Spatio-temporal variability of phytoplankton in the southern Benguela upwelling system

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SPATIO-TEMPORAL VARIABILITY OF PHYTOPLANKTON IN THE SOUTHERN BENGUELA UPWELLING SYSTEM

G. C. PITCHER, P. C. BROWN* and B. A. MITCHELL-INNES**

The overall spectrum of phytoplankton heterogeneity within the southern Benguela is classified and presented on the basis of spatial and temporal scales, ranging from the macro- to the microscale. State variables in terms of floristic and biomass changes and rate variables in terms of physiological changes are reviewed and related to the physical and biological mechanisms important to their generation and maintenance. Biological and physical processes acting alone and in concert give rise to the spatial and temporal patterns of phytoplankton distribution, making categorization by causative mechanisms both difficult and artificial. Nevertheless, all scales and types of patchiness in the southern Benguela are strongly influenced by the hydrodynamic process of upwelling, both through redistribution of existing biological variability and through the creation of spatial variability in the richness and suitability of the physical and chemical environment. Physical influences override biotic interactions during upwelling whereas, with the onset of stratification, physical processes become less dynamic, allowing biological and chemical factors to become the major determinants of phytoplankton variability. These observations are spatially confirmed, with physical forcing dominant close to the source of upwelling and biological influences more important downstream of upwelling.

Die algehele spektrum van heterogeneïteit in die fitoplankton binne die suidelike Benguela word geklassifeer en aangebied volgens ruimtelike en tydskale wat van die makro- tot die mikroskaal wissel. Standveranderlikes soos floristiese en biomassaveranderings en koersveranderlikes soos fisiologiese veranderings word in oënskou geneem en in verband gebring met die fisiese en biologiese meganismes van belang by hul ontstaan en handhawing. Biologiese en fisiese prosesse op sigself of gesamentlik gee aanleiding tot die verspreidingspatrone van fitoplankton in ruimte en tyd. Dit maak die klassifikasie volgens die aanleidende meganismes sowel moeilik as kunsmatig. Nogtans word alle skale en tipes van kol-kol-verspreiding in die suidelike Benguela sterk beïnvloed deur die hidrodinamiese proses van opwelling - deur herverdeling van bestaande biologiese veranderlikheid en ook deur die skepping van ruimtelike veranderlikheid in die rykheid en geskiktheid van die fisiese en chemiese omgewing. Fisiese invloede oorheers biologiese wisselwerking tydens opwelling, maar soos gelaagdheid ontwikkel, word fisiese prossese minder dinamies en laat dus toe dat biologiese en chemiese faktore die vernaamste bepalers van die fitoplankton se veranderlikheid word. Hierdie bevindings word ruimtelik bevestig, want fisiese forsering oorheers digby die bron van opwelling en biologiese invloede is belangriker stroomaf van opwelling.

The pelagic environment provides a hierarchy of forcing functions resulting in variability in the planktonic ecosystem throughout a spectrum of scales of space and time. These scales of variability are intimately linked, and when viewed from the standpoint of how data are often collected, space and time are indistinguishable. Therefore, any physical or biological perturbation of the ecosystem that is not constant in time can create potential variability in space. The resulting non-uniformity in the availability of food may in turn have a profound effect on the trophic dynamics of the marine ecosystem (Platt and Denman 1980).

Although phytoplankton species aggregations and biomass peaks appear to occur on a continuum of scales, it is convenient in the sections that follow to break the continuum into categories. The overall spectrum of phytoplankton heterogeneity within the southern

Benguela is therefore classified on the basis of spatial and temporal scales of variability, considering first the larger scales and proceeding sequentially to smaller scales.

Phytoplankton variability of both state and rate variables are presented and reviewed at the various scales, and related to the physical and biological forcing mechanisms important to their generation and maintenance.

MACROSCALE (>100 km, seasons/years)

Upwelling is a feature of oceanic circulation along the entire west coast of southern Africa, from Cape Agulhas in the south to Cape Frio in the north

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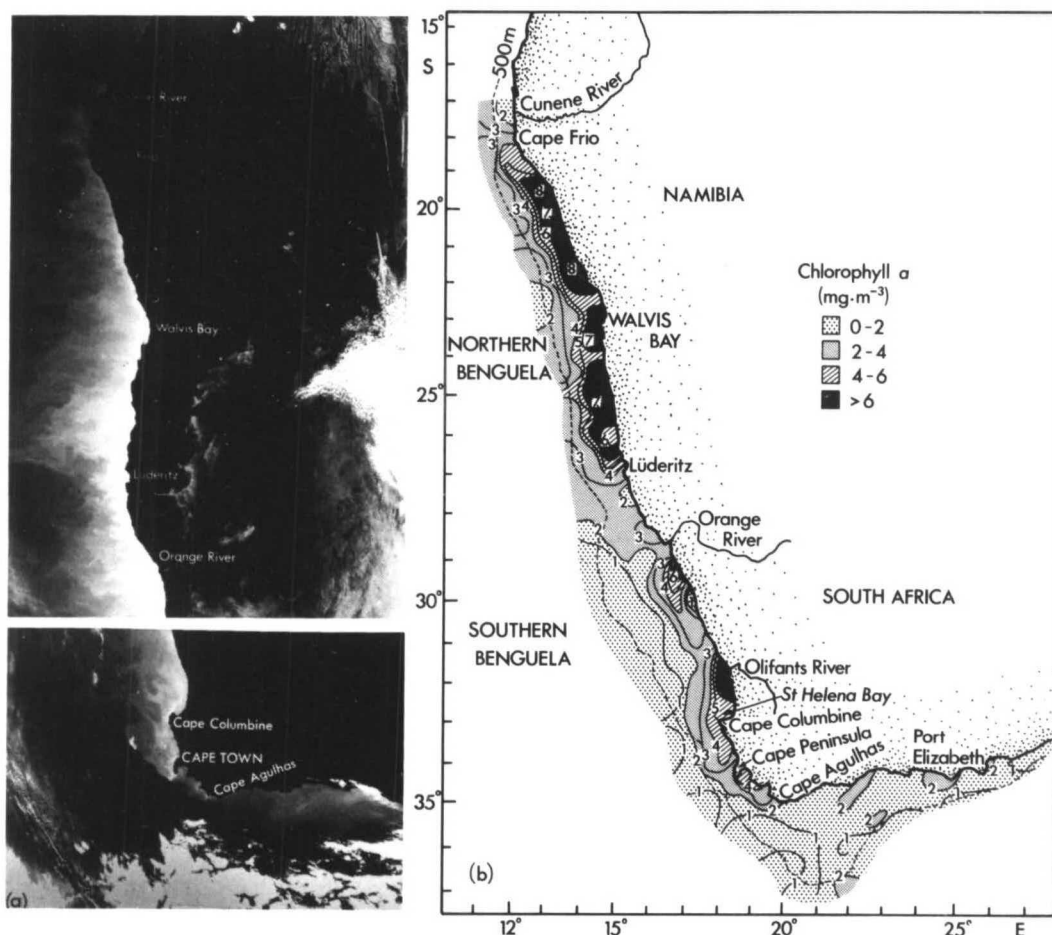
Fig. 1: (a) NOAA enhanced infra-red image of the Benguela; (b) Mean distribution of chlorophyll *a* (for 0–30 m) in the northern and southern Benguela for samples collected from 1971 to 1989 (after Brown *et al.* 1991)

(Fig. 1a). The prevailing upwelling winds are determined by the South Atlantic high pressure system, the pressure field over the adjacent continent and by east-moving cyclones in the south (Shannon 1985).

Boundaries to the southern Benguela

The principal upwelling centre of the Benguela system is in the vicinity of Lüderitz, and it comprises an environmental barrier in the Benguela, effectively dividing the system into northern and southern components. Meteorologically these areas are distinct. In the south, wind-induced upwelling reaches a maximum during spring and summer, whereas the northern

region exhibits relatively less seasonal variation (Shannon 1985). The perennial nature of upwelling in the northern Benguela most likely accounts for the consistently higher biomass of phytoplankton so evident there relative to that in the southern Benguela (Fig. 1b).

Changes in the orientation of the coastline and wind field are evident at both Cape Point and Cape Agulhas, but the latter is considered the more appropriate southern boundary because upwelling typically extends that far during summer (Fig. 1a). In response to reduced upwelling, phytoplankton biomass decreases east of Cape Agulhas (Fig. 1b). Therefore, a combination of meteorological, oceanographic and topographic factors produce the southern boundary of the Benguela, with
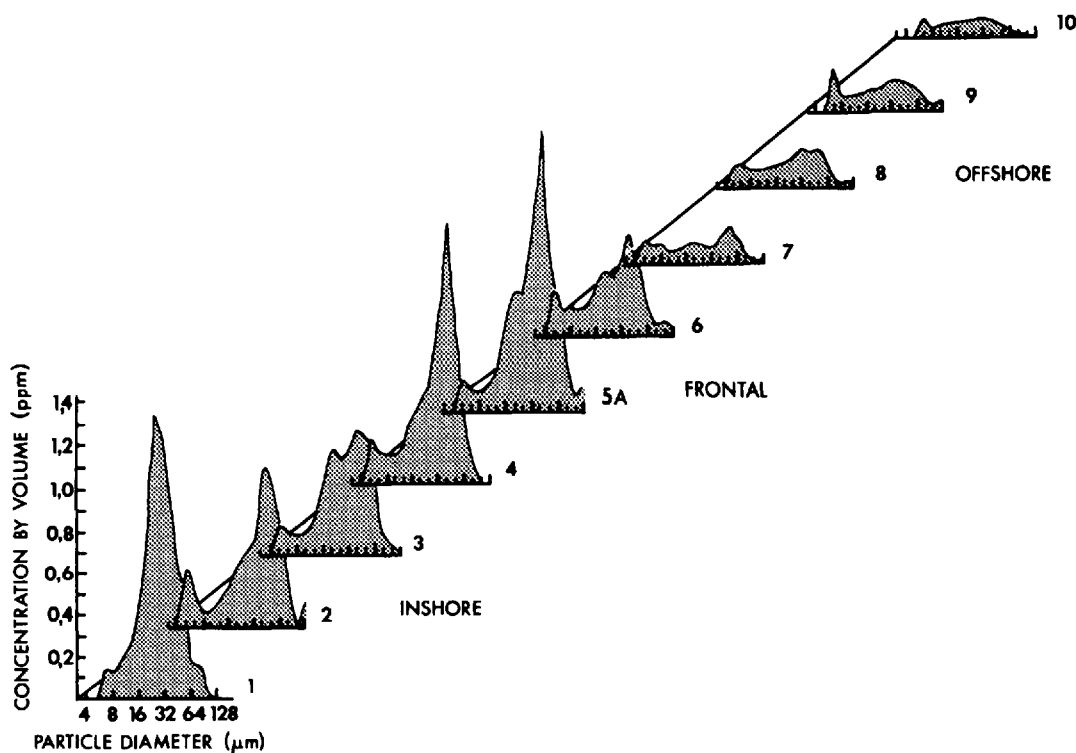
Fig. 2: Particle spectra of samples from the particle volume maximum in the water column, at stations along a transect of the upwelling front of the Cape Columbine upwelling cell (after Armstrong *et al.* 1987)

the western Agulhas Bank ecologically an integral part of the productive West Coast regime (Shannon 1985).

Offshore and longshore variability

Continental shelf bathymetry and upwelling winds provide a large-scale upwelling mechanism in the southern Benguela, whereas local topography and meteorology create an alternating pattern of active and passive upwelling circulations along the coast. Longshore variability is therefore often as dramatic as the expected offshore changes.

A well-defined thermal front separates the coastal waters with their high biomass from the smaller stocks of phytoplankton typical of oceanic waters (Fig. 1). Bang (1974) distinguished two fronts within the system, the upwelling front and the shelf-break front. The surface manifestation of the upwelling front is highly variable in position, responding rapidly to changes in wind stress and direction, moving offshore during upwelling and onshore during relaxation. The shelf-

break front appears to be more permanent; it can persist off the Cape Peninsula as a subsurface structure for most of the year. The two fronts coalesce during periods of sustained upwelling in the austral summer, creating a strong thermal gradient in the vicinity of the shelf-break (Hutchings *et al.* 1986).

Most primary production takes place over the shelf. North of Cape Columbine, the broadness of the shelf creates a wide zone rich in chlorophyll, whereas off Cape Columbine and the Cape Peninsula, where the shelf narrows, the plankton-rich zone also narrows. Frontal eddies and meanders are considered by Lutjeharms (1981) to form from the growth of instabilities in the frontal jet, whereas filaments of cool nutrient-rich water extending away from the coast may be connected to passing Agulhas rings (Duncombe Rae *et al.* 1989).

Examination of particle size spectra along a transect of the upwelling front off Cape Columbine reveals dramatic differences in the phytoplankton on either side of the front (Fig. 2). At coastal and frontal zone stations, phytoplankton biomass is high and nitrate forms the major portion of nitrogen taken up by the
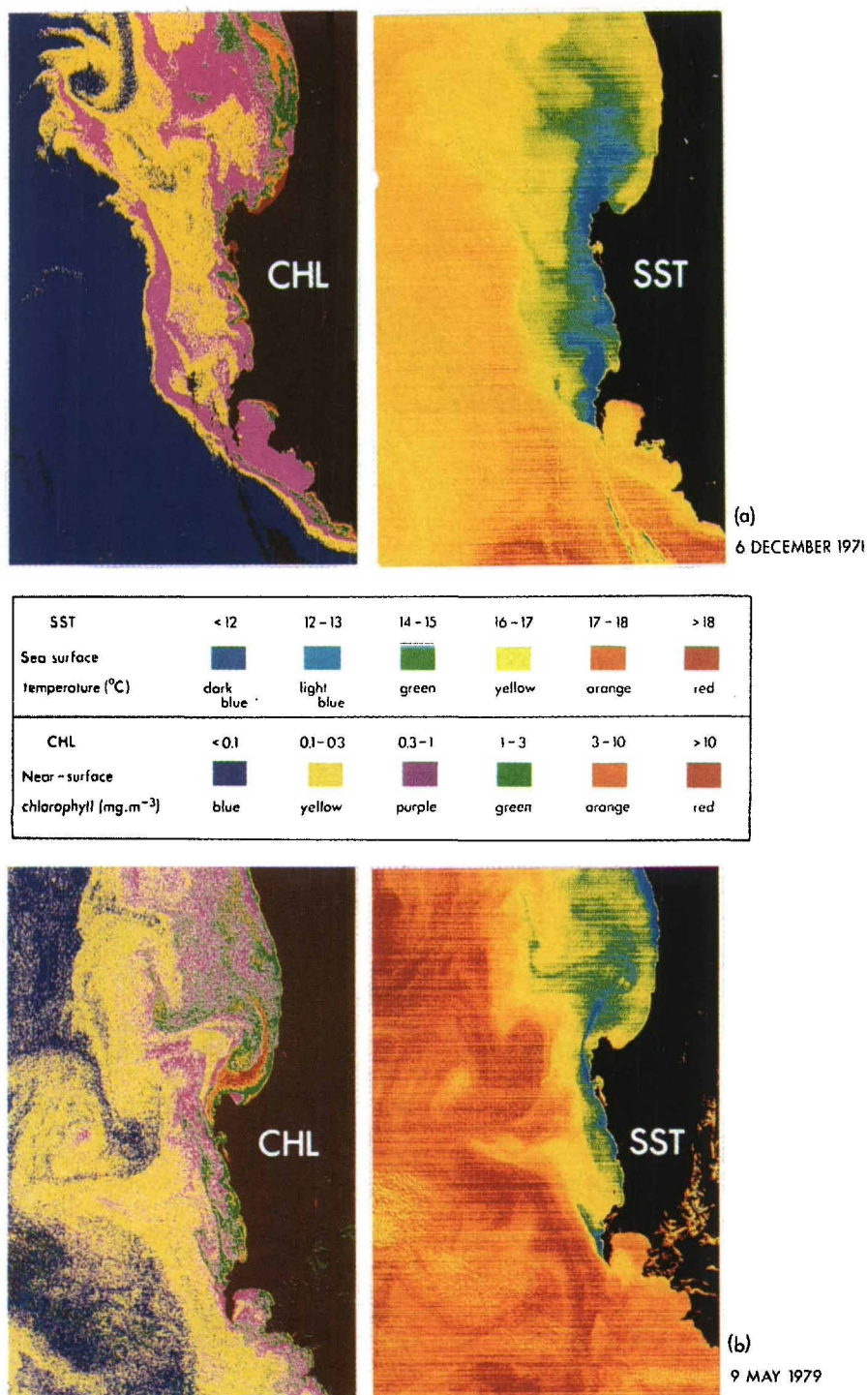
Fig. 3: *Nimbus*-7 CZCS imagery for (a) 6 December 1978 and (b) 9 May 1979 showing the distribution of near-surface chlorophyll and sea surface temperature in the southern Benguela (after Shannon *et al.* 1985)
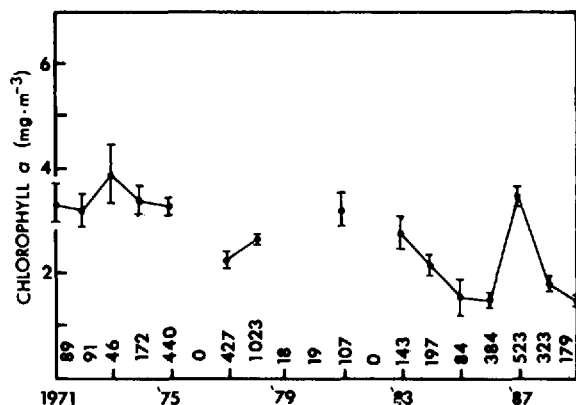
Fig. 4: Time-series (1971–1989) of annual arithmetic means of chlorophyll *a* concentrations in the upper 30 m for the southern Benguela (including the South Coast). Bars represent standard errors and numbers on the time axis represent the number of measurements for each year. Years with less than 20 measurements are excluded (adapted from Brown and Cochrane 1991)

phytoplankton community, which is usually dominated in terms of volume by diatoms. Offshore, the biomass is reduced, diatoms are fewer and a relatively larger portion of the population volume is contributed by pico- and nanoplankton, identified as being mostly small flagellates and supported principally by regenerated nitrogen (Probyn 1985).

Satellite imagery has provided striking documentation of the intensity and degree of correlation of biological and physical processes along the west coast of southern Africa (Fig. 3). Synoptic images of sea surface temperature and chlorophyll depict essentially the same complex patterns. The significance of the apparent correlation is as evidence that the variability in both the physical and biological fields is in many cases created by a locally shared pattern of environmental forcing.

Sea surface temperature and phytoplankton pigment are non-conservative tracers. The apparent relationship evident from satellite imagery between these tracers is one of low pigment at low sea surface temperature, increasing at intermediate temperatures, reaching a maximum value and then decreasing at the highest temperatures. This is consistent with the scenario of rapid phytoplankton growth as sea surface temperature increases following exposure of newly upwelled,. cold, nutrient-rich, low-pigment water to high solar radiation with an eventual decrease in pigment concentration after exhaustion of nutrients while sea surface temperatures continue to increase. Warm offshore waters not directly influenced by upwelling have low

concentrations of pigment.

During periods of sustained upwelling, highest concentrations of chlorophyll *a* in the southern Benguela are therefore found downstream from the main upwelling centres or otherwise in bays. The largest areas of high concentrations of chlorophyll are, on the other hand, evident during periods following relaxation or reversal of upwelling-favourable winds, when aged upwelled water tends to predominate (Shannon *et al.* 1985).

Interannual and seasonal fluctuations

Climatic fluctuations may influence characteristics of the water mass on interannual and seasonal timescales. Whereas meteorologists have been able to observe and document changes in large-scale atmospheric processes, there are very few long-term data sets resulting from the direct observation of planktonic communities.

In examining interannual variations in concentrations of chlorophyll *a*, Brown and Cochrane (1991) found an apparent overall decline in mean annual chlorophyll *a* from 1971 to 1989 (Fig. 4). These results indicate that trends are driven by large-scale meteorological forces. Time-series analysis, however, shows little autocorrelation or trend in the chlorophyll *a* time-series and only weak positive correlation between concentrations of chlorophyll *a* and both temperature and longshore winds.

Wind-induced upwelling in the southern Benguela is highly seasonal and takes place in response to the migration of the South Atlantic high and the east-moving cyclones. It reaches a maximum in spring and summer (Shannon 1985). Seasonal changes in chlorophyll distribution are evident from satellite imagery. South of Cape Columbine the seasonality of upwelling is greatest, maximum upwelling being in summer, when the chlorophyll-rich belt may extend southwards to Cape Agulhas. The highest near-surface concentrations of chlorophyll *a* are therefore present during summer and autumn, shorewards of the well-defined oceanic front. During winter the front is more diffuse, and lower near-surface concentrations are to an extent compensated by the existence of a broader productive zone. North of Cape Columbine, more-persistent upwelling contributes to a wider chlorophyll-rich zone with less seasonal variation (Shannon *et al.* 1984). Brown and Cochrane (1991) found that the productive area of the southern Benguela in summer is about double that in winter for chlorophyll concentrations >2 and >4 mg·m^{-3}, but areas with mean concentrations >6 mg·m^{-3} are found only in summer (Fig. 5).
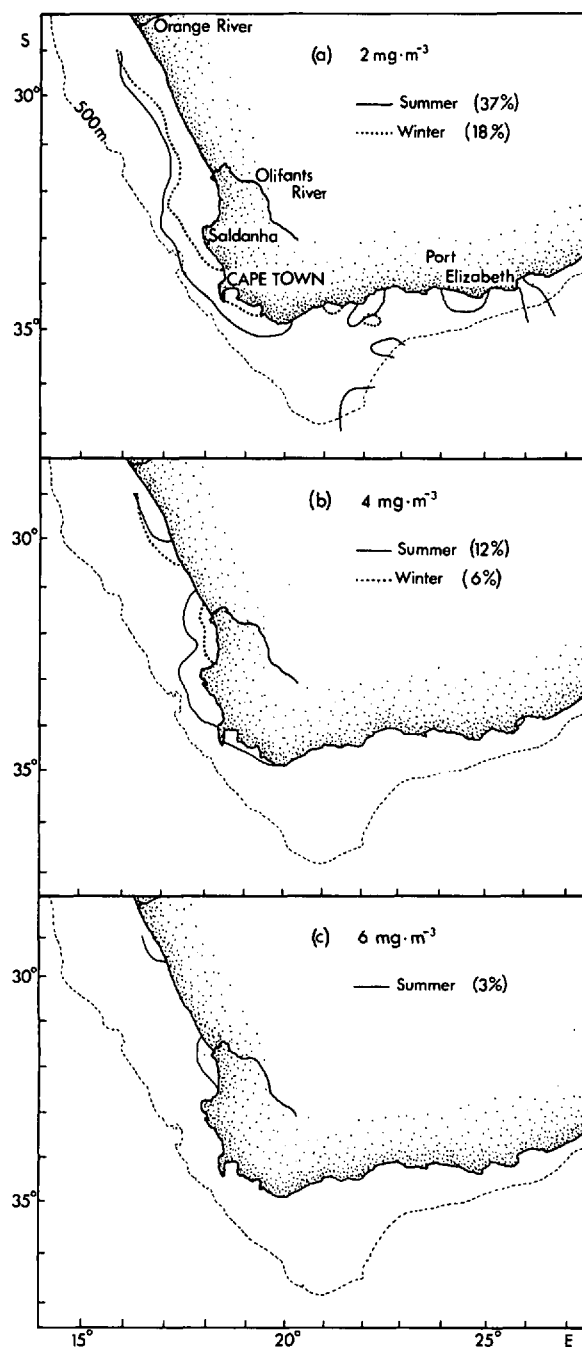
Fig. 5: Seasonal changes in the productive area of the southern Benguela as determined by the mean (a) 2, (b) 4 and (c) 6 mg·m^{-3} chlorophyll *a* isolines for summer (September–May) and winter (June–August). Values in parentheses are the areas landwards of the various isolines expressed as a percentage of the area within the 500 m isobath (after Brown and Cochrane 1991)

In their examination of the standing stock of phytoplankton off the Cape Peninsula, Andrews and Hutchings (1980) found considerably higher stocks during the upwelling season than between April and August. Variability in summer was nevertheless considerable and they attributed it to the very low stocks present in newly upwelled water. In their large-scale perspective of average concentrations of chlorophyll *a* in the southern Benguela, Brown and Cochrane (1991) similarly found estimates of the monthly arithmetic means of chlorophyll *a* to be higher and more variable in summer than winter.

Surprisingly few studies have examined seasonal variations in the composition of the phytoplankton of the southern Benguela. However, examination by Horstman (1981) of the monthly incidence of reported red tides for the period 1959–1980 has provided evidence that red tides occur most frequently towards the end of summer and autumn (February–May). Then, water column stability is increased as the pressure gradients responsible for equatorward winds weaken, thereby reducing upwelling activity. The increased thermal stratification in turn favours the presence of dinoflagellate-dominated red tides.

MESOSCALE (0,1–100 km, days/weeks/months)

Superimposed on seasonal variation are shorter cycles of upwelling and relaxation provided by wind abatement or reversal associated with the zonal passage of east-moving cyclones. Resulting rapid changes in the intensity and the frequency of upwelling winds alter the hydrography and plankton distributions dramatically, creating a highly variable mesoscale environment (Shannon *et al*. 1984). Furthermore, not only are the duration of wind events important, but so are the duration of the periods of relaxation, because these periods determine the productivity and availability of food to grazers.

It is at this event-scale that much of the research on phytoplankton variation in the southern Benguela has been conducted. Transect or grid studies have examined spatial variability along inferred axes of upwelling tongues or other hydrographic features; drogue studies have tagged parcels of upwelled water in order to monitor phytoplankton processes; microcosm studies have examined phytoplankton bloom development in newly upwelled waters, following incubation in the laboratory; and anchor station studies have enabled temporal variability at a single fixed station to be examined in response to coastal upwelling. Because these approaches focus on either spatial or temporal variability, the mesoscale changes in the southern Benguela are examined below in terms of these
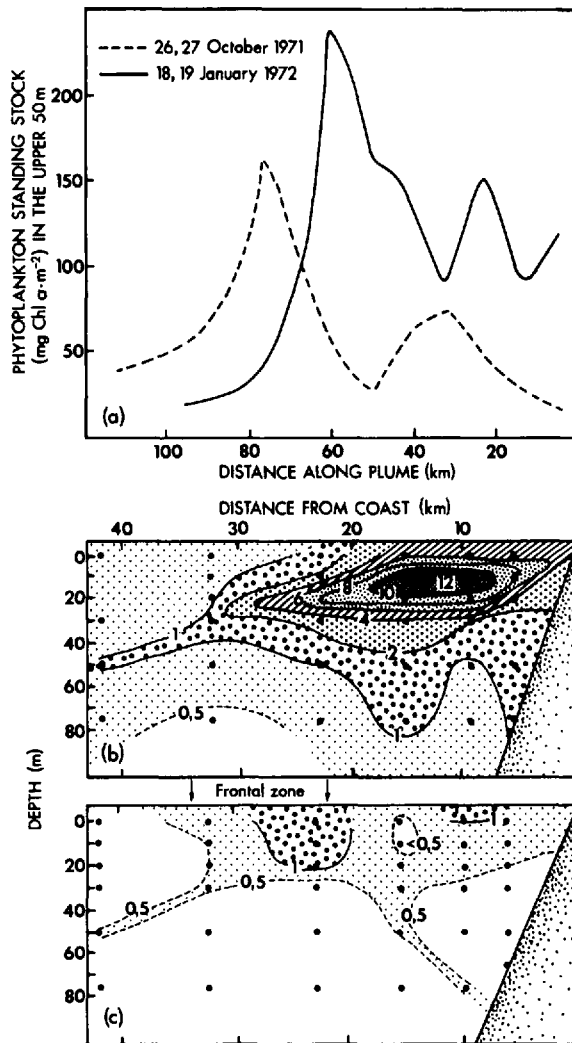
Fig. 6: (a) Selected profiles of the phytoplankton standing stock of the upper 50 m along the upwelling monitoring line off the Cape Peninsula. Distribution of chlorophyll *a* (mg·m^{-3}) during (b) downwelling on 13 December 1969 and (c) upwelling on 16 December 1969 along the upwelling monitoring line (adapted from Andrews and Hutchings 1980)

methods of study.

Transect and grid studies

Andrews and Hutchings (1980) monitored a line of stations transecting the Cape Peninsula upwelling plume on a monthly basis for 2½ years. Repeated transects demonstrated the semi-permanent nature of the plume as well as the high wind-generated variability of the phytoplankton biomass during the upwelling season. Chlorophyll concentrations increased somewhat irregularly down the plume, peaking in the photic layer inshore of the oceanic front (Fig. 6a) and tending to mirror nutrient concentrations. On average, an exponential increase in the chlorophyll concentrations was evident within the inshore 20 km.

Although the upwelling plume of the Cape Peninsula is considered a semi-permanent feature during summer, northerly winds do cause onshore transport of water (Andrews and Hutchings 1980). The resulting downwelling would seem to have only a superficial and temporary effect on the upwelling plume, but chlorophyll distributions change quite dramatically, markedly increasing in concentration inshore (Fig. 6b). Strong upwelling in turn displaces the phytoplankton out of the area (Fig. 6c) before high concentrations of phytoplankton again become evident during quiescent periods (Andrews and Hutchings op. cit.).

Another source of variation influencing bloom development in upwelling systems is that of seeding. The variability observed in seed populations of different upwelling events off the Cape Peninsula has been attributed to varying offshore phytoplankton developmental processes, the success of various species' seeding strategies and variation in circulation patterns. Such variability may in turn be instrumental in determining the species composition and the time required for bloom development (Pitcher 1989, 1990).

Two extreme types of seeding strategies are distinguishable. In one type, seeding is effected by fugitive cells in the surface layer and the other by deep-living refuge cells. It is the latter strategy which phytoplankton in upwelling systems are more likely to employ, although both strategies could well be followed. Phytoplankton moving downward out of the offshore-flowing Ekman layer will be entrained in the deeper onshore flow and so recycled through the upwelling circulation. Seeding is therefore effected by the sinking out or active migration of phytoplankton from nutrient-depleted offshore surface waters into nutrient-rich deeper waters. The prevalence of diatom resting spores in newly upwelled water (Pitcher 1990) and their germination following incubation (Pitcher 1989) provides evidence of the initiation of vegetative blooms by spores and demonstrates their ability to utilize mixing and current patterns in order to seed upwelling systems. Thereby, their reproductive success is increased in a physically dynamic environment. Coastal upwelling circulation therefore physically sorts phytoplankton, the rate of downward movement and temporal variations in the circulations permitting phytoplankton with different sinking and migration characteristics to predominate at different times in newly upwelled water.
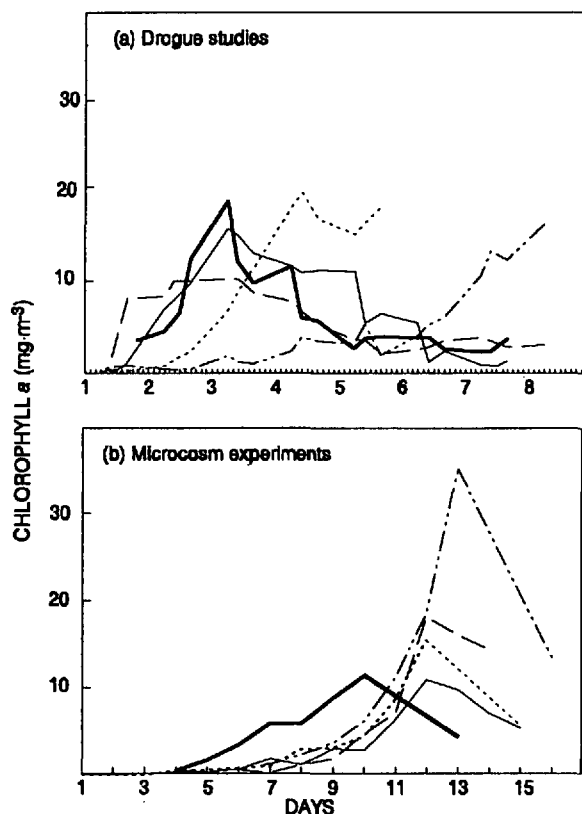
Fig. 7: Phytoplankton bloom development off the Cape Peninsula in terms of chlorophyll *a* as determined by (a) drogue studies (adapted from Brown 1986) and (b) microcosm studies (adapted from Pitcher 1989). Each line represents a different experiment

Drogue and microcosm studies

Drogue studies examined phytoplankton development in upwelled water from the perspective of the time-scale of bloom events (Brown 1986, Brown and Hutchings 1987a, b), thereby complementing transect studies, which emphasized spatial variations across the shelf.

Drogues were used to tag parcels of newly upwelled water off the Cape Peninsula on five different occasions in order to follow the temporal sequence of events after upwelling. Near the sea surface, temperatures increased along the drogue tracks, thereby increasing the stability of the water column. Changes in phyto-plankton biomass (Fig. 7a) and nutrient concentration along each drogue track exhibited considerable variation. Chlorophyll *a* increased from concentrations of usually <1 mg·m⁻³ in upwelling water to 10–20 mg·m⁻³ at the peak of the bloom, with nutrient con-

centrations exhibiting an inverse trend. Concentrations of chlorophyll *a* then decreased to 1–3 mg·m⁻³ after the bloom peak, when recycling of nutrients probably maintained phytoplankton stocks at moderately low levels. During one of the drogue studies, the depth of the upper mixed layer was markedly greater than the euphotic zone depth, limiting maximum biomass concentrations to about half of those of the other cruises.

Changes in productivity along each drogue track ranged from 0,84 to 14,02 gC·m⁻²·day⁻¹ and roughly reflected chlorophyll *a* distribution near the sea surface, suggesting that the rate of productivity is a function of phytoplankton biomass. Little trend was observed in the productivity indices during different phases of bloom development, but there was considerable variation, ranging from 2 to 17 mgC·mgChla^{-1}·h⁻¹. Low physiological rates in newly upwelled water were not identified, possibly as a result of the drogues having been deployed in recently rather than newly upwelled water.

Phytoplankton productivity during the drogue studies was undoubtedly nutrient-controlled in terms of the gross amount of nutrients which upwelled. On the other hand, about half the biomass in the upper 50 m occurred below the 1 per cent light depth, indicating that low light, due to self-shading, is an important factor limiting the primary productivity of the system. Comparison of estimates of phytoplankton biomass calculated from productivity measurements with observed changes in the standing stocks gives some indication of the loss of primary organic matter during the drogue studies. Calculated biomass coincided roughly with the observed biomass until the latter peaked. Although nutrient depletion and self-shading are considered to play a major role in limiting the bloom, grazing, senescence, sinking and dispersal are thought to contribute to the discrepancy between calculated and observed biomass following the bloom peak.

Brown (1986) concluded that each upwelling event appears to invoke a sequence of phytoplankton development which varies mainly with the relative stability of the upwelled water. The pulsed and strongly three-dimensional upwelling in the southern Benguela does not necessarily result in discrete parcels of water moving offshore with blooms developing and declining intact. Strong shearing motions, vertical turbulence and horizontal advection cause considerable mixing of new and old water, which influences the expected pattern of bloom development. The drogue studies do, however, reflect the *in situ* conditions after the net action of the physical and biological processes which occur after upwelling.

The development of phytoplankton blooms in the southern Benguela as determined by microcosm experiments (Pitcher 1989), in which newly upwelled water

was incubated in the laboratory under conditions approximating those in the ocean, was in many respects similar to bloom development as monitored during the drogue studies (Fig. 7b). The most notable difference between the two studies was the longer time required for bloom development in the microcosm experiments, which may be attributed to a number of important circumstances. As mentioned, the drogues were deployed in recently as opposed to newly upwelled water, and therefore growth had already occurred when monitoring commenced. The low physiological rates observed during the initial stages of the microcosm experiments, perhaps partially attributable to the artificial light supply, were not apparent during the drogue studies. The seed population in the microcosm experiments was found to be most important in determining both the time required for bloom development and also the species present in the developing bloom. Seeding in these studies is effected only by deep-living refuge cells that reappear in the surface waters after upwelling, whereas during the drogue studies, mixing with older water subsequent to upwelling will increase the size and diversity of the seed population, so further reducing the time required for bloom development. Such mixing with older waters was evident during the drogue studies by the occasional recording of unrealistic changes from one station to another. It is this mixing which is thought to be most important in influencing the pattern of bloom development following upwelling.

Anchor station studies

The time-series or anchor studies, whereby a single fixed station is regularly sampled, enables phytoplankton variability to be monitored during consecutive periods of upwelling and relaxation in such a manner that the time-scale of phytoplankton responses may be assessed.

Barlow (1982a) classified nearshore waters off the Cape Peninsula into three types, which followed sequentially after water had upwelled and merged with surface water. Type 1 water corresponded to newly upwelled water with a temperature of <10°C, a chlorophyll *a* concentration of <1 mg·m⁻³ and high concentrations of inorganic nutrients. Type 2 water corresponded to maturing upwelled water and was characterized by temperatures >10°C, chlorophyll *a* concentrations of 1–20 mg·m⁻³ and nitrate concentrations of 2–15 mmol·m⁻³. Finally, Type 3 water (12–16°C) corresponded to aged upwelled water and contained low concentrations of nitrate (<2 mmol·m⁻³) and chlorophyll *a* concentrations of 5–30 mg·m⁻³.

Low primary production in Type 1 water following active upwelling was attributed to the low initial biomass of phytoplankton in upwelling water (Brown

1984, Brown and Field 1986). Mean estimates of biomass and production were markedly higher in Type 2 water, in response to reduced wind stress and increased water column stability. Maximum levels of biomass and production were recorded in Type 3 water. Strong correlation was observed between production and chlorophyll *a*, particularly when concentrations of chlorophyll *a* were <12 mg·m⁻³. As biomass levels increased from Type 2 to Type 3 water, the correlation weakened, indicating a decrease in productivity indices from Type 2 to Type 3 water. This decrease suggests that factors such as light and nutrients play an increasingly important role in regulating production in aged upwelled water. The decrease in production indices is, however, countered by an increase in chlorophyll *a*, so that the production at the sea surface is highest in aged upwelled water.

Physiological changes in the phytoplankton community were observed as the water changed from one type to another (Barlow 1982a). The protein:carbohydrate ratio declined from >1 in Type 1 and 2 water to <1 in Type 3 water as nutrient availability declined, indicating that the community changed from an active phase of growth to a slow-growing phase in Type 3 water. Phytoplankton production in upwelled water off the Cape Peninsula is therefore limited at first, primarily by biomass, and later, as the population matures, by nutrients and light, both of which play increasingly important roles in determining production.

Phytoplankton blooms recorded during a 27-day anchor study in St Helena Bay were directly related to upwelling events or the intrusion of recently upwelled water into the study area (Pitcher *et al.* 1991). Stabilization of the water column following upwelling was accompanied by an initial increase in concentration of chlorophyll *a*, the formation of a subsurface chlorophyll *a* maximum and the eventual disappearance of the phytoplankton bloom from the euphotic zone. The period of relaxation was finally characterized by a low concentration of chlorophyll *a* and extensive nitrate-limitation in the surface waters prior to the next upwelling event.

Production rates during the study varied between 0,99 and 7,85 gC·m⁻²·day⁻¹ and generally tracked chlorophyll biomass changes (Mitchell-Innes and Walker 1991). Productivity indices (*PI*) varied considerably, from <1 to 10 mgC·mgChl⁻¹·h⁻¹, and were attributed to both successional changes in species and changing physiological conditions. Size-dependent changes in the productivity indices were observed, with the high productivity indices during the small-diatom and flagellate blooms decreasing during the large-diatom stage (Fig. 8). Size-dependent differences in the productivity indices were observed under optimal growth conditions when size dependent dif-
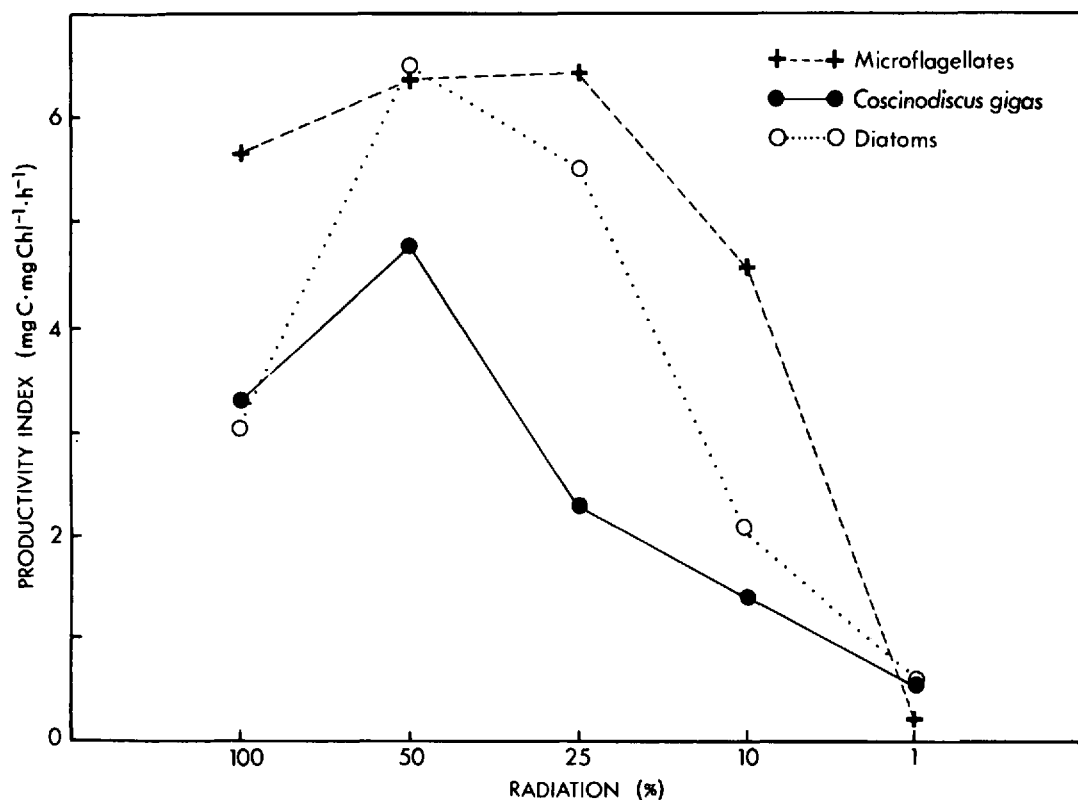
Fig. 8: The light-dependent response of productivity indices of microflagellate, small-diatom and *Coscinodiscus gigas* populations during a 27-day anchor study in St Helena Bay (after Mitchell-Innes and Walker 1991)

ferences should be most pronounced. The general assumption that nanoplankton have higher productivity indices than netplankton at all times is, however, not borne out by these data (Mitchell-Innes and Walker op. cit.). Generalizations about the productivity indices of different taxonomic and size groups of phytoplankton is complicated by the influence of factors such as light and nutrient availability. However, in maturing upwelled water, prior to nutrient limitation, small chain-forming diatoms have similar *PI* values to small flagellates (Walker 1990). Day-to-day variability of incident light, differences in C:Chl ratios and changing ambient temperatures are other factors which may have contributed to the spread in productivity indices.

Many independent factors are collectively involved in controlling changes in the phytoplankton. However, progression in species composition results primarily from two different mechanisms, namely succession (change in species composition within a given water mass resulting from changing physical, chemical and biological factors within that water mass) and sequential changes (change in species composition resulting

from a change in water-mass type). Both these mechanisms were evident during the St Helena Bay anchor study (Pitcher *et al.* 1991). True succession involves the original or autochthonous populations, whereas introduced or allocthonous populations are involved in the sequential changes. The species changes observed during periods of relaxation resulted from true successional changes, whereas the dramatic changes in the phytoplankton assemblage following upwelling events resulted from a change in water-mass type, which disrupts succession and is sequential in nature. Patterns of species succession are therefore influenced by the frequency of upwelling, which will play an important role in determining the phasic nature of phytoplankton succession.

During the St Helena Bay anchor study, the successional cycle following upwelling, during the subsequent period of relaxation, started with mixing and high availability of nutrients and ended with water-mass stratification and low availability of nutrients (Fig. 9). Initially, the growth of diatoms was favoured by a mixed water column with high levels of inorganic
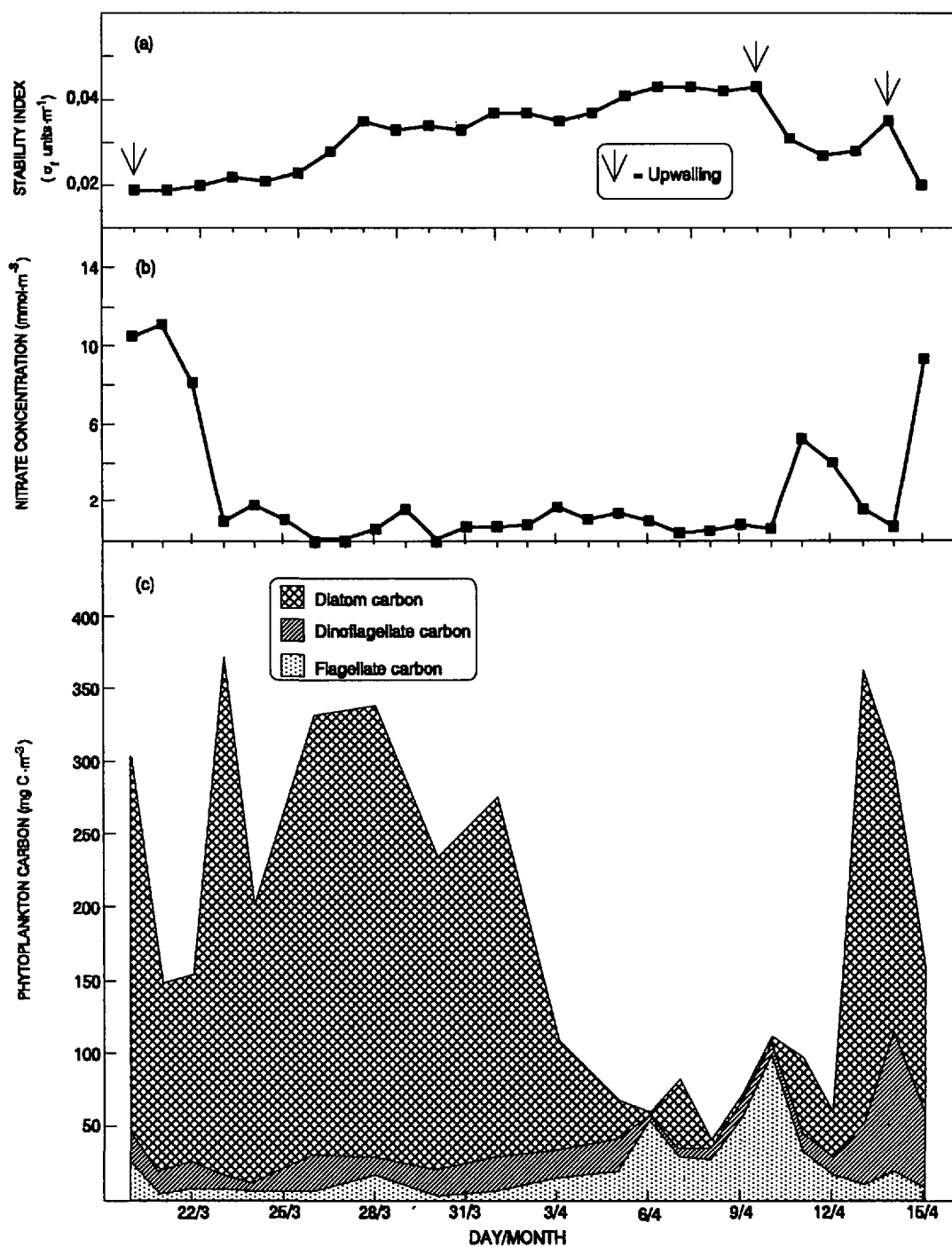
Fig. 9: Time-series of (a) water column stability (vertical density gradient over the upper 30 m), (b) surface nitrate concentration and (c) mean phytoplankton carbon concentration for the euphotic zone during a 27-day anchor study in St Helena Bay (adapted from Pitcher *et al.* 1991)

nutrients. Under conditions of low concentration of nutrients, the diatom bloom was terminated and small flagellates dominated the phytoplankton. The phytoplankton community was therefore closely associated with the vertical stability of the water column, with the stratification index giving good qualitative prediction of the relative dominance of diatoms and flagellates (Fig. 9). Succession progressed from a predominance of small-celled diatoms to larger species, followed then by a flagellate community, including representatives of several algal classes. The size composition of the phytoplankton responded somewhat predictably, large cells dominating the periods following upwelling and small cells during periods of water-mass stratification. The predominance of flagellate species in stratified waters with low concentrations of nutrients may possibly result from their increased ability to take up nutrients through motility.

The studies of Probyn (1985) support the hypothesis that netplankton production is largely nitrate-controlled, whereas picoplankton and nanoplankton productivity is regulated by regenerated nitrogen. The proportions of picoplankton and nanoplankton are therefore likely to increase with a reduction in upwelling intensity and nitrate supply. Hence, picoplankton and nanoplankton were found by Probyn *et al.* (1990) to dominate in terms of biomass and activity in aged upwelled water.

At the mesoscale, the phytoplankton community typically remains unpredictable at the species level, but it shows systematic spatial trends in the dominance pattern of higher taxonomic levels, such as diatoms, dinoflagellates and microflagellates. In terms of carbon, Pitcher *et al.* (1991) demonstrated that different components of the phytoplankton were associated with different stages of the upwelling cycle (Fig. 9). The variation and peaks in the phytoplankton biomass were therefore caused primarily by pulses in the diatom fraction of the total carbon, which tend to be greater in amplitude than the pulses in the microflagellate biomass. Not surprisingly, the system was therefore dominated by the >10 μm fraction, which constituted 81, 87 and 83 per cent of the total chlorophyll, production and phytoplankton carbon respectively during the St Helena Bay anchor study (Mitchell-Innes and Walker 1991). Probyn *et al.* (1990) also found inter-station variability in nitrogen productivity to be largest for netplankton, supporting the claim for an intermittent distribution of netplankton activity superimposed on relatively constant nanoplankton and picoplankton activity. This apparent constancy of nanoplankton biomass compared with that of netplankton could reflect a closer coupling between nanoplankton production and zooplankton.

Phytoplankton sinking was considered during the St Helena Bay anchor study (Pitcher *et al.* 1989, 1991) to have an impact on phytoplankton composition as a result of the variable sinking rates of different assemblage components. In particular, the onset of thermal stratification resulted in the replacement of heavy non-motile diatoms by motile or buoyant species. In this respect, a number of the changes in the species composition of the phytoplankton may have resulted from the interaction between turbulence and variable sinking rate.

Observed sinking rates of phytoplankton populations were not significantly correlated to any of the environmental parameters measured, possibly because of lags between environmental variations and the accompanying physiological responses associated with modifications of cell density. Variation of phytoplankton sinking rates was rather attributed to shifts in the population size distribution and taxonomic composition, sinking rates being significantly correlated with the taxonomic properties of the assemblage itself (Pitcher *et al.* 1989).

Although sinking may influence the successional patterns of various species and size-classes of phytoplankton, flux estimates made from both SETCOL measurements and sediment-trap recoveries indicate that losses from the euphotic zone resulting from the sinking of intact phytoplankton were of limited importance to the time-dependent changes of phytoplankton biomass. The natural mortality and breakdown of phytoplankton cells within the surface layers was considered to have been the most important factor accounting for the decline in phytoplankton biomass (Pitcher *et al.* 1991).

Longshore comparisons

The southern Benguela upwelling system is one in which changes in bottom topography and longshore wind stress result in locally enhanced upwelling, producing longshore variations in water temperature, nutrient concentration and plankton biomass as well as the expected changes offshore. Therefore in comparing an active upwelling site, such as the Cape Peninsula, to St Helena Bay, which is downstream on the leeward side of an upwelling centre, essential differences in bloom development may be found.

The hydrographic conditions present in an active site of upwelling such as the Cape Peninsula may be detrimental to the occurrence of an autochthonous flora and its succession. The reason is that wind-driven upwelling may be so intense that the autochthonous populations are continuously translocated, succession is prevented and the system is likely to be held in an immature state. However, in the relatively shallow, less hydrodynamically active system of St Helena

Bay, the ratio of autochthonous to allochthonous species is greater owing to less periodic incursions of different water-mass types and their associated flora (Pitcher *et al.* 1991). The progression of phytoplankton succession is therefore less likely to be disrupted in St Helena Bay and the development and retention of late successional forms is more likely (Walker and Pitcher 1991).

The rapid short-term changes that occur in the oceanography of an intense, pulsed upwelling site such as the Cape Peninsula have been illustrated by Brown and Field (1986). Mitchell-Innes and Walker (1991), on the other hand, found the biological variability inherent in upwelling areas to be tempered in St Helena Bay. The high rates of production and productivity indices reported for the Cape Peninsula upwelling plume were therefore not found in St Helena Bay, but neither were the very low rates of production. The duration of blooms in St Helena Bay also appear to be substantially longer than the duration of blooms off the Cape Peninsula, because of the longer retention times of the water masses. Although advection of recently upwelled water with high concentrations of nutrients appears to be the primary mechanism for nutrient replenishment off the Cape Peninsula and in St Helena Bay, nutrient regeneration within the water column and enhanced nutrient flux across the thermocline are very important processes in maintaining the bloom in St Helena Bay. The high productivity of St Helena Bay is therefore the result of a combination of relative stability of the physical environment, with the intermittent replenishment of nutrients in the upper water column by advection of recently upwelled water into the Bay, by nutrient regeneration within the water column (Probyn 1987) and enhanced nutrient flux across the thermocline from the bottom mixed layer (Bailey 1985).

These differences prompted Mitchell-Innes and Walker (1991) to liken St Helena Bay to a continuous culture system, where nutrient input is more or less continuous and high levels of biomass are maintained. In contrast, they considered the Cape Peninsula system more akin to a batch culture, where very fast rates of growth are attained and cycles of bloom development are normally completed within 5–8 days. These differences confirm the observations of Hutchings (1981) that St Helena Bay is an area of comparative homogeneity, where the standing crop of phytoplankton is both higher and more consistent than in the plume area off the Cape Peninsula. Hence, Shannon *et al.* (1984) observed high concentrations of chlorophyll *a* in St Helena Bay throughout the year, which have been assumed by Bailey (1985) to reflect enhanced primary production resulting from the establishment of a semi-closed system on the leeward side of the

Cape Columbine upwelling centre. Although both systems are very productive, there is likely to be a closer coupling between primary and secondary production in St Helena Bay and therefore a more continuous food supply for higher trophic levels (Mitchell-Innes and Walker 1991).

MICROSCALE (<0,1 km, hours/day)

Horizontal and vertical distributions

Phytoplankton patchiness at the microscale is likely to be as ephemeral in time as are the physical features on which it is dependent. Many of the plankton patches at this scale are too small and transitory to be the result of reproductive population increase. Behavioural factors are rather thought to play an important role in the formation and persistence of these micropatches. The transitional scale at which aggregative processes become more effective than reproduction varies strongly between taxa because of the opposing trends of mobility and reproductive rate (Mackas *et al.* 1985).

Red tides, which occur frequently within the southern Benguela, are considered to result from interaction between advection and behaviour. Buoyancy and positive phototaxis contribute to the shoreline accumulation of red-tide organisms under gentle onshore wind stress (Pitcher *et al.* in press). Especially nearshore, the spatial mosaic of accumulation and retention foci can be extremely complex and selective for individual taxa. It is possible that several biological and physical processes combine to produce a given abundance peak; active behavioural migration could occur within a zone of hydrodynamic accumulation which could in turn provide environmental conditions favourable for rapid growth and reproduction (Mackas *et al.* 1985).

Turbulent mixing, internal waves and advection are physical processes, and growth, sinking, grazing and vertical migration are the biological processes known to affect the vertical distribution of phytoplankton. Brown and Hutchings (1985) conclude that the vertical distribution of phytoplankton off the Cape Peninsula is largely dependent on the operative physical mechanisms. In summer, the shallower upper mixed layer, the increased concentrations of nutrients caused by upwelling, and the increased light result in the accumulation of high concentrations of phytoplankton in surface waters. In winter the phytoplankton is generally more sparsely, yet evenly, distributed in the water column owing to increased north-westerly winds, storm-mixing and reduced light.

Mitchell-Innes and Walker (1991) found a subsurface phytoplankton maximum layer in St Helena Bay
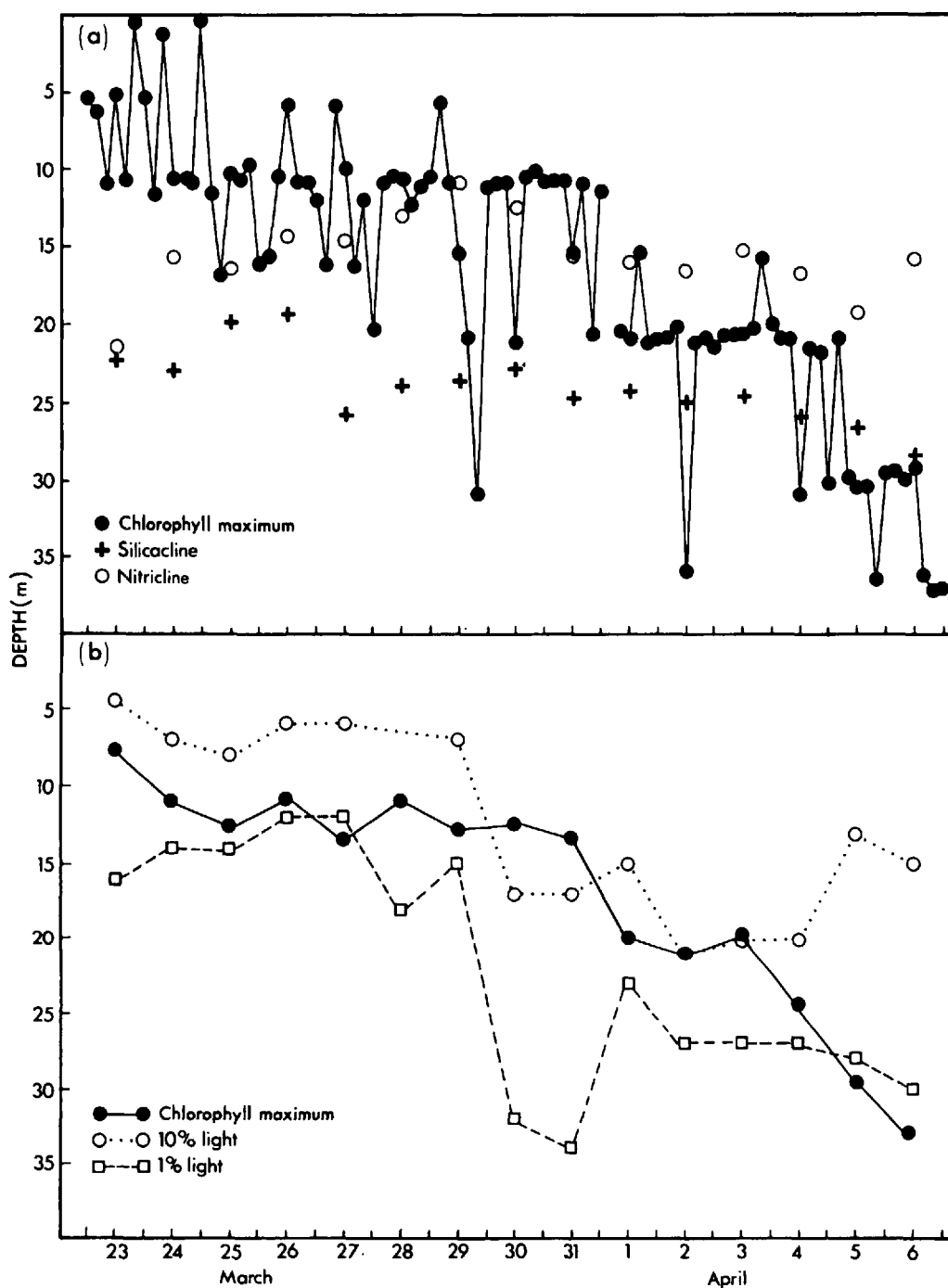
Fig. 10: (a) The position of the chlorophyll maximum in relation to the mean daily position of the maximum nitrate and silicate gradients and (b) the mean daily position of the chlorophyll maximum in relation to the 10 and 1 per cent light depths during a diatom bloom dominated by *Coscinodiscus gigas* in St Helena Bay (after Mitchell-Innes and Walker 1991)
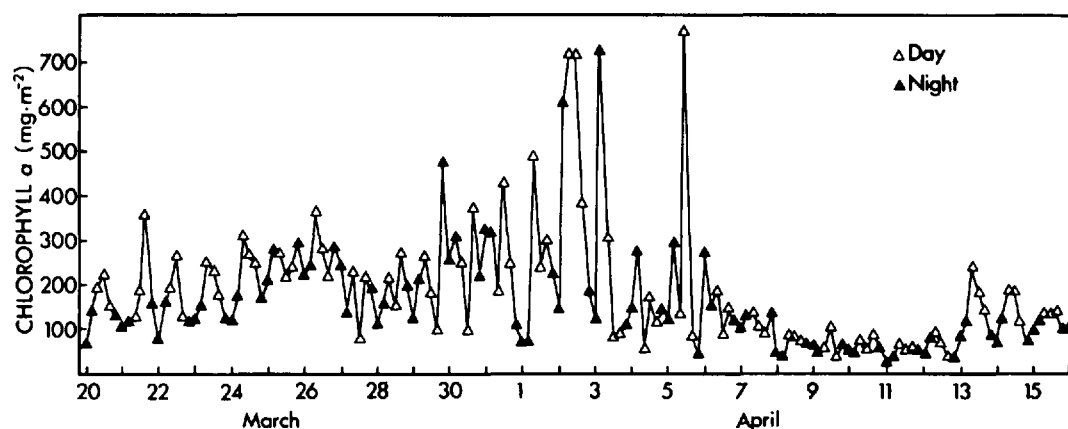
Fig. 11: Four-hourly changes in total chlorophyll *a* within the water column to 40 m during a 27-day anchor study in St Helena Bay (after Mitchell-Innes and Walker 1991)

shortly after the onset of nutrient depletion in the surface layer during the period of relaxation between upwelling events. Populations declined in the surface layers, presumably because of reduced growth and increased rates of sedimentation, but increased lower in the water column. The position of the chlorophyll maximum in relation to the nitri- and silicacline remained relatively constant as nutrients were progressively stripped from the surface layers by the large phytoplankton population and the nutrient-depleted surface layer deepened (Fig. 10a). The chlorophyll maximum layer maintained a close association with the nitricline, but lay above the silicacline, suggesting that silica rather than nitrate requirements were limiting and that nitrogen requirements were being supplemented by regenerated nitrogen. The chlorophyll maximum layer eventually collapsed as a result of light limitation after it had sunk below the 1 per cent light level (Fig. 10b). Low grazing probably permitted the accumulation of such high concentrations of chlorophyll within this layer while sinking deceleration (Pitcher *et al.* 1989) may have played an important role in the formation of the chlorophyll maximum layer. Biological processes, namely enhanced growth near the nitricline and perhaps buoyancy regulation, were therefore considered the major factors controlling the maintenance of the layer.

The most important factor affecting the vertical distribution of productivity indices is the decreasing availability of photosynthetically active radiation with increasing depth. Mitchell-Innes and Walker (1991), however, found that the productivity indices for different groups of phytoplankton responded differently to decreasing ambient light. The productivity indices for microflagellate populations were, for example, higher over a wider range of light levels than for other groups,

while both small and large diatom groups were light-inhibited at the surface (Fig. 8).

Diel changes

Total water column chlorophyll *a* in St Helena Bay varies in a cyclic fashion in the short term, with the highest values generally attained during daylight and the lowest at night (Fig. 11). Daytime mean concentrations of chlorophyll *a* were significantly higher than night-time mean concentrations and the diel change in total chlorophyll ranged from 1 to 144 per cent. These variations are most likely to have resulted from either the effects of internal waves or from biological processes. Although current-meter data indicated the occurrence of both inertial (22,37 h) and tidal (12,5 h) fluctuations, the increases in chlorophyll *a* observed towards the afternoon could not be closely linked to these factors. Mitchell-Innes and Walker (1991) therefore considered biological processes, namely growth and diel changes in cellular chlorophyll content coupled with predominant nocturnal grazing by zooplankton and fish, to be responsible for these short-term changes in chlorophyll concentration. Between advection or upwelling events, short-term variability in chlorophyll structure was therefore primarily regulated by biological factors. Although fluctuations in total water column chlorophyll *a* were greater and more irregular when there was a pronounced subsurface chlorophyll maximum layer, this may have been an artifact of discrete sampling in a region of strong phytoplankton gradients.

Diel periodicity in the productivity and productivity indices of surface samples, with peaks during the day and minima overnight, have been demonstrated by

Brown and Field (1985). The time of the peaks varies and the amplitude of the fluctuation is greatest when day and night are of equal length and smallest when day and night periods are most different. The timing of the daily peak appeared to be related to previous and ambient light levels and possibly to nutrient concentrations.

Barlow (1984) observed diel physiological changes in the phytoplankton, carbohydrate concentrations generally increasing during the day and decreasing at night. The percentage carbon incorporated into protein was, however, greater at night than during the day (Barlow 1982b). Probyn *et al.* (1990) have demonstrated various diel responses by different size-classes of phytoplankton to the uptake of nitrate. Whereas nitrogen uptake by netplankton declines dramatically at night, the pico- and nanoplankton maintain rates close to daylight levels. The active synthesis of protein by pico- and nanoplankton at night is indicated by higher uptake efficiencies, as calculated from uptake rates normalized to chlorophyll for pico- and nanoplankton relative to netplankton. This decline in netplankton activity at night indicates that the disparity between small and large phytoplankton in terms of nitrogen utilization may not be demonstrated from daylight incubations alone.

CONCLUDING REMARKS

As concluded by Haury *et al.* (1978), there is clearly a variety of causes of both physical and biological origin, acting both in concert and independently to shape the spatial scale and temporal longevity of phytoplankton patches. These processes vary in time in both a cyclic and random manner, so the causal factors and their temporal variation make any categorization by causative mechanism both difficult and artificial.

All scales and types of patchiness are strongly influenced by hydrodynamic processes, both through turbulent redistribution of existing biological variability and through the creation of variability in the richness and suitability of the physical and chemical environment. There is a general correspondence between scale and the variance-generating mechanism. As demonstrated by Harris (1980) and Legendre and Demers (1984), small rapid perturbations induce only behavioural and physiological responses, but if the stimulus is of greater amplitude or longer lasting, the responses are higher in the hierarchy until ultimately growth rates and taxonomic changes occur. State variables

therefore tend to vary over longer periods on larger scales while rate variables react rapidly on small scales, so that the latter cannot be studied independently from time, whereas the former are more structured in space.

Wind is a key determinant of variability in the southern Benguela over a wide spectrum of time and space, having a direct influence on large-scale currents, local upwelling and the dynamics of the surface mixed layer. Short-term wind events and upwelling constitute a major disruption and override biotic interactions. The physical environment is therefore of considerable importance in controlling the distribution of nutrients and phytoplankton cells in the water column following upwelling. With the onset of stratification, physical processes become less dynamic, allowing biological and chemical factors to become the major determinants of phytoplankton variability. In turn, primary and secondary production become more closely coupled the longer the period of relaxation. This cycle is repeatedly initiated and terminated by upwelling events which, with increased frequency, tend to minimize biological influences on subsequent bloom development. Similar comparisons may be observed spatially with physical processes more dominant close to the source of upwelling and biological influences more important downstream of upwelling.

From the similarity of patterns between biological and physical tracers, it is clear that turbulent advection plays a major role in controlling the morphology of phytoplankton patchiness. What is not clear is how the potential of plankton for population growth and decline, by reproduction and mortality or by immigration and emigration, will alter their spatial patterns from those that would result for a conserved tracer. Typical approaches of the past have been to identify and study particular biological processes and to hypothesize about the controlling physical processes on comparable scales. In future, more well-designed, well-integrated biological-physical studies are required to observe and understand the "switching" between physical and biological control.

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