



PERGAMON

Deep-Sea Research II 49 (2002) 2425–2442

DEEP-SEA RESEARCH  
PART II

[www.elsevier.com/locate/dsr2](http://www.elsevier.com/locate/dsr2)

# Carbon fluxes in the equatorial Pacific: a synthesis of the JGOFS programme

Robert Le Borgne<sup>a,\*</sup>, Richard A. Feely<sup>b</sup>, Denis J. Mackey<sup>c</sup>

<sup>a</sup> Centre IRD de Nouméa, B.P. A5, Nouméa Cedex, New Caledonia

<sup>b</sup> Pacific Marine Environmental Laboratory, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070, USA

<sup>c</sup> CSIRO Marine Research, P.O. Box 1538, Hobart 7001, Tasmania, Australia

Received 13 June 2001; received in revised form 28 August 2001; accepted 28 September 2001

## Abstract

This paper synthesizes published results on the carbon cycle of the equatorial Pacific which accounts for a major fraction of the net exchange of CO<sub>2</sub> between the atmosphere and the oceans. Most of the CO<sub>2</sub> evasion takes place in the upwelling-influenced region in the eastern Pacific, while atmospheric and sea-surface partial pressures of CO<sub>2</sub> are near equilibrium in the warm pool, located to the west. Large changes in the surface area of the upwelling region, which occur as a result of the ENSO (El Niño—Southern Oscillation) phenomenon, account for up to 70% of the interannual variability in the net air–sea flux of CO<sub>2</sub>. On average, the export of biological production, which is approximately the same as new primary production, is similar to that of CO<sub>2</sub> evasion (0.8–1.0 Pg C yr<sup>−1</sup>), but there is less temporal variability due to the very slow uptake of new macronutrients in the equatorial ecosystem. As in other tropical ecosystems, both the warm pool and upwelling areas are characterized by: (i) the dominance of picophytoplankton, and (ii) the steady state, achieved by the balance between predation and growth. In addition to the basic tropical population of nano- and picoplankton, larger phytoplankton are more abundant in the nutrient-replete waters of the upwelling region with the result that biomass, mean organism size and export fluxes are greater than in the nutrient-depleted waters of the warm pool. However, the difference in export flux of carbon between the two regions is rather modest (2–4 fold per unit area) because of the limitation of primary production in the upwelling zone by iron and, possibly, other nutrients. The latter is a typical HNLC (high-nutrient–low-chlorophyll) zone with very low rates of uptake of macronutrients and an essentially constant export flux of carbon due to the ‘biological pump’. This general pattern is temporarily disturbed by the passage of equatorial Kelvin waves and tropical instability waves (TIW) in the upwelling region through horizontal advection and possible inputs of micronutrients from the deeper layers. Finally, low-frequency variations on decadal time scales could influence the values of the CO<sub>2</sub> evasion and the ‘biological pump’. Studying their impact will require long-term monitoring. © 2002 Elsevier Science Ltd. All rights reserved.

## 1. Introduction

At the JGOFS (Joint Global Ocean Flux Study) Pacific Planning Workshop held in Honolulu in

September 1989, the Working Group on the Equatorial Pacific proposed three questions to be addressed as the basis for an Equatorial Pacific JGOFS Programme (JGOFS, 1989). The three questions were: (i) Does the equatorial Pacific biogeochemical cycling determine what happens in the global ocean; (ii) What is the capacity of the

\*Corresponding author.

E-mail address: [leborgne@noumea.ird.nc](mailto:leborgne@noumea.ird.nc) (R. Le Borgne).

biological pump in the equatorial Pacific; (iii) What is the response of the equatorial Pacific to ENSO fluctuations? It was further suggested that the timing was right due to the wealth of physical oceanographic data that had been recently collected by the TOGA (Tropical Ocean Global Atmosphere) project and the complementary data and oceanographic insights that would be gained from the TOGA-COARE (Coupled Ocean-Atmosphere Response Experiment) programme. A decade later, we now know that the timing was extremely fortunate, not only because of the range of ENSO fluctuations that we experienced during the 1990s but also because of the many improvements in technology that have occurred (e.g., Bricaud et al., 2002). We now routinely measure and characterize picoplankton, photosynthetic and carotenoid pigments, trace elements, and inorganic carbon species at concentrations and sensitivities that could not have been imagined during the planning stages. In 2002, we look at what we have learned, what we need to study, and, in particular, whether we are closer to answering the three questions above. We use results previously published in three volumes of *Deep-Sea Research* (Murray et al., 1995, 1997; Murray, 1996) and the present volume, which presents synthetic papers and some new results originating from recent cruises (other papers published in various journals will be used also in this synthesis).

## 2. Equatorial Pacific data resources

This synthesis of the equatorial Pacific JGOFS Programme includes data from specific research cruises, ships of opportunity, Tropical Ocean Atmosphere (TAO) moorings, and satellites between 1989 and 1999. A list of the research cruises that contributed to this programme is given in Appendix A. More than 50 oceanographic cruises to study biogeochemical processes were arranged by scientists from Australia, France, Japan and the United States. At the same time, our knowledge of the physical processes in the equatorial Pacific was greatly enhanced by the TAO mooring network that has been in place since 1984 (Kessler and McPhaden, 1995). In 1992 and 1993, bio-optical

sensors were added to the TAO mooring at 0°, 140°W (Foley et al., 1997), and in 1996 bio-optical and chemical sensors were added to the moorings at 0°, 155°W and 2°S, 170°W (Chavez et al., 1999). Since the fall of 1996, the Ocean Color-Temperature Sensor (OCTS), the Polarization Detection Environmental Radiometer (POLDER) and, the SeaViewing Wide Field-of-View Sensor (SeaWiFS) on earth orbiting satellites have provided a nearly continuous record of biological processes in surface waters in this region (McClain et al., 2002). These highly resolved data sets have allowed us to study the physical, chemical and biological processes over very large spatial scales. The enormous amount of disparate data from this large-scale international programme has proved to be an extraordinary challenge for each of the various national data management groups charged with maintaining and distributing the data sets. Numerous problems, associated with different data types and formats, had to be resolved by many investigators participating in the JGOFS programme, and it has become increasingly apparent that data management is a fundamental component of any such large-scale international effort that must be carefully planned and supported from the beginning of the programme. A summary of the major data management web sites for the equatorial Pacific data sets is given in Table 1. In most cases the data can be downloaded directly from the web site. In addition, a CD-ROM of the JGOFS equatorial Pacific data is being prepared and will be made available from the International JGOFS Project Office (Table 1).

Some JGOFS-related fieldwork in the equatorial Pacific is still underway. For example, Japanese JGOFS cruises are ongoing in the western and central equatorial Pacific, France is continuing to support underway chemical and biological measurements on ships of opportunity in the central equatorial Pacific (Gep&Co programme, LODYC, Paris), and the United States is still supporting the underway and mooring measurements as part of the maintenance of the TAO buoys (PMEL, Seattle). These new data sets are also being distributed via the existing data management web sites.

Table 1  
Data management web sites for JGOFS equatorial Pacific data

| Participating country              | WWW site URL   |
|------------------------------------|--|
| Australia                          | <a href="http://www.marine.csiro.au/datacentre/JGOFSweb/cmr_jgofs.htm">http://www.marine.csiro.au/datacentre/JGOFSweb/cmr_jgofs.htm</a>  |
| France                             | France JGOFS <a href="http://www.obs-vlfr.fr/jgofs/html/bdjgofs_eng.html">http://www.obs-vlfr.fr/jgofs/html/bdjgofs_eng.html</a>   |
| Japan                              | Japan JGOFS <a href="http://www.jodc.jhd.go.jp/JGOFS.DMO/index.html">http://www.jodc.jhd.go.jp/JGOFS.DMO/index.html</a>  |
| United States                      | US JGOFS <a href="http://www1.whoi.edu/jgdms_info.html">http://www1.whoi.edu/jgdms_info.html</a><br>CDIAC <a href="http://cdiac.esd.ornl.gov/oceans/home.html">http://cdiac.esd.ornl.gov/oceans/home.html</a><br>NOAA <a href="http://www.aoml.noaa.gov/ocd/oaces/index.html">http://www.aoml.noaa.gov/ocd/oaces/index.html</a><br>NOAA <a href="http://www.pmel.noaa.gov/uwpc02/">http://www.pmel.noaa.gov/uwpc02/</a><br>JGOFS IPO <a href="http://ads.smr.uib.no/jgofs/jgofs.htm">http://ads.smr.uib.no/jgofs/jgofs.htm</a> |
| JGOFS International Project Office |  |

### 3. Significant results of the JGOFS equatorial programme

#### 3.1. The physical environment: warm pool vs. HNLC region

The equatorial Pacific is subject to physical forcings that differ markedly from west to east. In the warm pool of the western Pacific, a deep thermocline and nutricline, combined with a barrier layer produced by shallow haloclines, prevent the upwelling of dissolved inorganic carbon (DIC)- and nutrient-rich water into the euphotic zone even when surface winds from the east would be favourable. In contrast, the region east of the warm pool is subject to the divergence of the South Equatorial Current (SEC), north and south of the equator. Such a divergence generates upwelling of waters from the Equatorial Undercurrent (EUC), which brings waters with higher salinity, DIC, and nutrient concentrations to the surface. Since phytoplankton pigment concentrations remain low and the macronutrients are not depleted, this region of the equatorial Pacific is usually called the HNLC (high-nutrient–low-chlorophyll) area after the definition given originally by Minas et al. (1986). The border between the warm pool and the HNLC region on the equator is clearly delineated by higher sea-surface salinity and  $p\text{CO}_2$  and the occurrence of nitrate in the surface waters in the east (Fig. 1; Feely et al., 1995, 1997, 1999; Inoue et al., 1996; Rodier et al., 2000; Feely et al., 2002; Kobayashi and Takahashi, 2002; Le Borgne et al., 2002). As illustrated by Fig. 1, zonal variations of sea-surface temperature (SST) are rather low and SST can be  $>29^\circ\text{C}$  in the

HNLC region of the western and central Pacific. Because the longitude of the border undergoes very significant temporal variations, the equatorial Pacific should not be partitioned into western, central and eastern regions, but rather into the warm pool and the HNLC region, each of which displaying very different properties.

The biogeochemical features of the HNLC region vary with latitude, and there is also a pronounced asymmetry with respect to the equator. This meridional asymmetry is due to the equatorial counter currents, with a marked boundary to the north produced by the North Equatorial Counter Current (NECC) and a less pronounced one to the south (west of  $140\text{--}150^\circ\text{W}$ ) formed by the South Equatorial Counter Current (SECC) when it exists. Asymmetry is generated also by the water masses originating north and south of the equator which supply different concentrations of nutrients such as silicate (Dugdale et al., 2002b). Finally, latitudinal variations are linked to the meridional divergence which result in a gradient of parameters such as  $p\text{CO}_2$  (Feely et al., 2002) and organic matter, and to the evolution of the ecosystem with increased heterotrophic biomass and activity away from the equator (Kirchman et al., 1995; White et al., 1995; Roman et al., 2002; Brown et al., submitted; Le Borgne and Landry, submitted).

#### 3.2. Export of $\text{CO}_2$ from the equatorial Pacific: an outstanding role in the global carbon budget

The equatorial belt plays a significant role in the global carbon cycle. It annually supplies approximately  $0.7\text{--}1.5\text{ Pg C}$  as  $\text{CO}_2$  to the atmosphere, and

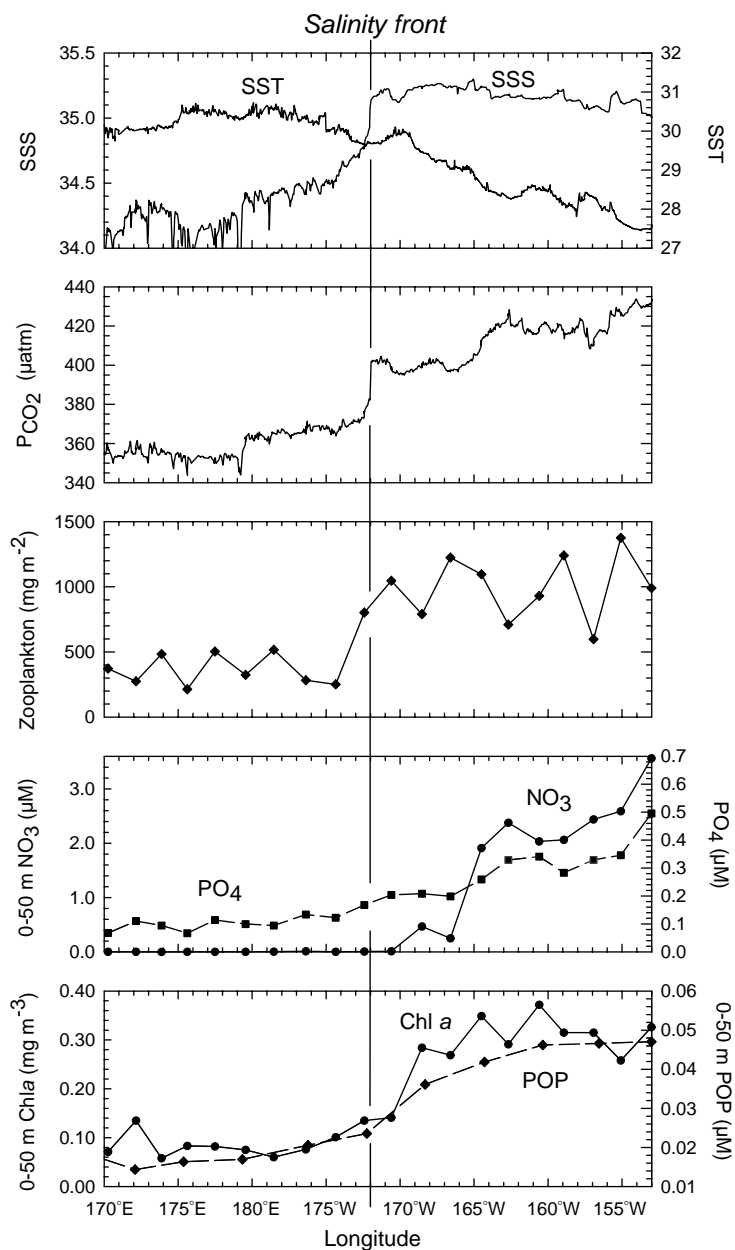


Fig. 1. The border between the warm pool and the HNLC region is clearly delineated by an increase of the partial pressure of carbon dioxide ( $p\text{CO}_2$ ), sea surface salinity (SSS), zooplankton biomass and higher concentrations of nitrate ( $\text{NO}_3$ ), chlorophyll  $a$  (Chla) and particulate organic phosphorus (POP). Note that variations in the sea surface temperature (SST) and phosphate ( $\text{PO}_4$ ) concentrations are less pronounced (Flupac transect in October 1994, Rodier et al., 2000).

is the largest natural source from the ocean (Tans et al., 1990; Takahashi et al., 1997, 1999; Feely et al., 1999). The large number of  $\text{CO}_2$  measure-

ments since the beginning of the JGOFS equatorial Pacific process study indicate that as much as 72% of the outgassing of  $\text{CO}_2$  from the world's

oceans can be attributed to the equatorial Pacific. Most of this flux originates from the HNLC area since Inoue et al. (2002) estimated that, in 1996, the CO<sub>2</sub> outflux per unit area was about 30-fold less in the warm pool than in the HNLC region.

The distributions of DIC and  $p\text{CO}_2$  (CO<sub>2</sub> partial pressure) are regulated by physical mixing and upwelling processes, biological uptake, and air–sea gas exchange. The border between the HNLC region and the warm pool is a region of strong zonal gradients in DIC and  $p\text{CO}_2$ , while there are also strong latitudinal gradients in the shear zone between the SEC and the NECC. Interannual and seasonal variations in the location of these borders play a significant role in controlling the amount and areal extent of CO<sub>2</sub> evasion in this region (Feely et al., 1995; Inoue et al., 1996).

### 3.3. The biological pump in the warm pool and HNLC regions

Both the level of primary production and the size–structure of phytoplankton are related to the availability of macronutrients in the euphotic zone, which leads to significant differences in the strength of the biological pump between the HNLC and warm-pool regions. The warm-pool waters, which are essentially always depleted in macronutrients, are dominated by small phytoplankton cells. Flow cytometry data showed that the autotrophic community is largely composed of picoeukaryotes and two classes of bacterioplankton, *Prochlorococcus* and *Synechococcus*, while HPLC/pigment analyses showed that the main contributions to chlorophyll were from *Prochlorococcus*, *Synechococcus* and haptophytes. No size fractionated pigment data has been reported but it seems likely that the picoeukaryotes are predominantly haptophytes (Mackey et al., 2002). Diatoms contribute about 15% of the biomass, and the standing stock of pennate diatoms is almost uniform across the entire equatorial Pacific (Kobayashi and Takahashi, 2002). The dominance of picoplankton is consistent with the fact that smaller cells have a higher surface to volume ratio and thus are more efficient in obtaining nutrients present at low concentrations. The vertical distribution of chlorophyll shows a pronounced

maximum (the deep chlorophyll maximum or DCM) at about 80–100 m due to the competing requirements for light, which decreases with depth, and macronutrients, which increase in concentration with depth (Fig. 2). These conditions are similar to those that characterize the oligotrophic mid-ocean gyres although the depth-integrated chlorophyll concentrations and gross productivity are higher in the warm pool. Compared with the mid-ocean gyres, which are subject to downwelling, the warm pool has higher nitrate concentrations at 80–100 m and there is usually uplifting of the nutricline at the equator (Radenac and Rodier, 1996) as well as intermittent upwelling at 2–5°N by Ekman pumping (Mackey et al., 1997).

The HNLC region of the equatorial Pacific is characterized by abundant macronutrients and comparatively high concentrations of chlorophyll in surface waters (0.2–0.3 vs. 0.05  $\mu\text{g l}^{-1}$ ). As for the warm pool, the autotrophic community is also dominated by picoeukaryotes, *Prochlorococcus* and *Synechococcus* (Binder et al., 1996; Landry et al., 1996), but with a greater contribution of larger cells, > 3  $\mu\text{m}$  (Rodier and Le Borgne, 1997), such as centric diatoms (Kobayashi and Takahashi, 2002). While the biomass of *Synechococcus* and picoeukaryotes is higher in the HNLC area than in oligotrophic waters, the biomass of *Prochlorococcus* is similar in both regions (Landry and Kirchman, 2002). Such an increase of larger cells is in agreement with the finding of Le Bouteiller et al. (1992) that there is a higher proportion of cells > 1  $\mu\text{m}$  in nitrate-containing waters of tropical areas whatever the depth of their occurrence in the photic layer. This led Landry and Kirchman (2002) to state that ‘the general impression is that marine microbes exist at relatively constant concentrations, providing the background upon which the dynamics of larger organisms are overprinted’. In addition, the size–structure of the phytoplankton in the HNLC region appears to be constant along the equator west of the Galapagos islands, regardless of macronutrient concentrations (Le Bouteiller and Blanchot, 1991), which suggests rather uniform populations.

Despite the differences in physical and chemical forcings between the warm pool and the HNLC,

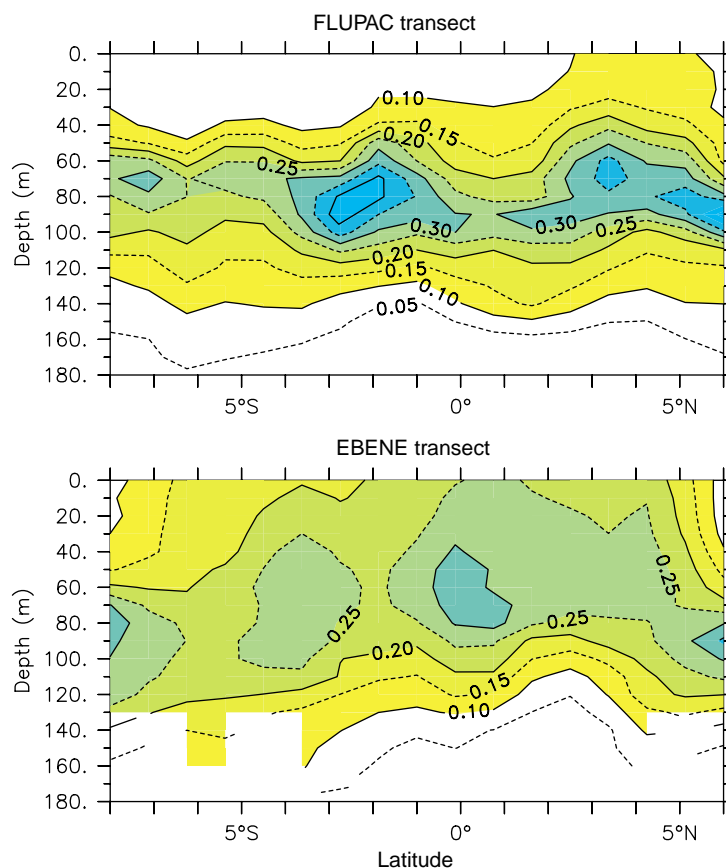


Fig. 2. Chlorophyll *a* equatorial cross sections in the warm pool (Flupac transect in September 1994 along 165°E) and HNLC regions (Ebene transect, November 1996 along 180°). Note the deep chlorophyll maximum in the warm pool and the homogeneous distribution in the HNLC region between 4°S and 5°N.

the depth-integrated chlorophyll concentrations in the HNLC (25–36  $\text{mg m}^{-2}$ ) region are only slightly higher (Figs. 1 and 2) than those observed in the warm pool under normal or El Niño conditions (20–30  $\text{mg m}^{-2}$ , Mackey et al., 1997). This does not necessarily imply a similarity in biomass since the chlorophyll tends to lie much deeper in the water column in the warm pool and the carbon to chlorophyll ratio decreases with depth (Chavez et al., 1996; Brown et al., submitted). Whereas the biomass and productivity in the warm pool are clearly limited by the availability of macronutrients, the IronEx experiments in the eastern Pacific confirmed that iron limits production and the development of larger cells (Coale et al., 1996; Landry et al., 2000a) in the HNLC region. Aeolian

deposition of iron is low in the central and eastern Pacific (Duce and Tindale, 1991), and the major source of iron is thought to be upwelled water from the top of the EUC (Gordon et al., 1997). This iron must be rapidly and efficiently recycled within the upwelling waters of the top 150 m (Landry et al., 1997). Temporary iron inputs from the EUC have been ascribed to increases in vertical advection (Loukos et al. 1997) linked to the passage of upwelling Kelvin waves and TIW (Barber et al., 1996; Foley et al., 1997; Leonard et al., 1999; Friedrichs and Hofmann, 2001; Aufdenkampe and Murray, 2002), although direct measurements of iron concentrations still remain to be made in order to check these hypotheses. Production of diatoms also may be limited by

$\text{Si(OH)}_4$  and a 1-D model by Chai et al. (2002) and Dugdale et al. (2002a) suggests that the HNLC region acts like a chemostat with limiting concentrations of  $\text{Si(OH)}_4$  and non-limiting  $\text{NO}_3$  in the feed water. The model demonstrates that low silicate concentrations in the equatorial Pacific would limit production of diatoms to approximately 16% of the total phytoplankton biomass. At present however, and following IronEx II experiments (Landry et al., 2000a), iron appears to be the primary element limiting new production in the equatorial Pacific HNLC region.

Export production, which is a function of the abundance and size-structure of the phytoplankton, was the focus of a wide range of studies conducted during the Equatorial Pacific JGOFS programme. These studies included: (i) a comparison between the warm pool and the HNLC region for planktonic populations (Kobayashi and Takahashi, 2002; Yamashita et al., 2002) and export fluxes (Le Borgne and Rodier, 1997; Rodier and Le Borgne, 1997), (ii) zonal variations in new production (Aufdenkampe et al., 2001; Turk et al., 2001) and sinking rates (Le Borgne et al., 1999; Dunne et al., 2000), (iii) latitudinal variations in new production (McCarthy et al., 1996; Le Bouteiller et al., submitted), (iv) sinking rates (Buesseler et al., 1995; Murray et al., 1996; Dunne et al., 1997), (v) export flux by diel migrants (Roman et al., 2002), and (vi) temporal variations in sinking fluxes of organic matter (Gupta and Kawahata, 2002) and foraminifera (Kawahata et al., 2002). In comparison with the warm pool, the average biological pump fluxes per unit area in the HNLC region appear to be greater by a factor of 4 for sinking rates (Rodier and Le Borgne, 1997), 1–9 for new production (Turk et al., 2001), and 2 for transfer by diel migration (Le Borgne and Rodier, 1997). In the HNLC region, macro-nutrient concentrations seem to have little or no effect on the export fluxes of the biological pump (Le Borgne et al., 2002) as long as there are no inputs of micronutrients by TIW or upwelling Kelvin waves. The situation seems to be more complex for new production (Aufdenkampe et al., 2001, 2002), which appears to be linked to nitrate and ammonium concentrations and phytoplankton total production, with nitrate being the

strongest predictor of new production within cruises. Differences in the relationships between new production and nitrate of the mixed layer between cruises are interpreted by Aufdenkampe and Murray (2002), who use a coupled nitrogen–iron model. These authors show that nitrogen and iron cycles are decoupled in the upper ocean as a result of physical forcing. Such a process may explain the small-scale variability in new production and the large variation in  $f$  ratios (0.06–0.38) found by Aufdenkampe et al. (2001).

Estimations of the export flux by sedimentation and zooplankton diel migrations should integrate the short-term variability and, in that sense, may be a better indicator of the strength of the biological pump than estimates of new production. Technical and methodological improvements made during the JGOFS equatorial Pacific programme improved the reliability of estimates of particulate sinking rates (Dunne et al., 1997, 2000). In the HNLC region, the active flux has been shown to be of secondary importance in exporting carbon from the euphotic zone (Le Borgne and Rodier, 1997; Roman et al., 2002) in agreement with Longhurst et al. (1989) who found that the active flux was relatively less in eutrophic regions than in oligotrophic ones. The combined sinking and active fluxes in the HNLC region are less than or equal to estimates of new production (Le Borgne et al., 2002), which requires a loss of DOC by horizontal advection (Murray et al., 1994; Hansell et al., 1997) for the budget to be balanced.

Chavez et al. (1996) estimated the average new production for the ‘Wyrtki box’ (Wyrtki, 1981), i.e. for the region extending from the Galapagos islands to  $180^\circ$  and from  $5^\circ\text{N}$  to  $5^\circ\text{S}$ , which corresponds to the average extent of the HNLC zone for the period 1980–2000 (Le Borgne et al., 2002). Their calculation, based on an estimation of upwelled nitrate and the assumption that 25–50% of this nitrate was advected out of the box, led to a new production of  $0.65\text{--}0.98\text{ Pg C yr}^{-1}$ , which is comparable to the mean estimate of  $\text{CO}_2$  evasion of  $0.8\text{--}1.0\text{ Pg C yr}^{-1}$  during non-El Niño years (Feely et al., 2002). In addition, Chavez et al. (1996) provide an  $f$  ratio value ranging from 0.18 to 0.27 (depending on the losses out of the ‘Wyrtki box’), which indicates that the HNLC ecosystem

works mainly (75–80%) on regeneration, as stressed by Murray et al. (1994).

### 3.4. Temporal variability of chemical and biological processes: from the diel to the interannual scale

#### 3.4.1. Short-term variability and the steady state

One of the main characteristics of tropical ecosystems is low temporal variability (Cushing, 1959; Walsh, 1976), and this is true also for both the warm pool and the equatorial upwelling systems. On time scales of less than a day, however, there can be substantial changes in abundance, cell size and in situ fluorescence (Binder and DuRand, 2002) due to active grazing at night by micrograzers, synchronized cell division (Vaulot and Marie, 1999), cell growth (Neveux et al., submitted), and changes in the chlorophyll to carbon content of individual cells as a function of irradiance (Kiefer, 1973; Dandonneau and Neveux, 1997; Neveux et al., submitted). There appears to be little variation in phytoplankton biomass caused by changes in the depths of the nutricline, thermocline, and DCM due to the passage of internal waves with a period of about 12 h (Mackey et al., 1995), leading to the conclusion that the main source of 24-h period variability is diurnal biological activity. In addition, vertical migration of mesozooplankton between the photic

layer and deeper ones also occurs on a diurnal time scale (Roman et al., 1995; Le Borgne and Rodier, 1997).

But, in spite of significant diel variations, planktonic biomasses remain the same from one day to another (Fig. 3). This has been observed in both the warm pool and the HNLC regions for: (i) phytoplankton cell numbers (Vaulot et al., 1995; Binder et al., 1996; Binder and DuRand, 2002); (ii) the particle load as measured by transmissometry (Walsh et al., 1995; Claustre et al., 1999); and (iii) other components of the pelagic food-web of the upper layer, i.e. mesozooplankton (Roman et al., 1995; Le Borgne and Rodier, 1997; Le Borgne et al., 2002, submitted). Such a steady state, however, requires an equilibrium between primary production and grazing or prey production and predators ingestion over a 24-h period. Most of the grazing on the microbial community is by micrograzers (Landry et al., 2000b, submitted; Landry and Kirchman, 2002; Le Borgne and Landry, submitted) since mesozooplankton only ingest a small fraction of the phytoplankton (Dam et al., 1995; Rollwagen Bollens and Landry, 2000; Roman et al., 2002; Champalbert et al., submitted). Micrograzers are protists that have growth rates similar to those of picophytoplankton (Landry et al., 2000b) and some taxa of microparticle feeders of mesozooplankton, such as

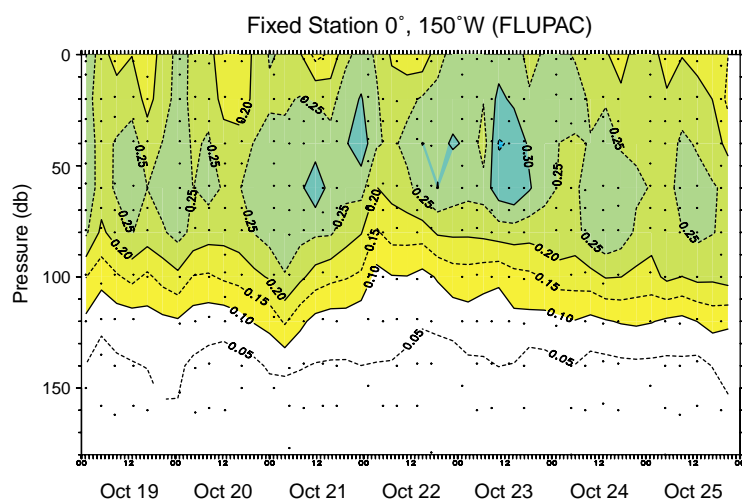


Fig. 3. Time series of chlorophyll *a* at a 7-d long fixed station in the HNLC region (0°, 150°W, Flupac cruise in 1994) showing constant values from the beginning to the end in spite of clear diel variations.



thaliaceans (larvaceans, doliolids and salps). However, for reasons which are not clear, thaliaceans have never been reported to make an important contribution of the total mesozooplankton biomass in the equatorial Pacific, which is dominated by copepods (Roman et al., 1995; Le Borgne and Rodier, 1997; Le Borgne et al., 2002, submitted). The top-down control seems to be so strong that, to our knowledge, phytoplankton blooms have only been reported in the equatorial area on two occasions. The first occurred during the recovery of the equatorial upwelling after the strong 1997–1998 El Niño when the chlorophyll *a* at 0°, 140°W increased by a factor of 3–4 in July–September 1998 (Murtugudde et al., 1999; McClain et al., 2002) and 10 at 2°N, 110°W (Chavez et al., 1999). The rapid change from oligotrophic conditions to unusually high phytoplankton biomass were ascribed to the effects of macronutrient and iron inputs to the photic zone, associated with strong TIW activity (Chavez et al., 1999; Murtugudde et al., 1999). Three months later, surface phytoplankton biomass had returned to normal HNLC chlorophyll values, which indicates that the top-down control may have been inefficient for 3 months or that the equatorial ecosystem had reached a different equilibrium, as demonstrated by IronEx II (Landry et al., 2000a). Conversely, when macronutrient inputs stop, following a cessation in upwelling, top-down control exceeds the bottom-up control and leads to lower chlorophyll concentrations in the western end of the HNLC region (Rodier et al., 2000). Such observations stress the importance of both bottom-up (nutrient inputs) and top-down (grazing) controls in establishing the steady state in the HNLC system. The second ‘bloom’ was of *Rhizosolenia* and was observed during EqPac (Yoder et al., 1994; Archer et al., 1997) on the leading edge of a TIW. The ‘bloom’ was, in fact, an accumulation of buoyant phytoplankton in the convergence zone (Archer et al., 1997), which was caused by physical processes rather than the lack of top-down control.

### 3.4.2. Effects of wave activity

On time scales longer than a day, wave activity may have an effect on biomasses and fluxes. TIW

and Kelvin waves affect primary production in the equatorial Pacific by changing the supply of macro- and micronutrients, including iron, to the euphotic zone (Eldin et al., 1997; Archer et al., 1997; McClain et al., 2002; Le Borgne et al., 2002). The westward propagating TIW have periods of 20–30 d, wavelengths of 1000–1500 km, phase speeds of 40–70 km d<sup>-1</sup>, and are associated with higher concentrations of nutrients and chlorophyll due to enhanced upwelling along the southernmost front of the wave (Harrison, 1996; Barber et al., 1996; Flament et al., 1996; Le Borgne et al., 2002; Aufdenkampe and Murray, 2002). The physical processes with TIW activity have been described by Flament et al. (1996) and Harrison (1996), and TIW have been observed as far west as the dateline (Eldin and Rodier, 2002). They are usually strongest between September and November when the wind fields in the central and eastern equatorial Pacific are most intense. The effect of TIW on the structure and functioning of the equatorial HNLC system appears to have an important impact on primary production. The increases in specific productivity associated with TIW in the equatorial Pacific have been interpreted as being ‘analogous to a natural iron enrichment experiment’ (Barber et al., 1996) because the productivity rates were found to be very close to the values observed during IronEx I (Coale et al., 1996). However, the interpretation of biological responses to TIW is still difficult because both horizontal and vertical advective processes need to be taken into account. Depending on the observer’s location with respect to the TIW, different effects will be observed which will not necessarily lead to an increase in biological productivity (Roman et al., 1995; Eldin and Rodier, 2002; Le Borgne and Landry, submitted). Any increase that occurred (e.g., during the autumn EqPac cruises in 1992) was ascribed to an increased input of iron (Barber et al., 1996; Foley et al., 1997). Similarly, Chavez et al. (1999) and McClain et al. (2002) proposed that increased iron inputs, related to strong TIW activity, caused the dramatic increase in chlorophyll concentrations of the central equatorial Pacific during the shift from oligotrophic to eutrophic conditions in June–September 1998. However, at this stage, no iron measurements

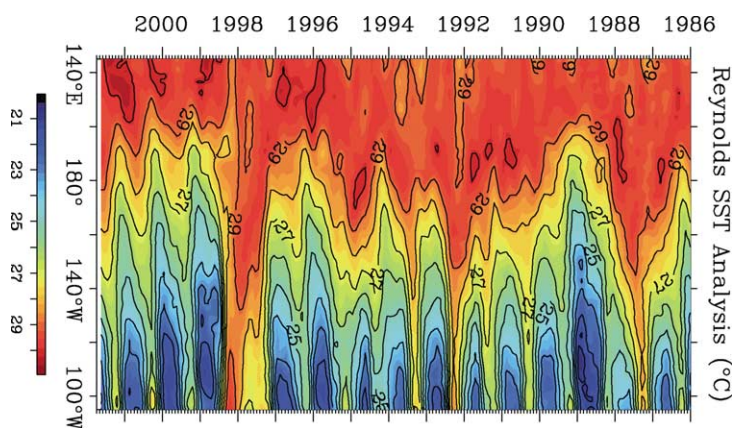


Fig. 4. Time-longitude distribution of sea surface temperature (in °C) from 1986 through 1998. The analysis is based on monthly averages between 2°S and 2°N from time series data from the TAO/Triton array. The migration of the 28°C isotherm past 140°W during the 1986–87, 1991–93, and 1997–98 El Niño events are examples of the eastward migration of the warm pool into the eastern equatorial Pacific.

have been made to support such an hypothesis. Nonetheless, TIW activity appears to play a crucial role in the interpretation of the spatial variability of planktonic parameters in the HNLC area, even though the net effect on productivity (over a complete cycle of a TIW) still needs to be estimated.

Downwelling Kelvin waves, which have periods of 40–70 d, wavelengths of up to 10,000 km and travel from west to east at speeds of approximately  $200 \text{ km d}^{-1}$ , are generated by westerly winds bursts. The leading edge of a Kelvin wave deepens the thermocline (and nutricline) and reduces the supply of macro- and micronutrients to the euphotic zone. The mooring data of Foley et al. (1997) for the 1992–1993 El Niño period indicate that primary production is reduced during the passage of the leading edge of these waves. Downwelling Kelvin waves produce surface water that is warmer and less nutrient-rich than the trailing edge of the upwelling wave. The lower productivity associated with the leading edge has been explained on the basis of reduced iron inputs from the core of the EUC (Foley et al., 1997) or

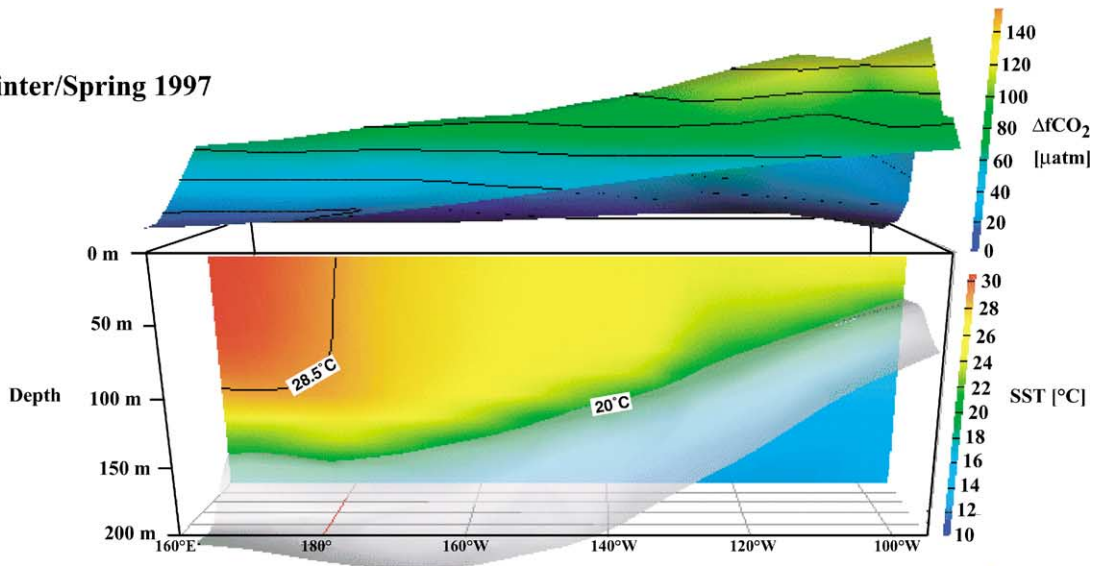
increased mixing associated with a deeper mixed layer (Le Borgne et al., 2002). Kelvin waves and TIW can either enhance or depress total primary production and new production (Aufdenkampe and Murray, 2002), depending on the balance between upwelling velocity and the concentration of nutrients being upwelled. Both depend on the phase of the wave (Foley et al., 1997). The net impact is that these two processes significantly enhance the overall variability of primary production near the equator.

#### 3.4.3. ENSO variability

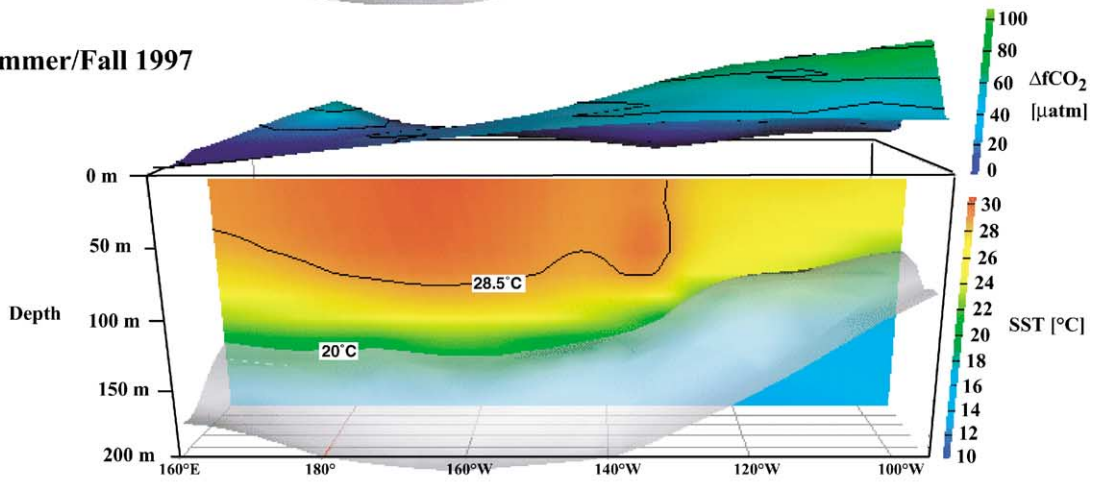
An important finding of the JGOFS programme is that the interannual variability of  $\text{CO}_2$  evasion in the equatorial Pacific is largely dependent upon the location of the eastern edge of the western equatorial Pacific warm pool (Fig. 4). The longitude of the border between the warm pool and the HNLC region is linked to the zonal displacement of the warm pool and is strongly correlated with the Southern Oscillation Index (SOI) (Inoue et al., 1996; Le Borgne et al., 2002). During all phases and intensities of the ENSO cycle,  $p\text{CO}_2$  in the

Fig. 5. 3-D view of the equatorial Pacific showing 6-month averaged temperature distributions and corresponding sea surface  $\text{CO}_2$  fugacity ( $\Delta f\text{CO}_2$ ) distributions for: (A) winter/spring 1997; (B) summer/fall 1997; and (C) winter/spring 1998. The approximate location of the warm pool is indicated in orange colours and the 20°C isotherm surface is highlighted in grey. Notice the eastward migration of the warm pool during the course of the 1997–98 El Niño event. Note: the fugacity of  $\text{CO}_2$  takes into account the non-ideal nature of  $\text{CO}_2$  as a gas; therefore, it is generally lower than  $p\text{CO}_2$  by about 1–1.5  $\mu\text{atm}$  in equatorial surface waters.

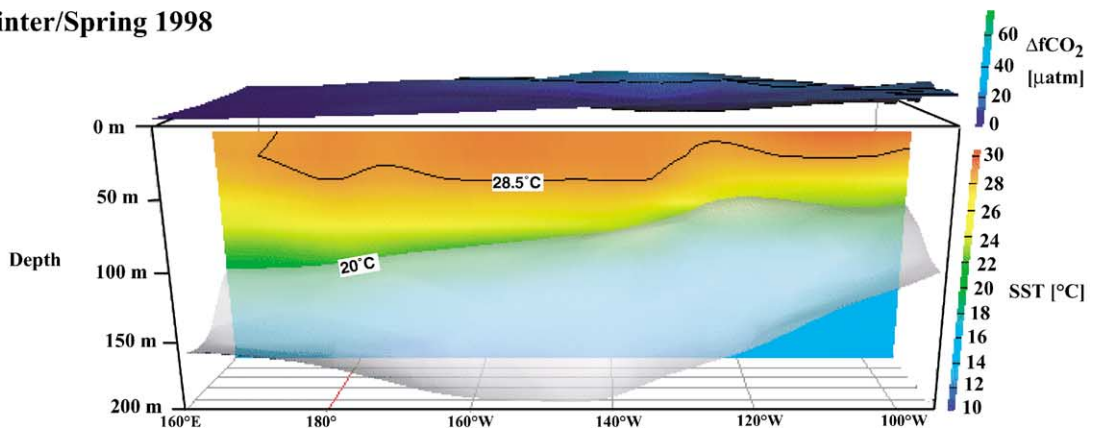
### Winter/Spring 1997



### Summer/Fall 1997



### Winter/Spring 1998



warm pool is close to equilibrium with the atmosphere and the region generally acts as a small source of CO<sub>2</sub> to the atmosphere. During an El Niño, this warm water forms an eastward-flowing ‘equatorial jet’ that effectively caps the water containing high CO<sub>2</sub> east of the dateline (Roemmich et al., 1994; Feely et al., 1995). In contrast, during a La Niña, the warm pool retreats to the western Pacific exposing water with high *p*CO<sub>2</sub> to the surface. Thus, the major impact on the global carbon cycle is due to the changing area of the warm pool as it shrinks during La Niña events and expands during El Niño events (Fig. 5).

One hypothesis of the JGOFS equatorial Pacific programme was that the ENSO-related variations of air–sea fluxes of carbon dioxide in the equatorial Pacific were a major contributor to the interannual variability of the carbon dioxide sources and sinks between the atmosphere and oceans. Consequently, a major objective of the JGOFS programme was to determine how much the source of CO<sub>2</sub> varied from year to year in the equatorial Pacific. Indirect oceanic and GCM model results suggest that the global ocean interannual variability is small. For example, the recent GCM model results of Le Quéré et al. (2000) suggest that the variability in the global air–sea flux of CO<sub>2</sub> from 1979 through 1997 averaged about  $\pm 0.4 \text{ Pg C yr}^{-1}$ , with approximately 70% of the variability originating from the equatorial Pacific. Somewhat smaller estimates were reported by Lee et al. (1998) from observations made up to the first half of the 1990s. The complete set of JGOFS measurements to date, suggest that ENSO-related interannual variability in the equatorial Pacific, efflux of CO<sub>2</sub> is about 0.3–0.7 Pg C yr<sup>-1</sup> (Feely et al., 1999, 2002). These flux variations can account for the negative atmospheric anomalies during some El Niño periods and can explain, for example, up to approximately one-third of the decrease in the growth rate of atmospheric CO<sub>2</sub> during the 1992–1993 El Niño event. Surface water *p*CO<sub>2</sub> data collected during the JGOFS era indicated significant seasonal and interannual variations. The largest decreases in fluxes were associated with the 1991–1993 and 1997–1998 El Niño events. The ENSO cycle has a controlling influence on surface *p*CO<sub>2</sub> levels by

affecting the three main processes controlling large-scale *p*CO<sub>2</sub> patterns: the longitude of the edge of the warm pool; the depth of the thermocline and; the strength of the upwelling. The key question that must be addressed in this regard is: are ocean models missing a large component of the oceanic variability in the air–sea exchange of CO<sub>2</sub>? There is evidence from satellite-based temperature and chlorophyll data in other equatorial and subtropical regions that suggests additional ENSO-related interannual variability of CO<sub>2</sub>, but we have insufficient observational *p*CO<sub>2</sub> data in these regions to determine yearly variations in CO<sub>2</sub> sources and sinks. The lack of observational data at appropriate temporal and spatial resolution has prevented a conclusive determination of this variability on a global scale.

As for estimates of the evasion of CO<sub>2</sub>, estimates of the magnitude of the biological pump depend heavily on the overall surface area of the HNLC region. Temporal variations in the biological pump of the HNLC region have been summarized by Le Borgne et al. (2002) for the 1°N–1°S equatorial band with a variable longitude of the western border. Even though only part of the equatorial upwelling region was considered, they found a smaller difference between strong El Niños and other periods (El Niño/other years ratio equals 0.67) than Feely et al. (2002) found for the CO<sub>2</sub> evasion (ratio equals 0.25). This reflects the basic steady-state nature of the biological pump, which is an important consequence of HNLC conditions in which nitrate uptake by phytoplankton is very slow, due to both a limitation by micronutrients and strong control by grazers.

#### 3.4.4. PDO/ENSO/global warming impacts

It has been proposed (Feely et al., 2002) that the CO<sub>2</sub> flux anomalies associated with large-scale ocean–atmosphere reorientations, such as the ENSO phenomenon, will be modulated by the 18–30 yr cycle of the Pacific decadal oscillation (PDO) which is a low-frequency pattern of Pacific climate variability. During the warm phase of the PDO, there are negative sea surface temperature (SST) anomalies in the central North Pacific and positive anomalies in the equatorial Pacific and

along the west coast of North America. The PDO tends to stay in a given phase (warm or cool) for decades at a time. For example, the PDO was in a warm phase from 1925–1945 and from 1977–1997 (Mantua et al., 1997). When the PDO and ENSO are both in the warm phase, as happened during the 1997–1998 ENSO event, the SST anomalies can be extremely large. The associated changes in biogeochemical processes due to the different phases of the ENSO and PDO might lead to significant variations in the CO<sub>2</sub> flux from the equatorial Pacific. Global warming-induced increases in SST also could enhance the SST anomalies when the ENSO and PDO cycles are in phase with each other. Long-term changes in *p*CO<sub>2</sub> in this region could thus significantly influence the global budget for carbon by decreasing the amount of CO<sub>2</sub> that is outgassed to the atmosphere. We need to gain a better understanding of the temporal patterns of surface ocean CO<sub>2</sub> concentrations and their variability. The seasonal and interannual variability of surface water *p*CO<sub>2</sub> gives information on how the carbon cycle functions, and can be used in conjunction with other methods to help understand the regional and global patterns of CO<sub>2</sub> sources and sinks. A promising benefit of the JGOFS effort to improve the temporal resolution of data is the development of new autonomous chemical sensors that will make it possible to measure CO<sub>2</sub> and biological properties on moorings (Chavez et al., 1999). An expanded network of time-series measurements on moorings is required to define the spatial distribution and temporal variability of CO<sub>2</sub> air–sea fluxes.

#### 4. Conclusion

We have come some way in answering the three questions posed at the start of the Equatorial Pacific JGOFS programme in 1989. It has been shown that the importance of this region in the global carbon budget is linked to the geographical extension of the area enriched by the upwelling. The warm pool region appears to have little, if any, direct role in the CO<sub>2</sub> evasion and only a minor role in the biological pump because it is

oligotrophic. However, interannual variations in the surface area of the HNLC region can account for most of the global variability (70%) of the air–sea flux of CO<sub>2</sub>. The surface area may be assessed by ocean-color imagery, estimated from the SOI or, obtained from combined observations of physical parameters and modelling. The latter also provide estimates of two other processes controlling the surface *p*CO<sub>2</sub>, namely the depth of the thermocline and the strength of upwelling. However, all these methods require reliable field data that can be provided by a network of time-series measurements on moorings and oceanographic cruises.

Process studies devoted to the biological pump have provided a wealth of new knowledge about the two regions of the equatorial Pacific. As in other tropical open-ocean areas, both systems are dominated by picophytoplankton and are in steady state. In the upwelling area, the presence of macronutrients over the entire photic zone leads to an increased contribution of larger phytoplankton cells with important consequences for the ecosystem size–structure and export fluxes due to sinking and diel migrations. However, the difference in biological fluxes per unit area between the warm pool and the macronutrient-enriched area is no more than a factor of 2–4, because primary production is limited in the latter zone. Although we still lack iron measurements, the IronEx experiments in the eastern Pacific suggest that iron is a more important limiting element than silicon. Such limitation reduces the uptake of macronutrients, which remain in the euphotic zone long after the cessation of upwelling. This contributes to the resiliency of the enriched area, which acts as a buffer to reduce the effect of temporal variability. The result is that the biological pump is less variable in time than the evasion of CO<sub>2</sub>.

The JGOFS programme has shown that TIW and Kelvin waves are important contributors to the variability on the equatorial Pacific. At present, we still ignore their overall effect on the pelagic production and do not know whether the associated increases in primary productivity are due to the input of iron. We need direct observations, including iron measurements,

throughout a complete sequence of a wave passage in all three dimensions, zonal, latitudinal and vertical. At present, we have to rely on models and partial observations. PDO also may affect the carbon budget of the equatorial Pacific and the long time scales associated with them highlight the need for long-term monitoring and ongoing modeling of this crucial zone.

### Acknowledgements

Authors are indebted to M.R. Landry and J.W. Murray who reviewed the manuscript. As guest editors, they appreciated the help of the referees in the review process of manuscripts of the present

volume. Finally, the JGOFS Equatorial Pacific Programme owes much to J.W. Murray who coordinated its activities from the beginning. This research was supported by the NOAA Climate and Global Change Program as part of the Global Carbon Cycle Program (contract number GC-99-220). Contribution number 2330 from the Pacific Marine Environmental Laboratory.

### Appendix A

List of the cruises made in the equatorial Pacific since the beginning of the JGOFS Equatorial Pacific programme in 1989 is shown in Table 2.

Table 2

| Month/year     | Latitude, longitude    | Ship             | Cruise            |
|----------------|------------------------|------------------|-------------------|
| July–Dec 89    | 20°S–8°N, 165°E        | Le Suroit        | SURTROPAC 12, 13  |
| Jan–Feb 90     | 0°, 160°E–160°W        | Natsushima       | JAPACS 90         |
| June–July 90   | 0°, 122°E–165°E        | Xiangyanghong    | US-PRC 08         |
| Sep–Oct 90     | 20°N–20°S, 180°–150°W  | Hakuho Maru      | KH-90-2           |
| Aug–Oct 90     | 45°N–8°S, 175°E        | Hakurei Maru     | NH-90-3           |
| Oct 90         | 10°S–5°N, 147°E–155°E  | Franklin         | FR08/90           |
| Nov 90         | 5°N–5°S, 160°E–179°E   | Hakuho Maru      | KH-90-3           |
| Jan–March 91   | 0°, 95°W–165°E         | Le Noroit        | Alizé 2           |
| Jan–Feb 91     | 0°, 160°E–160°W        | Natsushima       | JAPACS 91         |
| Aug–Oct 91     | 48°N–15°S, 175°E       | Hakurei Maru     | NH-91-2           |
| March, July 91 | 20°S–8°N, 165°E        | Le Noroit        | SURTROPAC 14, 15  |
| Jan, Aug 92    | 20°S–8°N, 165°E        | Le Noroit        | SURTROPAC 16, 17  |
| Feb–March 92   | 12°S–12°N, 140°W–170°W | Thompson         | TT007             |
| March 92       | 2°N–10°S, 170°W        | Discoverer       | TAO               |
| March–Apr 92   | 0°, 140°W–143°W        | Thompson         | TT008             |
| March–May 92   | 8°S–10°N, 95°W–170°W   | Malcolm Baldrige | EqPac Spring 1992 |
| June–July 92   | 10°S–10°N, 155°E       | Franklin         | FR05/92           |
| Aug–Sept 92    | 12°S–12°N, 135°W–140°W | Thompson         | TT011             |
| Sept–Oct 92    | 0°, 140°W–145°W        | Thompson         | TT012             |
| Sept–Dec 92    | 10°N–10°S, 95°W–170°W  | Discoverer       | EqPac Fall 1992   |
| Aug–Oct 92     | 48°N–15°S, 175°E       | Hakurei Maru     | NH-92-2           |
| Sept–Oct 92    | 48°N–15°S, 175°E       | Hakuho Maru      | KH-92-4           |
| Nov–Dec 92     | 1.30°S, 156°E          | Alis             | Equalis           |
| Nov–Dec 92     | 0°, 135°E–160°W        | Kaiyo            | LIDAR             |
| Feb–May 93     | 8°S–8°N, 95°W–140°W    | Malcolm Baldrige | EqPac Spring 1993 |
| March 93       | 2°N–10°S, 170°W        | Discoverer       | TAO               |
| April–June 93  | 48°N–0°, 175°E         | Hakurei Maru     | NH-93-1           |
| Aug–Oct 93     | 48°N–15°S, 175°E       | Hakurei Maru     | NH-93-2           |
| Nov 93         | 89°W–93.5°W            | Iselin           | PlumEx            |
| Nov 93         | 10°S–10°N, 155°E       | Franklin         | FR08/93           |
| Oct–Nov 93     | 0°, 90°W–150°W         | Iselin           | IronEx-1          |
| Jan–Feb 94     | 0°, 138°E–165°W        | Kaiyo            | KY-94-1           |
| April–June 94  | 10°S–10°N, 95°W–140°W  | Malcolm Baldrige | EqPac Spring 1994 |
| April–June 94  | 48°N–15°S, 175°E       | Hakurei Maru     | NH-94-1           |

Table 2 (continued)

| Month/year   | Latitude, longitude  | Ship             | Cruise            |
|--------------|----------------------|------------------|-------------------|
| Aug–Nov 94   | 8°S–10°N, 95°W–180°  | Malcolm Baldrige | EqPac Fall 1994   |
| Sept–Oct 94  | 0°, 165°E–150°W      | L'Atalante       | Flupac            |
| Nov 94       | 16°S–1°N, 150°W      | L'Atalante       | Olipac            |
| Aug–Oct 94   | 48°N–3°S, 175°E      | Hakurei Maru     | NH-94-2           |
| Nov–Dec 94   | 9°S–8°N, 155°W–180°  | Malcolm Baldrige | EqPac Fall 1995   |
| Nov–Dec 94   | 0°, 147°E–165°W      | Kaiyo            | KY-94-6           |
| Jan 96       | 0°, 160°E–165°W      | Kaiyo            | KY-96-1           |
| April–May 96 | 2°S–2°N, 165°E–150°W | Thompson         | Zonal Flux        |
| May–June 96  | 8°S–10°N, 95°W–140°W | Malcolm Baldrige | EqPac Spring 1996 |
| May–June 96  |                      | Melville         | IronEx-2          |
| June–Dec 96  | 8°S–8°N, 180°–95°W   | Ka'imimoana      | TAO               |
| Oct–Nov 96   | 8°S–8°N, 180°        | L'Atalante       | Ebene             |
| Jan 97       |                      | Kaiyo            | KY-97-1           |
| Feb–Dec 97   | 8°S–8°N, 180°–95°W   | Ka'imimoana      | TAO               |
| Jan 98       | 0°, 138°E–165°W      | Kaiyo            | KY-98-1           |
| Jan 98       | 0°, 180°–163°W       | Mirai            | MR-98-1           |
| Feb 98       | 0°, 145°E–170°W      | Mirai            | MR98-2            |
| Feb–Oct 98   | 8°S–10°N, 180°–95°W  | Ka'imimoana      | TAO               |
| Oct–Nov 98   | 8°S–8°N, 180°–155°W  | Ka'imimoana      | TAO               |
| Oct–Nov 98   | 8°S–8°N, 95°W–110°W  | Ronald Brown     | TAO               |
| Feb 99       | 0°, 138°E–162°E      | Kaiyo            | KY-99-1           |
| Jan–May 99   | 8°S–10°N, 95°W–140°W | Ka'imimoana      | TAO               |

## References

- Archer, D., Aiken, J., Balch, W., Barber, D., 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., 1997. A meeting place of great ocean currents: shipboard observations of a convergent front at 2°N in the Pacific. *Deep-Sea Research II* 44, 1827–1849.
- Aufdenkampe, A.K., Murray, J.W., 2002. Controls on new production: the role of iron and physical processes. *Deep-Sea Research II* 49, 2649–2668.
- Aufdenkampe, A.K., McCarthy, J.J., Rodier, M., Navarette, C., Dunne, J., Murray, J.W., 2001. Estimation of new production in the tropical Pacific. *Global Biogeochemical Cycles* 15, 101–113.
- Aufdenkampe, A.K., McCarthy, J.J., Navarette, C., Rodier, M., Dunne, J., Murray, J.W., 2002. Biogeochemical controls on new production in the tropical Pacific. *Deep-Sea Research II* 49, 2619–2648.
- Barber, R.T., Sanderson, M.P., Lindley, S.T., Chai, F., Newton, J., Trees, C.C., Foley, D.G., Chavez, F.P., 1996. Primary productivity and its regulation in the equatorial Pacific during and following the 1991–1992 El Niño. *Deep-Sea Research II* 43, 933–969.
- Binder, B.J., Chisholm, S.W., Olson, R.J., Frankel, S.L., Worden, A.Z., 1996. Dynamics of picophytoplankton, ultraphytoplankton and bacteria in the central equatorial Pacific. *Deep-Sea Research II* 43, 907–931.
- Binder, B.J., DuRand, M.D., 2002. Diel cycles in surface waters of the equatorial Pacific. *Deep-Sea Research II* 49, 2601–2617.
- Bricaud, A., Roesler, C.S., Parslow, J.S., Ishizaka, J., 2002. Bio-optical studies during the JGOFS-equatorial Pacific program: a contribution to the knowledge of the equatorial system. *Deep-Sea Research II* 49, 2533–2599.
- Brown, S.L., Landry, M.R., Neveux, J., Dupouy, C., submitted. Microbial community abundance and biomass along a 180° transect in the equatorial Pacific during an ENSO cold phase. *Journal of Geophysical Research*, submitted for publication.
- Buesseler, K.O., Andrews, J.A., Hartman, M.C., Belostock, R., Chai, F., 1995. Regional estimates of the export flux of particulate organic carbon derived from thorium-234 during the JGOFS EqPac program. *Deep-Sea Research II* 42, 777–804.
- Chai, F., Dugdale, R.C., Peng, T.-H., Wilkerson, F.P., Barber, R.T., 2002. One-dimensional ecosystem model of the equatorial Pacific upwelling system, Part I: model development and silicon and nitrogen cycle. *Deep-Sea Research II* 49, 2713–2745.
- Champalbert, G., Neveux, J., Gaudy, R., Le Borgne, R., submitted. Diel variations of in situ grazing rates of copepods in the HNLC equatorial Pacific Ocean (0°, 3°S, 180°). *Journal of Geophysical Research*, submitted for publication.
- Chavez, F.P., Buck, K.R., Service, S.R., Newton, J., Barber, R.T., 1996. Phytoplankton variability in the central and eastern tropical Pacific. *Deep-Sea Research II* 43, 835–870.

- Chavez, F.P., Strutton, P.G., Friederich, G.E., Feely, R.A., Feldman, G.C., Foley, D.G., McPhaden, M.J., 1999. Biological and chemical response of the equatorial Pacific ocean to the 1997–1998 El Niño. *Science* 286, 2126–2131.
- Claustre, H., Morel, A., Babin, M., Cailliau, C., Marie, D., Marty, J.-C., Tailliez, D., Vulot, D., 1999. Variability in particle attenuation and chlorophyll fluorescence in the tropical Pacific: scales, patterns and biogeochemical implications. *Journal of Geophysical Research* 104, 3401–3422.
- Coale, K.H., Johnson, K.S., Fitzwater, S.E., Gordon, R.M., Tanner, S., Chavez, F.P., Ferioli, L., Sakamoto, C., Rogers, P., Millero, F., Steinberg, P., Nightingale, P., Cooper, D., Cochlan, W.P., Landry, M.R., Constantinou, J., Rollwagen, G., Travnica, A., Kudela, R., 1996. A massive phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the equatorial Pacific Ocean. *Nature* 383, 495–501.
- Cushing, D.H., 1959. The seasonal variation in oceanic production as a problem in population dynamics. *Journal Conseil International Exploration Mer* 24, 455–464.
- Dam, H.G., Zhang, X., Butler, M., Roman, M.R., 1995. Mesozooplankton grazing and metabolism at the equator in the central Pacific: implications for carbon and nitrogen fluxes. *Deep-Sea Research II* 42, 735–755.
- Dandonneau, Y., Neveux, J., 1997. Diel variations of in vivo fluorescence in the eastern equatorial Pacific: an unvarying pattern. *Deep-Sea Research I* 44, 1869–1880.
- Duce, R.A., Tindale, N.W., 1991. Atmospheric transport of iron and its deposition in the ocean. *Limnology and Oceanography* 36, 1715–1726.
- Dugdale, R.C., Barber, R.T., Chai, F., Peng, T.-H., Wilkerson, F.P., 2002a. One-dimensional ecosystem model of the equatorial Pacific upwelling system, Part II: sensitivity analysis and comparison with JGOFS EqPac data. *Deep-Sea Research II* 49, 2747–2768.
- Dugdale, R.C., Wischmeyer, A.G., Wilkerson, F.P., Barber, R.T., Chai, F., Jiang, M.-S., Peng, T.-H., 2002b. Meridional asymmetry of source nutrients to the equatorial Pacific upwelling ecosystem and its potential impact on ocean-atmosphere CO<sub>2</sub> flux; a data and modeling approach. *Deep-Sea Research II* 49, 2513–2531.
- Dunne, J.P., Murray, J.W., Rodier, M., Hansell, D.A., 2000. Export flux in the western and central equatorial Pacific: zonal and temporal variability. *Deep-Sea Research. I* 47, 901–936.
- Dunne, J.P., Murray, J.W., Young, J., Balistreri, S., Bishop, J., 1997. <sup>234</sup>Th and particle cycling in the central equatorial Pacific. *Deep-Sea Research II* 44, 2049–2083.
- Eldin, G., Rodier, M., Radenac, M.-H., 1997. Physical and nutrient variability in the upper equatorial Pacific associated with westerly wind forcing and wave activity in October 1994. *Deep-Sea Research II* 44, 1783–1800.
- Eldin, G., Rodier, M., submitted. Ocean physics and nutrient fields along 180° during an ENSO cold phase. *Journal of Geophysical Research*, submitted for publication.
- Feely, R.A., Wanninkhof, R., Cosca, C.E., Murphy, P.P., Lamb, M.F., Steckley, M.D., 1995. CO<sub>2</sub> distributions in the equatorial Pacific during the 1991–1992 ENSO event. *Deep-Sea Research II* 42 (2–3), 365–386.
- Feely, R.A., Wanninkhof, R., Goyet, C., Archer, D.E., Takahashi, T., 1997. Variability of CO<sub>2</sub> distributions and sea-air fluxes in the central and eastern equatorial Pacific during the 1991–1994 El Niño. *Deep-Sea Research II* 44 (9–10), 1851–1867.
- Feely, R.A., Wanninkhof, R., Takahashi, T., Tans, P., 1999. Influence of El Niño on the equatorial Pacific contribution of atmospheric CO<sub>2</sub> accumulation. *Nature* 398, 597–601.
- Feely, R.A., Boutin, J., Cosca, C.E., Dandonneau, Y., Etcheto, J., Inoue, H.Y., Ishii, M., Le Quéré, C., Mackey, D., McPhaden, M., Metzl, N., Poisson, A., Wanninkhof, R., 2002. Seasonal and interannual variability of CO<sub>2</sub> in the equatorial Pacific. *Deep-Sea Research II* 49, 2443–2469.
- Flament, P.J., Kennan, S.C., Know, R.A., Niiler, P.P., Bernstein, R.L., 1996. The three-dimensional structure of an upper ocean vortex in the tropical Pacific ocean. *Nature* 383, 610–613.
- Foley, D.G., Dickey, T.D., McPhaden, M.J., Bidigare, R.R., Lewis, M.R., Barber, R.T., Lindley, S.T., Garside, C., Manov, D.V., McNeil, J.D., 1997. Longwaves and primary productivity variations in the equatorial Pacific at 0°, 140°W. *Deep-Sea Research II* 44, 1801–1826.
- Friedrichs, M.A.M., Hofmann, E.E., 2001. Physical control of biological processes in the central equatorial Pacific ocean. *Deep-Sea Research I* 48, 1023–1069.
- Gordon, R.M., Coale, K.H., Johnson, K.S., 1997. Iron distributions in the equatorial Pacific: implications for new production. *Limnology and Oceanography* 141, 419–431.
- Gupta, L.P., Kawahata, H., 2002. Impact of ENSO variability on the flux and composition of sinking POM in the western equatorial Pacific Ocean: amino acids and hexosamines. *Deep-Sea Research II* 49, 2769–2782.
- Hansell, D.A., Carlson, C.A., Bates, N.R., Poisson, A., 1997. Horizontal and vertical removal of organic carbon in the equatorial Pacific ocean: a mass balance assessment. *Deep-Sea Research II* 44, 2115–2130.
- Harrison, D.E., 1996. Vertical velocity in the central tropical Pacific: a circulation model perspective for JGOFS. *Deep-Sea Research II* 43, 687–705.
- Inoue, H.Y., Ishii, M., Matsueda, H., Ahoyama, M., 1996. Changes in longitudinal distribution of the partial pressure of CO<sub>2</sub> (pCO<sub>2</sub>) in the central and western equatorial Pacific, west of 160°W. *Geophysical Research Letters* 23, 1781–1784.
- Inoue, H.Y., Ishii, M., Matsueda, H., Saito, S., Aoyama, M., Tokieda, T., Midorikawa, T., Nemoto, K., Kawano, T., Asanuma, I., Ando, K., Yano, T., Murata, A., 2001. Distributions and variations in the partial pressure of CO<sub>2</sub> in surface waters (pCO<sub>2</sub><sup>w</sup>) of the central and western equatorial Pacific during the 1997/98 El Niño event. *Marine Chemistry* 76, 59–75.
- JGOFS, 1989. Report of the JGOFS Pacific planning workshop, Honolulu, September 1989. JGOFS Report No. 3, pp. 69.



- Kawahata, H., Nishimura, A., Gagan, M.K., 2002. Seasonal change in foraminiferal production in the western equatorial Pacific warm pool: evidence from sediment trap experiments. *Deep-Sea Research II* 49, 2783–2800.
- Kessler, W.S., McPhaden, M.J., 1995. The 1991–1993 El Niño in the central Pacific. *Deep-Sea Research II* 42, 295–333.
- Kiefer, D.A., 1973. Chlorophyll *a* fluorescence in marine centric diatoms: responses of chloroplasts to light and nutrient stress. *Marine Biology* 23, 39–46.
- Kirchman, D.L., Rich, J.H., Barber, R.T., 1995. Biomass and biomass production of heterotrophic bacteria along 140°W in the equatorial Pacific: effect of temperature on the microbial loop. *Deep-Sea Research II* 42, 603–619.
- Kobayashi, F., Takahashi, K., 2002. Distribution of diatoms along the equatorial transect in the western and central Pacific during the 1999 La Niña conditions. *Deep-Sea Research II* 49, 2801–2821.
- Landry, M.R., Kirchman, D.L., 2002. Microbial community structure and variability in the tropical Pacific. *Deep-Sea Research II* 49, 2669–2693.
- Landry, M.R., Kirshtein, J., Constantinou, J., 1996. Abundances and distributions of picoplankton populations in the central equatorial Pacific from 12°N to 12°S, 140°W. *Deep-Sea Research II* 43, 871–890.
- Landry, M.R., Barber, R.T., Bidigare, R.R., Chai, F., Coale, K.H., Dam, H.G., Lewis, M.R., Lindley, S.T., McCarthy, J.J., Roman, M.R., Stoecker, D.K., Verity, P.G., White, J.R., 1997. Iron and grazing constraints on primary production in the central equatorial Pacific: an EqPac synthesis. *Limnology and Oceanography* 42, 405–418.
- Landry, M.R., Constantinou, J., Latasa, M., Brown, S.L., Bidigare, R.R., Ondrusek, M.E., 2000a. Biological response to iron fertilization in the eastern equatorial Pacific (IronEx II). III. Dynamics of phytoplankton growth and microzooplankton grazing. *Marine Ecology Progress Series* 201, 57–72.
- Landry, M.R., Ondrusek, M.E., Tanner, S.J., Brown, S.L., Constantinou, J., Bidigare, R.R., Coale, K.H., Fitzwater, S., 2000b. Biological response to iron fertilization in the eastern equatorial Pacific (IronEx II). I. Microplankton community abundances and biomass. *Marine Ecology Progress Series* 201, 27–42.
- Landry, M.R., Brown, S.L., Neveux, J., Dupouy, C., Blanchot, J., Christensen, S., Bidigare, R.R., submitted. Phytoplankton growth and microzooplankton grazing in HNLC waters of the equatorial Pacific: community and taxa-specific rate assessments based on pigment and flow cytometric analyses. *Journal of Geophysical Research*, submitted for publication.
- Le Borgne, R., Landry, M.R., submitted. EBENE: A JGOFS investigation of plankton variability and trophic interactions in the equatorial Pacific (180°). *Journal of Geophysical Research*, submitted for publication.
- Le Borgne, R., Rodier, M., 1997. Net zooplankton and the biological pump: a comparison between the oligotrophic and mesotrophic equatorial Pacific. *Deep-Sea Research II* 44, 2003–2023.
- Le Borgne, R., Rodier, M., Le Bouteiller, A., Murray, J.W., 1999. Zonal variability of plankton and particle export flux in the equatorial Pacific upwelling between 165°E and 150°W. *Oceanologica Acta* 22, 57–66.
- Le Borgne, R., Champalbert, G., Gaudy, R., submitted. Mesozooplankton biomass and composition in the equatorial Pacific along 180. *Journal of Geophysical Research*, submitted for publication.
- Le Borgne, R., Barber, R.T., Delcroix, T., Inoue, H.Y., Mackey, D.J., Rodier, M., 2002. Pacific warm pool and divergence: temporal and zonal variations on the equator and their effects on the biological pump. *Deep-Sea Research II* 49, 2471–2512.
- Le Bouteiller, A., Blanchot, J., 1991. Size distribution and abundance of phytoplankton in the Pacific equatorial upwelling. *La Mer* 29, 175–179.
- Le Bouteiller, A., Blanchot, J., Rodier, M., 1992. Size structure patterns of phytoplankton in the western Pacific: towards a generalization for the tropical ocean. *Deep-Sea Research I* 39, 805–823.
- Le Bouteiller, A., Leynaert, A., Le Borgne, R., Neveux, J., Rodier, M., Blanchot, J., submitted. Changes of total and new primary production with nutrient in the equatorial Pacific (180°) during an ENSO cold event. *Journal of Geophysical Research*, submitted for publication.
- Lee, K., Wanninkhof, R., Takahashi, T., Doney, S.C., Feely, R.A., 1998. Low interannual variability in recent oceanic uptake of atmospheric carbon dioxide. *Nature* 396, 155–159.
- Leonard, C.L., McClain, C.R., Murtugudde, R., Hofmann, E.E., Harding Jr., L.W., 1999. An iron based ecosystem model of the central equatorial Pacific. *Journal of Geophysical Research* 104, 1325–1341.
- Le Quéré, C., Orr, J.C., Monfray, P., Aumont, O., 2000. Interannual variability of the oceanic sink of CO<sub>2</sub> from 1979 through 1997. *Global Biogeochemical Cycles* 14, 1247–1265.
- Longhurst, A.R., Bedo, A., Harrison, W.G., Head, E.J., Horn, E.P., Irwin, B., Morales, C., 1989. NFLUX: a test of vertical nitrogen flux by diel migrant biota. *Deep-Sea Research* 36, 1705–1719.
- Loukos, H., Frost, B., Harrison, D.E., Murray, J.W., 1997. Ecosystem model with iron limitation of primary production in the equatorial Pacific at 140°W. *Deep-Sea Research II* 44, 2221–2250.
- Mackey, D.J., Parslow, J., Higgins, H.W., Griffiths, F.B., O'Sullivan, J.E., 1995. Plankton productivity and biomass in the western equatorial Pacific: biological and physical controls. *Deep-Sea Research II* 42, 499–533.
- Mackey, D.J., Parslow, J.S., Griffiths, F.B., Higgins, H.W., Tilbrook, B., 1997. Phytoplankton productivity and the carbon cycle in the western equatorial Pacific under ENSO and non-ENSO conditions. *Deep-Sea Research II* 44, 1951–1978.
- Mackey, D.J., Blanchot, J., Higgins, H.W., Neveux, J., 2002. Phytoplankton abundances and community structure in the equatorial Pacific. *Deep-Sea Research II* 49, 2561–2582.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal climate oscillation with

- impacts on salmon production. *Bulletin of the American Meteorological Society* 78 (6), 1069–1079.
- McCarthy, J.J., Garside, C., Nevins, J.L., Barber, R.T., 1996. New production along 140°W in the equatorial Pacific during and following the 1992 El Niño event. *Deep-Sea Research II* 43, 1065–1093.
- McClain, C.R., Christian, J.R., Signorini, S.R., Lewis, M.R., Asanuma, I., Turk, D., Dupouy, C., 2002. Satellite ocean-color observations of the tropical Pacific Ocean. *Deep-Sea Research II* 49, 2533–2560.
- Minas, H.J., Minas, M., Packard, T.T., 1986. Productivity in upwelling areas deduced from hydrographic and chemical fields. *Limnology and Oceanography* 31, 1182–1206.
- Murray, J.W., 1996. A US JGOFS Process study in the equatorial Pacific. Part 2. *Deep-Sea Research II* 43 (4–6), 687–1435.
- Murray, J.W., Barber, R.T., Roman, M.R., Bacon, M.P., Feely, R.A., 1994. Physical and biological controls on carbon cycling in the equatorial Pacific. *Science* 266, 58–65.
- Murray, J.W., Johnson, E., Garside, C., 1995. A US JGOFS Process Study in the equatorial Pacific (EqPac): introduction. *Deep-Sea Research II* 42, 275–293.
- Murray, J.W., Young, J., Newton, J., Dunne, J., Chapin, T., Paul, B., McCarthy, J.J., 1996. Export flux of particulate organic carbon from the central equatorial Pacific determined using a combined drifting trap-<sup>234</sup>Th approach. *Deep-Sea Research II* 43, 1095–1132.
- Murray, J.W., Le Borgne, R., Dandonneau, Y., 1997. JGOFS studies in the equatorial Pacific. *Deep-Sea Research II* 44, 1759–1763.
- Murtugudde, R.G., Signorini, S.R., Christian, J.R., Busalacchi, A.J., McClain, C.R., Picaut, J., 1999. Ocean color variability of the tropical Indo-Pacific basin observed by SeaWiFS during 1997–1998. *Journal of Geophysical Research* 104, 18351–18366.
- Neveux, J., Dupouy, C., Blanchot, J., Le Bouteiller, A., Landry, M.R., Brown, S.L., submitted. Diel dynamics of chlorophylls in HNLC waters of the equatorial Pacific (180°W): Interactions of growth, grazing, physiological responses and mixing. *Journal of Geophysical Research*, submitted for publication.
- Radenac, M.-H., Rodier, M., 1996. Nitrate and chlorophyll distributions in relation to thermohaline and current structures in the western tropical Pacific during 1985–1989. *Deep-Sea Research II* 43, 725–752.
- Rodier, M., Le Borgne, R., 1997. Export flux of particles at the equator in the western and central Pacific ocean. *Deep-Sea Research II* 44, 2085–2113.
- Rodier, M., Eldin, G., Le Borgne, R., 2000. The western boundary of the equatorial Pacific upwelling: some consequences of climatic variability on hydrological and planktonic properties. *Journal of Oceanography* 56, 463–471.
- Rollwagen Bollens, G.C., Landry, M.R., 2000. Biological response to iron fertilization in the eastern equatorial Pacific (IronEx II). II. Mesozooplankton abundance, biomass, depth distribution and grazing. *Marine Ecology Progress Series* 201, 43–56.
- Roemmich, D., Morris, M., Young, W.R., Donguy, J.R., 1994. Fresh equatorial jets. *Journal of Physical Oceanography* 24, 540–558.
- Roman, M.R., Dam, H.G., Gauzens, A.L., Urban-Rich, J., Foley, D.G., Dickey, T.D., 1995. Zooplankton variability on the equator at 140°W during the JGOFS EqPac study. *Deep-Sea Research II* 42, 673–693.
- Roman, M.R., Dam, H.G., Le Borgne, R., Zhang, X., 2002. Latitudinal comparisons of equatorial Pacific zooplankton. *Deep-Sea Research II* 49, 2695–2711.
- Takahashi, T., Feely, R.A., Weiss, R.F., Wanninkhof, R., Chipman, D.W., Sutherland, S.C., Takahashi, T.T., 1997. Global air–sea–flux of CO<sub>2</sub>: an estimate based on measurements of sea–air pCO<sub>2</sub> difference. *Proceedings of the National Academy of Science USA* 94, 8292–8299.
- Takahashi, T., Wanninkhof, R.H., Feely, R.A., Weiss, R.F., Chipman, D.W., Bates, N., Olafsson, J., Sabine, C., Sutherland, S.C., 1999. Net sea–air CO<sub>2</sub> flux over the global oceans: an improved estimate based on the sea–air pCO<sub>2</sub> difference. 2nd International Symposium on CO<sub>2</sub> in the Oceans, the 12th Global Environment Tsukuba, 18–22 January 1999, Tsukuba, Japan, pp. 9–15.
- Tans, P.P., Fung, I.Y., Takahashi, T., 1990. Observational constraints on the global atmospheric CO<sub>2</sub> budget. *Science* 247, 1431–1438.
- Turk, D., Lewis, M.R., Harrison, W.G., Kawano, T., Asanuma, I., 2001. Geographical distribution of new production in the western/central equatorial Pacific during El Niño and non El Niño conditions. *Journal of Geophysical Research* 106, 4501–4515.
- Vaulot, D., Marie, D., 1999. Diel variability of photosynthetic picoplankton in the equatorial Pacific. *Journal of Geophysical Research* 104, 3297–3310.
- Vaulot, D., Marie, D., Olson, R.J., Chisholm, S.W., 1995. Growth of *Prochlorococcus*, a photosynthetic prokaryote, in the equatorial Pacific. *Oceanographic Science* 268, 1480–1482.
- Walsh, J.J., 1976. Herbivory as a factor in patterns of nutrient utilization in the sea. *Limnology and Oceanography* 21, 1–13.
- Walsh, I.D., Chung, S.P., Richardson, M.J., Gardner, W.D., 1995. The diel cycle in the integrated particle load in the equatorial Pacific: a comparison with primary production. *Deep-Sea Research II* 42, 465–477.
- White, J.R., Zhang, X., Welling, L.A., Roman, M.R., Dam, H.G., 1995. Latitudinal gradients in zooplankton biomass in the tropical Pacific at 140°W during the JGOFS EqPac study: effects of el niño. *Deep-Sea Research II* 42, 715–733.
- Wyrki, K., 1981. An estimate of equatorial upwelling in the Pacific. *Journal of Geophysical Research* 11, 1205–1214.
- Yamashita, H., Takahashi, K., Fujitani, N., 2002. Zonal and vertical distribution of radiolaria in the western and central equatorial Pacific in January 1999. *Deep-Sea Research II* 49, 2823–2862.
- Yoder, J.A., Ackleson, S.G., Barber, R.T., Flament, P., Balch, W.M., 1994. A line in the sea. *Nature* 371, 689–693.