

10 Biome and province analysis of the oceans

Satellite chlorophyll

All of oceanography, particularly its physical and biological aspects, has been intensely challenged by satellite data. Snapshots from space of temperature distributions have challenged physical oceanographers because earlier analyses of data taken from ships were blurred by widely spaced stations and by motion of patterns during sampling (low "synopticity"). Satellites swing across the Earth in minutes, gathering images from very wide swaths. Some sit in geostationary orbits and get instantaneous, whole Earth images. In the mid-1970s, we were suddenly able to see the layout of variability on scales of a few kilometers. This reveals offshore jets and eddies, current meanders and surface ring structures. The dynamism of ocean processes was a major surprise and something of an embarrassment. There are only vague hints in the literature that anyone anticipated it would look as it does from this distant and instantaneous perspective. Physicists had dropped the necessary higher order terms in their hydrodynamic models, thinking they were too small to have significant, observable effects. From the shipboard perspective, they were right. From the instantaneous perspective they missed the boat (which delighted some biologists for reasons we understand very well). Biologists were surprised by similar data. The jets and swirls show up not only in satellite temperature maps (e.g. AVHRR), but in pictures based on ocean color, variation of which is mostly determined by chlorophyll content. Here, too, the swirls and jets are impressive. A picture (book cover)

from the Coastal Zone Color Scanner (CZCS) shows (albeit in "false" color) some of the dramatic features which changed the understanding of ocean processes.

Just as impressive are the short-term changes in quantities and distribution from one picture date or season to the next. Satellites provide new pictures on time scales less than a week, the usual time required for records from orbital swaths to accumulate as regional or global images. Short-term and seasonal comparisons become possible, and the general correlation between production rates and chlorophyll standing stock makes possible much more convincing estimates of regional and total primary production rates. We can add up approximations of how much carbon is being incorporated in organic matter and get at large scale biogeochemical transformation rates with more convincing precision. Currently active color satellites are called SeaWiFS and MODIS. You can find an archive of Level 3 (elaborately corrected, averaged and mapped) SeaWiFS images at <http://seawifs.gsfc.nasa.gov/SEAWIFS.html>. Monthly global averages available there show the dominant features of seasonal cycling of phytoplankton stock in all ocean regions, except for the most polar areas and the two subpolar zones in their respective winters.

SeaWiFS, operational since September 1997, records over swaths that add up to complete global coverage every two days. The Goddard Space Flight Center of NASA produces processed images rapidly, with weekly averages as global images appearing a few days after the data are in,

monthly averages right at the end of the month, and so on. The global picture (Plate 10.1) shows the layout of blue (low chlorophyll) and green to red (artificial colors indicating high chlorophyll) regions across the globe. Note that SeaWiFS also generates color pictures of the land, which has its own uses.

The exact algorithm for SeaWiFS is not cleanly presented anywhere; a sort of technical haze covers the methodology. Here is a general description; similar techniques were used for the CZCS algorithm. A suite of spectral sensors looks during daylight down a narrow tube, actually a telescope "folded" with prisms into a compact package. The image at the "eyepiece" of the telescope subtends a small ($\sim 1.2 \times 1.2$ km) sea surface pixel. The telescope swings left and right across the path passing under the satellite, recording light from successive pixels. Dichroic beam splitters and color filters divide light from each pixel into eight spectral bands, one for each recording sensor. Sensors are charge-coupled devices similar to those in digital cameras. The spacecraft periodically transmits recorded results to ground stations by radio.

Each sensor collects an amount of light (L_{total}) proportional to the water-leaving radiance from the pixel (L_W , which is the variable of interest) plus (i) light reflected from the sea surface in the pixel (L_r), plus (ii) light atmospherically scattered into the path from the pixel to the satellite that left the sea outside the pixel (part of L^*), plus (iii) light scattered directly from the atmosphere (another part of L^*). The collected amount will also depend upon the thickness of atmosphere between the sea and the sensor, which varies between pixels thus requiring a pixel-specific transmittance fraction (T_A). Transmittance can vary with atmospheric conditions, which can be estimated from various wavelength-specific features of the received light. So, we have:

$$L_{\text{total}} = L^* + T_A L_W + T_A L_r.$$

L_r is taken to be modest and proportional to L^* and is lumped with it, giving $L_{\text{total}} = L^* + T_A L_W$. L^* is estimated from solar irradiance, measured on the outward-looking side of the satellite, and a model, and T_A is estimated from some ratios of received

irradiance at several wavelengths known not to vary from each other in their L_W . Finally, L_W values are calculated for each wavelength.

In the SeaWiFS algorithms, L_W is next converted to $R_{rs} = L_W/E_t$, where E_t is the total downwelling irradiance of the same wavelength at the sea surface. That is estimated from the simultaneous measures of solar irradiance on the outward-looking side of the satellite (L^* , again), corrected for atmospheric absorbance.

With estimates in hand of R_{rs} at eight wavelengths, it turns out that the best empirical estimator of chlorophyll in the sea surface of the pixel is given by a function of the ratio:

$$R_{rs}(490 \text{ nm})/R_{rs}(555 \text{ nm}).$$

The current version of this function is called OC4 (O'Reilly *et al.* 2000). This is repeatedly updated as more sea surface measures are taken corresponding to satellite results from the same pixels. OC2 version 3 has the following formula in which $R = \log_{10}(R_{rs}490/R_{rs}555)$:

$$\text{Chl (mg m}^{-3}\text{)} = 10^{(0.2733 - 2.3534R + 1.1416R^2 - 0.2972R^3)} - 0.0788.$$

Such formulas appear to fit ship-based data well (Fig. 10.1) over a range from 0.02 to about 20 mg m^{-3} . As shown by the dashed confidence-limit (level unspecified) lines, virtually all surface estimates are within a factor of 5 (either high or low) of the satellite estimate, and a very large fraction of estimates are within the range half to double. Thus, while the satellite estimator is not closely accurate for any given pixel, with sufficient area averaging the data are useful because the estimator shows no obvious bias. Regional and global totals will benefit from massive averaging and should be reasonably accurate.

Mitchell and Flatau (1999) show (Fig. 10.2) some comparisons of SeaWiFS OC2v2 (closely comparable to OC2v3 from 0.2 to 10 mg m^{-3}) results with direct sampling from the sea surface off California (CalCOFI) and in the Southern Ocean which do indicate some bias. The plots of deviations between the satellite estimates

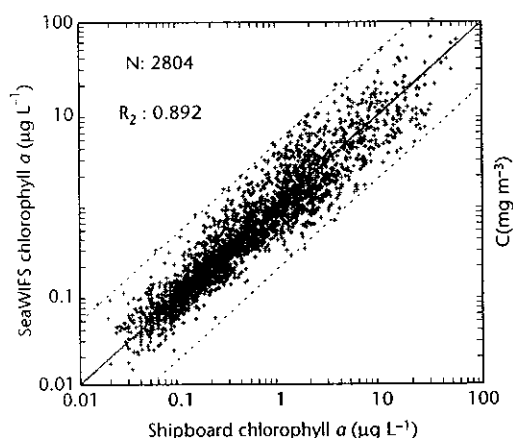


Fig. 10.1 Comparison of the OC2 version 4 chlorophyll estimate from R_{rs490}/R_{rs555} (ordinate) to shipboard measures of sea surface chlorophyll from a wide range of ocean sites. (After O'Reilly *et al.* 2000, workshop report.)

("model") and ship observations suggest that the satellite estimates are usually high by a factor of 1.25 to 2.0, except at the highest levels where they are too low. In all likelihood, these errors are "regional", that is, deviations in the areas of study from the general model that is a best-fit for the global ocean overall. Of course, it is possible to use regional models for detailed studies. The entire estimation process is under continuous study. It will improve, but it is also limited in fundamental ways.

Longhurst's analysis

Alan Longhurst was among the group (Abbott, Banse, Brown, Esaias, Longhurst, McClain, McGowan, Pelez, Platt, Sathyendranath and others) that took an early interest in the information from images made with the first visible-wavelength satellite radiometer, the CZCS, which was active from 1978 to 1986. In 1998 he published a book, *The Ecological Geography of the Sea*, attempting to define a geography of ecosystem types in the world's oceans based on CZCS images. He concluded that basically there are four "biomes" (a term from terrestrial ecology, where we recognize rainforest, desert, savannah, and

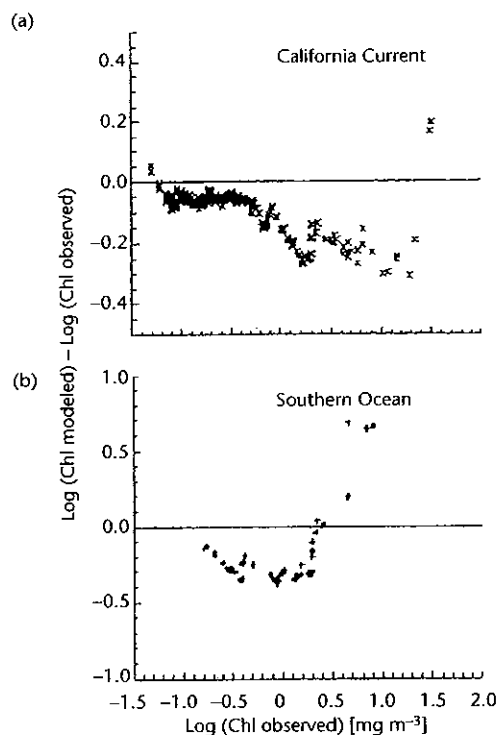


Fig. 10.2 Two regional comparisons, (a) California Current, and (b) Southern Ocean, of SeaWiFS chlorophyll estimates to shipboard measures. "Modeled" means estimated from satellite radiometer ratios. As an example of interpretation, above 1 mg m^{-3} (i.e. $\log [\text{observed Chl}] = 0.0$) the deviation of satellite estimates from the California Current average 1.58 times ($1/[-0.2]$) shipboard measures from the same pixels. (After Mitchell & Flatau 1999.)

other biomes) in the sea. These are polar, westerlies, trades and coastal zone biomes. Immediately after he defines them, however, he states that high nutrient-low chlorophyll (HNLC) habitats are large exceptions. He hesitates to define HNLC areas as a biome, because they span such a large range of latitude with obviously very different seasonality and ecology. At least the two polar and all the westerly biomes vary enough from each other that they really must be considered separately. It is also clear that the trades biome, in which Longhurst includes central gyre and equatorial areas, is not a suitable unit. In order to get to a division comparable to that indicated by the distributional patterns of organisms, he divides the biomes into

"provinces", ultimately arriving at a very complex scheme indeed. The general biogeographic observations reported in the previous chapter provide a more sensible division, a set of ocean sectors which the satellite observations also distinguish reasonably well. We will treat those as distinctive biomes and also accept Longhurst's distinction of coastal biomes, which again divide into several types.

Recent research in oceanic biological oceanography has been organized as programs targeting specific ones of these biomes or ecosystems. As examples, the subarctic Pacific was approached by the SUPER program (Miller 1993), the North Pacific central gyre by the Hawaii (HOTS) and Bermuda (BATS) ocean time series studies (e.g. Karl & Michaels 1996; Siegel *et al.* 2001), the Antarctic by the US Southern Ocean JGOFS-AESOPS Program (Smith & Anderson 2000a,b). There have been numerous other regional projects in the last two decades mounted by national and international teams. Output from these programs is usually in the form of stacked papers by participating research groups, sometimes including a good synthesis of the overall significance of the disparate components, sometimes not. Recent publishing practice has been to assemble these papers in single volumes of *Deep-Sea Research II* or *Progress in Oceanography*, which helps the uninitiated to approach the study of particular biomes. Full summaries of what is now known of each ecosystem type would take books larger than this. There follows the very rudimentary basics for each of these biomes.

Polar biomes

By polar biome Longhurst meant the zone covered permanently or seasonally by sea ice and consistently cold, with even surface temperatures remaining below about 5°C. Included are the Arctic Ocean, part of the Bering Sea and the Antarctic out to nearly the Antarctic circumpolar convergence. Ice has a high albedo and shades the water column below. Of course, in the seasons when the sea is frozen it is also dark, or nearly dark, and photosynthetic production drops to zero. Phytoplankton stocks are low. Not only

that, but lacking illumination, the satellites see nothing! When the sun does come out, the ice melts and recedes. From that point the outcome depends upon where you are. In the Atlantic side of the Arctic Ocean (from Greenland across to the Barents Sea) there is reasonably high availability of nutrients from the pre-freeze mixing, which supports a substantial spring bloom. It starts with an "epontic" community up in the porous "frazil" ice on the under-surface of the floating pack. Then the floating melt water left by the recession of the ice provides stability, and a bloom ensues immediately that follows the receding ice pole-ward. That bloom feeds some copepods and other plankton. Copepods (*Calanus glacialis* and *Calanus hyperboreus* in the Arctic) take two and even three years to complete a life cycle due to the short growing seasons. They rest at depth between bouts of growth.

In the central Arctic Ocean and Chukchi-Beaufort Sea the ice does not go out. This sector is stratified by a surface layer of low salinity that is primarily due to spreading of the outflow from Canadian and Siberian rivers. The low-density surface layer prevents contact of the ice with the underlying North Atlantic water that is warmer and saltier. During the winter night there is some upward mixing driven by recurring internal waves in the halocline, bringing up nutrients. During the lighted phase of the year, those nutrients drive production of epontic algae and very modest blooms in open leads in the ice. Recent results from Wheeler and others on the Shiva Expedition, aboard an icebreaker frozen into the ice for a year in this region, showed exactly that; somewhat more production than from previous estimates. The northern reach of the Bering Sea is underlain by continental shelf and is part of a coastal biome. By its proximity to the bottom (and tidal mixing) it generates a strong, continuous diatom bloom (red on satellite images) until freeze-up in the autumn.

In the Antarctic, in the seasonal ice zone, the upwelling of nutrient-rich deep water under the receding ice provides copious major nutrients. There is a phase in which epontic algae are abundant, then a strong bloom, dominated by diatoms, follows the ice melt southward. Dust accumulated on the ice over winter provides iron. Melt water

provides stability and critical depths are well below the mixing depth, so blooms (to $> 10 \text{ mg Chl m}^{-3}$) ensue. Northward from the winter ice, closer to the convergence, there is also upwelling from global-scale thermohaline circulation providing abundant major nutrients, and there can be spring (November–December) blooms ($\sim 1.5 \text{ mg Chl m}^{-3}$, Abbott *et al.* 2000). It is believed, but not fully established, that at each successive latitude southward depletion of trace metallic nutrients, most importantly iron, terminates this bloom well before major nutrients are consumed. Nitrate and phosphate remain in excess throughout the year (e.g. a minimum of $7 \mu\text{M}$ nitrate at 76°S in the Ross Sea, Gordon *et al.* 2000), sustaining modest levels of phytoplankton stock ($\sim 0.3 \text{ mg Chl m}^{-3}$) until darkness and ice return. Blooms are heavily dominated by diatoms that are grazed primarily by copepods in the open Antarctic and by krill, predominantly *Euphausia superba*, closer to the continent and in the outflow from Drake Passage around South Georgia. The oceanic copepods (principally *Calanus propinquus* and *Calanoides acutus*) resemble those of the Arctic (and subarctic), loading with lipid as a nutriment store and taking a deep siesta (copepodite “diapause”) during the dark season. Sedimentation from Antarctic diatom blooms accounts for a large fraction of silicic acid removal from the global ocean, producing a thick pad of opal-rich ooze on the seafloor. In the eastward outflow from Drake Passage, particularly in the vicinity of South Georgia which is probably a local iron source, the diatom production continues right through the summer, sustaining high secondary productivity (particularly of krill) and huge stocks of whales, seals, fish (e.g. the cod-like Nototheniids of the southern hemisphere) and seabirds (e.g. penguins). This Antarctic situation is, of course, much more complex and deserves more attention than it gets here.

Westerlies biomes

The westerlies zones are those also termed “sub-polar”: the subarctic Atlantic, subarctic Pacific and subantarctic. Discussion of these is limited here by

emphasizing the subarctic Pacific system. The subarctic North Atlantic was covered in the opening discussion of spring bloom dynamics, for which it is the main oceanic example. Much of our understanding of the subarctic Pacific came about because of its contrast to the North Atlantic. The subarctic Pacific is one of the cold versions of a high nitrate–low chlorophyll, or HNLC region. The other cold versions are the Antarctic (polar, of course) and subantarctic areas of the Southern Ocean. These have been studied (e.g. Miller 1993 and references therein) to determine why phytoplankton do not exhaust the surface supply of major nutrients during the warmer, illuminated summer season when the water column is stratified. The new dogma goes that iron limitation constrains the phytoplankton to small size ($< 10 \mu\text{m}$). This was initially demonstrated by Martin and Fitzwater (1988) who compared phytoplankton growth in large water samples augmented with iron and not augmented. After a lag in which enough large phytoplankton accumulated to contribute significantly to chlorophyll, there was a nutrient-depleting bloom in augmented containers, but not in the others (Fig. 10.3). The small size of primary producers allows protozoans to be the principal grazers. Protozoans can increase at least as rapidly, likely up to two doublings per day, as their phytoplankton food, if that food is abundant. So, they crop down every incipient bloom, recycling nutrients in the upper layers, preventing exhaustion of nitrate, phosphate and silicate. Surface nitrate drops by about $8 \mu\text{M}$ from March to August, but it never drops below $6 \mu\text{M}$ (Fig. 4.8d). Phosphate and silicate are never reduced to limiting levels, either. Another important part of this is that limitation of vertical mixing, by the halocline at approximately 100 m characteristic of the region (Fig. 10.4), keeps this microplanktonic food web in place right round the year. It is never disrupted by mixing to about 400 m as happens in most of the subarctic North Atlantic.

The mesozooplankton in the subarctic Pacific are dominated, especially from March to July, by five species of copepod: *Neocalanus plumchrus*, *Neocalanus flemingeri*, *Neocalanus cristatus*, *Eucalanus bungii* and *Metridia pacifica*.

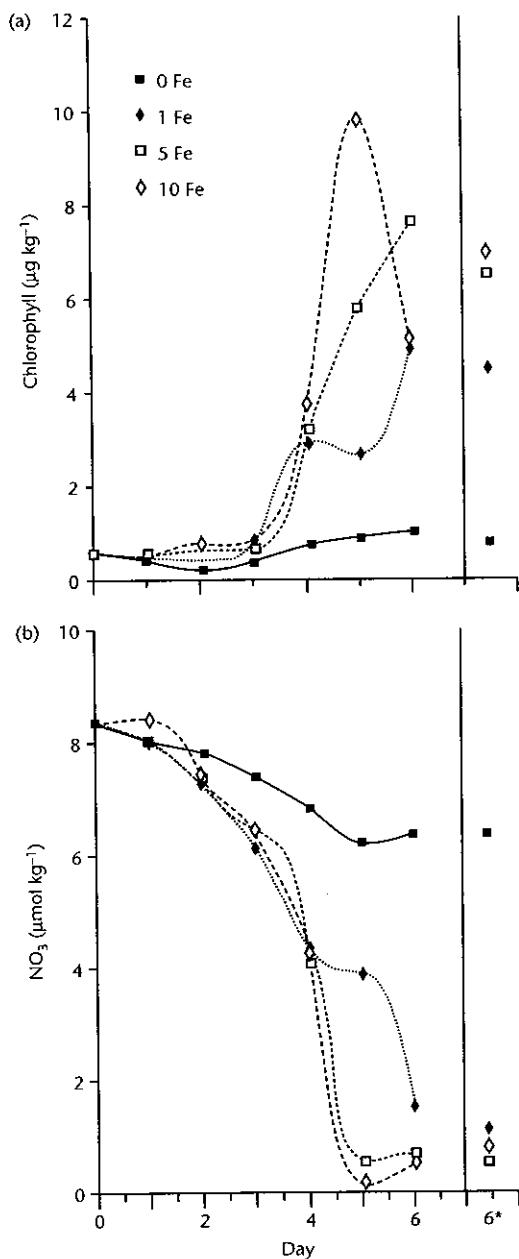


Fig. 10.3 Time series of (a) chlorophyll and (b) nitrate concentrations in incubation bottles of subarctic Pacific (Ocean Station P, 50°N, 145°W) surface water with and without iron enrichment. Three levels of enrichment were tested. Cells breaking out of background chlorophyll levels on Day 4 were large diatoms. Symbols over Day 6* are for separate incubations not opened for sampling until Day 6. (After Martin & Fitzwater 1988.)

Copepodite stages of the first two are abundant in the layer above the seasonal thermocline which sets up in late April at about 35 m. Those of the latter two species are abundant below the thermocline and probably primarily scavenge fecal matter sinking down from above it. *Metridia* is a strong diel migrator, the others are not. All but *Metridia* have a resting stage as fifth copepodites (C5). This stage loads with large amounts of nutrient stored as liquid wax, then descends to depths below 400 m (to 2000+ m) as a refuge from late summer warming and predation. The different species have somewhat different reproductive schedules as discussed in Chapter 8. The dominant species, *N. plumchrus*, distributes its spawning at depth from late summer through to early spring, apparently "spreading its bets" across the entire season. The winning nauplii that get food to grow are those arriving at the surface as first-feeding stages when production increase is strong due to rising insolation and surface thermal stratification. During the 1990s, the month in which these copepodite stocks were maximal moved progressively earlier by about 6 weeks from May in the 1980s to April (Mackas *et al.* 1998). All of these copepods feed primarily on protozoans, and they constitute the trophic level that shows strong seasonal cycling (Fig. 10.5). Thus, seasonality of primary production is first exhibited two trophic levels away from the primary producers.

The contrast of the subarctic Pacific with the North Atlantic north of the Gulf Stream and south of the polar front has four main parts. In the North Atlantic, (i) winter mixing is deep, and phytoplankton stocks are reduced very close to zero ($0.01 \mu\text{g Chl L}^{-1}$ is not unusual). (ii) Spring blooms are typical, reaching $2\text{--}4 \text{ mg Chl m}^{-3}$ all across from New England to Norway. Large diatoms dominate Atlantic blooms, whereas diatoms are only occasionally a major fraction of phytoplankton biomass in the Pacific and always as very small ($< 7 \mu\text{m}$) species. (iii) Proximity to continents apparently provides enough iron to fuel complete exhaustion of major nutrients, particularly nitrate from surface layers. It is important, also, that the concentration of nutrients at depth is about half that in the Pacific, so depletion is more readily reached before trace metal limitation is

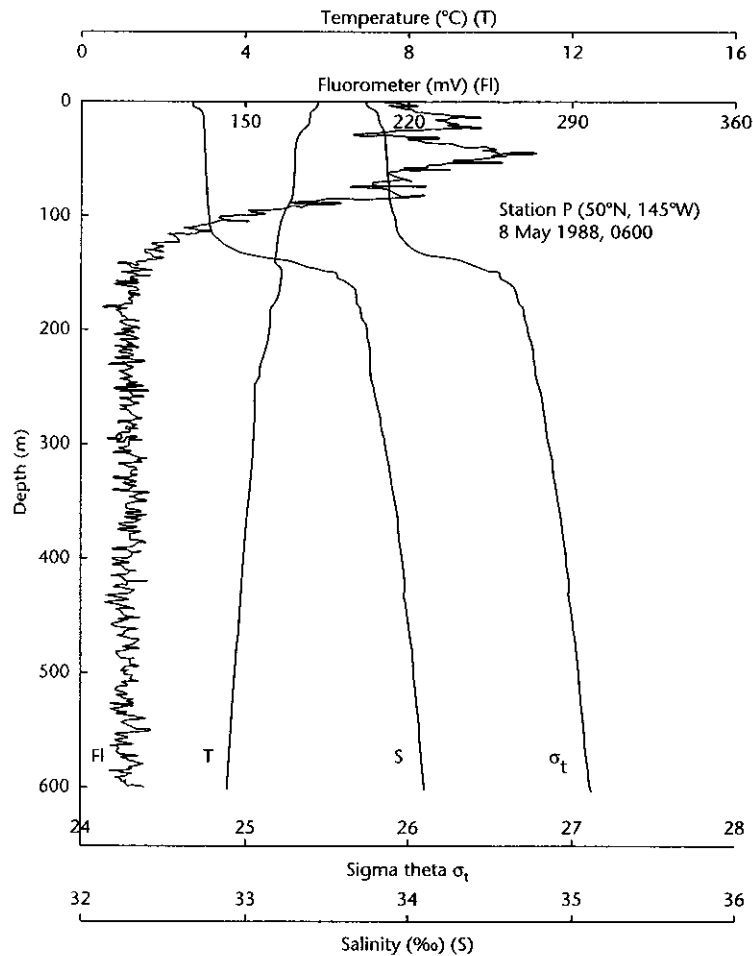


Fig. 10.4 Spring water column stratification in the oceanic subarctic Pacific at Ocean Station P. (After Miller *et al.* 1991.)

severe. (iv) The dominant grazing zooplankton species are from the genus *Calanus*. *Calanus helgolandicus* is dominant to the east and just north of the Gulf Stream. *Calanus finmarchicus* dominates in a northeasterly expanding stripe from Cape Cod across south of Iceland into the Norwegian and Barents Sea. *Calanus glacialis* is progressively more important approaching and under the Arctic ice. *Calanus finmarchicus*, the most abundant and best studied, shares the family trait of resting in late copepodite stages (C4 and C5). It matures at different dates according to subregion: January in the Gulf of Maine, February in the Norwegian Sea, March in the Irminger Sea in between (Planque *et al.* 1997). In each case, the timing anticipates

the spring bloom by weeks to months, so that females are matured and actively spawning when the spring bloom gets started. While the females can produce some eggs on the low stocks of phytoplankton (and microheterotrophs) available before the bloom, they depend upon the bloom to fuel maximum and sustained spawning. Unlike the subarctic Pacific *Neocalanus* species, *Calanus* females must eat to spawn. Most recent results (Niehoff *et al.* 1999) suggest that the pre-bloom spawning produces the copepodites that use the bloom to grow. Females are actually much less numerous during the bloom than before, and copepodites from eggs produced during the bloom must depend after the bloom upon microheterotrophs that con-

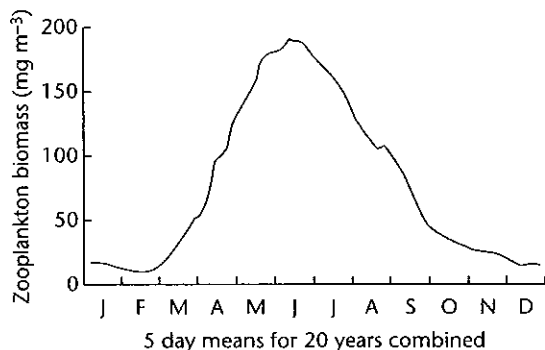


Fig. 10.5 Annual cycle of zooplankton biomass in the upper 150 m in the oceanic subarctic Pacific. The build-up in spring is from growth, mostly of large copepods. Decline in early summer is from descent of these copepods to depths below 500 m for diapause. (After Fulton 1983.)

stitute suitably sized food in that interval. In all regions except the Irminger Sea, rest at depth resumes in June or July. Irminger Sea stocks only rest after about October. Over most of the range, except for the northern Norwegian Sea, there are two generations, the first maturing immediately without rest to produce the second.

The subantarctic works much like the subarctic Pacific, although it isn't so well studied. The Antarctic sector of the Southern Ocean has attracted much more attention than the larger, adjacent subantarctic area. However, the subantarctic is another cold, HNLC region (Moore & Abbott 2000). Major nutrients are never exhausted, chlorophyll varies around $0.3\text{--}0.4\text{ mg m}^{-3}$ (Plate 10.2), and isolation from land suggests iron limitation, as do the chlorophyll "hot spots" around islands like Kerguelen. At least one abundant, circumglobal, subantarctic copepod, *Neocalanus tonsus*, has a lipid-loading and diapause scheme resembling that of the subarctic Pacific dominants.

Subtropical gyre biomes

Longhurst placed the boundaries of his trades zone at about 30°N and 30°S . That passes right through the ecologically quite uniform central gyres, and John McGowan and others have chosen 30°N as a

latitude at which to study the fundamentals of central gyre ecology (the Bermuda Atlantic Time Series, BATS, is at 32°N). There is a basis in biogeography for lumping all of the warmer ocean waters: many species ranges extend from 45 or 40°N to the equivalent southern latitude, stretching right across the equator. However, the satellite images show that the central gyres have lower chlorophyll (phytoplankton stocks), they are certainly less productive than the actual trade wind zone surrounding the equator, and many species live in the central gyres only. So, we will declare central gyre and trades biomes to be separable and consider them separately. We'll stick to the Pacific, since we can't cover everything. Thanks to McGowan's CLIMAX studies in the 1960s–1980s and to the Hawaii Ocean Time Series (HOTS, sampling at Station "ALOHA", e.g. Siegel *et al.* 2001), work that is part of the JGOFS program, we have lots of data about the North Pacific central gyre (NPCG). The similar JGOFS BATS time series (Steinberg *et al.* 2001) provides a comparison. JGOFS also mounted a series of equatorial zone production studies (Murray 1995; Murray *et al.* 1997) and the equatorial Pacific has been intensely studied by many other programs in recent decades.

The key feature of the central gyres is water column stability. Examination of north–south sections of temperature or σ_t shows flat isopleths in the gyres for 1000s of kilometers. The system is said to be "barotropic". This results from the anticyclonic direction of gyral flow, which tends to be convergent, piling water in the center under the tropical sun for stabilizing warming. There is a zone of moderately strong stratification from approximately 120 m down to about 1200 m, the permanent pycnocline. This is a barrier to mixing which ensures very slow provision of nutrients upward. The surface layer exhibits some temperature cycling ($\sim 18^{\circ}\text{C}$ winter to $\sim 25^{\circ}\text{C}$ summer) over a seasonal thermocline at about 50–70 m. Because of water clarity, net photosynthesis is possible to about 125 m (Fig. 10.6), and nutrients become depleted down to that level. Nitrate is removed to a level undetectable by standard analyses (sensitive to $\sim 0.1\text{ }\mu\text{M}$). Typically, free phosphate is not quite depleted (Fig. 10.7), but levels beneath the detection limits are not unusual. Pri

mary production runs mostly on recycled nutrients. Phytoplankton are found to have extreme affinity for ammonia and carry surface enzymes for stripping phosphate from organic complexes. Since there are always losses of organic matter to depth, however, the system cannot run entirely on recycled nutrients. At 125 m or just above is the top of a nutricline, a downward increase in available phosphate, nitrate and silicate, and it is the slow vertical mixing of the permanent pycnocline, moving this nutricline upward, which sets the rate of production via nutrient supply.

The NPCG ecosystem is certainly also iron-limited in a sense, but the long-term rate of aeolian iron transport is great enough to overcome the slow rate of fixed nitrogen supply, so that nitrogen becomes fully depleted from the surface. HNLC regions all are much more "baroclinic" and divergent, such that iron supply cannot keep pace with nitrogen supply, so iron becomes, as John Martin liked to put it, the Liebigian nutrient (Liebig, an early agricultural chemist, suggested that the one nutrient compound in least supply relative to plant requirements would be the factor limiting plant

growth). Probably the Sargasso Sea is different (Wu *et al.* 2000), because aeolian dust from North Africa supplies more iron to support nitrogen fixation. Thus, dissolved inorganic phosphorus becomes completely exhausted, typically leaving some dissolved nitrate behind (Fig. 10.8). Ratios of inorganic N:P differ between the central gyres in the two regions, about 15:1 in the NPCG and 17:1 in the Sargasso Sea, probably because of this quantitative difference in nitrogen fixation.

Primary productivity in the NPCG is relatively constant through the year, although data (Fig. 10.9) from Station ALOHA show a mid-winter low of about $350 \text{ mgC m}^{-2} \text{ day}^{-1}$ (integrated to 200 m) and an early summer high around $700 \text{ mgC m}^{-2} \text{ day}^{-1}$ (annual mean ~ 485). In the Sargasso Sea a small pulse of nutrients usually reaches the sea surface in February, with a modest increase in production and phytoplankton standing stocks (Steinberg *et al.* 2001). This is readily missed by gaps in sampling but probably does not happen every year. Interannual variations in productivity are also observed in the NPCG, and made much of by the HOTS team (e.g. Karl *et al.* 2002).

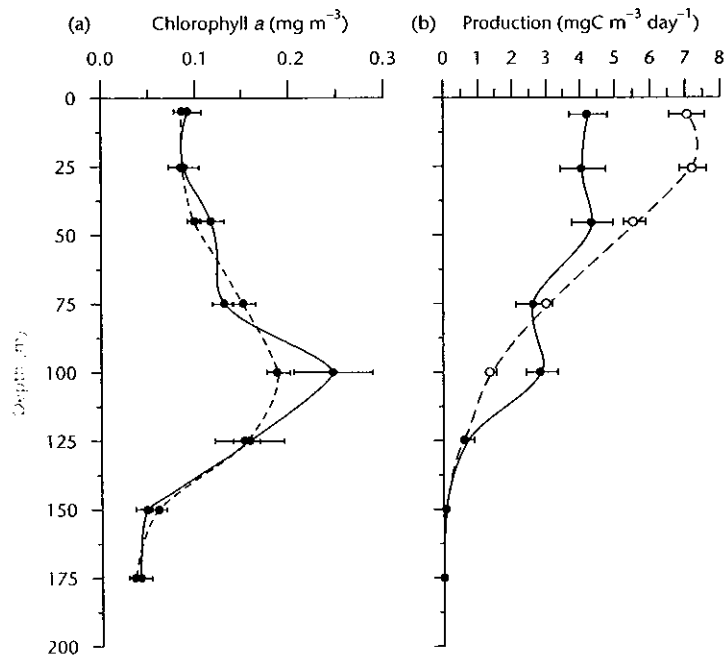


Fig. 10.6 Vertical profiles of (a) chlorophyll and (b) primary productivity from Station ALOHA (22.75°N, 158°W, the Hawaii Ocean Time Series site). Open circles for samples up through January 1991; filled circles for those afterward. (After Letelier *et al.* 1996.)

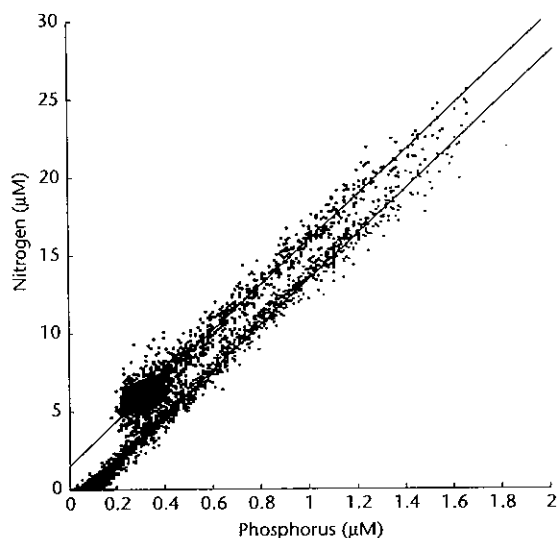


Fig. 10.7 Plot for Station ALOHA showing relationship between dissolved nitrogen and phosphorus. Higher values are deeper in the water column. The filled points and lower line are for nitrate plus nitrite vs. soluble reactive phosphorus (inorganic nutrients). The upper line is for total dissolved nitrogen (TDN = nitrate + nitrite + ammonia + dissolved organic nitrogen) vs. total dissolved phosphorus (TDP = inorganic + organic phosphorus). Nitrogen and phosphorus in the organic fractions are less available for uptake by phytoplankton. In surface layers (less than ~80 m) inorganic nitrogen is very close to undetectable, while reactive phosphorus is usually 0.02 to 0.15 μM . Relative to proportions required to form new organic matter, nitrogen generally is exhausted first. (After Karl *et al.* 2001.)

They are primarily seen as changes in assimilation number, which is ($\text{mgC m}^{-3} \text{ day}^{-1} / \text{mg Chl m}^{-3}$) (Fig. 10.9); this relative measure of production increased for the first seven years of the time series, then dropped somewhat. It is not certain whether a large increase of primary production in HOTS data (1991 on) compared to results from the 1980s is due to variant methods or to a real change. Data before 1980 were more than 2-fold lower, which is at least partly methodological, a change to very clean techniques. The high modern production values make a large difference in our estimates of global primary production. The importance of this change is a function of the scale of these ecosystems. The zone from 45°N to 45°S represents

about 70% of the world's oceans (just from similar latitude)).

Karl and colleagues (1999, 2001) have shown (Fig. 10.10) year-to-year decreases at ALOHA in unbound phosphate ions ("soluble, reactive phosphate," SRP), and that phosphate is occasionally replenished, as during 1994–95, by stronger than usual winter storm mixing or by passing mesoscale eddies. The decreases are about equal in magnitude to increases in organically bound phosphate. Karl believes that the fixed nitrogen required to accompany this phosphate assimilation has come from enhanced nitrogen fixation, principally by *Trichodesmium*, over the interval of the HOTS observations. There is also an annual, subsurface bloom (R. Letelier, pers. comm.) of the diatom *Hemiaulus*, which harbors a symbiotic, nitrogen-fixing cyanophyte called *Richelia*. Just this brief pulse of diatom production and symbiont nitrogen fixation adds substantially to the annual total of new production in the region and presumably to the drawdown of SRP. Karl argues that the system is in fact phosphate-limited at the low points of the declines, adducing as further evidence that the ratio of total (organic plus inorganic) nitrogen to total phosphate (Fig. 10.11) is far above the Redfield ratio (~16:1) that phytoplankton typically adopt when replete with nutrients and growing at their maximum rates. At ALOHA this ratio drops to about 16:1 only after the winter period of maximum mixing and highest seasonal phosphate concentration. Blooms of both *Trichodesmium* and *Hemiaulus/Richelia* occur elsewhere in warm oceans (e.g. Carpenter *et al.* 1999), so nitrogen fixation is a recurring feature of regions with depleted surface nutrients. As shown above, it is likely more important in the subtropical Atlantic. It has attracted increasing interest in recent years, and studies are going forward of its quantitative importance in global nitrogen and carbon cycles. There is very likely a complex interaction among (i) rates of iron supply, since iron is directly required for fixation biochemistry, (ii) vertical transfer of major nutrients, especially phosphate, (iii) the potential for growth of nitrogen fixers, and (iv) their success in competition for dilute nutrients with other phytoplankton.

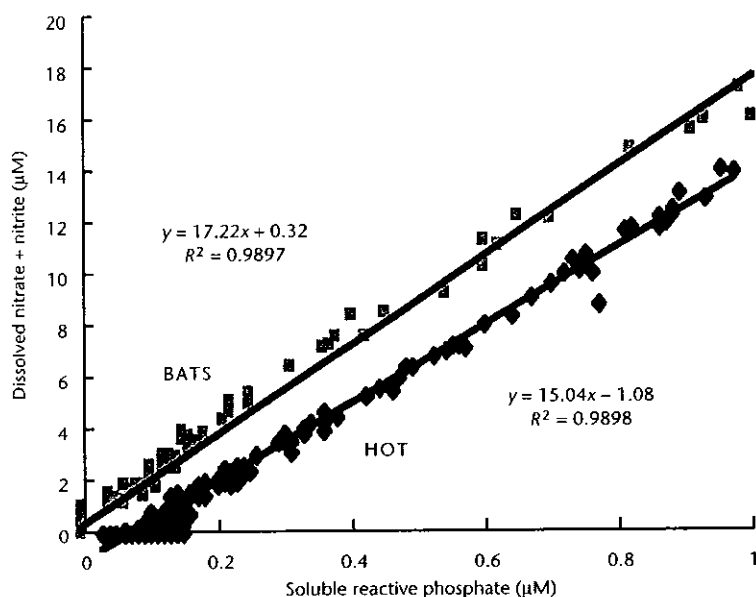


Fig. 10.8 Dissolved [nitrate + nitrite] vs. soluble reactive phosphate at Station ALOHA (HOTS) and at the BATS station (31°45'N, 64°10'W) in the Sargasso Sea. Probably the difference is attributable to greater relative importance of nitrogen fixation in the subtropical North Atlantic. (After Wu *et al.* 2000.)

The profile of primary production in the NPCG is maximum near the surface and tapers off with depth (Fig. 10.6). The taper is not perfectly exponential because chlorophyll increases sharply just above the nutricline (Fig. 10.6), forming a deep chlorophyll maximum (DCM). Profiles of cell counts have no comparable peaks, showing that this is generally not a significant increase in plant abundance, but an increase in amount of chlorophyll per cell. On the other hand, Venrick (1982) has shown for the "CLIMAX" station (30°N, 155°W) that at least the diatom component almost completely changes in species composition at a fairly sharp boundary just above the DCM. The flora is not simply shade-acclimated individuals of the phytoplankton above; it is a different, shade-adapted community. In recent data distinguishing pigments by liquid chromatography, more than half of the photosynthetic pigment in the DCM is divinyl chlorophyll *a*, implying dominance of primary production by *Prochlorococcus* (Karl *et al.* 2001).

Grazing in the NPCG and similar systems keeps the production almost exactly in balance; effectively grazers consume all production (not all biomass, all increase in biomass) every day. Banse (1995) has made an extended argument for this. He summarized (Fig. 10.12) vast quantities of

upper ocean, phytoplankton growth rate data for oligotrophic mid-ocean areas like the NPCG. Actual phytoplankton growth rates are not strongly affected by nutrient limitation; the plants that are present, mostly very small cells (*Synechococcus*, *Prochlorococcus*, microflagellates, naked Chlorophyta), are those most capable of obtaining sufficient nutrients from low concentrations. The growth rates range from 1 to 2 divisions per day. Banse argues convincingly that loss rates to cell sinking and vertical mixing can amount at most to a few percent of the growth rates, and therefore the apparent steady states which generally pertain must be attributed to cell death, most of it from grazing, although viral lysis could be important. Almost all actual herbivory (eating of phytoplankton) is by protozoans. Copepods, larvaceans and other large particle feeders are, then, carnivorous, feeding at the third trophic level.

So far as we know, all the mesozooplankton of the NPCG are continuously active, without a seasonal rest phase. Life cycles are not annual or twice-yearly as in subpolar habitats, but in surface layers are a few weeks or a month. Reproductive cohorts are not evident in the system.

At Station ALOHA collections to 150 m with 200 μm mesh nets demonstrate low amplitude

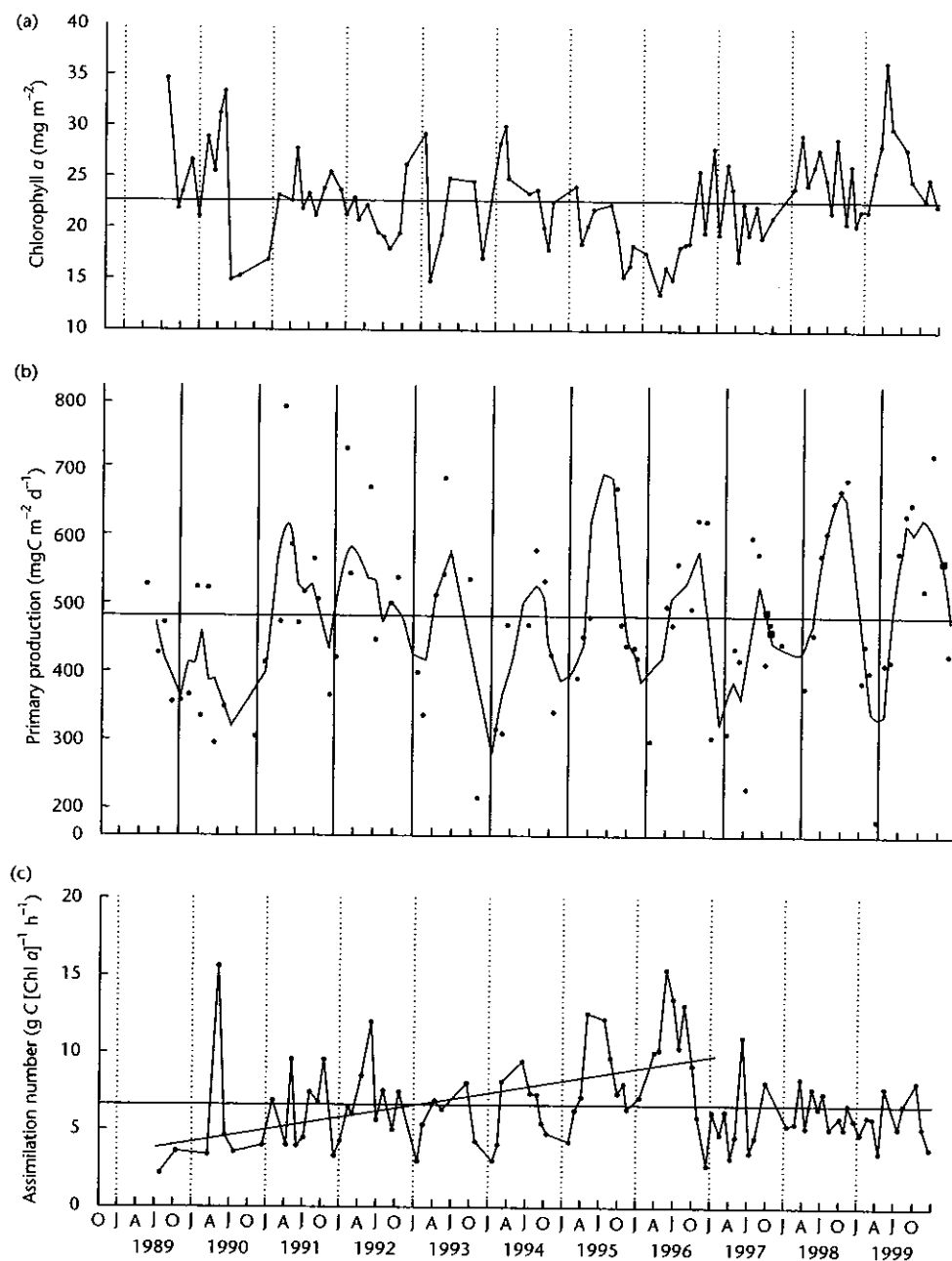


Fig. 10.9 Time series at Station ALOHA of (a) euphotic zone chlorophyll *a*, mg Chl m^{-2} , (b) integrated primary productivity (0–200 m), $\text{mgC fixed m}^{-2} \text{ day}^{-1}$, with a 3-point running mean showing the recurring seasonal pattern, and (c) assimilation numbers ($\text{mgC fixed m}^{-3} \text{ day}^{-1} / \text{mg Chl m}^{-3}$) at 5 m depth. (After Karl *et al.* 2001.)

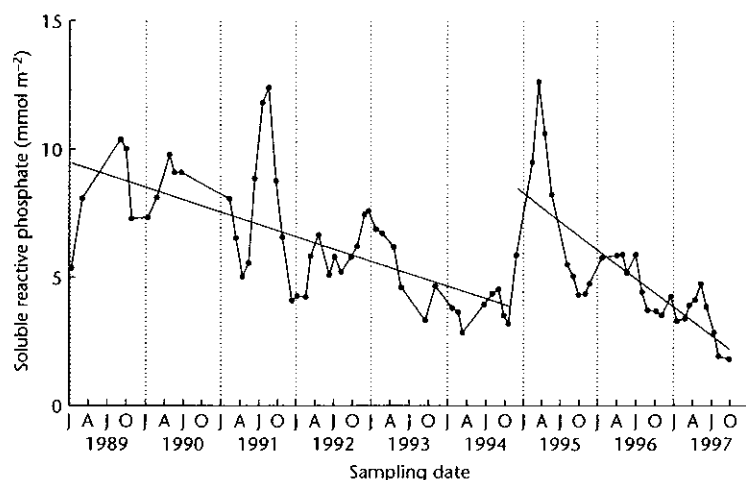


Fig. 10.10 Time series of soluble reactive phosphate at Station ALOHA with regressions for two periods of interannual decline. (After Karl *et al.* 2001.)

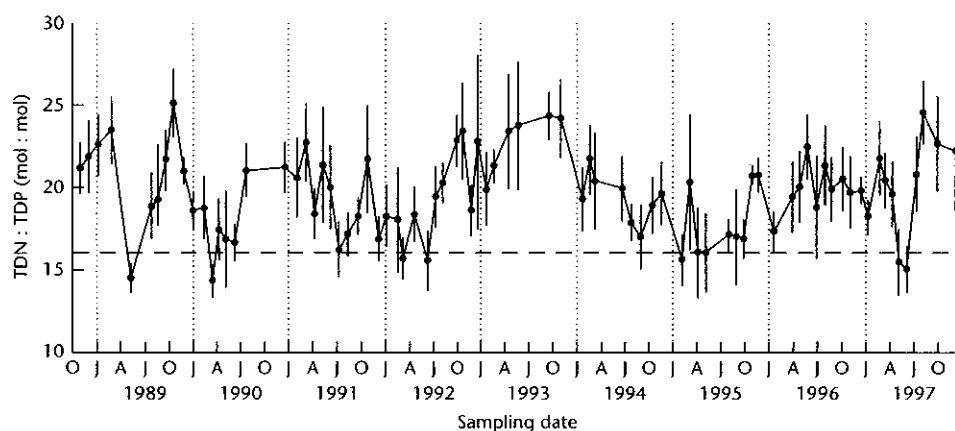


Fig. 10.11 Time series of the ratio between TDN, total dissolved nitrogen (inorganic + organic), and TDP, total dissolved phosphorus at Station ALOHA. The ratio usually drops to Redfield ($\sim 16:1$) only during the late winter period of strongest mixing. (After Karl *et al.* 2001.)

about 2-fold) seasonal cycles around an annual mean abundance of approximately 200 mgC m^{-2} (Landry *et al.* 2001). Zooplankton in the NPCG are a diverse array despite their low population biomasses, with two to three times more species than are found in higher latitudes. McGowan and Walker (1979) raised the issue of how so many species can persist together with so few obviously differing niches. The distinctive roles seem to sum up as (i) eat particles, or (ii) eat each other. As ecologists steeped in the "Law of Competitive Ex-

clusion", our expectation is that the system should simplify by competitive extinctions to just a few kinds in each role. The answer is still not complete. Part of it (Ambler & Miller 1987) is that the obvious trophic roles represented by the genera of plankton are dispersed vertically; congeners tend to separate into different depth levels.

Elaborate efforts are underway (e.g. Spitz *et al.* 2001) to model subtropical gyre ecosystem processes. The models do well in representing regional "climatology" (average seasonality) of nutrients

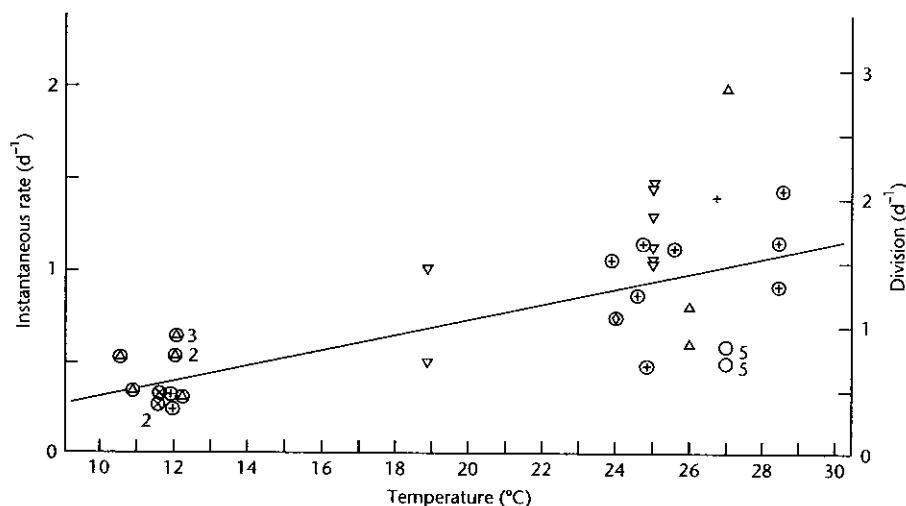


Fig. 10.12 Comparison of phytoplankton growth rates as a function of temperature in several oceanic, oligotrophic systems. Different symbol shapes from different workers. Plain symbols are from nitrate-depleted areas, mostly the NPCG. Circled symbols are from HNLC areas; those below 15 °C from the subarctic Pacific. Growth rates obtained in various ways (see original reference); all rates exceed the phytoplankton stock increase rates. Numbers indicate multiple samples. (Simplified from Banse 1995.)

and phytoplankton stock, and progress is apparent in predicting general phytoplankton stock and production responses to variations in mixing, irradiance, temperature, and seasonal timing of events. Models do less well, at least for now, with other components: primary productivity, dissolved and detrital organic matter, zooplankton. Data-assimilating calculations are under development that find best-fit parameters for modestly complex models. Resulting parameters appear to be better predictors than those selected on a more *ad hoc* basis.

Equatorial biomes

Equatorial biomes vary along the equatorial band. We will concentrate again on the Pacific example. Strong trade winds blow east to west from about 20°N to 5°N and from 5°S to 20°S, leaving a band of lighter winds, the doldrums, over the equator. Trades are one of the principal manifestations of the global heat transfer system. They push the ocean westward and the Coriolis effect carries the resulting flow pole-ward, away from the equator, replaced by upwelling along the equator. The flow

then slides under as it butts against the stratified central gyres. This upwelling is rich in major nutrients. In the Pacific, the westward force on the sea surface drives warmed surface water into a “warm pool” (recent terminology) in the west. This generates high evaporation rates, and also rain so that there is a halocline formed above the main thermocline. The warm pool is thus highly stratified by both warming and dilution, and it becomes fully depleted of major nutrients. So far as we know, it closely resembles the central gyres in ecology, and we won’t deal with it further.

In the eastern tropical Pacific and extending west past the date line, the elevated nutrients center right on the equator (Fig. 10.13), maximal just west of the Galapagos at 90°W. Typical nitrate concentration there is 6 μM , with concentrations decreasing westward (5 μM at 135°W, 3 μM at 160°W, and 1 μM at 170°E). Fall-off to the north and south is faster, with the southern isopleths more spread than the northern. As the surface current diverges slowly from the upwelling source at the equator, the nutrient is assimilated by phytoplankton and moved up the food chain. There is actually a progression, albeit rather subtle, in the mean trophic level from the equator to higher latitudes.

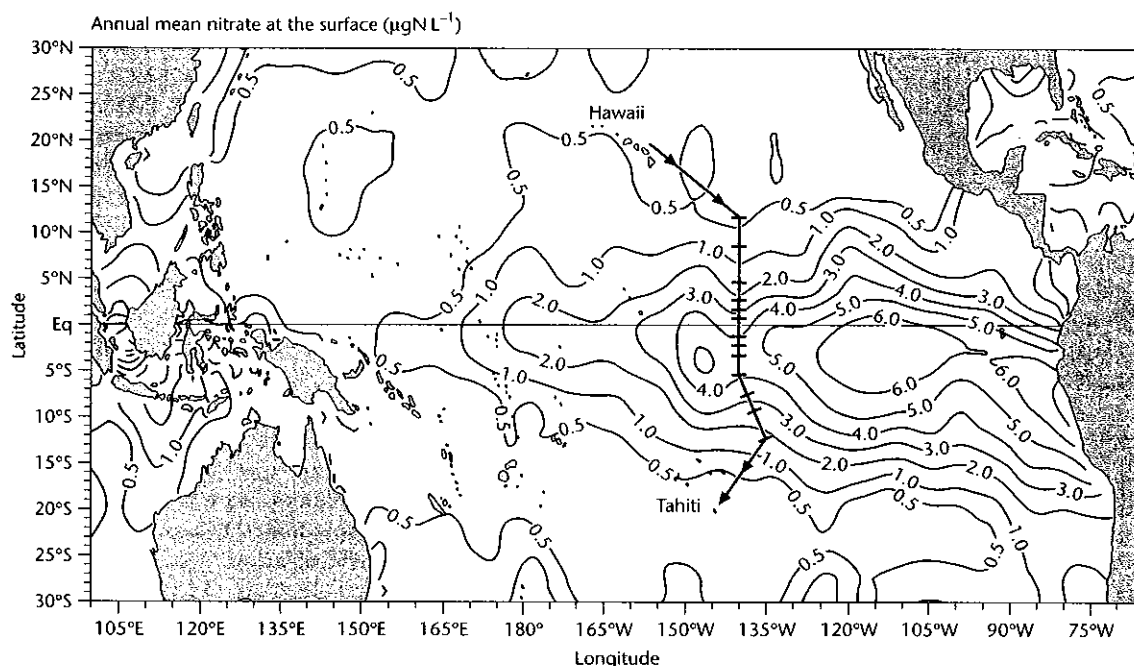


Fig. 10.13 Map of the equatorial Pacific with isopleths of annual mean surface nitrate concentration. Track line shows stations of the US JGOFS equatorial process study. (After Murray *et al.* 1995.)

Mesozooplankton closely resemble those of the central gyres in species list, with deletions and with additions of eastern tropical Pacific endemics, and in having short life cycle times. Standing stocks are higher, as are chlorophyll and primary productivity. Primary productivity shows slight surface photoinhibition, reaches a maximum at about 12 m, then tails off to zero just below 100 m. At typical surface levels of 0.2 to 0.35 $\mu\text{g Chl L}^{-1}$, self-shading is not a major factor. February–March and August–September transects (Fig. 10.14) of primary production stations across the equator at 140°W (Barber *et al.* 1996) showed a modest difference in vertically integrated primary production rates, especially from 5°N to 5°S. That difference was attributed by Barber *et al.* to the presence of El Niño conditions in the northern spring, then more normal (colder, richer) conditions in late summer, not to a recurring seasonal difference. The data were presented as $\text{mmol C m}^{-2} \text{ day}^{-1}$. Taking a mean for that equatorial strip as approximately 75 $\text{mmol C m}^{-2} \text{ day}^{-1}$ and multiplying

by 12 mg mmol C^{-1} , we get 900 $\text{mgC m}^{-2} \text{ day}^{-1}$, almost twice the central gyre average.

This eastern tropical Pacific region is important in the global exchange of carbon between the ocean and atmosphere. Since large volumes of water are brought from depth to the surface here, and since deep water is highly supersaturated with CO_2 , the region is a source of CO_2 to the atmosphere. Since large amounts of nutrient also surface, a much larger than average amount of production for the tropics returns a fraction of this carbon to the deep sea. The net flux is nevertheless to the atmosphere. The JGOFS transect work at 140°W included an extended particle trapping study. This gives a near-bottom carbon rain rate of 0.35 mmol C (4.2 $\text{mgC m}^{-2} \text{ day}^{-1}$), or about 0.5% of surface primary production. The rest is grazed and respired near the surface, with subsequent nutrient recycling contributing to total production, or respired as organic matter sinks through the ocean.

A study with transmissometers by Walsh *et al.* (1995) shows that most of the production is

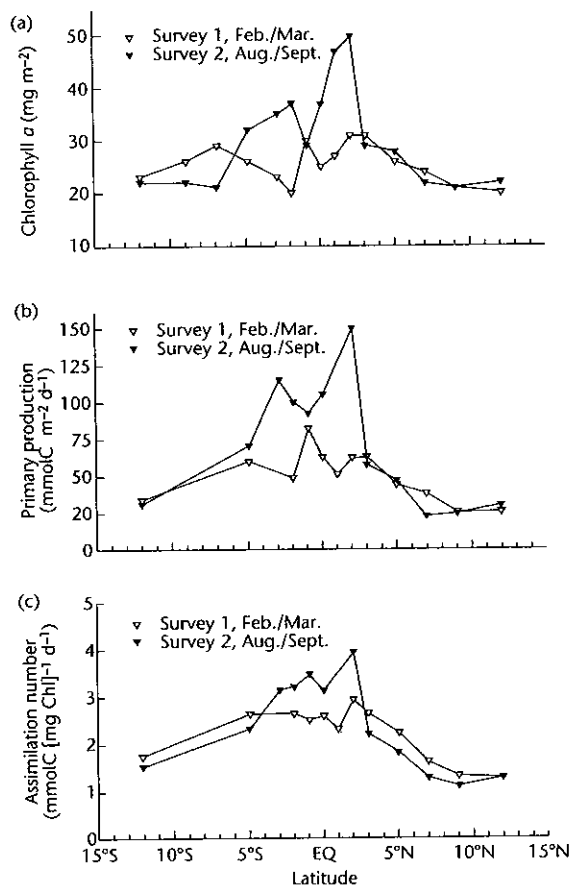


Fig. 10.14 Transequatorial transects at 140°W of (a) chlorophyll *a*, (b) primary production integrated to the 0.1% light level (mmol C m⁻² day⁻¹) and (c) assimilation number (mmol C (mg Chl *a*)⁻¹ day⁻¹) from two cruises in different seasons. Productivity is elevated just along the equator by nutrients supplied by upwelling supporting higher productive biomass. (After Barber *et al.* 1996.)

consumed every day, exactly as claimed above for subtropical areas. The transmissometer gives an estimate of the beam extinction coefficient for a laser diode (laser pointer) beam through ambient water but shielded from ambient sunlight. From calibration studies with filters, this can be converted to "particle load". Time series of profile data taken every three hours (Fig. 10.15) show early morning minima and evening maxima that recur over and over. Primary production and consumption of it nearly match on a daily basis. While

load may differ between cruises months apart, the daily cycles almost balance. Differences which could produce a longer-term change in particle standing stocks are invisible in the statistical noise of the observations. That is true all over the world's oceans. Except in strong spring blooms, almost all phytoplankton photosynthate is consumed on the day it is produced.

There are few useful studies of zooplankton biomass cycles or life history timing in the equatorial zone. One sampling program (Dessier & Donguy 1987) involving ship-of-opportunity sampling between Panama and Tahiti showed strong seasonal cycling in dominant copepod species right at the equator. It will be examined in connection with El Niño variations in Chapter 16 on climate variability. This seasonal cycling is both unexplained and likely caused by seasonal shifts of water mass boundaries across the equator.

Coastal biomes

Coastal waters generally are nutrient-rich and more productive compared to oceanic systems.

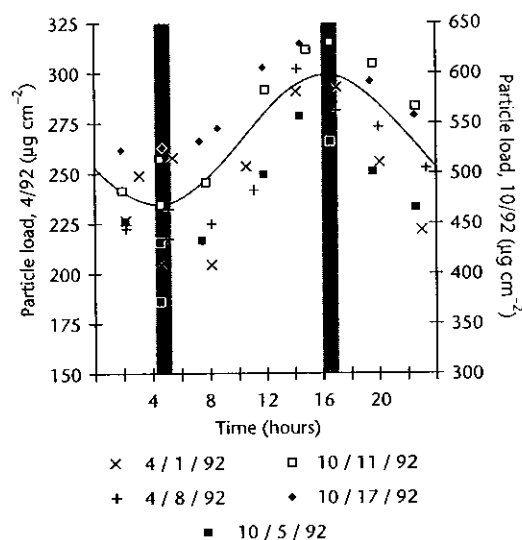


Fig. 10.15 Repeated daily cycles of euphotic zone particle abundance measured by transmissometry on five different days. (After Walsh *et al.* 1995.)

Inshore over shelves, mixing by tidal currents (of velocity u_s m s⁻¹) stirs the water column to the bottom over depths as great as h m, where $h/u_s^3 > \sim 80$. Maps of that criterion around the British isles and along the shelf of the northeastern US correlate with spring-summer stratification in waters to seaward. The phytoplankton inside that boundary is usually diatom dominated, although silicate can become limiting in summer. Beyond the boundary, diatoms are less important, except during spring blooms. Coastal seas are less frequently, but sometimes, iron-limited, especially where $h/u_s^3 > 80$, but major nutrients can be removed to very low concentrations both in the tropics and seasonally in high latitudes.

Coasts with an equator-ward component in the prevailing alongshore winds are the sites of coastal upwelling due to seaward acceleration of the surface layer by the Coriolis effect. After modest reduction in sea level height, the offshore flow is balanced by shoreward and rising flow in deeper layers. This carries nutrient-laden, relatively cold water into the euphotic zone. After an initial period of incubation, phytoplankton blooms develop and consume the nutrients. Depletion occurs at various distances offshore, and at least in the offshore California Current (Hutchins *et al.* 1998) iron can at times becoming limiting before major nutrients. These coastal upwelling zones are found (i) on the eastern shores of ocean basins at temperate latitudes (Baja California to Oregon, northern Peru to northern Chile, southwest Africa, northwest Africa, Spain, southwest Australia), (ii) in the Arabian Sea along the Somali and Omani coasts,

and (iii) along the northern shore of the Gulf of Guinea coast from Nigeria to Ghana.

Productivity in the Arabian Sea is high during the prolonged southwest monsoon, with sustained high levels of chlorophyll giving a very strong satellite signature. The coastal upwelling is reinforced offshore by a peculiar oceanic upwelling zone under the Findlater jet, the monsoonal wind blowing from the Somali coast directly across the open Arabian Sea to Pakistan from April to October. The upwelling and chlorophyll are much reduced, with blue waters during the winter monsoon. Intense production, supported by upwelled nutrients and continuous tropical irradiance, supplies unusually large amounts of organic matter to depth, where it is oxidized and creates thick suboxic and anoxic layers. Specialized mid-water fishes hide in the anoxic mesopelagic during the day, then migrate to the surface at night to feed on the abundant zooplankton. All upwelling areas support abundant zooplankton and fish stocks. In many of them some species of the copepod family Calanidae is dominant during the upwelling season. For example, *Calanoides carinatus* appears in the Gulf of Guinea (Binet & Suisse de Sainte Claire 1975) and Somali Current (Smith 1995) areas when upwelling is active, runs off four to six generations, then late copepodites move offshore and to mesopelagic depths, entering a diapause that lasts until upwelling returns them to the coast and surface.

All of this will receive recurring attention from oceanographers in the next few decades. Our understanding of these ocean biomes is rapidly improving, and readers of this are invited to contribute to the ongoing effort.