegut G, Avril B (1993) Vertical distribution and temporal variation of dissolved organic carbon in the north-western Mediterranean Sea. *Deep-Sea Res Pt I* 40:1963–1972
- Cronon W (1983) Changes in the land. Indians, colonists and the ecology of New England. Hill and Wang, New York, 241 pp
- Cullen JJ, Franks PJS, Karl DM, Longhurst A (2002) Physical influences on marine ecosystem dynamics. In: Robinson AR, McCarthy JJ, Rothschild BJ (eds) *The sea*, vol. 12. John Wiley & Sons, New York, pp 297–336
- Giorgio PA del, Cole JJ (1998) Bacterial growth efficiency in natural aquatic systems. *Annu Rev Ecol Syst* 29:503–541
- Giorgio PA del, Cole JJ (2000) Bacterial bioenergetics and growth efficiency. In: Kirchman DL (ed) *Microbial ecology of the oceans*. John Wiley & Sons, New York, pp 289–326
- Dietrich G (1963) General oceanography, an introduction. Interscience Publishers, New York, 588 pp
- Ducklow HW (1999) The bacterial content of the oceanic euphotic zone. *Fems Microbiol Ecol* 30:1–10
- Ducklow HW (2000) Bacterioplankton production and biomass in the oceans. Chap. 4. In: Kirchman DL (ed) *Microbial ecology of the oceans*. John Wiley & Sons, New York, pp 85–120
- Ducklow HW, Carlson CA (1992) Oceanic bacterial productivity. *Adv Microb Ecol* 12:113–181
- Ducklow HW, Harris R (1993) Introduction to the JGOFS North Atlantic Bloom Study. *Deep-Sea Res* 40:1–8
- Ducklow HW, Kirchman DL, Quinby HL, Carlson CA, Dam HG (1993) Stocks and dynamics of bacterioplankton carbon during the spring phytoplankton bloom in the eastern North Atlantic Ocean. *Deep-Sea Res Pt II* 40:245–263
- Ducklow HW, Smith DC, Campbell L, Landry MR, Quinby HL, Steward GF, Azam F (2001a) Heterotrophic bacterioplankton distributions in the Arabian Sea: basinwide response to high primary productivity. *Deep-Sea Res Pt II* 48:1303–1323
- Ducklow HW, Carlson CA, Church M, Kirchman DL, Smith DC, Steward G (2001b) The seasonal development of bacterioplankton in the Ross Sea, Antarctica, 1994–97. *Deep-Sea Res Pt II* 47:3227–3247
- Dugdale RC, Goering JJ (1967) Uptake of new and regenerated forms of nitrogen in primary production. *Limnol Oceanogr* 12:196–206
- Eppley RW, Ducklow HW (1986) Workshop on Upper Ocean Processes. US GOFs Report 3, Woods Hole, MA. US JGOFS Planning Office, WHOI, pp 1–141
- Falkowski PG, Raven JA (1997) *Aquatic photosynthesis*. Blackwell Scientific, Malden, MA, 375 pp
- Falkowski PG, Laws EA, Barber RT, Murray JW (2003) Phytoplankton and their role in primary, new, and export production. (this volume)
- Field CB, Behrenfeld MJ, Randerson JT, Falkowski PG (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281:237–240
- Frost BW (1987) Grazing control of phytoplankton stock in the open subarctic Pacific Ocean: a model assessing the role of mesozooplankton, particularly the large calanoid copepods *Neocalanus* spp. *Mar Ecol Prog Ser* 39:49–68
- Fuhrman J (2000) Impact of viruses on microbial processes. In: Kirchman D (ed) *Microbial ecology of the oceans*. John Wiley & Sons, New York, pp 327–351
- Gaillard JF, Tréguer P (eds) (1997) *Antares I: France-JGOFS in the Indian sector of the Southern Ocean: benthic and water column processes*. *Deep-Sea Res Pt II* 44:951–1176
- Giovannoni SJ, Rappe M (2000) Evolution, diversity, and molecular ecology of marine prokaryotes. In: Kirchman DL (ed) *Microbial ecology of the oceans*. John Wiley & Sons, New York, pp 47–84
- Hansell DA, Carlson CA (1998a) Deep-ocean gradients in the concentration of dissolved organic carbon. *Nature* 395:263–266
- Hansell DA, Carlson CA (1998b) Net community production of dissolved organic carbon. *Global Biogeochem Cy* 12:443–453
- Hansell DA, Carlson CA, Bates NR, Poisson A (1997) Horizontal and vertical removal of organic carbon in the equatorial Pacific Ocean: a mass balance assessment. *Deep-Sea Res Pt II* 44:2115–2130
- Harris RP, Boyd P, Harbour DS, Head RN, Pingree RD, Pomroy AJ (1997) Physical, chemical and biological features of a cyclonic eddy in the region of 61° 10' N 19° 50' W in the North Atlantic. *Deep-Sea Res Pt I* 44:1815–1839



- Harrison WG (1980) Nutrient regeneration and primary production in the sea. In: Falkowski PG (ed) Primary productivity in the sea. Plenum Publishing Co, pp 433–60
- Harrison WG, Head EJH, Horne EPW, Irwin B, Li WKW, Longhurst AR, Paranjape MA, Platt T (1993) The Western North Atlantic Bloom Experiment. *Deep-Sea Res Pt II* 40:279–306
- Harrison WG, Aristegui J, Head EJH, Li WKW, Longhurst AR, Sameoto DD (2001) Basin-scale variability in plankton biomass and community metabolism in the sub-tropical North Atlantic Ocean. *Deep-Sea Res Pt II* 48:2241–2270
- Hedges J, Farrington J (1993) Measurement of dissolved organic carbon and nitrogen in natural waters: workshop report. *Mar Chem* 41:5–10
- Hu D, Tsunogai S (1999) Margin fluxes in the East China Sea. China Ocean Press, Beijing, 247 pp
- Jarre-Teichmann A, Shannon LJ, Moloney CL, Wickens PA (1998) Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems. *S Afr J Marine Sci* 19:391–414
- Johnson PW, Sieburth JMcN (1979) Chroococcoid cyanobacteria in the sea: a ubiquitous and diverse phototrophic biomass. *Limnol Oceanogr* 24:928–35
- Kähler P, Bjørnsen PK, Lochte K, Antia A (1997) Dissolved organic matter and its utilization by bacteria during spring in the Southern Ocean. *Deep-Sea Res Pt II* 44:341–353
- Karl DM (1999) A sea of change: biogeochemical variability in the North Pacific subtropical gyre. *Ecosystems* 2:181–214
- Karl DM, Lukas R (1996) The Hawaii Ocean Time-series (HOT) program: background, rationale and field implementation. *Deep-Sea Res Pt II* 43:129–156
- Karl DM, Michaels AF (1996) Preface: The Hawaii Ocean Time Series (HOT) and the Bermuda Atlantic Time Series (BATS). *Deep-Sea Res Pt II* 43:127–129
- Karl DM, Christian JR, Dore JE, Hebel DV, Letelier RM, Tupas LM, Winn CD (1996) Seasonal and interannual variability in primary production and particle flux at Station ALOHA. *Deep-Sea Res Pt II* 43:539–56
- Karner MB, DeLong EF, Karl DM (2001) Archaeal dominance in the mesopelagic zone of the Pacific Ocean. *Nature* 409:507–510
- Kirchman DL, Keil RG, Simon M, Welschmeyer NA (1993) Biomass and production of heterotrophic bacterioplankton in the oceanic subarctic Pacific. *Deep-Sea Res* 40:967–988
- Knap A, Michaels A, Close A, Ducklow HW, Dickson A (eds) (1996) Protocols for the Joint Global Ocean Flux Study (JGOFS) core measurements. JGOFS Report No. 19, vi+170 pp Reprint of the IOC Manuals and Guides No. 29, UNESCO 1994
- Kumar MD, Rajendran A, Somasundar K, Haake B, Jenisch A, Shuo Z, Ittekkot V, Desai BN (1990) Dynamics of dissolved organic carbon in the northwestern Indian Ocean. *Mar Chem* 31:299–316
- Lal D (1994) Biogeochemistry of the Arabian Sea. Reprinted from *P Indian As-Earth* 103:399–352
- Landry MR, Barber RT, Bidigare RR, Chai F, Coale KH, Dam HG, Lewis MR, Lindley ST, McCarthy JJ, Roman MR, Stoecker DK, Verity PG, White JR (1997) Iron and grazing constraints on primary production in the central equatorial Pacific: An EqPac synthesis. *Limnol Oceanogr* 42:405–418
- Laws EA, Falkowski PG, Smith WO, Ducklow HW Jr., McCarthy JJ (2000) Temperature effects on export production in the open ocean. *Global Biogeochem Cy* 14:1231–1246
- Le Fèvre J, Tréguer P (1998) Special issue: carbon fluxes, dynamic processes in the Southern Ocean: present, past. *J Marine Syst* 17:1–4
- Letelier RM, Karl DM (1996) The role of *Trichodesmium* spp. in the productivity of the subtropical North Pacific Ocean. *Mar Ecol Prog Ser* 133:263–273
- Letelier RM, Karl DM (1998) *Trichodesmium* spp. physiology and nutrient fluxes in the North Pacific subtropical gyre. *Aquat Microb Ecol* 15:265–276
- Li WKW, Subba Rao DV, Harrison WG, Smith JC, Cullen JJ, Irwin B, Platt T (1982) Autotrophic picoplankton in the tropical ocean. *Science* 219:292–95
- Longhurst AR (1995) Seasonal cycles of pelagic production and consumption. *Prog Oceanogr* 36:77–167
- Longhurst AR (1998) Ecological geography of the sea. Academic, San Diego, 398 pp
- Longhurst AR, Sathyendranath S, Platt T, Caverhill C (1995) An estimate of global primary production in the ocean from satellite radiometer data. *J Plankton Res* 17:1245–1271
- Malone TC (1980) Size-fractionated primary productivity of marine phytoplankton. In: Falkowski PG (ed) Primary productivity in the sea. Plenum Publishing Co., pp 301–319
- Margalef R (1978) Life forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol Acta* 1:493–509
- McGillicuddy DJ Jr., Robinson AR, Siegel DA, Jannasch HW, Johnson R, Dickey TD, McNeil J, Michaels AF, Knap AH (1998) Influence of mesoscale eddies on new production in the Sargasso Sea. *Nature* 394:263–265
- Michaels AF, Knap AH (1996) Overview of the U.S. JGOFS Bermuda Atlantic Time-series Study and the Hydrostation S Program. *Deep-Sea Res Pt II* 43:157–198
- Monaco A, Biscaye PE, Laborde P (1999) France-JGOFS/ECOMARGE: The ECOFER (ECOsystème du Canyon du Cap FERret) Experiment on the Northeast Atlantic Continental Margin. *Deep-Sea Res Pt II* 46:1944–2379
- Moran MA, Zepp RG (2000) UV radiation effects on microbes and microbial processes. In: Kirchman DL (ed) Microbial ecology of the oceans. John Wiley & Sons, New York, pp 201–228
- Morel A (1996) An ocean flux study in eutrophic, mesotrophic, and oligotrophic situations: the EUMELI program. *Deep-Sea Res Pt I* 43:1185–1190
- Murray JW, Barber RT, Roman M, Bacon MP, Feely RA (1994) Physical and biological controls on carbon cycling in the equatorial Pacific. *Science* 266:58–65
- Nagata T (2000) Production mechanisms of dissolved organic matter. In: Kirchman DL (ed) Microbial ecology of the oceans. Wiley-Liss, New York, pp 121–152
- Odum EP (1969) The strategy of ecosystem development. *Science* 164:262–270
- Peltzer E, Hayward N (1996) Spatial distribution and temporal variability of total organic carbon along 140° W in the Equatorial Pacific Ocean in 1992. *Deep-Sea Res Pt II* 43:1155–1180
- Pfannkuche O, Lochte K (eds) (2001) Biogeochemistry of the deep Arabian Sea: German research programmes in the Arabian Sea. *Deep-Sea Res Pt II* 47:2615–3072
- Platt T, Sathyendranath S (1988) Oceanic primary production: estimation by remote sensing at local and regional scales. *Science* 241:1613–1622
- Platt T, Sathyendranath S (1999) Spatial structure of pelagic ecosystem processes in the global ocean. *Ecosystems* 2:384–394
- Platt T, Caverhill C, Sathyendranath S (1991) Basin-scale estimates of oceanic primary production by remote sensing: the North Atlantic. *J Geophys Res* 96:147–159
- Pomeroy LR (1974) The ocean's food web, a changing paradigm. *Bioscience* 24:499–504
- Pomroy A, Joint I (1999) Bacterioplankton activity in the surface waters of the Arabian Sea during and after the 1994 SW Monsoon. *Deep-Sea Res Pt II* 46:767–794
- Pondaven P, Ruiz-Pino D, Fravalo C, Tréguer P, Jeandel C (2000) Interannual variability of Si and N cycles at the time-series station KERFIX between 1990 and 1995 – a 1-D modeling study. *Deep-Sea Res Pt I* 47:223–257
- Rich J, Gosselin M, Sherr E, Sherr B, Kirchman DL (1998) High bacterial production, uptake and concentrations of dissolved organic matter in the central Arctic Ocean. *Deep-Sea Res Pt II* 44:1645–1663
- Roy S, Sundby B (2000) A Canadian JGOFS Process Study in the Gulf of St. Lawrence (Canada): carbon transformations from production to burial. *Deep-Sea Res Pt II* 47:385–760
- Sarmiento JL, Slater RD, Fasham MJR, Ducklow HW, Toggweiler JR, Evans GT (1993) A seasonal three-dimensional ecosystem model of nitrogen cycling in the North Atlantic euphotic zone. *Global Biogeochem Cy* 7:417–450
- Sathyendranath S, Longhurst AR, Caverhill CM, Platt T (1995) Regionally and seasonally differentiated primary production in the North Atlantic. *Deep-Sea Res Pt I* 42:1773–1802
- Savenkoff C, Lefevre D, Denis M, Lambert CE (1993) How do microbial communities keep living in the Mediterranean outflow within N.E. Atlantic intermediate waters? *Deep-Sea Res* 40:627–641



- SCOR (1990) JGOFS science plan. JGOFS Report No. 5. Halifax NS: SCOR and JGOFS
- Sharp JH, Suzuki Y, Munday WL (1993) A comparison of dissolved organic carbon in North Atlantic Ocean nearshore waters by high temperature combustion and wet chemical oxidation. *Mar Chem* 41:253–259
- Sherr E, Sherr B (2000) Marine microbes: an overview. In: Kirchman DL (ed) *Microbial ecology of the oceans*. John Wiley & Sons, New York, pp 13–46
- Sherry ND, Boyd PW, Sugimoto K, Harrison PJ (1999) Seasonal and spatial patterns of heterotrophic bacterial production, respiration, and biomass in the subarctic NE Pacific. *Deep-Sea Res Pt II* 46:2557–2578
- Sieburth JMcN, Smetacek V, Lenz J (1978) Pelagic ecosystem structure: heterotrophic compartments of plankton and their relationship to plankton size fractions. *Limnol Oceanogr* 23:1256–1263
- Smetacek V, De Baar HJW, Bathmann UV, Lochte K, Van Der Loeff MM, Rutgers (1997) Ecology and biogeochemistry of the Antarctic Circumpolar Current during austral spring: a summary of Southern Ocean JGOFS cruise ANT X/6 of R.V. Polarstern. *Deep-Sea Res Pt II* 44:1–21
- Smith SL (1998) The 1994–1996 Arabian Sea Expedition: oceanic response to monsoonal forcing, Part I. *Deep-Sea Res Pt II* 45:1917–2501
- Smith WO Jr., Anderson RF, Moore JK, Codispoti LA, Morrison JM (2000a) The U.S. Southern Ocean Joint Global Ocean Flux Study: an introduction to AESOPS. *Deep-Sea Res Pt II* 47:3073–3093
- Smith WO Jr., Marra J, Hiscock MR, Barber RT (2000b) The seasonal cycle of phytoplankton biomass and primary productivity in the Ross Sea, Antarctica. *Deep-Sea Res Pt II* 47:3119–3140
- Strom SL, Miller CB, Frost BW (2000) What sets lower limits to phytoplankton stocks in high-nitrate, low-chlorophyll regions of the open ocean? *Mar Ecol Prog Ser* 193:19–31
- Sugimura Y, Suzuki Y (1988) A high-temperature catalytic oxidation method of non-volatile dissolved organic carbon in seawater by direct injection of liquid samples. *Mar Chem* 14:105–131
- Sverdrup HU (1953) On the conditions for the vernal blooming of phytoplankton. *J Cons Perm Int Explor Mer* 18:287–295
- Tindale NW, Pease PP (1999) Aerosols over the Arabian Sea: Atmospheric transport pathways and concentrations of dust and sea salt. *Deep-Sea Res Pt II* 46:1577–1595
- Tomczak M, Godfrey JS (1994) *Regional oceanography: an introduction*. Pergamon, Oxford, 422 p
- Tsunogai S (1997) Biogeochemical processes in the North Pacific. *Proceedings of the International Marine Science Symposium held on 12–14 November 1996 at Mutsu, Aomori, Japan*. Tokyo: Japan Marine Science Foundation
- Turner D, Owens N, Priddle J (1995) Southern Ocean JGOFS: The U.K. 'STERNA' study in the Bellingshausen Sea. *Deep-Sea Res Pt II* 42:905–906
- Van der Spoel J, Heymann RP (1983) *A comparative atlas of zooplankton*. Springer-Verlag, Berlin
- Walsh JJ (1976) Herbivory as a factor in patterns of nutrient utilization in the sea. *Limnol Oceanogr* 21:1–13
- Waterbury JB, Watson SW, Guillard RR, Brand LE (1979) Widespread occurrence of a unicellular, marine, planktonic cyanobacterium. *Nature* 277:392–394
- Welschmeyer N, Strom SL, Goericke R, diTullio G, Belvin M, Peterson W (1993) Primary production in the subarctic Pacific Ocean: project SUPER. *Prog Oceanogr* 32:101–135
- Wiebinga CJ, Veldhuis MJW, De Baar HJW (1997) Abundance and productivity of bacterioplankton in relation to seasonal upwelling in the northwest Indian Ocean. *Deep-Sea Res Pt I* 44:451–476
- Williams PJ leB (1981) Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web. *Kieler Meeresforschung* 5:1–28
- Williams PJ leB (1984) Bacterial production in the marine food chain: the emperor's new suit of clothes? In: Fasham M (ed) *Flows of energy and materials in marine ecosystems: theory and practice*. Plenum Press, pp 271–299
- Williams PJ leB (2000) Heterotrophic bacterial and the dynamics of dissolved organic material. In: Kirchman DL (ed) *Microbial ecology of the oceans*. John Wiley & Sons, New York, pp 153–201
- Winn CD, Campbell L, Letelier R, Hebel D, Fujieki L, Karl DM (1995) Seasonal variability in chlorophyll concentrations in the North Pacific subtropical gyre. *Global Biogeochem Cy* 9:605–620
- Wong GTF, Chao S-Y, Li Y-H, Shiah F-K (2000) The Kuroshio edge exchange processes (KEEP) study – an introduction to hypotheses and highlights. *Cont Shelf Res* 20:335–347
- Wu J, Sunda W, Boyle EA, Karl DM (2000) Phosphate depletion in the Western North Atlantic Ocean. *Science* 289:759–762