7 The Northeastern Pacific Abyssal Plain

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7.1 Introduction

Abyssal plains occupy approximately two-thirds of the global sea floor, or two-fifths of the total surface of the earth. Owing to their large distance from the heavily populated continental margins, they are influenced only indirectly by land-based human activities, e.g. through atmospheric perturbations. However, planned *in situ* activities, such as the mining of manganese nodules, iron fertilization and commercial fishing may dramatically affect abyssal ecosystems in the future. In this chapter, we review the major geochemical and ecological characteristics of the northeastern Pacific abyssal plains, a comparatively well-studied region by deep sea standards, and examine the system's resilience in view of climatic change and *in situ* human activities.

For the purposes of this review, we define the northeastern Pacific abyssal plain (NEPAP) as the oceanic region north of the equator and east of 180^o W with waters deeper than 4000 m and slope angles less than 0.001 (Seibold & Berger, 1996). Although some recent authors consider the abyssal region in the world oceans to extend, ecologically speaking, from approximately 2000 to 6000 m depth (Gage & Tyler, 1991), the continental slope and rise in the northeast Pacific (which reach ~4000 m) are ecologically distinct from the general abyssal plain. This is because the narrowness of the continental shelf and slope in the northeast Pacific yields steeper inclines and more energetic hydrodynamic conditions between 2000 and 4000 m depths than on the abyssal plains, allowing significant downslope transport of material from the continental margin (e.g. Smith & Demopoulos, 2003). Figure 7.1 and Table 7.1 indicate the region under consideration and major study sites and stations referred to here.

7.2 Key habitat parameters of deep seafloor communities

Deep seafloor communities are shaped by a number of key parameters that directly affect the nature and abundance of living organisms and their interactions with seafloor geochemistry. These parameters include (a) substratum type, (b) near-bottom hydrodynamic regime, (c) bottom-water oxygen concentration, (d) sinking particulate-organic-carbon (POC) flux, and (e) sediment redox conditions. Below, we describe these parameters and their variation in the northeastern abyssal Pacific.

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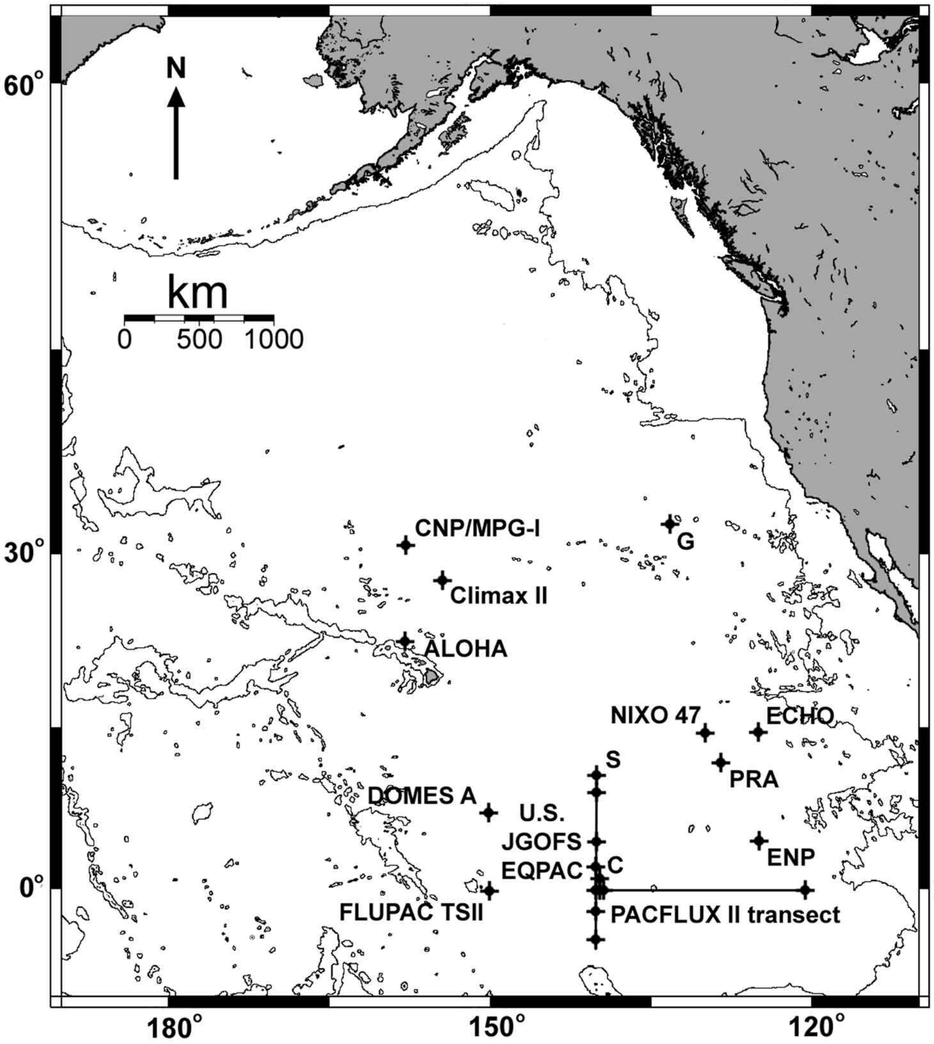

Fig. 7.1 Major study sites and stations in the northeastern abyssal Pacific referred in this chapter (see Table 7.1 for details). The 4000 m bathymetric contour is also shown.

7.2.1 Key habitat parameters

7.2.1.1 Substratum type

The type of substratum often determines, or at least is correlated with, trophic mode of many of the dominant animals, particularly the macro- and megafauna. Hard substrata are mostly inhabited by suspension feeders, whereas sediments typically are dominated by deposit feeders feeding primarily on surface sediments.

Most of the deep seafloor is covered by sediments, consisting of silica and calcium carbonate tests of phytoplankton, and of terrigenous clays and other

Table 7.1 Major study sites and stations in the northeastern Pacific referred to in this chapter

Region	Site or study name	Site location	References
Eutrophic	EqPac transect	5^{o} S-5^{o} N 140^{o} W	Honjo *et al.* (1995); Hammond *et al.* (1996); Berelson *et al.* (1997); Smith *et al.* (1997); Brown *et al.* (2001)
	PACFLUX II	0-1^{o} N 103-140^{o} W	Hammond *et al.* (1996)
	FLUPAC TSII	0^{o} N 150^{o} W	Dunne *et al.* (2000)
	MANOP station C	1^{o} N 139^{o} W	Cochran (1985); Dymond and Collier (1988)
Mesotrophic	EqPac transect	5-9^{o} N 140^{o} W	Honjo *et al.* (1995); Hammond *et al.* (1996); Berelson *et al.* (1997); Smith *et al.* (1997); Brown *et al.* (2001)
	ENP	5^{o} N 125^{o} W	Mullineaux (1987)
	DOMES A	8^{o} 27’ N 150^{o} 47’ W	Paterson *et al.* (1998); Glover *et al.* (2002)
	MANOP station S	11^{o} N 140^{o} W	Cochran (1985); Dymond and Collier (1988)
	PRA	12^{o} 57’ N 128^{o} 19.5’ W	Paterson *et al.* (1998); Glover *et al.* (2002)
	ECHO	14^{o} 40’ N 125^{o} 26’ W	Paterson *et al.* (1998); Glover *et al.* (2002)
	NIXO 47	14^{o} 0-40’ N 130^{o} 40-60’ W	Renaud-Mornant and Goubault (1990)
Oligotrophic	ALOHA-HOT	22 ^{o} 45’ N 158^{o} W	Glover *et al.* (2002); Smith *et al.* (2002)
	Climax II	Diameter of 50 km centered on 28^{o} 28’ N 155^{o} 20’ W	Hessler and Jumars (1974); Paterson *et al.* (1998)
	CNP/MPG-I	30-32^{o} N 157-159^{o} W	Smith *et al.* (1983); Snider *et al.* (1984); Mullineaux (1987); Smith (1987); Smith (1992)
	G	34 ^{o} N 133^{o} W	Smith *et al.* (1983); Smith (1987)

mineral grains transported by turbidites or by winds (Seibold & Berger, 1996). Hard substrata are limited to regions of recent volcanic activity, such as mid-ocean ridges, submarine canyons, seamounts and volcanic islands, and areas of very low sedimentation conditions, which allow the accretion of ferromanganese nodules (Ghosh & Mukhopadhyay, 2000; McMurtry, 2001).

7.2.1.2 Near-bottom currents.

Current regimes are also correlated with feeding mode. Very slow currents yield low horizontal particle flux and allow even fine particles to settle. This, combined with the absence of primary production in the dark abyss, yield very low concentrations of suspended food particles, often making suspension feeding unsustainable. High currents can cause sediment erosion and transport, disrupting most feeding activities and burying slow-moving organisms (Aller, 1989). Intermediate currents allow for a diversity of feeding modes and redistribute organic matter (e.g. phytodetritus) deposited on the sediment surface, causing spatial and temporal heterogeneity in resources (Lampitt, 1985; Smith *et al.*, 1996; Bett *et al.*, 2001).

7.2.1.3 Bottom-water oxygen.

Oxygen is a metabolic requirement for all metazoans and for aerobic metabolism in microbial taxa. Below a concentration of approximately 0.5 ml l^{-1}, oxygen availability may affect community structure by excluding less tolerant taxa (Diaz & Rosenberg, 1995; Levin and Gage, 1998). Deep sea regions underlying high productivity areas and/or bathed in *old* water masses (i.e. water masses not recently in contact with the atmosphere) are particularly likely to experience low oxygen concentrations (Diaz & Rosenberg, 1995).

7.2.1.4 Sinking POC flux.

Organic matter synthesized at the ocean's surface through photosynthesis constitutes the primary source of energy for seafloor communities (excluding hydrothermal vents and cold seeps). During sinking, most of the photosynthesized POC decomposes in the water column (Field *et al.*, 1998; Hartnett *et al.*, 1998). The amount of decomposition depends, in part, on oxygen presence, sinking velocity and water column depth (Suess, 1980; Jahnke, 1990; Hartnett *et al.*, 1998). Sinking matter containing ballast minerals such as silica and calcium carbonate will sink faster and therefore may dominate POC flux to the deep ocean (Armstrong *et al.*, 2001). Because very little of the primary production in the surface ocean reaches the abyssal seafloor (typically a few percent), the seafloor communities in abyssal regions are among the most food- and biomass-poor on the planet. The total biomass of many components of abyssal benthic communities appear to be correlated with annual POC flux (Rowe *et al.*, 1991; Smith *et al.*, 1997), whereas only microbes have been shown to respond to seasonal fluctuations in POC flux (reviewed by Gooday, 2002).

7.2.1.5 Redox conditions.

The most common reduction reactions taking place in the deep-sea are aerobic respiration, denitrification, and iron and manganese reduction. In this respect, deep sea sediments differ from most coastal sediments. This difference is attributed to relatively high POC flux and sediment organic-carbon content in shallow water, where organic-carbon decomposition depletes oxygen and, in turn, other thermodynamically preferred microbial electron acceptors (in sequence, nitrate, iron, manganese), leaving sulphate reduction as the major metabolic process (Berner, 1980). In abyssal sediments, labile POC typically becomes depleted prior to the advent of sulphate reduction. Nonetheless, along gradients of POC flux to the abyssal seafloor, the relative importance of the various electron acceptors in microbial metabolism, and hence sediment redox conditions, will vary (e.g. Hammond *et al.*, 1996).

7.2.2 Variation of key habitat parameters in the northeastern Pacific abyssal plain

7.2.2.1 Sediment types

Most of the NEPAP is covered with soft sediments. The character of these soft sediments is largely determined by the surface productivity of the overlying ocean. Within the equatorial divergence zone, sediments shallower than ~4600 m are rich in calcium carbonate (50-90% by weight) and poor in organic carbon (<0.3% by weight) because of the large contribution of foraminiferan and pteropod tests (Jahnke, 1996); at greater depths, sediments are primarily siliceous muds comprised of diatom and radiolarian tests. Beyond the equatorial zone of high productivity (spanning roughly 5° S-5° N at 140° W), aeolian red clay particles (typically <6 μm in diameter) of terrigenous and volcanic origin dominate abyssal sediments (Hessler & Jumars, 1974; Smith *et al.*, 1983). These sediments are poor in organic matter (<0.25% organic carbon by weight; Hessler and Jumars, 1974) relative to siliceous muds, which contain 0.25-0.5% of organic carbon by weight (Berger, 1974).

The dominant hard substratum in the NEPAP is the exposed surface of ferromanganese nodules. These nodules precipitate over millions of years in areas of very low sedimentation, and range in size from 0.5 to 20 cm (McMurtry, 2001). In regions of high occurrence, such as between the Clarion and Clipperton fracture zones, they may cover more than 75% of the seafloor, whereas in sediments underlying the North Pacific oligotrophic gyre, they cover approximately 30% (Hessler & Jumars, 1974; Mullineaux, 1987; Ghosh & Mukhopadhyay, 2000).

7.2.2.2 Near-bottom currents and oxygen concentrations

Most of the deep waters in contact with the abyssal sediments are a mixture of North Atlantic and Antarctic bottom-water masses. They are relatively saline and fairly cold (0.5-1.5° C). Currents at these depths typically are slow and do not impose shear stress of sufficient magnitude to transport sediments (Gardner *et al.*, 1984; Demidova, 1999).

Although bottom-water masses are relatively old in the NEPAP, bottom-water oxygen concentrations remain well above 2 ml l^{-1} and hence they probably do not influence benthic community structure (Levin & Gage, 1998). In the eastern tropical Pacific, oxygen-minimum zones appear in mid-water (100-1000 m) due to intense water column decomposition, but they do not extend to abyssal depths (Wishner *et al.*, 1990).

7.2.2.3 POC flux and redox conditions

Due to the extreme food limitation of the NEPAP and its isolation from many other potential sources of energy and matter, POC flux constitutes a critical variable determining a multitude of habitat characteristics, such as sediment type (oozes and the presence or absence of ferromanganese nodules), redox conditions, rates of biogeochemical processes, and the biomass and structure of benthic communities (Hammond *et al.*, 1996; Levin & Gage, 1998; McMurtry, 2001). Two major conditions determining POC flux to aphotic marine sediments are surface primary production and sinking time (Field *et al.*, 1998). Since the depth of the water column within the NEPAP is relatively constant, any observed variations in most of the above characteristics will be determined by variations in surface primary productivity, or more accurately, export production, at each location. Based on POC flux to the sediments, then, the NEPAP along roughly 140^o W can be divided into three zones:

(a) the *eutrophic abyss*, from the equator up to 5^o N, where the POC flux is ~1-2 g C m^{-2} y^{-1} (Berelson *et al.*, 1997; Dymond & Collier, 1988; Honjo *et al.*, 1995). This zone is restricted to 1-2^o N as one moves west towards 180^o W (Jahnke & Jackson, 1992).
(b) the *mesotrophic abyss*, from 5^o N to 15^o N, where the POC flux is ~0.5-1.6 g C m^{-2} y^{-1} (Dymond & Collier, 1988; Honjo *et al.*, 1995); and
(c) the *oligotrophic abyss*, underlying the central North Pacific gyre, where POC fluxes typically are lower than 0.5 g C m^{-2} y^{-1} (Smith, 1987; Smith *et al.*, 2002).

In consequence, seafloor geochemical conditions across these different zones co-vary with primary production rates and POC fluxes to the sediments. Profiles of dissolved O_2 in sedimentary porewater exhibit deeper oxygen penetration with increasing distance from the equator (Hammond *et al.*, 1996). This pattern is explained by the observed oxygen consumption by metabolism within sediments, which decreases from 0.24-0.6 mol m^{-2} y^{-1} in the eutrophic abyss to less than 0.06 mol m^{-2} y^{-1} in the oligotrophic abyss (Hammond *et al.*, 1996; Jahnke & Jackson, 1992). As a consequence, oxygen becomes significantly depleted within 4-6 cm of the sediment-water interface within eutrophic abyssal sediments, suggesting an increasing importance of anaerobic decomposition in eutrophic abyssal sediments relative to oligotrophic sediments (Hammond et al., 1996).

7.3 Northeastern Pacific abyssal zones

Due to the overarching significance of POC flux in shaping abyssal communities, our discussion of the Northeastern Pacific abyssal plain ecosystem is organized into sections on the eutrophic, mesotrophic and oligotrophic abyss. The gradients in POC flux across the NEPAP explain gradients in the total benthic biomass, sediment community oxygen consumption, other solute fluxes into and out of the sediments and, consequently, elemental cycling rates.

7.3.1 The eutrophic equatorial abyss

The eutrophic equatorial abyss is characterized by high primary productivity of surface waters within the equatorial divergence zone, and POC fluxes to the abyssal seafloor of ~ 1-2 g C m^{-2} y^{-1} (Dymond & Collier, 1988; Honjo *et al.*, 1995; Berelson *et al.*, 1997). The region of the abyssal seafloor impacted by this productivity extends to 5^{o} N and S at 140^{o} W, gradually narrowing as one moves west. At the 180^{th} meridian, the eutrophic abyss extends only to $1\text{-}2^{o}$ N and S (Jahnke, 1996; Jahnke & Jackson, 1992). This yields an area of approximately 4.5 million square kilometers that annually receives approximately 8000 Gt of POC from surface waters. At times, about 3% of this flux may be recently deposited phytodetritus (Smith *et al.*, 1996), which may constitute an important resource for surface-deposit-feeding epifauna not observed in other zones.

The composition of the living community is summarized in Table 7.2. The megafaunal community, and especially the burrowing fraction, remain poorly sampled. The dominant metazoan megafauna are urchins, hexactinellid sponges of the genus *Hyalonema*, and epibenthic holothurians (Hoover, 1995; Smith & Demopoulos, 2003). Various protozoan agglutinating xenophyophores, especially of the genera *Reticulammina* and *Stannophyllum*, also are numerous and actually dominate megafaunal abundance (Smith & Demopoulos, 2003) but because of their high water content (~98%), they are unlikely to contribute greatly to biomass (Levin & Gooday, 1992). An indirect indicator of infaunal activities is feeding traces on the sediment surface and they suggest a significant presence of large echiurans (Smith & Demopoulos, 2003).

Macrofaunal abundance and biomass are both dominated by polychaetes (62% and 62% respectively), the rest being accounted for by tanaids, isopods and bivalves (Smith and Miller, in preparation). The vast majority (>90%) of individuals can be found at the top 3-5 cm of the sediment column (Smith & Demopoulos, 2003), an apparent response to localization of food resources near the sediment-water interface. Meiofauna are mostly represented by nematodes, which attain densities of 36-108000 individuals m^{-2} and biomasses of 1.3-12 mg m^{-2} at the top 1 cm of sediment (Brown *et al.*, 2001). Microbes, however, appear to contribute more to benthic biomass than macrofauna and meiofauna together. Where it has been quantified, microbial biomass may attain values of 0.2-0.3 g C m^{-2} (Smith *et al.*, 1997), roughly equivalent to a biomass of 1.3-1.6 g m^{-2}, assuming carbon constitutes approximately 16% of total biomass (Fenchel *et al.*, 1998; Madigan *et al.*, 2000).

Most of the polychaetes and nematodes in the eutrophic abyssal zone belong to families considered to be deposit feeders (e.g. Kukert & Smith, 1992). Their

Table 7.2 Benthic community components in the NEPAP. Large ranges in reported values may occasionally be due to differences in sediment depths analyzed. When possible, these differences have been normalized to a certain depth across regions

	Ecosystem Type		
Habitat Parameter	Eutrophic abyss	Mesotrophic abyss	Oligotrophic abyss
Sedimentary POC flux (g C m^{-2} y^{-1})	1.53-1.97(1)-(3)	0.26-1.65(2),(3)	0.04-0.76 (4),(5)
Megafaunal abundance (ind. m^{-2})	0.17-0.25(6),[a]	0.10-0.17(6),[b]	0.15 (7)
Megafaunal biomass (g wet wt m^{-2})	Not available	Not available	> 12.4-12.6 (7),[c]
Macrofaunal abundance (ind. m^{-2})	1200-2000(6),(8),(9)	60-1200(6),(8),(10)	12-160 (5),(10),(11)
Macrofaunal biomass (mg wet wt m^{-2})	400-600(6),(9)	120-400(6)	2.1-137 (5),(7)
Meiofaunal abundance (10^3 ind. m^{-2})	> 36-108(12),[d]	> 23-189(12),(13),[d]	10-232 (11),(12),(14),[e]
Meiofaunal biomass (mg wet wt m^{-2})	> 2.26-20.20(12),[f]	> 2.07-17.01(13),[g]	0.24-243 (11),(12),(14)
Microbial abundance (10^{12} ind. m^{-2})	20-25[h]	13-20[h]	0.56-2.4 (4),(14)
Microbial biomass (mg wet wt m^{-2})	1250-1563[i]	813-1250[i]	95-172 (4),(14)
Manganese nodule faunal abundance (10^3 ind. 0.25 m^{-2})	-	1.05-1.40(15)	0.7-1.0 (15)

[a] With xenophyophores, 1.9-5.9 ind. m^{-2} (Smith & Demopoulos, 2003).

[b] With xenophyophores, 2.35 ind. m^{-2} (C. Smith & Demopoulos, 2003).

[c] Estimated ash-free dry weight (AFDW) of the dominant holothurians and sea anemones at Station CNP back-calculated from reported AFDW carbon mass per unit area (Smith, 1992).

[d] Data available only for nematodes at 0-1 cm.

[e] Data available for foraminifera and metazoa, including nematodes.

[f] Biomass data available only for nematodes at 0-1 cm; projected to 0-5 cm using reported contribution of 0-1 cm meiofaunal biomass to 0-5 cm meiofaunal biomass: average of 59.5% for 0-5° N and 50% at 9° N (Brown *et al.*, 2001).

[g] Meiofaunal biomass estimated using reported biomasses at Station NIXO 47 (Renaud-Mornant & Goubault, 1990) and corrected for an oligotrophic deep-sea site (wet wt/nematode=0.09 μg; Vanreusel *et al.*, 1995).

[h] Calculated using reported microbial biomass of 0.2-0.25 g C m^{-2} for 0-5° N and 0.13-0.2 g C m^{-2} for 5-9° N (Smith *et al.*, 1997), and a conversion factor of 10 fg C/cell (10×10^{-15} g C/cell) (Karl & Dobbs, 1998).

[i] Calculated using reported microbial biomass of 0.2-0.25 g C m^{-2} for 0-5° N and 0.13-0.2 g C m^{-2} for 5-9° N (Smith *et al.*, 1997), and a % wet weight carbon content of microbes of 16% (Fenchel *et al.*, 1998; Madigan *et al.*, 2000).

References: (1) Berelson *et al.* (1997); (2) Dymond and Collier (1988); (3) Honjo *et al.* (1995); (4) Smith *et al.* (2002); (5) Smith (1987); (6) Smith *et al.* (1997); (7) Smith (1992); (8) Glover *et al.* (2002); (9) Smith and Miller (in preparation); (10) Paterson *et al.* (1998); (11) Hessler and Jumars (1974); (12) Snider *et al.* (1984); (13) Brown *et al.* (2001); (14) Renaud-Mornant and Goubault (1990); and (15) Mullineaux (1987).

activities contribute to the relatively high abyssal bioturbation rates in this region. Biodiffusion coefficients at stations of the JGOFS EqPac transect determined using ^{234}Th and ^{210}Pb are correlated with POC flux, and decrease by an order of magnitude from the eutrophic to the mesotrophic abyss (Smith *et al.*, 1997). The depth of mixing in the eutrophic zone extends down to 6-8 cm (Smith *et al.*, 1997; Smith and Rabouille, 2002). Biodiffusion coefficients estimated using the short-lived ^{234}Th are much higher than those estimated using ^{210}Pb, which suggests age-dependent mixing, that is the preferential bioturbation of newly deposited particles (Smith *et al.*, 1993). Additionally, the activity of burrowing urchins appears to homogenize surface sediments down to 3 cm, a feature recognizable in ^{210}Pb profiles (Hoover, 1995; Smith *et al.*, 1997).

Diagenetic modeling has aided in the estimation of organic matter residence times in eutrophic abyssal sediments. Two fractions appear to be present: a labile fraction with a residence time of 7-150 d, and a refractory fraction with residence times between 44 and 289 years (Hammond *et al.*, 1996). The average time needed for surface-deposited organic matter to reach a certain depth in the sediment may be calculated using the average depth of the mixed layer and the average bioturbation coefficient. At the eutrophic NEPAP, using a bioturbation coefficient of 0.31 cm^2 y^{-1} from ^{210}Pb profiles (0-5^o N; Cochran, 1985; Smith et al., 1997), it is estimated that reaching 1 cm into the sediments takes 3.2 years while reaching the bottom of the mixed layer at 6-8 cm (Smith & Rabouille, 2002) may take 116-206 years. This suggests that benthic organisms living on or within 1 cm from the sediment surface may show very little resistance and resilience to changes in POC flux, relative to the infauna living deeper into the sediment.

Benthic oxygen flux into the equatorial abyssal sediments varies between 0.24 and 0.6 mol m^{-2} y^{-1} and is roughly correlated to the supply of organic matter from above, decreasing as one moves away from the equator (Jahnke & Jackson, 1992; Hammond *et al.*, 1996). Roughly 90% of this oxygen flux results from the decomposition of the labile fraction of organic matter. As inferred from flux data, eutrophic abyssal sediments are the site of regeneration and release of various nutrients including nitrate, phosphate and silica (Hammond *et al.*, 1996). Finally, the high oxygen consumption rates (Jahnke & Jackson, 1992) and steep porewater oxygen profiles (Hammond *et al.*, 1996) in the equatorial abyss suggest that anaerobic processes may occasionally constitute significant metabolic pathways compared to meso- and oligotrophic sediments.

In general, this region demonstrates high organic-matter processing rates and rapid elemental cycling by abyssal standards, performed to a large extent by abundant microbiota. The flux of organic matter from the surface appears to be high enough to support a significant surface-deposit feeding megafaunal community, and densities and biomasses of macrofauna and meiofauna that are high by abyssal deep sea standards. Diversity has only been determined for certain taxa and shown to be high on local scales. For example, within the polychaetes, there may be up to 83 species per 163 individuals (Glover *et al.*, 2002). However, the very small sampled area does not allow reliable estimates of diversity on regional scales. Because patterns of biodiversity and their causes are so poorly constrained in the eutrophic abyss, it is not fruitful to speculate on biodiversity responses to ecosystem change.

7.3.2 The mesotrophic (sub-equatorial) abyss

The mesotrophic (or sub-equatorial) abyss constitutes a zone of transition between the region of high POC beneath equatorial upwelling and the regions of very low fluxes beneath the oligotrophic central gyres. North of the equator roughly along 140^o W, this zone stretches between approximately 5^o and 15^o N, or for 10^o N of the boundary of the eutrophic abyss. A major characteristic of this region is the concentration of manganese nodules dotting vast areas of the seafloor, covering up to 75% of its plan area (Ghosh & Mukhopadhyay, 2000). The surrounding sediments contain between 0.25 and 0.5% organic carbon and significantly less $CaCO_3$ than the equatorial abyssal sediments (Berger, 1974; Jahnke, 1996; Smith et al., 1997).

The mesotrophic abyssal benthic standing stocks are summarized in Table 7.2. One major difference between the eutrophic and mesotrophic abyss is a large reduction in the abundance of surface-burrowing urchins and echiuran worms, indicated by the disappearance of urchin furrows and spoke traces (Hoover, 1995; Smith, unpublished data). Protozoan xenophyophores do remain common (approximately 2.35 m^{-2}; Smith & Demopoulos, 2003), but metazoan megafaunal abundance drops to almost half that of the eutrophic abyss (Table 7.2; Smith *et al.*, 1997). The metazoan megafauna appear to be dominated primarily by hexactinellid sponges of the genus *Hyalonema* (55-87%), and secondarily by surface-deposit feeding holothurians (Hoover *et al.*, 1994; Smith & Demopoulos, 2003).

Macrofaunal abundance and biomass are diminished even further, down to a third of those in the equatorial abyss (Table 7.2). A similar pattern is observed for meiofaunal biomass and abundance (Brown *et al.*, 2001), which in this region are dominated by nematodes followed by copepods and foraminifera (Renaud-Mornant and Goubault, 1990). Microbial biomass also declines (Table 7.2); however, the decline in microbial biomass is smaller than in the larger size classes, yielding a greater contribution of microbes to total mesotrophic community biomass (Smith *et al*., 1997). The vast majority of macrofauna in the mesotrophic abyss have been determined to be deposit feeders (Paterson *et al.*, 1998), whereas meiofaunal abundances are correlated with microbial biomass, suggesting that they may be bacterial grazers (Brown *et al.*, 2001).

Manganese nodules in this region (site ENP) harbor sessile eukaryotic epibionts, with 98.2% of the abundance attributed to foraminifera and rhizopod protozoans, with sponges, mollusks, polychaetes, bryozoans, and nematodes also present (Mullineaux, 1987). Although nodule-associated nematodes are not as abundant as in the surrounding sediments, they appear to be as diverse (Mullineaux, 1987).

Accompanying the decrease in POC flux relative to the eutrophic abyss is a decrease in sedimentary oxygen consumption rates, varying between 0.06 and 0.24 mol m^{-2} y^{-1} (Jahnke & Jackson, 1992; Hammond *et al.*, 1996). Nutrients such as nitrate, phosphate and silica are regenerated from sediments at rates lower than those of the eutrophic abyss, as predicted by differences in POC supply (Hammond *et al.*, 1996). The presence of a labile, short-lived organic matter fraction predicted by modeling in eutrophic sediments has not been verified for mesotrophic sediments. Instead, only one, relatively refractory pool of organic matter appears to be present with estimated residence time of 9-50 years (Hammond *et al.*, 1996). As in the previous section, using an average bioturbation coefficient of 0.19 cm^2 y^{-1} (5^o N; Smith et al., 1997) and an average mixed layer depth of 4 cm (C. Smith and Rabouille, 2002) for the mesotrophic Pacific, it is estimated that it may take an average of 84 years for freshly deposited organic matter to reach the bottom of the mixed layer. The shallower mixed layer and the consequent shorter time period needed for mixing suggest that benthos at the mesotrophic abyss may be even less resilient than that of the eutrophic abyss to changes in POC fluxes.

On local scales, species diversity in the mesotrophic abyss is lower than in the eutrophic abyss. On average, 45-75 different species of polychaetes have been identified for every 150-163 individuals examined (Paterson *et al.*, 1998; Glover *et al.*, 2002), and 780 nematode individuals could belong to as many as 45 species (Renaud-Mornant & Goubault, 1990). Because of the high abundance of nickel- and cobalt-rich manganese nodules in this region, mining of nodules from this area has been contemplated since the 1950s (Glasby, 2000). The paucity of ecological and biogeographic information from this region, e.g. concerning colonization rates of benthos and species ranges, constitutes a major hurdle in assessing the potential environmental impacts of nodule mining.

7.3.3 The oligotrophic central gyre abyss

A large proportion of the NEPAP features some of the lowest POC fluxes, and lowest biological standing stocks and rates recorded at the seafloor. POC fluxes in the NE Pacific oligotrophic abyss are typically lower than 0.5 g C m^{-2} y^{-1} (Smith, 1992; Smith *et al.*, 2002), although some seasonality is present as demonstrated by massive pulses of organic matter of up to 2 mg C m^{-2} d^{-1} to the seafloor (Karl, unpublished data; Karl *et al.*, 1996; Smith *et al.*, 2002). The very low supply of organic matter to the seafloor results in deep penetration of oxygen into sediment porewaters (Hammond *et al.*, 1996) and very low sedimentary oxygen consumption rates (<0.06 mmol m^{-2} y^{-1}; Jahnke & Jackson, 1992).

Sediments reflect these conditions, consisting mostly of red clay particles smaller than 6 μm transported on winds from the continents (Hessler & Jumars, 1974; Smith *et al.*, 1983), and carrying very little organic matter, typically less than 0.25% by weight (Berger, 1974; Smith *et al.*, 1983).

The oligotrophic conditions yield very low biomass and abundance for all components of the benthic community (Table 7.2). The megafauna consists of epibenthic holothurians (primarily *Amperima* sp.), cnidarians, and xenophyophores at densities about half those of the eutrophic abyss. In spite of the oligotrophic conditions, bottom-associated mobile scavengers, such as lysianassid amphipods, rattail fish and decapods, appear to be important components of this community (Dayton & Hessler, 1972; Ingram & Hessler, 1983; Smith *et al.*, 1992; Priede *et al.*, 1994). These scavengers are not typically encountered during surveys of the seafloor, but are attracted to bait-fall experiments within minutes to hours and form large aggregations (tens to hundreds per fall) that consume 10-100 kg of carrion within days (Dayton & Hessler, 1972; Ingram & Hessler, 1983; Priede *et al.*, 1994).

Macrofaunal assemblages are dominated by polychaetes (55% of individuals) with other major components being tanaids (18%), bivalves (7%) and isopods (6%) (Hessler & Jumars, 1974). Macrofaunal biomass and abundance are substantially lower than those of the eutrophic abyss, and the average macrofaunal body size is approximately an order of magnitude smaller than that of the eutrophic and mesotrophic abyssal regions (Smith & Demopoulos, 2003). Meiobenthic biomass at the CNP/MPG-I site is dominated by foraminifera (87%), which account for 50 % of the total abundance, with nematodes contributing 45 % (Snider *et al.*, 1984). The microbial community dominates biomass of total benthos in the oligotrophic abyss, exceeding that of macrofauna and meiofauna combined by approximately ten times (Table 7.2). Moreover, microbial biomass appears to fluctuate seasonally with POC flux, unlike other community groups (Smith *et al.*, 2002). Manganese nodules in this region (station CNP) host assemblages similar to the mesotrophic region (station ENP), with foraminifera and rhizopod protozoans accounting for 99.5% of the abundance (Mullineaux, 1987).

Considering the scarcity and high degree of specialization of scavengers in the oligotrophic abyss, the major source of energy for the abyssal communities appears to be sinking particulate matter, and due to the very low fluxes, the oligotrophic abyss appears to be food-deficient (Smith, 1992; Smith *et al.*, 2002). The majority of macrobenthos and meiobenthos are deposit feeders (Hessler & Jumars, 1974) while the very low community metabolic rates are presumably dominated by the microbial component (Smith, 1992). Low standing stocks and relatively high species diversities (more than 45 species for every hundred polychaete individuals; Hessler & Jumars, 1974; Glover *et al.*, 2002) suggest that the study of metazoan life histories, which requires collection of large numbers of individuals per species, will be particularly difficult in the oligotrophic abyss. Knowledge of these life histories is essential in addressing impacts of global change and anthropogenic disturbance in all abyssal regions.

7.4 Sensitivity and resilience to natural and anthropogenic change

7.4.1 General thoughts

The NEPAP ecosystems are characterized by extremely low energy inputs and elemental cycling rates, very low biological rates, high species diversity and, usually, high physical stability. The structure of the community and the intensity of cycling rates at any one abyssal location are predominantly determined by the POC flux regime at that location. As a consequence, these abyssal ecosystems are probably extremely sensitive to long-term changes in POC fluxes; even modest sustained changes may yield substantial alterations in community structure. For example, if eutrophic to oligotrophic trends are representative, a three-fold drop in mean POC export to the deep sea may yield a 10-fold decline in macrofaunal and microbial abundance and biomass (Table 7.2). However, these abyssal ecosystems may be surprisingly resilient (i.e. change little) when faced with short-term variations in POC flux. This is because POC flux to the NEPAP seafloor can vary substantially within and between years, e.g. due to ENSO events and phytodetrital pulses (Dymond & Collier, 1988; Honjo *et al.*, 1995; Smith *et al.*, 1996; Smith *et al.*, 2002). In addition, abyssal species are likely to (1) be well adapted to extended periods of low food availability, and (2) have very low growth and reproduction rates (Gage & Tyler, 1991). As a consequence, flux-induced changes in macrofaunal community structure may occur relatively slowly, i.e. over at least several years. Thus, we expect that the NEPAP ecosystems would ultimately exhibit high sensitivity to moderate, but long-term, changes in POC flux; however, the consequent changes in benthic community structure would probably occur slowly.

In contrast, benthic community structure and processes in the NEPAP region are likely to be both extremely sensitive to, and have very little resistance to, physical perturbations (e.g. mining disturbance). This is because the natural ecosystem is relatively very stable (compared to virtually all other ecosystems), most animals are small and/or very delicately constructed, and critical habitat structure for the entire benthic fauna is concentrated within a few centimeters of the sediment-water interface. Thus, it would require very little physical energy to disrupt the animals and the thin veneer of surface sediments that define this ecosystem. The extremely low sediment accumulation rates, bioturbation rates, nodule growth rates, and macrofaunal recolonization rates of the NEPAP seafloor ecosystem, compared to other seafloor habitats (Smith & Demopoulos, 2003), suggest that recovery from physical disturbance is likely to be extremely slow relative to other ecosystems.

Global biogeochemical cycles may respond to natural or anthropogenic changes, such as variations in El Niño-Southern Oscillation (ENSO) frequency or global warming, and in the process cause perturbations in oceanic ecosystem functions, including primary production and the export of POC to the abyssal ocean. Human activities on the abyssal seafloor and in the overlying water column, e.g., mining of ferromanganese nodules and iron fertilization, could impact abyssal communities more rapidly and dramatically than atmosphere-mediated changes. In the following paragraphs, we discuss potential impacts of a number of natural and anthropogenic influences on NEPAP benthic communities.

7.4.2 Potential sensitivity and resilience to specific changes

7.4.2.1 Climate variation in the equatorial and North Pacific.

A number of large-scale climatic cycles and their impacts have been recognized and thoroughly studied in the 1990s. Two of the climatic cycles that impact the central and northern Pacific are the ENSO and the Pacific Decadal Oscillation (PDO).

ENSO events are characterized by reversals of the atmospheric pressure systems in the south and central Pacific, and switching of the sources of the intensely upwelled water masses along the southeastern Pacific continental margin. An El Niño event results in warmer surface waters, greater stratification and reduced upwelling of nutrients in the central and eastern equatorial Pacific, reducing primary productivity. While reduced equatorial-subequatorial productivity during El Niño is observed in the central eastern Pacific in all studied events (Barber & Chavez, 1983; Barber *et al.*, 1996; Strutton and Chavez, 2000), the effects of ENSO events on POC flux to the seafloor are not clear.

At least three studies from the central equatorial Pacific contrast deep POC fluxes under El Niño and non-El Niño conditions. Dymond and Collier (1988) explored the effects of the 1982 El Niño on POC export at MANOP stations C and S (Fig. 7.1 and Table 7.1). They found decreased export to the eutrophic abyss during the El Niño event, but saw an increase in export to the mesotrophic abyss at 11° N over the same time period (Fig. 7.2). POC flux data were also recorded along the US JGOFS EqPac transect during and after the moderate El Niño event of 1991-92 (Honjo *et al.*, 1995; see Murray *et al.*, 1995, for study description). The POC fluxes at 700 m above the bottom during El Niño were higher at the equator, 2° N and 9° N but lower at 5° N, 2° S and 5° S relative to non-El Niño conditions (Fig. 7.2). However, the French JGOFS FLUPAC and Zonal Flux studies reported no statistical differences between POC fluxes calibrated using ^{234}Th out of the euphotic zone (150 m) at 0° N 150° W during the following El Niño event of 1994 (FLUPAC TSII) and during non-El Niño conditions (Zonal Flux) (Dunne *et al.*, 2000). Considering the evident increase in frequency of El Niño events during the latter part of the 20th century (Trenberth &

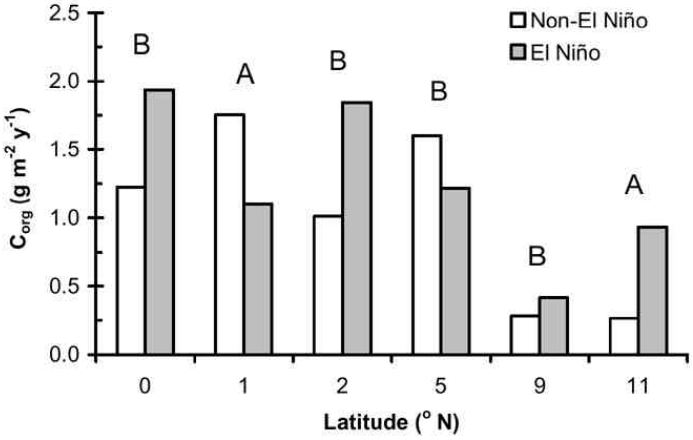

Fig. 7.2 Deep sea POC fluxes in the equatorial and sub-equatorial Pacific during El Niño and non-El Niño periods. All sediment trap stations are along 139-140^{o} W. Data for latitudes 1^{o} N (MANOP station C, 2908-3495 m) and 11^{o} N (MANOP station S, 3400 m) are from Dymond and Collier (1988) for the 1982-83 event (marked A). Data for latitudes 0^{o} (3618 m), 2^{o} N (2200 m), 5^{o} N (3800 m) and 9^{o} N (4400 m) along the U.S. JGOFS transect are from Honjo *et al.* (1995) for the 1991-92 event (marked B). Courtesy of R. Collier, US JGOFS, http://usjgofs.whoi.edu/jg/dir/jgofs/eqpac/.

Hoar, 1996, 1997; Timmermann *et al.*, 1999) and the defining role of POC fluxes on NEPAP communities, the impact of ENSO events on the seafloor has yet to be resolved.

The PDO climate pattern appears to be teleconnected to ENSO and is characterized by interdecadal climate shifts in the North Pacific, as observed using a variety of environmental indices from sea surface temperatures to fish productivity in the region (Mantua *et al.*, 1997; Minobe, 1999). Two recent climate-regime shifts in the North Pacific, in 1976-77 and in 1989, have been explored and documented extensively (Ebbesmeyer *et al.*, 1991; Hare & Mantua, 2000). North Pacific climate indices generally correlate very well with both North Pacific environmental indices and ENSO indices (Mantua *et al.*, 1997), and are expected to affect, among other things, primary productivity in the North Pacific sub-tropical gyre. Past productivity changes have been suggested to occur due to variation in mixed-layer depth over decadal scales (Polovina *et al.*, 1994, 1995) and lengthened periods of stratification and reduced turbulence (Karl *et al.*, 1995, 2001a).

In particular, it has been suggested that chlorophyll concentrations in the euphotic zone at stations Climax and ALOHA document the impact of PDO, and specifically the climate shift of 1976-77, on oligotrophic gyre productivity (Karl, 1999; Karl *et al.*, 2001b). The current hypothesis suggests a shift from a eukaryotic phytoplankton community to one dominated by nitrogen-fixing prokaryotes. The shift to prokaryotic dominance is caused by physical conditions that restrict nutrient supply to the euphotic zone and encourage nitrogen fixation either by free-living cyanobacteria or by diatom endosymbionts (Karl *et al.*, 1995, 2001a; Zehr *et al.*, 2000). Due to the presence of these nitrogen-fixing endosymbionts, the otherwise plausible translation of this regime shift into a decrease in diatom and coccolithophorid populations and productivity, and consequently POC export changes (Smith *et al.*, 2002), is not possible. Time series data from deep-sea sediment traps at station ALOHA (D.M. Karl, unpublished data) have continuously been collected well after the last proposed regime shift in 1989 (Hare and Mantua, 2000), and they may prove useful in interpreting the role of community structure changes on POC export from the ocean surface layers on the occasion of the next shift.

The effects of ENSO and PDO on communities of the NEPAP are far from being resolved. Whereas their impacts in the regions immediately affected (equatorial and sub-equatorial Pacific for ENSO and northeastern Pacific for PDO) can be speculated, their impacts on larger-scale regional conditions appear to be synergistic for some regions and opposing for others (e.g. Mestas-Nuñez and Enfield, 2001). For example, it has been suggested that subtropical waters of the Pacific experience increased productivities during El Niño events whereas equatorial productivity drops (Leonard *et al.*, 2001). In any case, from the data available at present it appears that all regions of the NEPAP are experiencing interannual to interdecadal variations in export due to large-scale climate patterns. During El Niño events, zones of the eutrophic abyss may be starved whereas zones of the mesotrophic abyss may be enriched. This pattern will probably be longer lasting, considering the increased frequency of ENSO. As a result of larger-scale climatic teleconnections, the oligotrophic abyss is undergoing similar starvation-enrichment oscillations on the frequency of decades.

7.4.2.2 Global increase in atmospheric greenhouse gases and temperatures

Fossil fuel burning is now accepted to have increased the concentrations of greenhouse gases in the atmosphere and is expected to lead to global warming (IPCC, 2001). Global climate change may affect primary productivity directly, by physiological effects on the photosynthetic taxa dominating POC export, and indirectly, by enhancement of regional climatic conditions which result in shifts in photosynthetic-community structure. In turn, alterations of primary production processes will impact the export of organic matter from the surface waters to the abyssal plain and the benthic biota that rely on this export.

Mechanisms connecting changes in dissolved inorganic carbon (DIC) concentrations and water temperatures and the physiology of photosynthesizing taxa dominating POC export, such as diatoms and coccolithophorids, are well studied. Marine diatoms have been shown to concentrate DIC by using extra-cellular and intracellular carbonic anhydrase (Burkhardt *et al.*, 2001; Tortell *et al.*, 1997), thus avoiding the limitation of concentration-dependent diffusive uptake. Raven (1991) suggested that photosynthesizers which are now DIC-limited because they lack similar active uptake mechanisms may become more competitive if DIC concentrations increase, resulting in a change in the community structure of primary producers. Additionally, similar experiments performed with coccolithophorid species demonstrate a decrease in calcification rates and calcite:POC ratios with increasing DIC concentrations associated with a simultaneous increase in POC production rates (Riebesell *et al.*, 2000). Data from station ALOHA suggest that the surface waters of the oligotrophic gyre have tracked the atmospheric increases in DIC for the last decade (Fig. 7.3; Karl *et al.*, 2001b), although it is uncertain whether the magnitude of these changes is sufficient to alter the key primary producers or export production to the oligotrophic NEPAP.

In contrast, surface water temperatures in the same region do not show any consistent pattern during the last decade and are presumably controlled by the

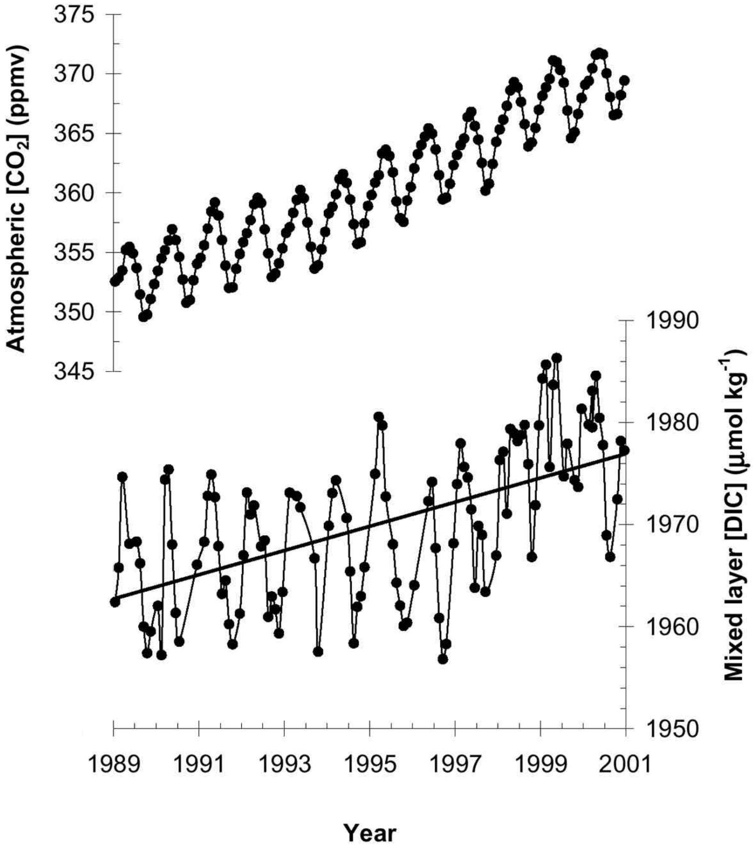

Fig. 7.3 Trends in inorganic carbon concentrations between 1989 and 2001. *Above*: atmospheric carbon dioxide concentrations as measured at the Manoa Loa observatory. Data courtesy of the Carbon Dioxide Information Analysis Center, http://cdiac.ornl.gov/ndps/ndp001.html. *Below*: mixed layer (0-50 m; Karl & Lukas, 1996) DIC concentrations, normalized to a salinity of 35 per mil, at station ALOHA. Data courtesy of D.M. Karl, The Hawaii Ocean Time-series (HOT), http://hahana.soest.hawaii.edu (Karl *et al.*, 2001b).

climate cycles operating in the Pacific as described above. Nonetheless, higher water temperatures have been shown to decrease the size of most diatom species examined from the open ocean (Montagnes & Franklin, 2001). This matches widely observed patterns of decreasing ectotherm size with increasing temperature (see Atkinson, 1994, for a review). A reduction in size will result in a reduction in sinking rate, although the extent of the effect also depends on the associated changes in the cell's specific gravity. If all cell components, including vacuoles and frustules, decrease proportionately then the specific gravity will not change, and any observed changes may be attributed only to size (Jackson, 1990; Montagnes & Franklin, 2001). Since the major seasonal POC fluxes at Station ALOHA are dominated mostly by diatoms during the late summer bloom (Scharek *et al.*, 1999a,b) and by coccolithophorids during the winter-spring bloom (Cortés *et al.*, 2001), they may be explained in part by inter-annual variations in average temperatures of the surface layers at this region (Fig. 7.4). Indeed, a fairly significant relationship between temperature and production export has been demonstrated to exist on a global scale and modeled (Laws *et al.*, 2000) although it may not be robust at low primary productivity zones such as those overlying the NEPAP.

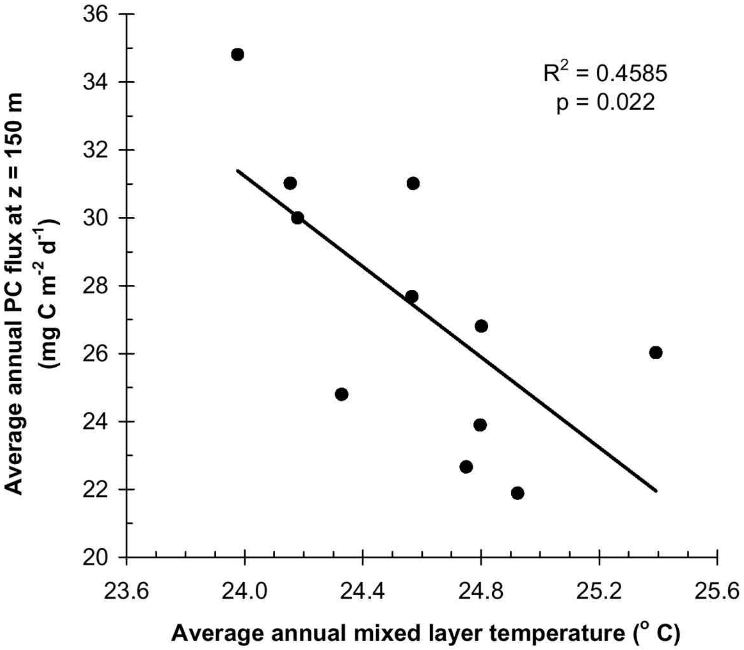

Fig. 7.4 Relationship between average annual particulate carbon flux at 150 m and mixed layer temperatures (0-50 m; Karl & Lukas, 1996) at station ALOHA. The relationship was tested using ANOVA (F=7.62, p=0.022). Data courtesy of D.M. Karl, The Hawaii Ocean Time-series (HOT), http://hahana.soest.hawaii.edu.

Apart from physiological effects on major photosynthetic eukaryotes, global climate change has been connected to the increasing frequency of El Niño-La Niña cycles in the later part of the twentieth century (Trenberth & Hoar, 1996, 1997; Timmermann *et al.*, 1999). Increased surface water stratification will certainly result in nutrient depletion, an amplified importance of nitrogen fixation, and variable changes in particulate matter export to the abyss as described above (Karl *et al.*, 2001a). Modeling of the interaction between ENSO and global climate change suggests that not only the frequency but also the intensity of El Niño and La Niña events will increase in the future, if current trends in atmospheric carbon dioxide concentrations remain unchanged (Timmerman *et al.*, 1999). Ultimately, the consequence of these changes may be a prolonged period of atrophic conditions in the abyssal plains subjecting the eutrophic and mesotrophic abyss to an energetic imbalance and a continuous demand for organic matter similar to that of the oligotrophic abyss (Karl, 1999; Smith *et al.*, 2002).

7.4.2.3 Manganese nodule mining

Manganese nodule mining may ultimately be the largest-scale human activity to directly impact the NEPAP, or any other abyssal habitat worldwide (Thiel, 2001). Twelve pioneer investigator countries and consortia, including the International Seabed Authority, have carried out more than two hundred exploratory cruises around the globe to investigate locations of high manganese nodule coverage, especially the area between the Clipperton and the Clarion fracture zones (Fig. 7.5; Glasby, 2000). This region covers approximately 6 million km^2 (out of a total of 46 million nodule-rich km^2 worldwide) and is estimated to contain approximately 7.5 billion metric tons of manganese, 78 million tons of cobalt, 340 million tons of nickel and 265 million tons of copper (Ghosh & Mukhopadhyay, 2000; Morgan, 2000). At present, six contractors

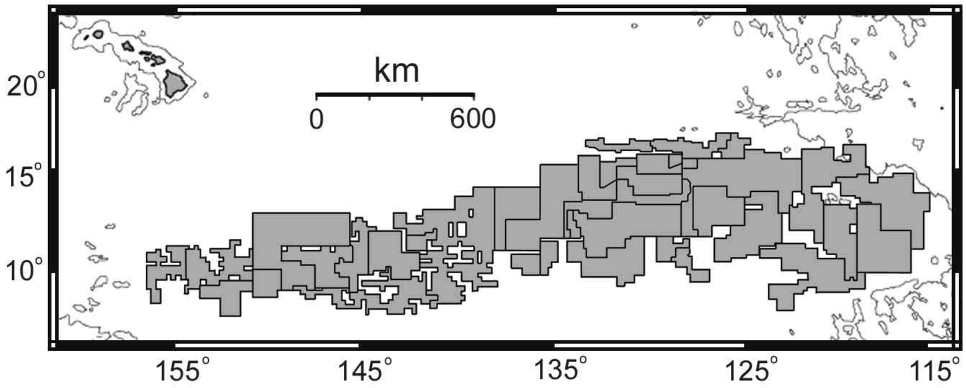

Fig. 7.5 Extent of the general Pacific area under prospecting for manganese nodule mining. The shaded sectors have either been allocated to, reserved for or claimed by pioneer investors and consortia. Maps courtesy of the International Seabed Authority, http://www.isa.org.jm.

are licensed by the International Seabed Authority (the international body charged with managing deep-sea mining) to explore nodule resources and to test mining techniques in six claim areas, each covering 75000 km^2 (i.e. an area roughly half the size of the state of Florida).

When mining ultimately begins (probably not for another 10-20 years), each mining operation is projected to directly disrupt, through nodule *harvesting*, ~800 km^2 of seafloor per year, and to disturb the sediment-dwelling fauna over an area 5-10 times that size due to redeposition of suspended sediments (data from the International Seabed Authority). Thus, in any given year, nodule mining might severely damage abyssal seafloor communities over areas of 20000-40000 km^2 (a zone of devastation at least the size of the state of Massachusetts). One obvious direct effect of manganese nodule mining will be removal of the nodules themselves, which will require millions of years to re-accrete (Ghosh & Mukhopadhyay, 2000, McMurtry, 2001). Nodule mining will thus remove the only hard substrate present at the NEPAP seafloor, yielding habitat loss and at least local extinction of the nodule fauna, which differs dramatically from that in surrounding sediments (Mullineaux, 1987).

The nodule-collecting process will also undoubtedly remove at least the top 5 cm of sediment, broadcasting much of this material into the sediment column (e.g. Gage & Tyler, 1991). In the direct path of the collection device, most animals will be killed immediately, and compacted relatively organic-poor subsurface sediments will be exposed (Jumars, 1981). Resuspended sediments will rain out onto the seafloor, burying benthos to varying depths, and covering the sediment-water interface with layers of subsurface sediments (Jumars, 1981). Because the NEPAP habitat is normally very stable, and is dominated by very small and/or fragile animals, the direct effects of nodule collection will be devastating the benthos (Jumars, 1981). The indirect impacts of sediment redeposition may also be deleterious because much the NEPAP macrofauna and megafauna appear to be surface-deposit feeders that consume the meager flux of POC from the water column. Redeposition of subsurface, presumably food-poor sediment from the mining plume may dilute food resources, causing nutritional stress to the benthos. This effect would be enhanced if redeposition were chronic, i.e. if it occurred over extended time periods (months to years) due to concentration of mining activities at a single site.

A number of small-scale studies (relative to full-scale mining) have been conducted to begin to evaluate the sensitivity and recovery times of abyssal benthic communities subjected to nodule-mining disturbance. These studies have used disturbances of the following two types: (1) A plowing disturbance, in which an 8-m wide frame with multiple plow heads was dragged over the ocean floor in the south equatorial abyss, directly disturbing about 20% of the seafloor within a circular area of 11 km^2 [the DISCOL experiment (Thiel, 2001)]; (2) A sediment removal and redeposition disturbance, in which a sediment-pumping system has been towed along seafloor swathes 200-400 m wide and 2- 3 km long, removing sediments from a track ~10 cm deep and 2 m wide and disgorging them as a plume at an altitude of 5 m [the BIE-type experiments (Thiel, 2001]. Both types of studies have addressed community disturbance and recolonization within directly disturbed tracks, as well as in areas subjected to rapid resedimentation to thicknesses of ≥7 mm.

Although these experiments produced disturbances of much lower intensity and much smaller spatial scale than would result from commercial-scale mining, they provide some insights into the sensitivity and recovery times of abyssal nodule communities exposed to mining disturbance. Direct plowing disturbance (DISCOL) yielded a dramatic reduction in the abundances of macrofaunal polychaetes (51.4%), tanaids (72%), isopods (81.5%) and bivalves (90.7%) (Borowski & Thiel, 1998). Megafauna was also heavily impacted immediately after the disturbance, decreasing sharply in abundance within plow tracks (Bluhm *et al.*, 1995). In areas of resettling sediment, the disturbances of macrofaunal and megafaunal abundance varied from quite low to negligible (Bluhm *et al.*, 1995; Borowski & Thiel, 1998). Three years after the disturbance event, the abundance of dominant macrofaunal taxa, especially polychaetes, had reached pre-disturbance levels, but macrofaunal diversity remained depressed even after seven years (Borowski & Thiel, 1998; Borowski, 2001). The abundance and diversity of megafauna also remained below pre-disturbance levels seven years after disturbance (Bluhm, 2001). Nematode densities and biomass were not detectably affected by the disturbance event, while copepods only showed some decrease in diversity at the species level seven years after (Ahnert & Schriever, 2001; Vopel & Thiel, 2001).

Results from sediment removal/redeposition (or BIE-type) experiments show similar sensitivity of abyssal seafloor communities to physical disturbance. Immediately following apparent redeposition of <1 cm of sediment (Yamazaki *et al.*, 1997; Fukushima *et al.*, 2000), reductions have been observed in the abundance of many components of the biological community, including megafauna (21-48%), macrofauna (up to 63%), meiofauna (23%) and microbiota (one to three orders of magnitude), possibly due to burial by settling sediment, and interference with respiratory and feeding functions (Fukushima, 2000; Ingole *et al.*, 2001; Raghukumar *et al.*, 2001; Rodrigues *et al.*, 2001). Two years after redeposition, the abundance of surface-deposit-feeding and mobile megafauna may remain low, suggesting a lingering impact on their food resources (Fukushima *et al.*, 2000).

One must be very cautious in extrapolating these experimental results to the impacts of commercial mining, which would be much more intense, and would devastate much larger areas of seafloor (i.e. 100-1000 km^2 versus 1-11 km^2). One can only say that NEPAP benthos will be substantially disturbed by even modest amounts (~1 cm) of sediment redeposition resulting from mining activities, and that full sediment-community recovery from major mining disturbance will take much longer than seven years. We cannot predict the likelihood of species extinctions from nodule mining because we do not know the typical geographic ranges of species living within the nodule region (are the ranges large or small relative to the potential spatial scales of mining disturbance?). We can predict that the recovery of the nodule fauna within a mined area will take millions of years because of the extremely slow regeneration rate of their required substrate, manganese nodules. It is clear that to fully predict commercial mining impacts, substantially more information is required concerning species ranges, burial sensitivity and the spatial-scale dependence of recolonization in the NEPAP biota.

7.4.2.4 Iron fertilization

The goal of iron fertilization of the oceans would be to stimulate primary production and export production in iron-limited, high-nutrient-low-chlorophyll (HNLC) regions of the ocean, such as the eutrophic Pacific. This stimulation of the *biological pumping* of CO_2 from the atmosphere to the deep ocean would be expected to reduce the atmospheric *greenhouse effect*, mitigating global warming (Fuhrman & Capone, 1991; Raven & Falkowski, 1999). The stimulation of primary production on a scale of 100-300 km^2 with the addition of iron was demonstrated in the equatorial Pacific during the IronEx I and II experiments in 1993 and 1995 respectively (Martin *et al.*, 1994; Coale *et al.*, 1996) and during the SOIREE experiment in the Southern Ocean (Boyd *et al.*, 2000). Where measured, the export of particulate carbon from the mixed layer did not increase significantly during these iron-enrichment experiments (days to weeks) (Coale *et al.*, 1996; Trull & Armand, 2001). However, longer-term effects of iron fertilization on POC export were modeled for the SOIREE experiment (Hannon *et al.*, 2001). The modeling suggested that POC export out of the fertilized patch of ~ 150 km^2 may have increased by two to three-fold within two months after iron addition. Longer monitoring of POC export is needed in subsequent fertilization experiments to test these predictions.

An extreme iron fertilization scenario modeled by Sarmiento and Orr (1991) relies on the sustained depletion of phosphorus in Southern Ocean surface waters by continuous iron addition. The three-dimensional, multi-layer model predicts a global increase of export production and the possibility of anoxia in deep oceanic waters. Specifically, the results indicate a POC export increase of 6-30 Gt C y^{-1}, i.e. a doubling of export production, after 100 years of fertilization. In addition, anoxia is predicted for certain parts of the southwest Indian Ocean. Considering the enormous scale of this hypothesized fertilization operation (0.6 Mt utilizable Fe y^{-1}; Sarmiento & Orr, 1991) and the low spatial resolution of the model, the exercise provides limited insights into more realistic iron fertilization scenarios.

Because of the potential magnitude and uncertainty of environmental impacts, proposals to fertilize the ocean to mitigate global warming (or to earn *carbon credits*) have been controversial (e.g. ASLO, 2001; Chisholm *et al.*, 2001;

Johnson & Karl, 2002). Quite simply, existing models and experimental studies are inadequate to predict the ecosystem consequences of large-scale, prolonged iron fertilization. It is clear that if iron fertilization were successful on a large enough scale to mitigate global warming, POC fluxes to large areas of the deep-sea floor (possibly including the NEPAP) would be increased dramatically. Because of the sensitivity of abyssal ecosystems to patterns of POC flux, community structure (including abundance, biomass, species diversity) and ecosystem rates (e.g. organic-carbon mineralization and burial rates) would also be dramatically altered (cf. Smith *et al.*, 1997; Glover *et al.*, 2002). If hypoxic or anoxic conditions were created over large areas of abyssal seafloor, species extinctions would be likely and the nature of sediment geochemical processes (e.g. organic-carbon burial and phosphorous regeneration) would be fundamentally altered (e.g. Canfield, 1994; Van Cappellen & Ingall, 1996). More detailed speculation on the abyssal benthic impacts of ocean fertilization is premature, however, until better resolution of the consequent magnitude and spatial scales of enhanced deep sea POC flux is available.

7.5 Concluding remarks

Because of the low flux of food materials from the euphotic zone, ecosystem structure and function on the NEPAP is largely controlled by annual patterns of POC flux to the seafloor. In particular, the standing crop of NEPAP communities is likely to be very sensitive to long-term changes in export production from the surface ocean. Particles reaching the abyssal seafloor from the euphotic zone appear to be drawn, on an annual basis, from large areas of the surface ocean (in the order of 10000 km^2; Siegel & Deuser, 1997). This fact, plus the low growth and reproduction rates of abyssal benthos (Gage & Tyler, 1991) mean that macro- and megabenthic abundance and biomass integrate surface-ocean production conditions (in particular, export production) over large space and time scales (10000 km^2 and years). Thus, we suggest that the standing stock of NEPAP benthos might be used to monitor large-scale changes in the production regimes of the equatorial Pacific and the oligotrophic central gyre resulting from regional climate cycles, global warming, or iron fertilization. In essence, the export-production signal preserved in abyssal macro- and megabenthic biomass may be viewed as having passed through a low-pass filter that smooths short-period (days to months) and small-scale (1-10 km) variability in export production, but responds to broad trends in the flux of labile organic matter to the deep-sea. Because macro-benthos, in particular, occur throughout the oxygenated deep sea and are easily sampled using standard quantitative techniques (Gage & Tyler, 1991), macro-benthic standing crop could be readily used to monitor large-scale changes in the ocean's production cycles as a consequence of global change. Such measurements could augment the much more expensive and labor-intensive studies of export production using sediment-trap moorings (e.g. Honjo *et al.*, 1995; Lampitt & Antia, 1997).

Because of natural physical stability on the NEPAP, and the small size and fragility of habitat elements and fauna, the NEPAP ecosystem will be very sensitive to even moderate physical disturbance resulting from anthropogenic activities such as manganese-nodule mining. The vastness of the NEPAP habitat may reduce the chances of species extinctions, but commercial-scale mining would almost certainly devastate the biota, and alter geochemical processes, over tens of thousands of square kilometers of seafloor through direct (e.g. nodule removal) and indirect (e.g. sediment redeposition) effects. Recovery of the sediment fauna and geochemical processes following large-scale mining is likely to require decades, while recovery of the nodule biota in mined areas will take millions of years. Substantially more studies of disturbance and recolonization processes, and of biodiversity levels and species ranges, are required before the impacts of nodule mining, and similar large physical disturbances, can be predicted for the NEPAP.

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References

Ahnert, A. and Schriever, G. (2001) Response of abyssal Copepoda Harpacticoida (Crustacea) and other meiobenthos to an artificial disturbance and its bearing on future mining for polymetallic nodules. *Deep-Sea Research II*, **48**, 3779-3794.

Aller, J.Y. (1989) Quantifying sediment disturbance from bottom currents and its effect on benthic communities in a deep western boundary zone. *Deep-Sea Research*, **36**, 901-934.

Armstrong, R.A., Lee, C., Hedges, J.I., Honjo, S. and Wakeham, S.G. (2001) A new, mechanistic model for organic carbon fluxes in the ocean based on the quantitative association of POC with ballast minerals. *Deep-Sea Research II*, **49**, 219-236.

ASLO (2001) *The Scientific and Policy Uncertainties Surrounding the Use of Ocean Fertilization to Transfer Atmospheric Carbon Dioxide to the Oceans*, Workshop and Capitol Hill Briefing, April 23-24, 2001, American Society of Limnology and Oceanography, Washington D.C.

Atkinson, D. (1994) Temperature functions in biology and their application to algal growth constant. *Oikos*, **49**, 177-190.

Barber, R.T. and Chavez, F.P. (1983) Biological consequences of El Niño. *Science*, **222**, 1203-1210.

Barber, R.T., Sanderson, M.P., Lindley, S.T., Chai, F., Newton, J., Trees, C.C., Foley, D.G. and 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.

Berelson, W.M., Anderson, R.F., Dymond, J.A., DeMaster, D., Hammond, D.E., Collier, R., Honjo, S., Leinen, M., McManus, J., Pope, R., Smith, C. and Stephens M. (1997) Biogenic budgets of particle rain, benthic remineralization and sediment accumulation in the equatorial Pacific. *Deep-Sea Research II*, **44**, 2251-2282.

Berger, W.H. (1974) Deep-sea sedimentation, in *The Geology of Continental Margins* (eds C.A. Burke and C.D. Drake), Springer-Verlag, New York, pp. 213-241.

Berner, R.A. (1980) *Early Diagenesis*, Princeton University Press, Princeton, New Jersey.

Bett, B.J., Malzone, M.G., Narayanaswamy, B.E. and Wigham, B.D. (2001) Temporal variability in phytodetritus and megabenthic activity at the seabed in the deep Northeast Atlantic. *Progress in Oceanography*, **50**, 349-368.

Bluhm, H. (2001) Re-establishment of an abyssal megabenthic community after experimental physical disturbance of the seafloor. *Deep-Sea Research II*, **48**, 3841-3868.

Bluhm, H., Schriever, G. and Thiel, H. (1995) Megabenthic recolonization in an experimentally disturbed abyssal manganese nodule area. *Marine Georesources and Geotechnology*, **13**, 393-416.

Borowski, C. (2001) Physically disturbed deep-sea macrofauna in the Peru Basin, southeast Pacific, revisited 7 years after the experimental impact. *Deep-Sea Research II*, **48**, 3809-3839.

Borowski, C. and Thiel, H. (1998) Deep-sea macrofaunal impacts of a large-scale physical disturbance experiment in the Southeast Pacific. *Deep-Sea Research II*, **45**, 55-81.

Boyd, P.W., Watson, A.J., Law, C.S., Abraham, E.R., Trull, T., Murdoch, R., Bakker, D.C.E., Bowie, A.R., Buesseler, K.O., Chang, H., Charette, M., Croot, P., Downing, K., Frew, R., Gall, M., Hadfield, M., Hall, J., Harvey, M, Jameson, G., LaRoche, J., Liddicoat, M., Ling, R., Maldonado, M.T., McKay, R.M., Nodder, S., Pickmere, S., Pridmore, R., Rintoul, S., Safi, K., Sutton, P., Strzepek, R., Tanneberg, K., Turner, S., Waite, A. and Zeldis, J. (2000) A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. *Nature*, **407**, 695-702.

Brown, C.J., Lambshead, P.J.D., Smith, C.R., Hawkins, L.E. and Farley, R. (2001) Phytodetritus and the abundance and biomass of abyssal nematodes in the central, equatorial Pacific. *Deep-Sea Research I*, **48**, 555-565.

Burkhardt, S., Amoroso, G., Riebesell, U. and Sültemeyer, D. (2001) CO_2 and HCO_3^- uptake in marine diatoms acclimated to different CO_2 concentrations. *Limnology and Oceanography*, **46**, 1378-1391.

Canfield, D.E. (1994) Factors influencing organic carbon preservation in marine sediments. *Chemical Geology*, **114**, 315-329.

Chisholm, S.W., Falkowski, P.G. and Cullen, J.J. (2001) Dis-crediting ocean fertilization. *Science*, **294**, 309-310.

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., Trasvina, A. and Kudela, R. (1996) A massive phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the equatorial Pacific Ocean. *Nature*, **383**, 495-501.

Cochran, J.K. (1985) Particle mixing rates in sediments of the eastern equatorial Pacific: Evidence from ^{210}Pb, $^{239,240}Pu$ and ^{137}Cs distributions at MANOP sites. *Geochimica et Cosmochimica Acta*, **49**, 1195-1210.

Cortés, M.Y., Bollman, J. and Thierstein, H.R. (2001) Coccolithophore ecology at the HOT station ALOHA. *Deep-Sea Research II*, **48**, 1957-1981.

Dayton, P.K. and Hessler, R.R. (1972) Role of biological disturbance in maintaining diversity in the deep sea. *Deep-Sea Research*, **19**, 199-208.

Demidova, T. (1999) The physical environment in nodule provinces of the deep sea, in *Deep-seabed Polymetallic Nodule Exploration: Development of Environmental Guidelines*. International Seabed Authority, Kingston, pp. 79-116.

Diaz, R.J. and Rosenberg, R. (1995) Marine benthic hypoxia: a review of its ecological effects and the behavioral responses of benthic macrofauna. *Oceanography and Marine Biology: an Annual Review*, **33**, 245-303.

Dunne, J.P., Murray, J.W., Rodier, M. and Hansell, D.A. (2000) Export flux in the western and central equatorial Pacific: zonal and temporal variability. *Deep-Sea Research I*, **47**, 901-936.

Dymond, J. and Collier, R. (1988) Biogenic particle fluxes in the equatorial Pacific: Evidence for both high and low productivity during the 1982-1983 El Niño. *Global Biogeochemical Cycles*, **2**, 129-137.

Ebbesmeyer, C.C., Cayan, D.R., McLain, D.R., Nichols, F.H., Peterson, D.H. and Redmond, K.T. (1991) 1976 step in the Pacific climate: forty environmental changes between 1968-1975 and 1977-1984, in *Proceedings of the 7th Annual Pacific Climate (PACLIM) Workshop* (eds J.L. Betancourt and V.L. Tharpe), California Department of Water Resources, Interagency Ecological Studies Program Technical Report 26, pp. 115-126.

Fenchel, T., King, G.M. and Blackburn, T.H. (1998) *Bacterial Biogeochemistry: the Ecophysiology of Mineral Cycling*, 2nd edn, Academic Press, London.

Field, C.B., Behrenfeld, M.J., Randerson, J.T. and Falkowski, P. (1998) Primary Production of the Biosphere: Integrating Terrestrial and Oceanic Components. *Science*, **281**, 237-240.

Fuhrman, J.A. and Capone, D.G. (1991) Possible biogeochemical consequences of ocean fertilization. *Limnology and Oceanography*, **36**, 1951-1959.

Fukushima, T., Shirayama, Y. and Kuboki, E. (2000) The characteristics of deep-sea epifaunal megabenthos community two years after an artificial rapid deposition event. *Publications of the Seto Marine Biological Laboratory*, **39**, 17-27.

Gage, J.D. and Tyler, P.A. (1991) *Deep-sea biology: a natural history of organisms at the deep-sea floor*, Cambridge University Press, Cambridge.

Gardner, W.D., Sullivan, L.G. and Thorndike, E.M. (1984) Long-term photographic, current, and nephelometer observations of manganese nodule environments in the Pacific. *Earth and Planetary Science Letters*, **70**, 95-109.

Ghosh, A.K. and Mukhopadhyay, R. (2000) *Mineral Wealth of the Ocean*, A.A. Balkema, Rotterdam, Netherlands.

Glasby, G.P. (2000) Lessons learned from deep-sea mining. *Science*, **289**, 551-553.

Glover, A.G., Smith, C.R., Paterson, G.L.J., Wilson, G.D.F., Hawkins, L. and Sheader, M. (2002) Polychaete species diversity in the central Pacific abyss: local and regional patterns, and relationships with productivity. *Marine Ecology Progress Series*, **240**, 157-170.

Gooday, A.J. (2002) Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review. *Journal of Oceanography*, **58**, 305-332.

Hammond, D.E., McManus, J., Berelson, W., Kilgore, T. and Pope, R. (1996) Early diagenesis of organic material in equatorial Pacific sediments: stoichiometry and kinetics. *Deep-Sea Research II*, **43**, 1365-1380.

Hannon, E., Boyd, P.W., Silvoso, M. and Lancelot, C. (2001) Modeling the bloom evolution and carbon flows during SOIREE: Implications for future in situ iron-enrichments in the Southern Ocean. *Deep-Sea Research II*, **48**, 2745-2773.

Hare, S.R. and Mantua, N.J. (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, **47**, 103-145.

Hartnett, H.E., Keil, R.G. Hedges, J.I. and Devol, A.H. (1998) Influence of Oxygen Exposure Time on Organic Carbon Preservation in Continental Margin Sediments. *Nature,* **391**, 572-574.

Hessler, R.R. and Jumars, P.A. (1974) Abyssal community analysis from replicate box cores in the central North Pacific. *Deep-Sea Research,* **21**, 185-209.

Honjo, S., Dymond, J., Collier, R. and Manganini, S.J. (1995) Export production of particles to the interior of the equatorial Pacific Ocean during the 1992 EqPac experiment. *Deep-Sea Research II*, **42**, 831-870.

Hoover, D.J. (1995) *Burrowing Urchins in the Abyssal Equatorial Pacific: sediment reworking rates estimated using two independent tracer techniques*. M.S. Thesis, University of Hawaii at Manoa.

Hoover, D.J., Smith, C.R. and Doan, S.E. (1994) Megafaunal mixing rates along the JGOFS equatorial Pacific transect estimated using phytodetritus as a time marker. *EOS*, **75**, 70.

Ingole, B., Ansari, Z.A., Rathod, V. and Rodrigues, N. (2001) Response of deep-sea macrobenthos to a small-scale environmental disturbance. *Deep-Sea Research II*, **48**, 3401-3410.

Ingram, C.I. and Hessler, R.R. (1983) Distributional and behavioral patterns of scavenging amphipods from the central North Pacific. *Deep-Sea Research*, **30**, 683-706.

IPCC (2001) *IPCC Third Assessment Report-Climate Change 2001*, Intergovernmental Panel on Climate Change, Geneva, Switzerland.

Jackson, G.A. (1990) A model of the formation of marine algal flocs by physical coagulation processes. *Deep-Sea Research*, **37**, 1197-1211.

Jahnke, R.A. (1990) Early Diagenesis and Recycling of Biogenic Debris at the Seafloor, Santa Monica basin, California. *Journal of Marine Research,* **48**, 413-436.

Jahnke, R.A. (1996) The global ocean flux of particulate organic carbon: areal distribution and magnitude. *Global Biogeochemical Cycles,* **10**, 71-88.

Jahnke, R.A. and Jackson, G.A. (1992) The spatial distribution of sea floor oxygen consumption in the Atlantic and Pacific oceans, in *Deep-sea Food Chains and the Global Carbon Cycle*, vol. 360 (eds G.T. Rowe and V. Pariente), NATO ASI Series, Series C, Kluwer Academic Publishers, Dordrecht, pp 295-307.

Johnson, K.S. and Karl, D.M. (2002) Is ocean fertilization credible and creditable? *Science*, **296**, 467.

Jumars, P.A. (1981) Limits in predicting and detecting benthic community responses to manganese nodule mining. *Marine Mining*, **3**, 213-229.

Karl, D.M. (1999) A sea of change: Biogeochemical variability in the north Pacific subtropical gyre. *Ecosystems*, **2**, 181-214.

Karl, D.M. and Dobbs, F.C. (1998) Molecular Approaches to Microbial Biomass Estimation in the Sea, in *Molecular Approaches to the Study of the Ocean* (ed K.E. Cooksey), Chapman and Hall, London, pp. 29-81.

Karl, D.M. and Lukas, R. (1996) The Hawaii Ocean Time-series (HOT) program: Background, rationale and field implementation. *Deep-Sea Research II*, **43**, 129-156.

Karl, D.M., Bidigare, R.R. and Letelier, R.M. (2001a) Long-term changes in plankton community structure and productivity in the North Pacific Subtropical Gyre: The domain shift hypothesis. *Deep-Sea Research II,* **48**, 1449-1470.

Karl, D.M., Christian, J.R., Dore, J.E., Hebel, D.V., Letelier, R.M., Tupas, L.M. and Winn, C.D. (1996) Seasonal and interannual variability in primary production and particle flux at Station ALOHA. *Deep-Sea Research II*, **43**, 539-568.

Karl, D.M., Dore, J.E., Lukas, R., Michaels, A.F., Bates, N.R. and Knap, A. (2001b) Building the long-term picture: the U.S. JGOFS time-series programs. *Oceanography*, **14**, 6-17.

Karl, D.M., Letelier, R., Hebel, D., Tupas, L., Dore, J., Christian, J. and Winn, C. (1995) Ecosystem changes in the North Pacific subtropical gyre attributed to the 1991-92 El Niño. *Nature,* **373**, 230-234.

Kukert, H. and Smith, C.R. (1992) Disturbance, colonization and succession in a deep-sea sediment community: artificial-mound experiments. *Deep-Sea Research*, **39**, 1349-1371.

Lampitt, R.S. (1985) Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. *Deep-Sea Research*, **32**, 885-897.

Lampitt, R.S. and Antia, A.N. (1997) Particle flux in deep seas: regional characteristics and temporal variability. *Deep-Sea Research I,* **44**, 1377-1403.

Laws, E.A., Falkowski, P.G., Smith, W.O. Jr., Ducklow, H. and McCarthy, J.J. (2000) Temperature effects on export production in the open ocean. *Global Biogeochemical Cycles*, **14**, 1231-1246.

Leonard, C.L., Bidigare, R.R., Seki, M.P. and Polovina, J.J. (2001) Interannual mesoscale physical and biological variability in the North Pacific Central Gyre. *Progress in Oceanography*, **49**, 227-244.

Levin, L.A. and Gage, J.D. (1998) Relationships between oxygen, organic matter and the diversity of bathyal macrofauna. *Deep-Sea Research II*, **45**, 129-163.

Levin, L.A. and Gooday, A.J. (1992) Possible roles for xenophyophores in deep-sea carbon cycling, in *Deep-sea Food Chains and the Global Carbon Cycle*, vol. 360 (eds G.T. Rowe and V. Pariente), NATO ASI Series, Series C, Kluwer Academic Publishers, Dordrecht, pp. 93-104.

McMurtry, G. (2001) Authigenic deposits, in *Encyclopedia of Ocean Sciences, Volume One* (eds S.A. Thorpe and K.K. Turekian), Academic Press, an imprint of Elsevier Science, London, pp. 201-220.

Madigan, M.T., Martinko, J.M. and Parker, J. (2000) *Brock Biology of Microorganisms*, 9th edn, Prentice Hall, New Jersey.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. and Francis, R.C. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Metereological Society*, **78**, 1069-1079.

Martin, J.H., Coale, K.H., Johnson, K.S., Fitzwater, S.E., Gordon, R.M., Tanner, S.J., Hunter, C.N., Elrod, V.A., Nowicki, J.L., Coley, T.L., Barber, R.T., Lindley, S., Watson, A.J., Van Scoy, K., Law, C.S., Liddicoat, M.I., Ling, R., Stanton, T., Stockel, J., Collins, C., Anderson, A., Bidigare, R., Ondrusek, M., Latasa, M., Millero, F.J., Lee, K., Tao, W., Zhang, J.Z., Friedriech, G., Sakamoto, C., Chavez, F., Buck, K., Kolber, Z., Greene, R., Falkowski, P., Chisholm, S.W., Hoge, F., Swift, R., Yungel, J., Turner, S., Nightingale, P., Hatton, A., Liss, P. and Tindale, N.W. (1994) Testing the iron hypothesis in ecosystems of the equatorial Pacific Ocean. *Nature*, **371**, 123-129.

Mestas-Nuñez, A.M. and Enfield, D.B. (2001) Eastern equatorial Pacific SST variability: ENSO and non-ENSO components and their climatic associations. *Journal of Climate*, **14**, 391-402.

Minobe, S. (1999) Resonance in bidecadal and pentadecadal climate oscillations over the North Pacific: Role in climate regime shifts. *Geophysical Research Letters*, **26**, 855-858.

Montagnes, D.J.S. and Franklin, D.J. (2001) Effect of temperature on diatom volume, growth rate, and carbon and nitrogen content: reconsidering some paradigms. *Limnology and Oceanography*, **46**, 2008-2018.

Morgan, C.L. (2000) Resource estimates of the Clarion-Clipperton manganese nodule deposits, in *Handbook of Marine Mineral Deposits* (ed D.S. Cronan), CRC Press, Boca Raton, pp. 145-170.

Mullineaux, L.S. (1987) Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. *Deep-Sea Research*, **34**, 165-184.

Murray, J.W., Johnson, E. and Garside, C. (1995) A U.S. JGOFS Process Study in the equatorial Pacific (EqPac): Introduction. *Deep-Sea Research II*, **42**, 275-293.

Paterson, G.L.J., Wilson, G.D.F., Cosson, N. and Lamont, P.A. (1998) Hessler and Jumars (1974) revisited: abyssal polychaete assemblages from the Atlantic and Pacific. *Deep-Sea Research II*, **45**, 225-251.

Polovina, J.J., Mitchum, G.T. and Evans, G.T. (1995) Decadal and basin-scale variation in mixed layer depth and the impact on biological production in the Central and North Pacific, 1960-88. *Deep-Sea Research*, **42**, 1701-1716.

Polovina, J.J., Mitchum, G.T., Graham, N.E., Craig, M.P., DeMartini, E.E. and Flint, E.N. (1994) Physical and biological consequences of a climate event in the central North Pacific. *Fisheries Oceanography*, **3**, 15-21.

Priede, I.G., Bagley, P.M. and Smith Jr., K.L. (1994) Seasonal change in activity of abyssal demersal scavenging grenadiers *Coryphaenoides (Nematonurus) armatus* in the eastern North Pacific Ocean. *Limnology and Oceanography*, **39**, 279-285.

Raghukumar, C. Loka Bharathi, P. A., Ansari, Z. A., Nair, S., Ingole, B., Sheelu, G., Mohandass, C., Nagender Nath, B. and Rodrigues, N. (2001) Bacterial standing stock, meiofauna and sediment-nutrient characteristics: indicators of benthic disturbance in the Central Indian Basin. *Deep Sea Research II*, **48**, 3381-3399.

Raven, J.A. (1991) Physiology of inorganic acquisition and implications for resource use efficiency by marine phytoplankton - Release to increased CO_2 and temperature. *Plant Cell and Environment*, **14**, 779-794.

Raven, J.A. and Falkowski, P.G. (1999) Oceanic sinks for atmospheric CO_2. *Plant, Cell and Environment*, **22**, 741-755.

Renaud-Mornant, J. and Goubault, N. (1990) Evaluation of abyssal meiobenthos in the eastern central Pacific (Clarion-Clipperton fracture zone). *Progress in Oceanography*, **24**, 317-329.

Riebesell, U., Zondervan, I., Rost, B, Tortell, P.D., Zeebe, R.E. and Morel, F.M.M. (2000) Reduced calcification of marine plankton in response to increased atmospheric CO_2. *Nature*, **407**, 364-367.

Rodrigues, N., Sharma, R. and Nagender Nath, B. (2001) Impact of benthic disturbance on megafauna in Central Indian Basin. *Deep-Sea Research II*, **48**, 3411-3426.

Rowe, G.T., Sibouet, M.S., Deming, J., Kiripounoff, A., Tietjen, J., Macko, S. and Theroux, R. (1991) "Total" sediment biomass and preliminary estimates of organic carbon residence time in deep-sea benthos. *Marine Ecology Progress Series*, **79**, 99-114.

Sarmiento, J.L. and Orr, J.C. (1991) Three-dimensional simulations of the impact of Southern Ocean nutrient depletion on atmospheric CO_2 and ocean chemistry. *Limnology and Oceanography*, **36**, 1928-1950.

Scharek, R., Latasa. M., Karl, D.M. and Bidigare, R.R. (1999a) Temporal variations in diatom abundance and downward vertical flux in the oligotrophic North Pacific gyre. *Deep-Sea Research I*, **46**, 1051-1075.

Scharek, R., Tupas, L.M. and Karl, D.M. (1999b) Diatom fluxes to the deep sea in the oligotrophic North Pacific gyre at station ALOHA. *Marine Ecology Progress Series*, **182**, 55-67.

Seibold, E. and Berger, W.H. (1996) *The Seafloor: an Introduction to Marine Geology*, 2nd edn, Springer-Verlag, Berlin, Heidelberg, New York.

Siegel, D.A. and Deuser, W.G. (1997) Trajectories of sinking particles in the Sargasso Sea: modeling of statistical funnels above deep-ocean sediment traps. *Deep-Sea Research I*, **44**, 1519-1541.

Smith, C.R. and Demopoulos, A.W.J. (2003) Ecology of the deep Pacific Ocean floor, in *Ecosystems of the World, Volume 28, Ecosystems of the Deep Ocean* (ed. P.A. Tyler), Elsevier, Amsterdam, pp. 179-218.

Smith, C.R. and Rabouille, C. (2002) What controls the mixed-layer depth in the deep-sea sediments? The importance of POC flux. *Limnology and Oceanography*, **47**, 418-426.

Smith, C.R., Berelson, W., DeMaster, D.J., Dobbs, F.C., Hammond, D., Hoover, D.J., Pope, R.H. and Stephens, M. (1997) Latitudinal variations in benthic processes in the abyssal equatorial Pacific: control by biogenic particle flux. *Deep-Sea Research II*, **44**, 2295-2317.

Smith, C.R., Hoover, D.J., Doan, S.E., Pope, R.H., DeMaster, D.J., Dobbs, F.C., and Altabet, M.A. (1996) Phytodetritus at the abyssal seafloor across 10^o of latitude in the central equatorial Pacific. *Deep-Sea Research II*, **43**, 1309-1338.

Smith, C.R., Pope, R.H., DeMaster, D.J. and Magaard, L. (1993) Age-dependent mixing of deep-sea sediments. *Geochimica et Cosmochimica Acta*, **57**, 1473-1488.

Smith Jr., K.L. (1987) Food energy supply and demand: A discrepancy between particulate organic carbon flux and sediment community oxygen consumption in the deep ocean. *Limnology and Oceanography*, **32**, 201-220.

Smith Jr., K.L. (1992) Benthic boundary layer communities and carbon cycling at abyssal depths in the central North Pacific. *Limnology and Oceanography*, **37**, 1034-1056.

Smith Jr., K.L., Baldwin, R.J., Karl, D.M. and Boetius, A. (2002) Benthic community responses to pulses in pelagic food supply: North Pacific Subtropical Gyre. *Deep-Sea Research I*, **49**, 971-990.

Smith Jr., K.L., Kaufmann, R.S., Edelman, J.L. and Baldwin, R.J. (1992) Abyssopelagic fauna in the central North Pacific: comparison of acoustic detection and baited trap collections to 5800 m. *Deep-Sea Research*, **39**, 659-685.

Smith Jr., K.L., Laver, M.B. and Brown, N.O. (1983) Sediment community oxygen consumption and nutrient exchange in the central and eastern North Pacific. *Limnology and Oceanography*, **28**, 882-898.

Snider, L.J., Burnett, B.R. and Hessler, R.R. (1984) The composition and distribution of meiofauna and nanobiota in a central North Pacific deep-sea area. *Deep-Sea Research*, **31**, 1225-1249.

Strutton, P.G. and Chavez, F.P. (2000) Primary productivity in the equatorial Pacific during the 1997-1998 El Niño. *Journal of Geophysical Research - Oceans*, **105**, 26,089-26,101.

Suess, E. (1980) Particulate Organic Carbon Flux in the Oceans – Surface Productivity and Oxygen Utilization. *Nature*, **288**, 260-263.

Thiel, H. (2001) Use and protection of the deep sea - an introduction. *Deep-Sea Research II*, **48**, 3427-3431.

Timmermann, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M. and Roeckner, E. (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature*, **398**, 694-697.

Tortell, P.D., Reinfelder, J.R. and Morel, F.M.M. (1997) Active uptake of bicarbonate by diatoms. *Nature*, **390**, 243-244.

Trenberth, K.E. and Hoar, T.J. (1996) The 1990-1995 El Niño-Southern Oscillation event: longest on record. *Geophysical Research Letters*, **23**, 57-60.

Trenberth, K.E. and Hoar, T.J. (1997) El Niño and climate change. *Geophysical Research Letters*, **24**, 3057-3060.

Trull, T.W. and Armand, L. (2001) Insights into Southern Ocean carbon export from the $\delta^{13}C$ of particles and dissolved inorganic carbon during the SOIREE iron release experiment. *Deep-Sea Research II*, **48**, 2655-2680.

Van Cappellen, P. and Ingall, E.D. (1996) Redox stabilization of the atmosphere and oceans by phosphorus-limited marine productivity. *Science*, **271**, 493-496.

Vanreusel, A., Vincx, M., Bett, B.J. and Rice, A.L. (1995) Nematode biomass spectra at two abyssal sites in the NE Atlantic with a contrasting food supply. *Internationale Revue der Gesamten Hydrobiologie*, **80**, 287-296.

Vopel, K. and Thiel, H. (2001) Abyssal nematode assemblages in physically disturbed and adjacent sites of the eastern equatorial Pacific. *Deep-Sea Research II*, **48**, 3795-3808.

Wishner, K., Levin, L., Gowing, M. and Mullineaux, L. (1990) Involvement of the oxygen-minimum in benthic zonation on a deep seamount. *Nature*, **346**, 57-59.

Yamazaki, T., Kajitani, Y., Barnett, B.G. and Suzuki, T. (1997) Development of image analytical technique for resedimentation induced by nodule mining, in *Proceedings of the ISOPE Ocean Mining Symposium*, ISOPE, Seoul, pp. 159-164.

Zehr, J.P., Carpenter, E.J. and Villareal, T.A. (2000) New perspectives on nitrogen-fixing micro-organisms in tropical and sub-tropical oceans. *Trends in Microbiology*, **8**, 68-73.