

ECOLOGICAL FEATURES OF HARMFUL ALGAL BLOOMS IN COASTAL UPWELLING ECOSYSTEMS

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Upwelling regions are the most complex habitats in which dinoflagellates produce red tides, but the flora is not unique. Many species also bloom in nutrient-enriched, non-upwelling systems, share the collective dinoflagellate trait of low-nutrient affinity, and can achieve relatively fast growth rates. Blooms occur over the range of nutrient – mixing – advection combinations found in upwelling habitats, rather than being restricted to the high-nutrient high-irradiance low-turbulence conditions posited by Margalef's classical Mandala and its Bowman *et al.* and Pingree versions. The bloom species are primarily ruderal strategists (R-species), which typify "mixing – drift" life-forms adapted to the velocities associated with frontal zones, entrainment within coastal currents, and vertical mixing during upwelling relaxations. Collectively, dinoflagellates appear capable of surviving fairly high turbulence spectra formed at representative Kolmogorov length scale – wind speed conditions. This biophysical protection might be the result of cell size-facilitated entrainment within the micro-eddies formed during turbulent energy dissipation. The swimming speeds of 71 clones of dinoflagellates are compared and related to reported rates of vertical motion in coastal upwelling systems. There are slow and fast swimmers; many exhibit motility rates that can exceed representative *in situ* vertical and horizontal water mass movements. At least four dinoflagellates from upwelling systems form chains leading to increased swimming speeds, and may be an adaptation for growth in coastal upwelling habitats. Red tides are frequent and fundamental features of upwelling systems, particularly during intermittent upwelling relaxations, rather than dichotomous (sometimes catastrophic) interruptions of the diatom blooms characteristically induced by upwelling. Successional sequences and the "red tide" zone may differ between upwelling and non-upwelling systems. In the latter, red tides diverge from the main sequence and are appropriately positioned in the Mandala's ecological space of high nutrients and low turbulence. An amended Mandala based on Pingree's *S-kh* model and the Smayda and Reynolds life-form model is presented to accommodate the range of red tide development and their successional routing found in coastal upwelling systems. Ecophysiological data support the Pitcher and Boyd seeding mechanism model, which can lead to red tides in upwelling systems. Nutrients, phyto-stimulation and grazing pressure as triggering factors in upwelling-system red tides are considered. Some red tides may be stimulated by nutrients and growth promoting factors excreted by migrating shoals and "boils" of clupeoid stocks, with selective zooplankton grazing contributory. Substantial collapses in grazing pressure may be essential in anoxic red tide events. The mass mortalities that accompany anoxia, common to the Benguela and Peru upwelling systems, may be a trophic control mechanism to maintain biogeochemical balance and regional homeostasis, which are vital to upwelling ecosystem dynamics. Some traditional concepts of phytoplankton ecology may not completely apply to dinoflagellate bloom events in coastal upwelling systems.

Upwelling regions, the most fertile of the seas' habitats, are also sites of massive, episodic die-offs of fish and invertebrate communities, induced by red tides. This dichotomy, vividly documented in Brongersma-Sanders' (1957) classical summary, suggests that, whereas diatom blooms are normal responses to upwelling, outbreaks of red tide and their trophic consequences are anomalous. However, substantial evidence reveals that red tides are neither infrequent nor dichotomous in coastal upwelling systems. Over a 21-year period (ending 1980), 177 red-water outbreaks developed along the South African coast (Horstman 1981), and during 1992/93 alone, 60 red tides were reported for the southern Benguela upwelling system (Pitcher *et al.* 1995). The toxic and harmful nature of many of these red tides is documented by Pitcher and

Calder (2000). A major, unresolved issue is: what ecological, adaptational, bloom cycle and successional features characterize dinoflagellates indigenous to upwelling systems, and how do these compare to species in non-upwelling systems? Do their blooms conform to expected successional behaviour? Since Blasco's (1975) pioneering review, much new information allows re-examination of these issues. The present analysis will focus on the ecophysiological and bloom commonalities of red tides in eastern boundary current and minor upwelling regions generally, rather than be a region-by-region assessment. Because red tides, their regulation and dynamics are subsets of basic bloom phenomena (Smayda 1997a, b), the analysis is placed within the context of phytoplankton ecology generally.

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THE UPWELLING HABITAT

Upwelling systems are attenuated relicts of the wider evolutionary arena within which dinoflagellates and diatoms evolved and refined their specific phytoplanktonic life modes. The salient feature in this evolutionary struggle is the hallmark requirement of upwelling systems: the ability of species to cope with strong physical forcing and the biophysical consequences of entrainment within advective currents, frontal zones and turbulence. For dinoflagellates, the problem is to survive turbulent water masses without biophysical impairment, to access mixing zones and strata of high nutrient availability and to achieve population growth over a time-period adequate for completion of their life cycles. The phylogenetic struggle of diatoms and dinoflagellates to cross the turbulence barrier, to function at low irradiance, and to access nutrient-rich waters is mimicked in upwelling systems. Specifically played out is the role of turbulence in the selection of swim (dinoflagellate) versus sink (diatom) strategies. This selection establishes the life mode, successional stage and bloom species characteristics of the assembled communities.

Two classical views need to be unified in assessing the dynamics of red tides in coastal upwelling systems, the physical nature of upwelling and the habitat conditions needed by dinoflagellates to bloom. The classical (narrow) physical view is that coastal upwelling systems are generated by an onshore, wind-induced inflow of deeper, colder, nutrient-rich water, which upwells to maintain the hydrostatic balance required by the offshore displacement of the near-surface, nutrient-depleted waters. The more appropriate view is that the energy of wind stress moves water masses in singular (i.e. advective) and multiple (i.e. turbulence) directions, and their subsequent speed and direction are further modified by shoreline and bottom topographies, by local accelerations and reductions in velocity and meanderings of the upwelled waters. The variable transfer of momentum from air to sea creates a discontinuous habitat of chemical and thermal fronts, plumes, filaments, eddies, turbulence-cascade cells, mobile upwelling core centres and longshore currents.

The nutrient environment produced by the physics of upwelling is likewise spatially heterogeneous and temporally variable. Advected delivery and concentrations of nutrients are neither fixed, continuous, chemostatic, nor depend solely on upwelling rates. Remineralization is a major source of nutrients; excretion by zooplankton usually exceeds that from the herbivorous-omnivorous clupeoid stocks, for which upwelling systems are famous (Whitledge 1981). Even nutrient limitation occurs, both by nitrogen

(Dortch and Maske 1982, Shannon and Pillar 1986) and silicon (Harrison *et al.* 1981, Nelson *et al.* 1981). Nutrient supply regulates biomass levels and, through nutrient ratio modification, probably species composition. There are also onshore-offshore and longshore gradients of chemically seasoned ("biologically conditioned") waters, ranging from freshly upwelled, "pioneer" waters to the outermost, "mature" or "aged" plume waters (Barlow 1982a, b, Shannon and Pillar 1986). Considerable leakage of pelagic production to bottom sediments leads to conspicuously high dissolved organic carbon content, which reaches 26% off Namibia and varies from 7 to 11% in the North-West African, Californian and Peruvian upwelling systems (Diester-Haass 1978). This sedimentation of pelagic carbon promotes denitrification and episodic anoxic events, the latter causing faunal die-offs that alter the pelagic chemical milieu, trophic processes and benthic-pelagic coupling. Copenhagen (1953) presents a vivid account of "milky seas" in the vicinity of Walvis Bay, Namibia, during an anoxic event. This discolouration was attributed to colloidal sulphur formed by oxidation of H₂S emitted from depth by sulphurous eruptions.

Upwelling habitats, accordingly, are mosaics of multiple and shifting sub-habitats, whose physical and chemical properties exhibit sharp spatial and temporal heterogeneities, a variability that leads to frequent niche disruptions. Upwelling regions are the most complex and extreme of the habitats in which dinoflagellates are found. These habitat irregularities represent an anisentropic, open system, unlike non-upwelling regions (seasons) where (when) the phytoplankton habitat usually is spatially more uniform and temporally persistent. Rapid, unpredictable, episodic openings and closings of red tide bloom niches, usually of brief duration, intercalate upwelling pulses and their relaxations. This results in an alternating series of bloom-support and bloom-repression "habitat-windows", which restrict dinoflagellate blooms to narrow temporal periods of unpredictable occurrence and duration. A key determinant of whether a red tide then develops is the duration of the upwelling relaxation period relative to cellular growth rates. The favoured species must then contend with the combined problems of cellular biophysical damage and advective dispersion of the developing population accompanying spin-up of the temporarily relaxed upwelling winds. If turbulence remains too intense, cellular growth may be diminished; if advection is too strong, the balance between population washout and growth may preclude a bloom event. These variable, intermittent and unpredictable growth opportunities open and close during coastal upwelling. This feature and the degree of niche disruption differ from non-

Table I: Species reported to have caused red tides or harmful blooms in coastal upwelling systems, their cell size, and whether they have bloomed in nutrient-enriched, non-upwelling systems – denoted by * (from Braarud 1945, Lackey and Glendenning 1963, Lasker and Zweifel 1978, Horstman 1981, Fraga *et al.* 1989, Pitcher and Boyd 1996, Pitcher and Cockcroft 1998, Pitcher and Calder 2000; see text also)

Species	Cell size (µm)
Dinoflagellates	
<i>Alexandrium affine</i>	24–71
<i>A. catenella</i>	21–48
<i>A. tamarense</i> *	27–44
<i>Ceratium dens</i>	> 75
<i>C. furca</i> *	100–200
<i>C. fusus</i> *	300–600
<i>C. kofoidii</i>	> 75
<i>C. lineatum</i> *	> 75
<i>Cochlodinium</i> sp.	?
<i>C. cf. catenatum</i> (? <i>polykrikoides</i>)	30–40
<i>Dinophysis acuminata</i>	40–50
<i>Gonyaulax peruviana</i>	?
<i>G. polygramma</i> *	35–66
<i>G. spinifera</i>	35–40
<i>Gymnodinium arcuatum</i>	69
<i>G. breve</i>	15–70
<i>G. catenatum</i>	48–65
<i>G. flavum</i>	26–35
<i>G. galatheanum</i> *	14–17
<i>G. sanguineum</i> *	54–56
<i>Heterocapsa triquetra</i> *	21–32
<i>Lingulodinium polyedrum</i> *	40–50
<i>Noctiluca scintillans</i>	150–2 000
<i>Prorocentrum baltica</i>	5–30
<i>P. gracile</i>	40–60
<i>P. micans</i> *	35–70
<i>P. triestinum</i> *	18–27
<i>P. rostratum</i>	45–60
<i>P. reticulatum</i> (= <i>Gonyaulax grindleyi</i>)	30–53
<i>Scrippsiella trochoidea</i> *	16–36
Raphidophytes/others	
<i>Heterosigma akashiwo</i> *	11–25
<i>Eutreptiella gymnastica</i> *	18–38
<i>Mesodinium rubrum</i> *	30–50

upwelling habitats, where blooms and supporting habitat conditions are often more predictable, and occur along defined successional gradients. For example, late summer–early autumn ceratium blooms (Hickel 1982, Edler 1984, Granéli *et al.* 1989), predictably occur during a period of prolonged water mass stratification and high temperature. In regions of anthropogenic nutrient enrichment, dinoflagellates usually have a prolonged growth season in which to exploit available nutrients. The greater unpredictability of red tides in upwelling regions reflects the greater physical and chemical habitat variability accompanying upwelling physics. Dinoflagellates must accommodate habitat variability through their life cycle, swim-

based behavioural strategies, and biophysical tolerance to turbulence. Do coastal upwelling species exhibit unique ecophysiological properties?

THE UPWELLING FLORA

Components

A distinct upwelling diatom community has not evolved, based on species checklists for the major eastern boundary currents (Benguela, Peru, North-West Africa and California) and regionally contiguous, minor upwelling centres (Gulf of Panama, Baja California – De Jager 1955, Kollmer 1962, Smayda 1966, 1975, Blasco 1971, Blasco *et al.* 1980, 1981, Margalef 1973, 1978a, Rojas de Mendiola 1979, 1981, Kruger 1980, Olivieri 1983). The diatom communities and major bloom species are not only similar among the geographically dispersed upwelling regions, they are virtually identical to those in contiguous, non-upwelling habitats. *Asterionellopsis glacialis*, *Chaetoceros affinis*, *Chaetoceros compressus*, *Chaetoceros didymus*, *Chaetoceros socialis*, *Lauderia borealis* (*annulata*), *Lithodesmium undulatum*, *Pseudo-nitzschia delicatissima*, *Pseudo-nitzschia seriata*, *Rhizosolenia delicatula*, *Rhizosolenia stolterfothii* and *Skeletonema costatum* are among the diatom bloom-species common to coastal upwelling and non-upwelling systems. Where there are differences, they are relatively minor, for example, the unique predominance of *Delphineis karstenii* in the Benguela system (Hart and Currie 1960, Kruger 1980, Schuette and Schrader 1981), the relative rarity of *S. costatum* in the northern Benguela (Shannon and Pillar 1986) and the blooms of *Coenobiodiscus muriformis* in the Baja California system (Smayda 1975). The remarkable fertility of upwelling regions is not attributable to unique diatom communities having high photosynthetic and growth rates, but is more likely explained by the duration of the upwelling growth seasons (Cushing 1981).

Dinoflagellates, likewise, have not evolved assemblages unique to upwelling systems (see references above for diatoms). Of the 28 dinoflagellate species listed in Table I, all are common to coastal waters; only *Gymnodinium catenatum* and *Alexandrium affine* appear to occur preferentially in upwelling systems (Hallegraeff and Fraga 1998). However, certain dinoflagellate life-forms – ceratium, prorocentroid, gymnodinian – may be selected over others in being better adapted to upwelling habitats; this selection will be discussed later. The rarity of other phytoflagellate groups in developing blooms in upwelling systems

Table II: Half-saturation constants for nitrogen and phosphorus uptake and growth (*) by dinoflagellates

Species	Half-saturated constants K_s (μM)			
	NH_4	NO_3	PO_4	Source
Dinoflagellates:				
<i>Alexandrium tamarense</i>	2.0	1.5–2.8	–	4
<i>A. tamarense</i>	1.5–2.0	–	–	3
<i>A. tamarense</i>	–	–	0.40	4
<i>A. tamarense</i>	–	–	1.85	4
<i>A. tamarense</i>	–	–	2.64	5
<i>Amphidinium carterae</i>	–	–	0.01	4
<i>A. carterae</i>	–	~2.0	–	4
<i>Cryptocodinium microadriaticum</i>	–	–	0.01	4
<i>Gonyaulax polyedra</i>	5.3–5.7	8.6–10.3	–	4
(Red tide populations)	7.5–15.0	–	–	4
<i>Gymnodinium bogoriense</i>	20.0	–	3.2	4
<i>G. breve</i>	–	–	0.18*	4
<i>G. nagasakiense</i>	0.6*	0.78*	0.14*	4
<i>G. sanguineum</i> (= <i>splendens</i>)				
18°C	1.1	3.8	–	4
18°C	–	1.02*	–	4
25°C	–	6.55*	–	4
<i>Heterocapsa triquetra</i>	–	–	3.1	4
<i>Peridinium cinctum</i>	27.0	29.0	0.18–0.31	4
<i>Peridinium</i> sp.	3.6	–	–	4
<i>Peridinium</i> sp.	–	–	6.3	4
<i>Prorocentrum minimum</i>	–	–	1.96	4
<i>P. minimum</i>	3.1–7.4	–	–	2
<i>Pyrocystis noctiluca</i>	–	–	1.7–2.2.8	4
<i>P. noctiluca</i>	–	–	0.15*	4
<i>P. noctiluca</i>	4.4 ± 2.2	5.0 ± 4.0	–	1
<i>Pyrocystis fusiformis</i>	1.4 ± 1.1	3.0 ± 6.0	–	1
<i>Dissodinium lunula</i>	3.8 ± 5.1	1.7 ± 2.0	–	1

(1) Bhovichitra and Swift 1977; (2) Kondo *et al.* 1990; (3) MacIsaac 1978; (4) Smayda 1997b, (5) Yamamoto and Tarutani 1997

is notable: those of the raphidophyte *Heterosigma akashiwo* and the euglenid *Eutreptiella gymnastica* are the most conspicuous (Table I). Intense blooms of the microbial loop predator, *Noctiluca scintillans*, and endosymbiotic *Mesodinium rubrum* are ubiquitous in upwelling regions.

The bloom species recorded in Table I undoubtedly are only a partial listing, but some tentative conclusions can be drawn. Unlike diatoms, and despite evidence of a generally common bloom-species pool, dinoflagellate bloom taxa may not be as ubiquitous among upwelling regions, and the major bloom species may differ. *G. catenatum* primarily blooms in the upwelling regions along the Iberian peninsula and Moroccan coast (Hallegraeff and Fraga 1998). *Gymnodinium sanguineum* blooms are particularly notable in the Peruvian system (Packard *et al.* 1978b, Huntsman *et al.* 1981). *Lingulodinium polyedrum* is known primarily for its blooms in the Californian system (see Sweeney 1975, Lewis and Hallett 1997), but these are seemingly becoming less frequent. A similar decline in bloom importance of *L. polyedrum* has been observed along the Spanish coast, where it has been re-

placed by *G. catenatum*, *A. affine* and *Prorocentrum triestinum* (= *redfieldii*) (Fraga and Bakun 1993). Although *L. polyedrum* occurs in the Benguela system (Kruger 1980), it is not among the red tide producers reported for that system (Grindley and Taylor 1964, Horstman 1981, Pitcher and Boyd 1996, Pitcher and Calder 2000). Dinoflagellate diversity and occurrences of red tides are particularly high in the Benguela system (Horstman 1981, Pitcher and Calder 2000), unlike in the North-West African system where red tides appear to be less frequent, despite a similar species diversity (Margalef 1973, Blasco *et al.* 1981). This may be linked to the intense physical upwelling features of the North-West African system (Walsh 1976). Neither the species (Table I) nor their distributional patterns suggest that red tide species in upwelling systems differ from dinoflagellates generally in being exceptionally fast-growing, *r*-selected species.

Nutrient features of dinoflagellates

It is remarkable that 14 of the 28 species listed in

Table III: Half-saturation constants and their frequency of occurrence (%) for nutrient uptake reported for dinoflagellates and diatoms (from Smayda 1997b)

Group	Half-saturated constants K_s (μM)			
	<1.0	≥ 1.0	≥ 2.0	≥ 5.0
<i>n</i> = 22; maxima: 27 μM (NH_4), 29 μM (NO_3), 6.3 μM (PO_4)				
Dinoflagellates	4 (18%)	18 (82%)	15 (68%)	7 (32%)
<i>n</i> = 28; maxima: 5.5 μM (NH_4), 5.1 μM (NO_3), 1.7 μM (PO_4)				
Diatoms	12 (43%)	16 (57%)	6 (18%)	2 (7%)

Table I also produce prodigious blooms in nutrient-enriched, non-upwelling coastal systems. *Ceratium furca*, *Ceratium lineatum*, *Heterocapsa triquetra*, *Prorocentrum micans* and *Scrippsiella trochoidea* produce large blooms in eutrophicated, inner Oslofjord (Braarud 1945). *L. polyedrum* increasingly has become a major bloom species in progressively nutrified Kastela Bay in the Adriatic Sea (Marasovic *et al.* 1991). *Gonyaulax polygramma* and *G. sanguineum* bloom in polluted Omura Bay (Iizuka 1976), and *Gymnodinium galatheanum* blooms in enriched Walvis Bay (Braarud 1957, Pieterse and van der Post 1967). These field responses to elevated nutrients are consistent with experimental evidence that dinoflagellates and red tide flagellates generally, and paradoxically, lack the expected high nutrient affinity (low K_s – see Smayda 1997b). Red tide species found in upwelling systems share the common dinoflagellate preference for high nutrients (Tables I–III). Dinoflagellates would be expected to have low K_s coefficients to allow efficient uptake of nutrients at the low concentrations found in the warm, highly stratified, nutrient-depleted (poor) water masses, seasons and regions where they tend to predominate. The K_s values for inorganic nitrogen and phosphorus uptake by 24

species and clones of dinoflagellates (Table II) generally are substantially higher than those for diatoms (Table III). Values $>2.0 \mu\text{M}$ are common, and even exceed $10 \mu\text{M}$; diatom K_s values generally are $<1.0 \mu\text{M}$. The ecological consequences of this physiology and evolutionary adaptation that dinoflagellates may have evolved to offset the ecological disadvantages of high K_s are considered by Smayda (1997b).

Growth

Red tide species are commonly assumed to grow relatively slow, and their blooms are often the result of physical accumulation or low grazing pressure (Smayda 1997b). Whereas dinoflagellates collectively grow more slowly than diatoms, cellular growth rates $>1.0\text{-day}^{-1}$ in culture are not unusual (Table IV). Among the species forming red tides in upwelling regions, growth rates from 1.25 to 2.1-day^{-1} have been reported for *G. sanguineum*, *H. triquetra*, *P. micans*, *P. triestinum* (= *redfieldii*), *S. trochoidea* (Smayda 1997b) and *L. polyedrum* (Harrison 1976). *In situ* doubling rates and productivity (= assimilation numbers) of red tide species in coastal upwelling (Table V), although indirectly determined and representative of net population growth, support the notion that their blooms often result from active growth, rather than being physical aggregations of metabolically sluggish populations (see Franks 1992). The assimilation rate of $16.8 \text{ mgC}\cdot\text{mgChl}^{-1}\cdot\text{h}^{-1}$ measured during a *Mesodinium* bloom is one of the highest reported. Assimilation numbers and primary production rates during diatom- and dinoflagellate-dominated bloom communities are similar. This is consistent with the conclusion that differences in annual production among upwelling systems primarily reflect differences in the duration and intensity of upwelling, and not the bloom species.

Table IV: Daily growth rates *in situ* and in culture, and their frequency of occurrence (%), reported for various phytoplankton groups, exclusive of coccolithophorids (Smayda 1997b)

Group	Daily growth rates ($\mu\text{-day}^{-1}$)					
	≥ 1.0	≥ 1.5	≥ 2.0	≥ 3.0	≥ 3.5	≥ 4.0
<i>n</i> = 58; range 0.2–5.9 day^{-1}						
Diatoms	53 (91%)	50 (88%)	41 (70%)	23 (40%)	15 (26%)	14 (24%)
<i>n</i> = 24; range 0.1–2.7 day^{-1}						
Dinoflagellates	10 (42%)	7 (29%)	3 (12%)	0	0	0
<i>n</i> =22; range 1.3–5.2 day^{-1}						
Other flagellates	22 (100%)	17 (77%)	10 (45%)	1 (5%)	1(5%)	0

Table V: Growth and productivity rates of red tide species in coastal upwelling systems

Species	Location	Growth and productivity rates			Source
		<i>In situ</i> doubling (day^{-1})	Assimilation number ($\text{mg C}\cdot\text{mg chl}^{-1}\cdot\text{h}^{-1}$)	Primary production rates ($\text{gC}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$)	
<i>Lingulodinium polyedrum</i>	Mexico	0.2–0.9			11
<i>L. polyedrum</i>	California	0.6–0.8			10
<i>L. polyedrum</i>	California	0.8–1.4			8
<i>Ceratium tripos</i>	California	0.25			7
Dinoflagellates	Peru	0.7			2
“Phytoplankton”	S. Benguela	0.42			6
	N. Benguela	0.08			6
<i>Gymnodinium sanguineum</i>			5.0		4
<i>Lingulodinium polyedrum</i>			4.3		4
<i>L. polyedrum</i>			3.3		10
<i>Gyrodinium aureolum</i>			4.0		3
<i>Mesodinium rubrum</i>			9.6		9
<i>M. rubrum</i>			16.8		1
“Dinoflagellate bloom”	False Bay (S. Benguela)			3.7	5

(1) Barber and Smith 1981; (2) Beers *et al.* 1971; (3) Bjørnson and Nielsen 1991; (4) Blasco 1975; (5) Brown *et al.* 1979; (6) Brown *et al.* 1991; (7) Eppley *et al.* 1984; (8) Harrison 1976; (9) Harrison *et al.* 1981; (10) Holmes *et al.* 1967; (11) Walsh *et al.* 1974

INTERACTION OF PHYSICAL HABITAT AND LIFE-FORMS IN SELECTING FOR DINOFLAGELLATE BLOOMS IN COASTAL UPWELLING SYSTEMS

Margalef's Mandala and Bowman *et al.* model

Margalef (1978b) formulated his classical, theoretical Mandala (Fig. 1) to provide a conceptual basis to the conundrum: what mechanisms select for specific phytoplankton life-forms and their blooms? This model incorporates the well-established observation that diatoms become dominant in turbulent waters rich in nutrients (spring bloom period; coastal upwelling), and dinoflagellates often dominate in stratified waters poor in nutrients. A water mass initially well-mixed and nutrient-replete becomes progressively nutrient-poorer during its seasonal transformation into a stratified state. Intermittent and seasonal relaxations in upwelling intensity have corresponding effects on nutrient supply. Margalef *et al.* (1979) considered that nutrient concentrations and turbulence usually go hand in hand and are the main abiotic determinants of ecological space that drive phytoplankton community organization. Hence, diatom and dinoflagellate communities, as depicted in the Mandala, are linked by a species succession – the main sequence – occurring in response to the seasonal consumption (availability) of nutrients and accompanying decay in turbulence. In this scheme, *K*-selected species better adapted to utilize the diminishing nutrient

base progressively displace *r*-selected (fast growing, opportunistic) species.

Red tides were considered by Margalef *et al.* (1979, p. 93) to be “representative of a rather exceptional sort of phytoplankton community”, and the Mandala positions their occurrences in the ecological space of relatively high nutrients and low turbulence along a trajectory separate from, but leading off the main sequence from, diatom- to dinoflagellate-dominated communities (Fig. 1). In this routing, the seasonal decrease in nutrients normally accompanying the progressive decay in turbulence and increased stratification is interrupted by a nutrient flux, which exceeds delivery by the seasonally weakened turbulence. This leads to the unique, transitory matrix combination of high nutrient levels and low turbulence (Fig. 1). Margalef (1978b, p. 505) concluded that this habitat condition of high nutrient–low turbulence “might represent a sort of illness, not completely ironed out by evolution, since it produces red tides that may end in catastrophe”. The prospect that catastrophic die-offs accompanying outbreaks of red tides in upwelling systems (Brongersma-Sanders 1957) might reflect such trophic imbalance is considered in a later section.

Whereas the red tide dinoflagellates in upwelling and non-upwelling coastal systems are taxonomically and ecophysiologicaly similar (Tables I–IV), are their required bloom conditions also similar (Fig. 1)? Although the Mandala treats red tides collectively, Margalef *et al.* (1979, p. 89) characterized those that develop in coastal areas, or are associated with up-

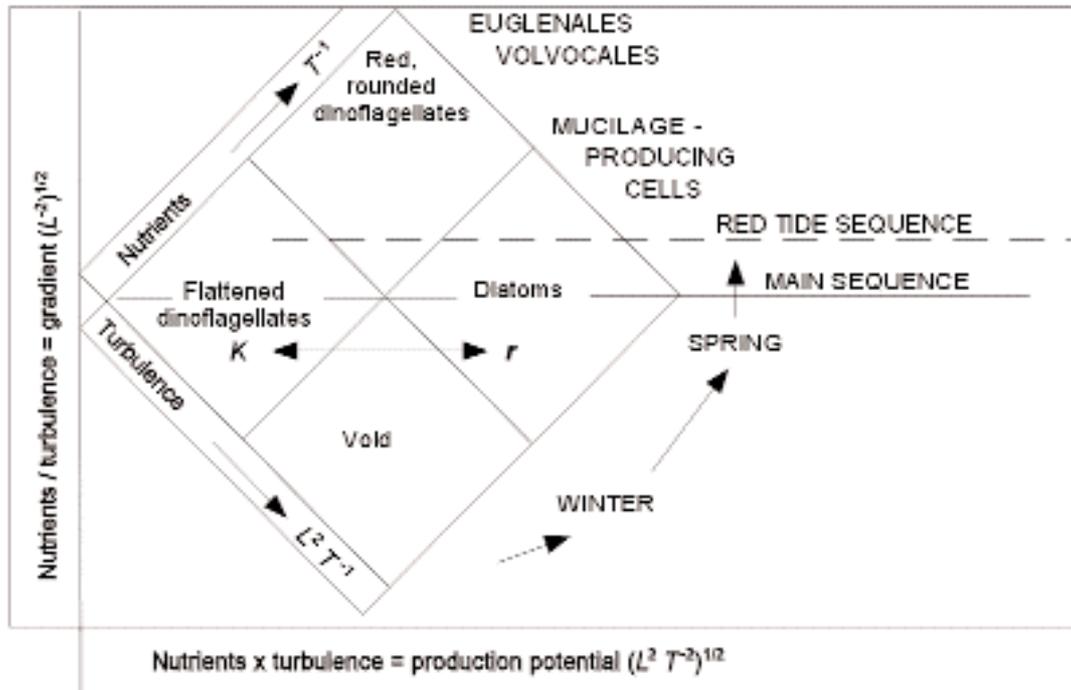


Fig. 1: The Margalef Mandala and its red tide trajectory (from Margalef *et al.* 1979)

welling, as “two situations [which] are so different” and further (p. 93), that “red tides associated with upwelling conditions are more difficult to understand and pose challenging problems in the interface between hydrography and planktology”. Blooms and successional events are processes, the result of both cellular and population growth; dispersion rates, grazing and other losses also affect the outcome. The ecological space (nutrients v. turbulence) delineated qualitatively in the Mandala (Fig. 1) is therefore re-stated and quantified (Fig. 2) to evaluate whether coastal upwelling red tides are accommodated by the Mandala. In the Bowman *et al.* (1981) model, phytoplankton growth (α) is conceptualized to occur in a horizontal and vertical diffusing (D) environment under advective influence, and within an ecological grid of net population growth rate, α (s^{-1}), v. turbulent mixing intensity parameterized through D ($cm^2 \cdot s^{-1}$). D is a strong function of stratification and pycnocline strength. Its effective value in the horizontal plane is many orders of magnitude greater than in the vertical plane. In the horizontal, velocity (v) is associated with surface divergences (as in upwelling) and frontal zone convergences. In the vertical, v is associated with down-

welling speeds and, for phytoplankton cells, sinking and swimming velocities.

The Bowman *et al.* model is basically a phytoplankton patch model, with the vertical axis $(\alpha/D)^{1/2}$ having the dimensions of a gradient representing the maximum wave number (corresponding to the minimum patch dimension) that can persist for a growing population in the presence of diffusion. The horizontal axis $(\alpha/D)^{1/2}$ is the “diffusion velocity” (v_f), conceptualized as the “production potential” in the Mandala (Fig. 1), i.e. a measure of a patch population’s tendency to expand into the surrounding environment. In the vertical plane, the diffusion velocity is the minimum swimming speed needed to allow dinoflagellate growth, or the maximum sinking speed that a diatom population can have, and remain within the euphotic zone. The ability of dinoflagellates to survive the turbulence structure during upwelling, its relaxations and to form blooms, is determined by their swimming speeds and cellular and population growth rates relative to the horizontal and vertical advection rates, the latter acting as both dispersal and aggregation mechanisms. The growth-supporting potential of these physical processes is shown schematically in

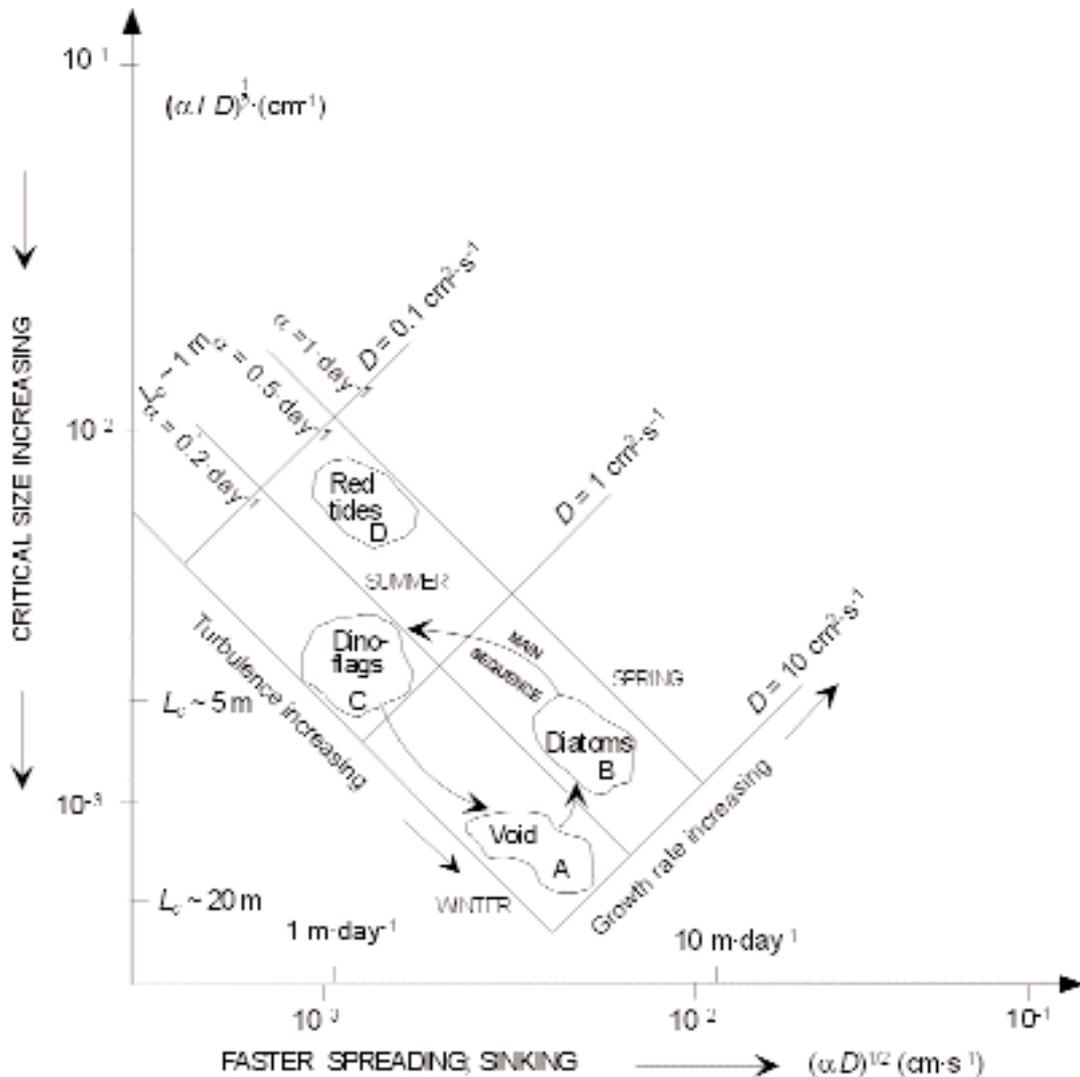


Fig. 2: The four basic phytoplankton growth regimes of Margalef's Mandala, restated in terms of population growth rate (α) and intensity of turbulent mixing parameterized through degree of vertical diffusivity (D) – From Bowman *et al.* 1981). See text for further details

Figure 2, where the orthogonal, intersecting straight lines (log-log scale) represent isopleths of growth (α) and turbulence (D) based on arbitrary, but realistic, coastal values.

Four distinct growth-vertical diffusion zones are delineated, and in each zone a distinctive phytoplankton community develops corresponding to their ecological placements within Margalef's Mandala (Figs 1, 2). Of these, the basic dinoflagellate growth zone (Region C), which develops along the main se-

quence and follows diatom blooms (Region B), is characterized as a habitat of low α potential and vertical diffusivity (D), with α limited by low nutrient levels. Flagellates are predicted to dominate in such highly stratified, oligotrophic waters (Fig. 1), despite low growth rates, because excessive sinking losses select against diatoms. For dinoflagellate communities in this ecological space to produce a red tide, both versions of the Mandala (Figs 1, 2) require α to increase, transforming the habitat into the "red tide zone"

characterized by high α and low D (Fig. 2). If the red tide develops as a result of local growth (as assumed in the following), and not physical aggregation, then for α to increase an energy input is required to heighten photosynthesis. Because high irradiance characteristically accompanies strong stratification, it is nutrient limitation of α that must be overcome. This is a requirement of both versions of the Mandala. The source of this nutrient to satisfy the mandated, anomalous combination of high nutrient levels and low D is less obvious. It cannot be new nutrients that are physically pumped up from the nutrient-rich reservoir underlying the stratified water mass, because D is then predictably low; in fact, the water mass progressively may acquire even greater seasonal inertia against mixing (Fig. 2). Anthropogenic delivery, a major potential source of the elevated nutrient flux in non-upwelling, coastal waters, is unlikely in upwelling systems, which are characteristically off arid, scantily populated coastlines.

Leaving open the unresolved issue of the sources of nutrients favouring development of red tide ecological zones (Figs 1, 2), do the Margalef and Bowman *et al.* versions of the Mandala accommodate red tide development in upwelling regions? Red tides are grouped as similar phenomena in the Mandala. Yet, in addition to the distinction made between non-upwelling and upwelling-associated red tides (Margalef *et al.* 1979), upwelling systems display at least two spatially distinct types of red tides, shelf-blooms and nearshore (coastal embayment) blooms. These can be further sub-grouped into blooms that develop during intermittent upwelling relaxations (Walsh *et al.* 1974, Pitcher and Boyd 1996), and red tide outbreaks that develop during the post-upwelling (rainy) season (Smayda 1966, Reyes-Vasquez *et al.* 1979). Nearshore red tides are considered here first. The Benguela upwelling system has a series of coastal embayments (Walvis Bay, St Helena Bay, False Bay, Walker Bay), where both upwelling and red tides are important events (De Jager 1955, Pieterse and van der Post 1967, Grindley and Nel 1970, Shannon and Pillar 1986, among others). Nutrient data are limited, but suggest that red tide blooms in these embayments do not meet the high concurrent nutrient criterion of either version of the Mandala, with the notable exception of Walvis Bay. During the post-upwelling period, particularly December–January, when fish factory effluent was copiously discharged into this small, phosphorus-enriched bay, prodigious blooms of *Alexandrium tamarense*, *G. galatheanum*, *H. triquetra* and *S. trochoidea* occurred, sometimes accompanied by fish and invertebrate die-offs (Pieterse and van der Post 1967). The conspicuous, year-round predominance of dinoflagellates in Walvis Bay (at least at that time) further distinguishes it as a unique dinoflagel-

late habitat similar to Phosphorescent Bay, Puerto Rico (Margalef 1961, Smayda 1970), and Oyster Bay, Jamaica (Seliger *et al.* 1970), where *Pyrodinium bahamense* var. *bahamense* predominates year-round.

Similar coastal embayments are relatively uncommon in other major (California, North-West Africa, Peru) and minor (Oregon, Baja California, Gulf of Panama) eastern boundary current regions. In those systems, as in the Benguela system, prominent shelf red tides often develop during intermittent periods of upwelling relaxation and/or at offshore frontal zones (see Packard *et al.* 1978a, Pitcher and Boyd 1996). Dinoflagellates can then out-compete diatoms, despite exposure to mixing conditions that are traditionally considered to be hostile (Blasco 1977). In the California upwelling system, dinoflagellates bloomed at times when the thermocline was shallow and steep, and nutrient enrichment did not reach the surface (Eppley and Harrison 1975). In an even more dynamic situation, a bloom of *L. polyedrum* persisted for 20 days off Baja California in upwelled water masses with elevated NO_3 concentrations, under conditions of relatively low water column stability and the absence of appreciable vertical gradients.

Offshore, frontal zone red tides, common in upwelling systems, also fall outside of the presumed habitat conditions of the “red tide zone” (Figs 1, 2), and are not readily explained by associated ecophysiological kinetics (Beers *et al.* 1971, Holligan 1979, 1985, 1987, Holligan *et al.* 1984, LeFèvre 1986, Pitcher and Boyd 1996, Pitcher *et al.* 1998). Frontal zone physical processes function as a nutrient pump and also aggregate and disperse populations entrained in downwelling convergences and upwelling divergences, respectively (Franks 1992). These dynamics yield nutrient intergrades between Region C and Region D habitats (Fig. 2), whereas the characteristic turbulence and diffusion velocities tend to create either Region B habitats, favouring diatom blooms, or the “void” of Region A, detrimental to phytoplankton growth. The importance of dinoflagellate swimming speeds in frontal system blooms is evaluated in a later section.

Pingree's *S-kh* model

The closeness of fit between observed upwelling system red tides and the Mandala's designated “red tide zone” is further evaluated using Pingree's *S-kh* model. Pingree *et al.* (1975, 1978) and Pingree (1978) applied a different approach in relating the seasonal occurrences, dispersions and abundance of red tide species in the tidally mixed Celtic Sea and English Channel. Pingree assumed that the availability of nutrients and light under variable mixing regimes

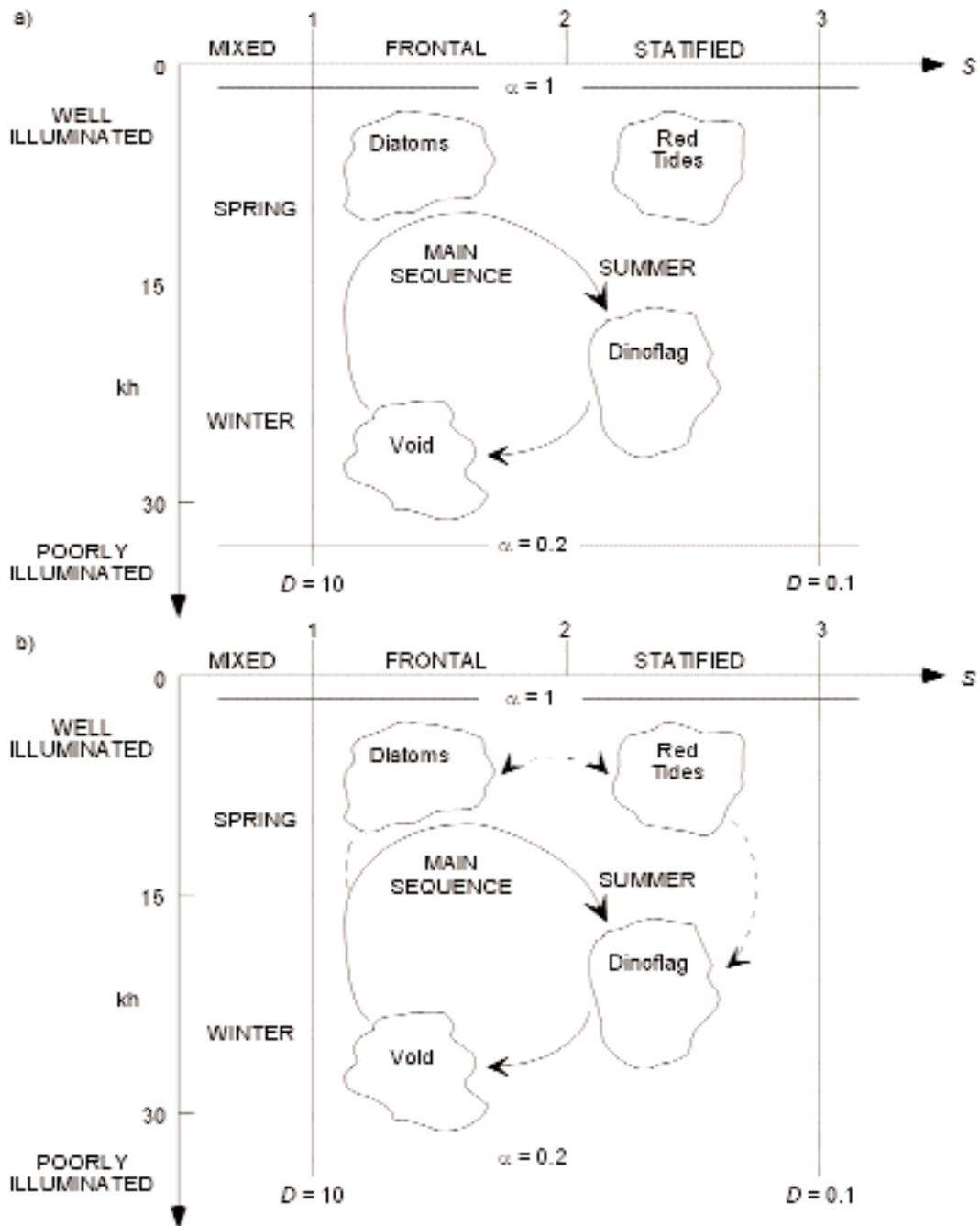


Fig. 3: (a) Schematic of Pingree's S - kh diagram and conceptual equivalence with Margalef's Mandala: α denotes population growth rate, D is vertical diffusivity and S is the stratification-mixing index, as defined in the text (From Bowman *et al.* 1981); (b) proposed successional sequence (dashed line) that can occur during upwelling cycles, including the reversible bloom responses between active upwelling (diatoms) and its intermittent relaxations (red tides). In the absence of upwelling relaxations favourable to red tide development, the depicted main sequence applies. See text for further details

could be gauged from two parameters: the stratification parameter, and water depth scaled by the light extinction coefficient. Stratification v. depth-scaled-by-light plots, i.e. *S-kh* diagrams, were constructed from a stratification index (*S*) and the number of optical depths (*kh*) in the water column. The stratification index, is defined as:

$$S = \log_{10} (h / C_D \mu^3) \quad ,$$

where *h* is water column depth, C_D the dimensionless friction drag coefficient and μ^3 is the mean cubed semi-diurnal tidal current. High values of *S* are associated with well-stratified waters, low values represent well-mixed water columns. The number of optical depths (*kh*) within the water is the product of the diffuse extinction coefficient (*k*) and the water column depth. The axis parameters of Pingree's *S-kh* diagram can be directly measured, in contrast to the difficulty in measuring *in situ* growth and diffusivity (Fig. 2), but they nonetheless are proxies of actual nutrient and light conditions. The *S-kh* diagram is schematized in Figure 3a, onto which Bowman *et al.* (1981) appended the Mandala, with appropriate rotation, showing their conceptual equivalence. The ability of the *S-kh* model to distinguish among different mixing regions is evident: values of $S < 1$ define well-mixed regions (high *D*) where nutrients are likely to be high. Values of $S > 2$ represent stratified conditions (low *D*), with a nutrient impoverished layer most likely overlying a nutrient-rich reservoir at the base of the euphotic zone. Under these conditions, nutrient-gathering migrations of motile phytoplankters should be facilitated, and sinking losses of diatoms would be high (Smayda 1997b). For $S < 2$, vertical nutrient fluxes play an increasing role; at $S > 2$, remineralization is more important. Pingree (1978) considered that at $S = c. 1.5$, a transition into frontal zone dynamics occurs, and the resultant combination of high nutrients and suitable light regime favours growth. In the intermediate region ($1 < S < 2$), stratification is marginal and variable, as is the bloom-support capacity of the vertical physical microstructure and associated irradiance. Those flagellates that have equivalent growth rates and the fastest swimming speeds would then be favoured. A virtue of the *S-kh* model, relative to the other Mandala versions (Figs 1, 2) is the greater spatial and temporal delineation of the physically diverse ecological space. The depicted orientation of the characteristic communities developing within this space, however, is virtually identical in all three versions of the Mandala. Once again, the "red tide zone", positioned in the upper right quadrant of Figure 3a, is characterized as a habitat of high light and low turbulence, but requiring a higher nutrient input than expected from the stratification index to support the high population growth rate leading to a red tide.

Table VI: Predominant dinoflagellate bloom taxa (vegetation) along an onshore-offshore gradient of decreasing nutrients, reduced mixing and deep-end euphotic zone (Smayda and Reynolds in prep.)

• Type I (= Gymnodinioids)
<i>Gymnodinium</i> spp., <i>Gyrodinium instriatum</i> , <i>Katodinium rotundatum</i>
• Type II (= Peridinioids / Prorocentroids)
<i>Heterocapsa triquetra</i> , <i>Scrippsiella trochoidea</i> , <i>Prorocentrum micans</i> , <i>Prorocentrum minimum</i>
• Type III (= Ceratians)
<i>Ceratium tripos</i> , <i>Ceratium fusus</i> , <i>Ceratium lineatum</i>
• Type IV (= Frontal Zone Taxa)
<i>Gymnodinium mikimotoi</i> , <i>Alexandrium tamarense</i>
• Type V (= Upwelling Relaxation Taxa)
<i>Gymnodinium catenatum</i> , <i>Lingulodinium polyedrum</i>
• Type VI (= Coastal Current Entrained Taxa)
<i>Gymnodinium breve</i> , <i>Ceratium</i> spp., <i>Pyrodinium bahamense</i> var. <i>compressum</i>
• Type VII (= Dinophysoids)
<i>Dinophysis acuta</i> , <i>Dinophysis acuminata</i>
• Type VIII (= Tropical Oceanic Flora)
<i>Amphisolenia</i> , <i>Histioneis</i> , <i>Ornithocercus</i> , <i>Ceratium</i> spp.
• Type IX (= Tropical Shade Flora)
<i>Pyrocystis noctiluca</i> , <i>Pyrocystis pyriformis</i>

Smayda and Reynolds life-form model

Smayda and Reynolds (in press.) reject two basic premises of the Mandala: that all dinoflagellate blooms cluster into a single category, and bloom species' selection follows an *r*- v. *K*-pathway. Nine distinct habitat types in which dinoflagellates bloom – each type characterized by a more or less specific bloom (vegetation) assemblage – and three basic life-form strategies (C, S and R) were recognized. Within each of the latter, *r*- v. *K*-species occur. These nine habitat and associated life-form types ordinate on a habitat-template along onshore-offshore gradients of decreasing nutrient, reduced mixing and deepened euphotic zone (= diminished irradiance – Fig. 4, Table VI). In relatively shallow, highly nutrient-enriched, nearshore waters, small gymnodinioid species tend to predominate (Type I, Table VI). In habitats of lower, but still elevated nutrient levels, peridinioids and prorocentroids predominate (Type II), whereas ceratians dominate Type III blooms in more open coastal waters. The "mixing-drift" adapted group, consisting of three habitat/bloom types, is of special interest to the present analysis. "Mixing-drift" species are adapted to the increased velocity streamlines associated with frontal zones (Type IV), they tolerate entrainment within coastal currents (Type VI) or exposure to the

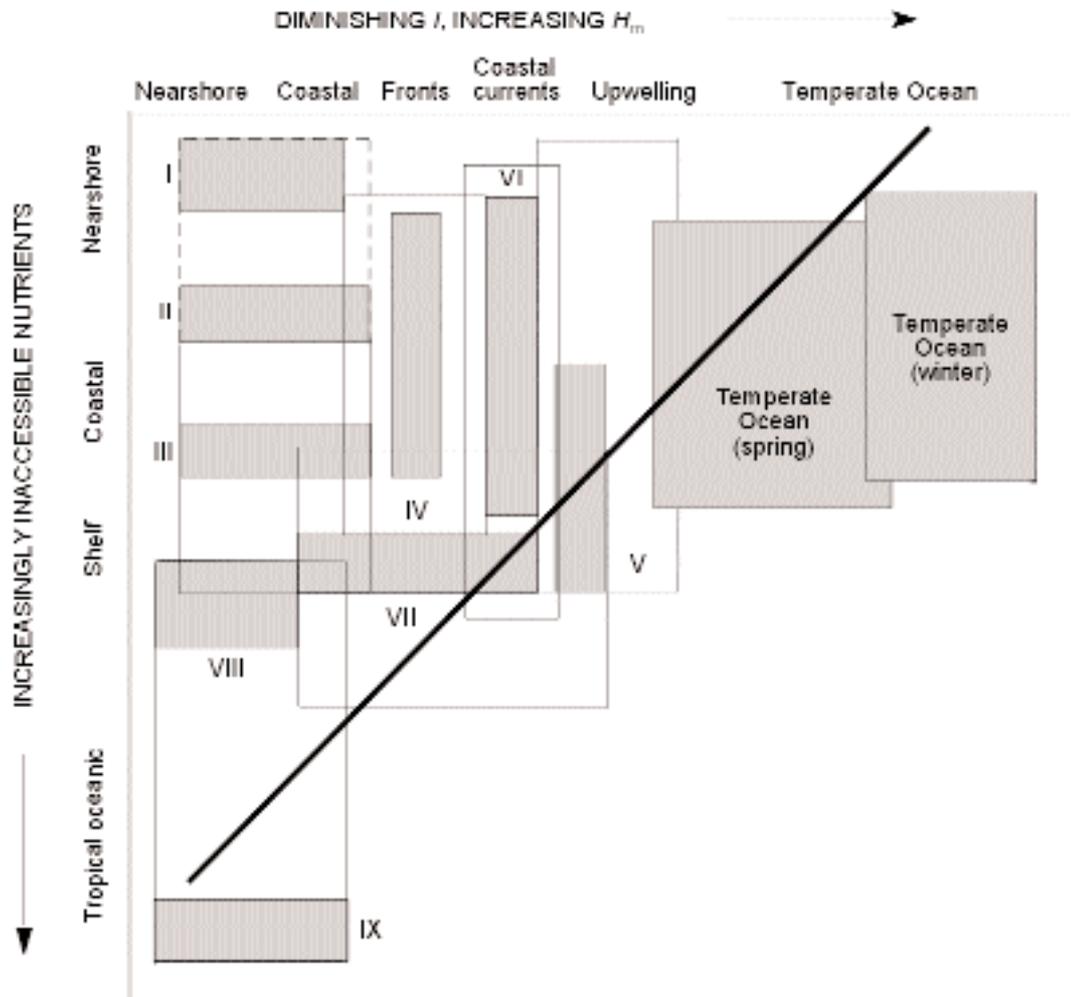


Fig. 4: Schematic matrix of pelagic marine habitats along an onshore-offshore gradient separating deep-mixed and well-stratified, but nutrient-deficient, systems. H_m represents depth of mixed layer and I refers to irradiance level received by cells within water column. Overlap of types within the habitat-template schema does not always imply their contiguity. Examples of dinoflagellate life-forms associated with the habitats designated by Roman numeral are given in Table VI. The diagonal approximates to Margalef's main successional sequence (Margalef *et al.* 1979) shown in Figure 2. (From Smayda and Reynolds in prep.)

dampened, but still high vertical mixing coefficients that accompany upwelling relaxations (Type V). The ecological space of Types IV–VI habitats is intermediate between the energy-limited, temperate winter-spring bloom period (favoured by diatoms) and habitat Types I–III and VII–IX, characterized by greater stratification and increased nutrient control under energy-replete conditions (Fig. 4).

Representative “mixing-drift” species include

Alexandrium tamarense (= *excavatum*, Type IV species), known for its frontal zone blooms in the Argentine Sea (Carreto *et al.* 1985, 1993), and *Gyrodinium aureolum* (= *Gymnodinium mikimotoi*), which blooms along frontal zones within the English Channel, North Sea, Skagerrak and Gulf of St Lawrence (Le Fèvre 1986, Holligan 1987, Dahl and Tangen 1993, Blasco *et al.* 1996). Highly adapted for entrainment and dispersal within coastal currents,

G. mikimotoi has spread rapidly throughout the North Sea and contiguous waters (Lindahl 1986), achieving great abundance since first recorded in the 1960s (Dahl and Tangen 1993). The toxic species, *A. tamarense* (Franks and Anderson 1992) and *P. bahamense* var. *compressum* (Seliger 1993), are notable Type VI dinoflagellates that survive entrainment and dispersal within coastal currents. The Type VI ichthyotoxic, *Gymnodinium breve*, is dispersed by the Gulf Stream from its "natural" habitat in the Gulf of Mexico (Tester *et al.* 1991). Although *G. breve* differs considerably from other Type VI species in certain autecological traits, its tolerance of shear/stress forces during coastal current entrainment is evident. It may be a relict from ancient conditions in the Gulf of Mexico, when upwelling was more common (Emslie and Morgan 1994). *L. polyedrum* (Blasco 1977) and *G. catenatum* (Round 1967, Fraga *et al.* 1988, Figueiras *et al.* 1994) are prominent "mixing-drift" dinoflagellates that survive upwelling events, and bloom during intermittent upwelling relaxations (Type V). Figueiras *et al.* (1994) concluded that a critical determinant of Type V blooms is whether the species' growth rate exceeds the ratio of upwelling velocity to depth of the stratified water layer.

"Mixing-drift"-adapted taxa, like dinoflagellates, generally are vulnerable to turbulence, which, if intense, can inhibit their growth, e.g. *A. excavatum* and *L. polyedrum* (White 1976, Carreto *et al.* 1986, Thomas and Gibson 1990). Future data may warrant recombination of the three distinct "mixing-drift"-type assemblages presently recognized into a single type. Taxa assigned to a specific type are not necessarily restricted to that particular habitat. Type VI *A. tamarense* and *P. bahamense* var. *compressum* also flourish in nutrient-enriched habitats, and *A. tamarense* can survive in frontal zones (Carreto *et al.* 1985, 1993). *G. catenatum*, a conspicuous Type V (upwelling relaxation) species, blooms in a shallow Tasmanian embayment where there is no upwelling. Its blooms there correlate with river runoff events in association with reductions in wind intensity (Hallegraeff *et al.* 1995).

Ordination of the life-form types on the habitat-template (Fig. 4, Table VI) suggests dinoflagellates have variable strategies consistent with the C-S-R strategies recognized among freshwater phytoplankton species (Reynolds 1984, 1988, 1995, Smayda and Reynolds in press). (Some, particularly Type III ceratium species, show intermediate C-S-R characters – Smayda and Reynolds in press). C-species are primarily *invasive* species, which often predominate following onset of elevated nutrient conditions, i.e. in chemically disturbed water bodies. Type I and II species are typically *invasive* competitors. Generally smaller than R- and S-species, C-species have faster growth rates, achieve greater abundance and, when toxic, are primarily

ichthyotoxic. S-species are primarily *acquisitive* species that are able to deal with the stress of low nutrient availability; they predominate among life-form Types VII, VIII and IX (Table VI). Typically very large and often highly ornamented, they are capable of maintaining depth through motility alone, or in combination with auto-regulated buoyancy (e.g. *Noctiluca*, *Pyrocystis*). Typically *K*-selected, they achieve modest, but persistent abundance, often possess endosymbionts, or supplement their photo-autotrophy by mixotrophy.

R-species occur in physically disturbed water masses. The "mixing-drift"-adapted species (Types IV–VI) are clearly disturbance-tolerant R-species. Primarily *attuning* or *acclimating* strategists, these *ruderal* species tolerate, or depend upon, entrainment within actively mixed or circulating water layers. They are pre-adapted to withstand shear/stress effects, and are anticipated to have slightly faster growth rates than other dinoflagellates (exclusive of Types I and II) to counterbalance wind-induced washout. Their light-harvesting pigment antennae, cellular shape, or form achieved through chain formation, enable their growth to become light-saturated at lower aggregate light levels than other phytoplankton types. They are generally characterized by strong phototactic capability, chain formation, a perennating stage in their life cycle, marked behavioural and auto-aggregative ability, and production of toxins and/or inducing mortality. The auto-regulated behaviour of toxic *G. catenatum* in Spanish upwelling rias is a particularly elegant example of the motility-based behaviour of R-strategists (Fraga *et al.* 1989). It forms chains of up to 64 cells and 2 mm long (Blackburn *et al.* 1989), which increase its swimming speed (Fraga *et al.* 1989). This increased motility facilitates both retention within the habitat and its diel nutrient-retrieval migrations into the underlying nutrient reservoir, a behaviour favourable to its blooms during upwelling relaxations (Fraga *et al.* 1989, Fraga and Bakun 1993). During nutrient deficiency, it reduces its chain size, ceases to swim, and the stationary phase cells then hang vertically within the water column (Blackburn *et al.* 1989).

Ecological space model of red tides in coastal upwelling systems

The Smayda and Reynolds life-form model, based on field evidence (Fig. 4), shows that dinoflagellate blooms are not restricted to nutrient-high, irradiance-low turbulence ecologies (Figs 1, 2, 3a). Diverse combinations of mixing – nutrients – irradiance support red tides: dinoflagellates exploit habitat diversity. They successfully grow in at least nine different

habitat types, under conditions ranging from high to low nutrient availability, and from highly stratified conditions to relatively intense mixing. The three versions of the Mandala examined call for C-strategists (Figs 1, 2, 3a), but *ruderal* strategists (R-species) are primarily responsible for coastal upwelling system red tides. Restriction of red tide development to the assigned ecological space ("red tide zone") in the three versions of the Mandala does not represent the diverse conditions under which red tides develop in upwelling regions: their nearshore, offshore (shelf, frontal system) and upwelling relaxation blooms. Whereas the Mandala and its versions may adequately account for red tides in non-upwelling coastal systems, those blooms may not always be successional equivalent to those developing in upwelling systems. The Mandala and its Bowman *et al.* and Pingree variations depict red tides as temporary deflections branching off the main successional sequence (Figs 1, 2, 3a). Red tide occurrences in upwelling systems, however, are not necessarily deflections, but part of the main sequence. An alternative "main sequence" might better characterize bloom succession in coastal upwelling systems (see Fig. 3b). The characteristic diatom blooms induced by upwelling are often interrupted during upwelling relaxations and temporarily replaced by dinoflagellate bloom-species, which may or may not bloom. Thereafter, diatoms bloom again in response to upwelling spin-up (see Walsh *et al.* 1974, 1977, Blasco 1977). In fact, both sequences (Fig. 3) might characterize coastal upwelling systems, the route taken partly dependent on the duration of the upwelling relaxation periods. Where (when) upwelling relaxations do not lead to red tide blooms, the main sequence depicted may apply. When (where) upwelling relaxations lead to red tides (which are reversible with diatom blooms), the alternative pathway (Fig. 3b) might apply. Exclusive of, and during the sequence of alternating diatom and dinoflagellate blooms, a distinct diatom species succession can occur and exhibit similar patterns from year to year (Smayda 1966). Community changes during offshore plume advections of upwelled water developing in response to nutrient utilization also lead to a sequence of diatoms \Rightarrow mixed diatom + dinoflagellate community \Rightarrow red tide blooms (at fronts subducting the plumes).

It is suggested here that there is a gradient in ecological space along which red tides develop, rather than at the fixed conditions of the Mandala (Figs 1, 2, 3a), and that this gradient is positioned in the region intermediate between the diatom and red tide bloom sites depicted in the Pingree *S-kh* diagram (Fig. 3). This region corresponds roughly to that lying between $S = 1.5$ and 3. Along this gradient, the

importance of nutrients relative to diffusion (stratification) in promoting red tides varies, and biophysical impairment of cells and advective washout can diminish population growth and become more significant than nutrients. At lower S values, at which upwelling system red tides cluster, strength of diffusion, both vertical and horizontal, becomes more important than the associated nutrient flux. At higher S values, at which non-upwelling, coastal red tides cluster, an influx of exogenous nutrients above the stratification-dampened, diffusive delivery becomes more important. In non-upwelling systems, anthropogenic nutrient sources are often available; in upwelling systems, remineralization in combination with unknown factors might provide the bloom stimulus. Tentatively, it is suggested that blooms of life-form Types I–III occur primarily at $S > 2$, and blooms of "mixing-drift" Types IV–VI at $S < 2$ (Figs 3, 4; Table VI). This qualitative re-definition of the ecological space supportive of red tide blooms and their successional occurrences (Fig. 3b) is a first approach towards more adequate accommodation of coastal upwelling system red tides within the Mandala (Figs 1, 2, 3b).

TURBULENCE AND DINOFLAGELLATE BEHAVIOUR

Turbulent kinetic energy introduced into the water mass by prevailing winds causes vertical mixing and turbulence (Mann and Lazier 1996). The energy of this turbulent motion, the intensity of which pulsates with variations in wind stress, is continuously transferred from large to ever smaller eddies, which progressively and ultimately completely dissipate. The rate of turbulent-energy dissipation (ϵ ; $W \cdot kg^{-1}$) during this energy cascade is the twisting, or shearing force, in the turbulence, the feature that makes turbulence so biophysically threatening to phytoplankton. With increasing wind stress, the size of the smallest eddies, i.e. Kolmogorov length scale (λ_1), formed during the eddy cascade decreases. A decrease in eddy size is accompanied by increases in the velocity gradient and the rate of strain (Fig. 5, Mann and Lazier 1996, Estrada and Berdalet 1998). The potential for negative effects on the exposed phytoplankton increases with the degree of mismatch between the size-shape characteristics of cells captured by eddies and the scale and velocity of the eddies (see Margalef 1978b). At wind speeds of between 20 and 5 $m \cdot s^{-1}$, Kolmogorov length scales range from 600 to 1 600 μm (Fig. 5), i.e. they overlap dinoflagellate size-classes (Table I). Cells (life-forms, colonies) whose maximum linear dimensions exceed local eddy widths are more likely

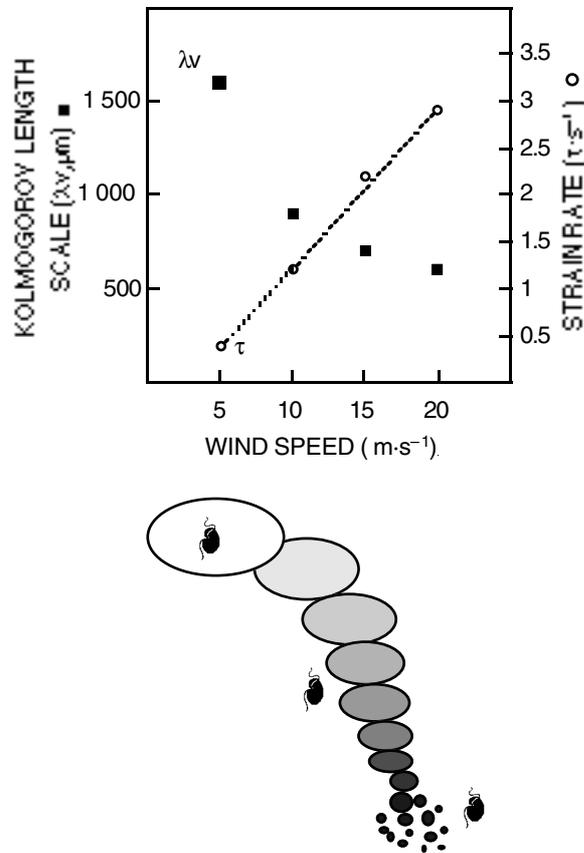


Fig. 5: Relationship between wind speed, Kolmogorov length scale and associated strain rates (data from Estrada and Berdalet 1998). Illustrated qualitatively is the potential of a flagellate of fixed size to be entrained within the wind-generated eddies of progressively decreasing length scales. See text for further discussion

to be damaged or selected against than smaller cells captured and entrained within larger eddies. Average longshore wind speeds in the Peruvian (15°S), Baja California and North-West African upwelling systems ranged from 4.6 to 5.5 m·s⁻¹ (Walsh 1976). Upwelling wind speeds along the Peruvian coast vary from 3.2 to 4.9 m·s⁻¹ (Guillén and Calienes 1981) and reached 7.0 m·s⁻¹ off North-West Africa during intense events (Codispoti 1981). These upwelling-inducing wind speeds are at the lower end of the Kolmogorov length scale-wind speed relationship (Fig. 5). The anticipated minimal Kolmogorov eddy size and associated rates of strain induced by these wind speeds seemingly would not select against many of the red tide species

found in upwelling regions (Table I). Many have a cell diameter of c. 50 μm, or less, suggesting that they would become entrained within (and survive) the micro-eddy cascade generated at wind speeds from c. 5 to 20 m·s⁻¹ (Table I). In contrast, large ceratians would be selected against at wind speeds >10 m·s⁻¹. Wind speeds are often >20 m·s⁻¹ in the Benguela (Bailey and Chapman 1991), setting up a turbulence regime expected to have strong selective pressure against dinoflagellate blooms (Fig. 5).

The ability of a dinoflagellate species to survive the upwelling turbulence spectrum, and to withstand the sheer/stress during entrainment within coastal currents, influences its potential to provide seed stock for red tide events during intermittent upwelling relaxations and the post-upwelling season. Because many red tide species lack resting stages, their recruitment from seabed seed banks is precluded. For such holoplanktonic species, pelagic survivors of the intense upwelling periods must seed such blooms, following advection into the bloom area (Pitcher and Boyd 1996, Pitcher *et al.* 1998). Under laboratory conditions, exposure to turbulence can inhibit dinoflagellate growth rate and, if sustained or intensified, lead to mortality (White 1976, Pollinger and Zemel 1981), disrupt the cellular clock, mitotic cycle, and alter nucleic acid concentrations (Pollinger and Zemel 1981, Berdalet and Estrada 1993). Motile cells of *L. polyedrum* that are exposed to high shear lose their longitudinal flagellum and ability to swim forward; such cells spin in place (Thomas and Gibson 1990). High shear rates can also induce cellular disintegration (Berdalet and Estrada 1993). Turbulence, at least in laboratory culture, can therefore negatively influence dinoflagellate survival and blooming by three mechanisms; physical damage, physiological impairment and behavioural modification. In the latter case, loss of flagella and increased turbulence can disrupt cellular swarming (= aggregation), phototaxis and diel vertical migration, i.e. behaviour presumably beneficial to bloom formation. Despite these responses, there is little definitive evidence that turbulence *in situ* selects for blooms of specific species. Boyd (1982) reported that mean shear speeds of 1.25 cm·s⁻¹·m⁻¹ between 2 and 10 m deep decreased to 0.8 cm·s⁻¹·m⁻¹ in the 10–20 m stratum. A patch of “particles” 2 m thick and centred 10 m deep would stretch horizontally from 10 m to hundreds of metres along axis of shear in a period of hours. Thomas and Gibson’s (1990) prediction that near-surface blooms of the upwelling species *L. polyedrum* become inhibited at wind speeds >2.1 m·s⁻¹ awaits confirmation. This intensity suggests an eddy structure and rate of strain (Fig. 4) below that encountered during its red tide occurrences in the Californian upwelling system (Table V); turbu-

lence induced by winds $>3.5 \text{ m}\cdot\text{s}^{-1}$ disrupted dinoflagellate blooms in the Dead Sea (Pollinger and Zemmel 1981). The effects of turbulence on dinoflagellate growth, including the upwelling species, *G. sanguineum*, *P. micans* and *S. trochoidea*, have been evaluated experimentally (Estrada and Berdalet 1998), but the mixed results and experimental procedures compromise application to natural populations. Dinoflagellates vary inter-specifically in their vulnerability to turbulent shear and strain (Berdalet and Estrada 1993); this may influence selection of bloom species.

SPATIAL AND TEMPORAL VARIABILITY, VERTICAL WATER MOTION, FRONTAL ZONES AND DINOFLAGELLATE SWIMMING BEHAVIOUR

Physical aspects

Coastal upwelling systems are not simple on-off (upwelling-non-upwelling) systems, spatially uniform, or continuous. Wind-induced structuring creates an extraordinarily complex upwelling habitat, to which phytoplankton must adapt. Upwelling is accompanied by turbulence, divergences, plumes, downwelling at frontal zones, and longshore and onshore-offshore currents whose velocities and spatial heterogeneity vary. These sub-habitats are neither regionally isolated nor form and persist independently of each other. Their formation, spatial and temporal behaviour, and dynamics are coupled to each other, and inter-linked over considerable spatial distances. The Benguela Current is about 200 km wide and 1 600 km long; the Peru Current is 3 200 km long (Hart and Currie 1960, Walker 1986), and tongues of upwelled water can extend 110–200 km offshore (Schuette and Schrader 1981). Fronts develop in upwelling regions and can attain vast spatial scales. The Benguela shelf-break front can be c. 10–20 km wide, with blooms concentrated in fronts 10–25 km offshore (Summerhayes *et al.* 1995). A Chilean frontal system 100 km offshore supported a *P. micans* bloom (Avaria 1979), and the width of a 300-km long patch of *L. polyedrum* in the California Current system ranged from a few km to 40 km (Lasker and Zweifel 1978). Most remarkable, a frontal zone bloom of *G. sanguineum* (up to 280 mgChl·m⁻³) stretched 2 000 km within the Peru Current (Lasker and Zweifel 1978, Packard *et al.* 1978b). Thus, where upwelling occurs (no matter its strength), frontal systems, and longshore and across-shelf currents also develop (Pitcher and Boyd 1996). These different sub-habitats, among which phytoplankton is exchanged, have dif-

Table VII: Intermittent physical processes contributing to vertical water motion, and depths and time constants of impact (after Kamykowski *et al.* 1988)

Process	Depth estimate (m)	Time estimate
Double diffusion	< 1	Minutes
Turbulent motion	0.5–20	Minutes–days
Langmuir cells	2–10	Minutes
Upwelling or subduction*	3.6–36	~1 day
Frontal circulation	1–50	1–10 days

*Ekman divergence/convergence

fering capacities to support cellular and population growth (Barlow 1982b, Barber and Ryther 1969), and to serve as refugia for seed stock.

The life cycles of bloom species must accommodate this spatial heterogeneity and three temporal event scales (seasonal, intermediate and diel) to survive and bloom in coastal upwelling systems. Seasonal and intermediate event time-scales differ among upwelling systems (Walsh *et al.* 1977), as does the degree of tolerance needed to withstand turbulence and niche disruptions. The annual upwelling cycle may be more or less continuous, as in Peruvian upwelling, or show marked seasonality, as in the Gulf of Panama where a prolonged rainy season follows the four-month upwelling period (Smayda 1966). Once in progress, upwelling is neither continuous nor equally intense. Periodic interruptions (upwelling relaxations) of variable duration result from temporary reductions in upwelling-inducing winds, which then resurge and lead to renewed upwelling (Estrada and Blasco 1979, Walsh *et al.* 1974, 1977). These intermediate events have periods ranging from days to several weeks. In the North-West African system, relaxation events occurred over a two-month period, producing upwelling (U)/downwelling (D) cycles averaging 12 days each (Codispoti 1981). Blasco *et al.* (1981) reported 7–10 day periods. In the southern Benguela, three upwelling-downwelling cycles occurred over a 24-day period, and 10-day (c. 7U:3D) and 20-day (2U:18D) cycles during the summer and winter seasons respectively were reported for this system (Branch and Griffiths 1988). In St Helena Bay, South Africa, complete upwelling cycles averaged 15–20 days (Mitchell-Innes and Walker 1991). In the Gulf of Cariaco, Venezuela, upwelling relaxations lasted 6–8 weeks (Ferraz-Reyes *et al.* 1979). Species able to exploit the opportunistic growth “windows” that open during upwelling relaxation periods seemingly tolerate turbulence, become available as seed stock (a stochastic feature) and are capable of fairly rapid growth.

Diel changes in the instantaneous rates of vertical

Table VIII: Some upwelling rates and near-surface longshore current speeds in coastal upwelling systems

Region	m·day ⁻¹	cm·s ⁻¹	km·day ⁻¹	Source
<i>Upwelling</i>				
Baja California	10	1.2×10 ⁻²		4
Baja California	22	2.5×10 ⁻²		5
Oregon	17	2.0×10 ⁻²		1
Peru (5°S)	1	1.3×10 ⁻³		1
Peru (8°S)	0.8	0.9×10 ⁻³		1
Peru (12°S)	2	2.2×10 ⁻³		1
Peru (15°S)	3	3.0×10 ⁻³		1
Peru (15°S)	36	4.1×10 ⁻²		8
North-West Africa	786	1.0×10 ⁻¹		1
Benguela	?			
<i>Longshore currents</i>				
Baja California		15–30	13–26	4
Benguela		7–50	6–43	2,3,7,10
North-West Africa		20–32	17–28	9
Oregon		35	30	9
Peru (5°S)		15–45	13–39	6
Peru (15°S)		10–20	9–18	6,8
<i>Across-shelf currents</i>				
Benguela: onshore		5	4	10
Oregon: onshore		5	4	9
Oregon: offshore		10	9	9
Baja California: onshore		5.2	5	5
Baja California: offshore		8–25	7–22	5
Peru: onshore (15°S)		5	4	8

(1) Guillén and Calienes 1981; (2) Shannon 1985; (3) Verheye *et al.* 1991; (4) Walsh *et al.* 1974; (5) Walsh *et al.* 1977; (6) Zuta *et al.* 1978; (7) Summerhayes *et al.* 1995; (8) Brink *et al.* 1981; (9) Barber and Smith 1981; (10) Pitcher *et al.* 1998

water motion pose other problems to dinoflagellates, which, biophysically and through growth in micro-structural refugia, must tolerate prolonged exposure to turbulence, if they are to survive and grow in upwelling systems. This is particularly the case for holoplanktonic species. Flagellates use swimming (Smayda 1997b) in vertical depth-keeping, to undertake nutrient-retrieval migrations, to achieve pycnocline blooms (or swarms) and to exploit the nutrient resource gradient and other habitat micro-structural features. Two important determinants of whether a given dinoflagellate species will bloom (and when) in coastal upwelling systems, irrespective of the temporal event scale, are the degree of vertical, micro-habitat structural differentiation developing during mixing, and whether the strength of turbulence allows dinoflagellates to utilize swimming to exploit this micro-structure. Six intermittent physical processes contribute to the vertical motion with which phytoplankters must contend (Table VII), and whose scales of vertical excursions range from centimetres to metres and last from minutes to days. The increased depth and duration of intermittent vertical mixing associated with upwelling relative to the other vertical motions are evident.

Representative coastal upwelling rates and longshore and across-shelf current speeds are given in Table VIII. Upwelling rates range from about 1 to 40 m·day⁻¹. The wide spread in rates reflects regional differences (as in the Peruvian system) and natural variability at the time and site of measurement. Longshore currents are generally much faster than across-shelf currents, whose direction and velocity vary partly in response to the intensity of winds favouring upwelling. Across-shelf flow is particularly important in bloom dynamics (Pitcher and Boyd 1996, Pitcher *et al.* 1998) and in the formation of fronts (Franks 1992). Fronts are capable of considerable onshore-offshore movements and serve multiple roles (Sournia 1994): as barriers to offshore displacement of advected populations, as concentration sites, as refugia, as sources of seed stock and as ecotones. Fronts are also zones of intensified motion and mixing whose vertical velocities are difficult to measure; maximal speeds of c. 200 μm·s⁻¹ (= 17.3 m·day⁻¹) have been theorized (see Franks 1992). The intensity of turbulence and rate of vertical eddy diffusion increase along the frontal gradients, from the stratified to the mixed side (Mann and Lazier 1996). The coefficient of eddy dif-

Table IX: Mean euphotic zone and mixed layer depths at four major upwelling centres along the coast of Peru (modified from Guillén and Calienes 1981)

Region	Euphotic zone (EZ, m)	Mixed layer (ML, m)	EZ:ML
Paita (5°S)	22.3	13.3	1.68
Chimbote (8°S)	19.1	10.8	1.76
Callao (12°S)	18.7	14.5	1.29
San Juan (15°S)	29.4	15.3	1.92

fusivity reached $190 \text{ cm}^2\text{s}^{-1}$ during an upwelling event in the southern Benguela (Boyd 1982). A mean coefficient of eddy diffusivity of $0.4 \text{ cm}^2\text{s}^{-1}$ has been suggested as the transition state between diatom and dinoflagellate predominance (Margalef 1978b), diatoms occurring in regions of high turbulence ($2\text{--}100 \text{ cm}^2\text{s}^{-1}$) and dinoflagellates at lower turbulence ($0.02\text{--}1 \text{ cm}^2\text{s}^{-1}$). Dinoflagellates commonly bloom along fronts, despite sharp horizontal and vertical velocity gradients (Carreto *et al.* 1986, Pingree *et al.* 1978, Pitcher and Boyd 1996, Pitcher *et al.* 1998). Velocity features, variable widths and offshore distances of fronts cause appreciable vertical and horizontal patchiness in dinoflagellate occurrences (Franks 1992).

In summary, the physics of coastal upwelling systems induces episodic onshore-offshore displacements of the primary growth habitats (fronts); episodically destroys and restores vertical microhabitats (= thin-layers); leads to fluctuations in turbulence and upwelling velocities, which impact cellular and population growth; and affects nutrient pulsing and exposure to grazer patches. Given this amplified spatial and temporal heterogeneity, some traditional concepts of phytoplankton ecology may not completely apply to red tide bloom-taxa in coastal upwelling regions. These include distinctions between indigenous and allochthonous species; the notion that seabed seed banks are the primary source of seed stock; the blurred role of mixing v. stratification in providing "critical depth" criteria essential to bloom and patch formation, given the interruptions in upwelling intensity and associated delivery of nutrients. Dinoflagellates forming red tides in upwelling systems confront continuous habitat (niche) destruction on a scale unlike that in other habitats. This suggests their need for multiple strategies to exploit the coupled physical and velocity structure of upwelling systems to achieve blooms. The mean euphotic zone depth during upwelling in the Peruvian system is 4–14 m deeper than the mixed-layer depth (Table IX). This irradiance-mixing feature should allow formation of a vertical micro-

Table X: Swimming speeds of dinoflagellates and other motile taxa that form red tides in upwelling or frontal systems

Species	Swimming speed ($\mu\text{m}\text{s}^{-1}$)	Source
<i>Alexandrium affine</i> *	410	5
<i>Ceratium furca</i>	278	9
<i>C. furca</i>	222	9
<i>C. furca</i>	206	4
<i>C. furca</i> (chain)	167	9
<i>Dinophysis acuta</i>	500	9
<i>Gyrodinium aureolum</i>	230	10
<i>Gonyaulax polygramma</i>	500	9
<i>Gymnodinium catenatum</i> *	247	5
<i>Gymnodinium sanguineum</i>	300	3
<i>G. sanguineum</i>	278	11
<i>G. sanguineum</i>	135	8
<i>G. sanguineum</i>	115	7
<i>G. sanguineum</i> "nelsoni"	32	7
<i>Heterosigma akashiwo</i>	140	10
<i>Lingulodinium polyedrum</i>	400	6
<i>L. polyedrum</i>	355	7
<i>L. polyedrum</i>	278	9
<i>L. polyedrum</i>	258	8
<i>Mesodinium rubrum</i>	2 217	1
<i>Prorocentrum micans</i>	236	4
<i>P. micans</i>	133	7
<i>P. micans</i>	100	2
<i>P. micans</i>	87	7
<i>Protoceratium reticulatum</i>	362	7
<i>Scrippsiella trochoidea</i>	153	8
<i>S. trochoidea</i>	82	2
<i>S. trochoidea</i>	69	9

* Single cells;

(1) Barber and Smith 1981; (2) Bauerfeind *et al.* 1986; (3) Cullen and Horrigan 1981; (4) Edler and Olsson 1985; (5) Fraga *et al.* 1989; (6) Jeong 1994; (7) Kamykowski *et al.* 1989; (8) Kamykowski *et al.* 1992; (9) Levandowsky and Kaneta 1987; (10) Thronsen 1973; (11) Blasco 1979

habitat structure favourable to growth below the turbulent upper layer, if accessed. Do (can) dinoflagellates when entrained into zones of high instantaneous rates of vertical water velocity undertake escape reactions by swimming down into, and remaining within, the nutrient-rich reservoir below the mixed upper layer? Photosynthetically available light in this stratum would enhance survival. Migration in quest of turbulence-avoidance would differ operationally from nutrient-gathering migrations.

Swimming behaviour of dinoflagellates

Vertical mixing and turbulence influence the horizontal and vertical distributions of the entrained species. Cells able to autoregulate their position in the water column would be better able to optimize

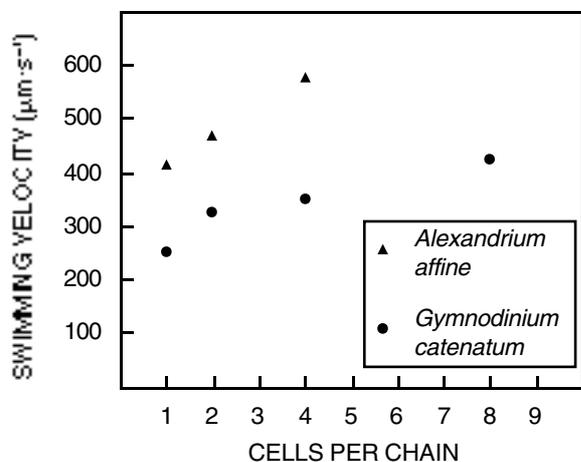


Fig. 6: Effect of colony size on swimming speed of *Alexandrium affine* and *Gymnodinium catenatum* (data from Fraga *et al.* 1989)

their metabolism and more closely achieve maximum rates of potential production under ambient conditions than physically translocated cells (Kamykowski and Yamazaki 1997). Are dinoflagellates able to autoregulate in response to upwelling, its relaxations and frontal zone dynamics or, more typically, are they controlled by the existing physical field, which determines their vertical distributions and disperses them into suboptimal habitats? At what upwelling and downwelling rates will dinoflagellate swimming speeds be compromised to the detriment of their behavioural migrations, depth-keeping, retention within the euphotic zone, and accumulation into "thin-layers"? Red tide taxa vary intrinsically in the adequacy of their motility-based behaviour to offset physical displacement induced by mixing, advection and turbulence in upwelling systems and frontal zones (Table X). *Noctiluca* is positively buoyant; *M. rubrum* is extremely fast ($2\,217\ \mu\text{m}\cdot\text{s}^{-1}$, equivalent to a vertical ascent of $8\ \text{m}\cdot\text{h}^{-1}$); autotrophic dinoflagellates exhibit intermediate to sluggish swimming speeds, which range about 15-fold, from $410\ \mu\text{m}\cdot\text{s}^{-1}$ (single-celled *A. affine*) to $32\ \mu\text{m}\cdot\text{s}^{-1}$ (*G. sanguineum*). Swimming rates of individual species are variable rather than fixed, as for *G. sanguineum* and *P. micans* (Table X), because they are influenced by temperature, nutrients and irradiance (Kamykowski and Yamazaki 1997). Their velocities of ascent and descent also differ (Bauerfeind *et al.* 1986).

Most dinoflagellates occur as solitary cells, but at least four coastal upwelling species form chains: *A. affine*, *A. catenella*, *C. cf. polykrikoides* and *G. cate-*

natum. Grindley and Sapeika (1969) reported that *A. tamarense* (Walvis Bay, Namibia) and *A. catenella* (Elands Bay, South Africa) formed up to four-celled chains during blooms in upwelling-influenced systems. *G. catenatum* commonly co-occurs with other chain-forming species: *A. affine* (Spain), *P. bahamense* (Mexico), and the rudimentary chain-forming ceratians, *Ceratium tripos*, *C. furca* and *C. fusus* (Hallegraeff and Fraga 1998). *Alexandrium cohorticula*, *A. fraterculum* and *A. monilatum* also form chains, but their association with upwelling regions is unclear. Because swimming speeds increase with chain formation (Fraga *et al.* 1989), the limited ability of some dinoflagellates to form chains may help them to cope with upwelling system dynamics. Swimming speed of four-celled chains of *G. catenatum* nearly doubled from 247 to about $440\ \mu\text{m}\cdot\text{s}^{-1}$; for *A. affine*, the increase was about 50%, from 410 to $580\ \mu\text{m}\cdot\text{s}^{-1}$ (Fig. 6). [The apparent decrease in motility rate of *C. furca* chains (Table X) needs confirmation.] Fraga *et al.* (1989) interpreted the increased swimming speed of *G. catenatum* and *A. affine* chains as a motility-based adaptation for retention within the euphotic zone during downwelling, or local divergences. Field observations support this view: *G. catenatum* overcame downwelling velocities of c. $10\ \text{m}\cdot\text{day}^{-1}$ and remained within the euphotic zone (Figuieras *et al.* 1995). The increased swimming speeds of *G. catenatum* chains allow it to access deeper, nutrient-rich strata during upwelling relaxations in Spanish rias, and lead to its blooms (Fraga and Bakun 1993). The habitat preference of *P. bahamense*, a Type VI "drift-community" component (Fig. 4, Table IV) and prominent chain-former, is also seemingly enhanced by the increased speed expected to accompany its chain-formation.

Are dinoflagellates in upwelling regions more energetic swimmers than those in other habitats? This is examined in Figure 7, where the ratio of swimming to sinking velocities is used as an index of the relative ease of migrational return to preferred depth that a species will have following its vertical displacement by upwelling or downwelling streamlines. Since the velocities of ascent and descent differ for a given species (Bauerfeind *et al.* 1986), sinking rates add to descent rates, but subtract from ascent rates. This finer point can not be incorporated into the analysis. The sources of the depicted rates for the species shown are among those identified in Table X and also based on data in Smayda and Bienfang (1983). Where sinking rates were not found, they were calculated using the Kamykowski *et al.* (1992) equation:

$$V_i = -22.90 (S/V) + 7.50$$

where V_i is the sinking velocity ($\text{m}\cdot\text{day}^{-1}$) as a function of the cell surface area:cell volume ratio ($S/V\cdot\mu\text{m}^{-1}$).

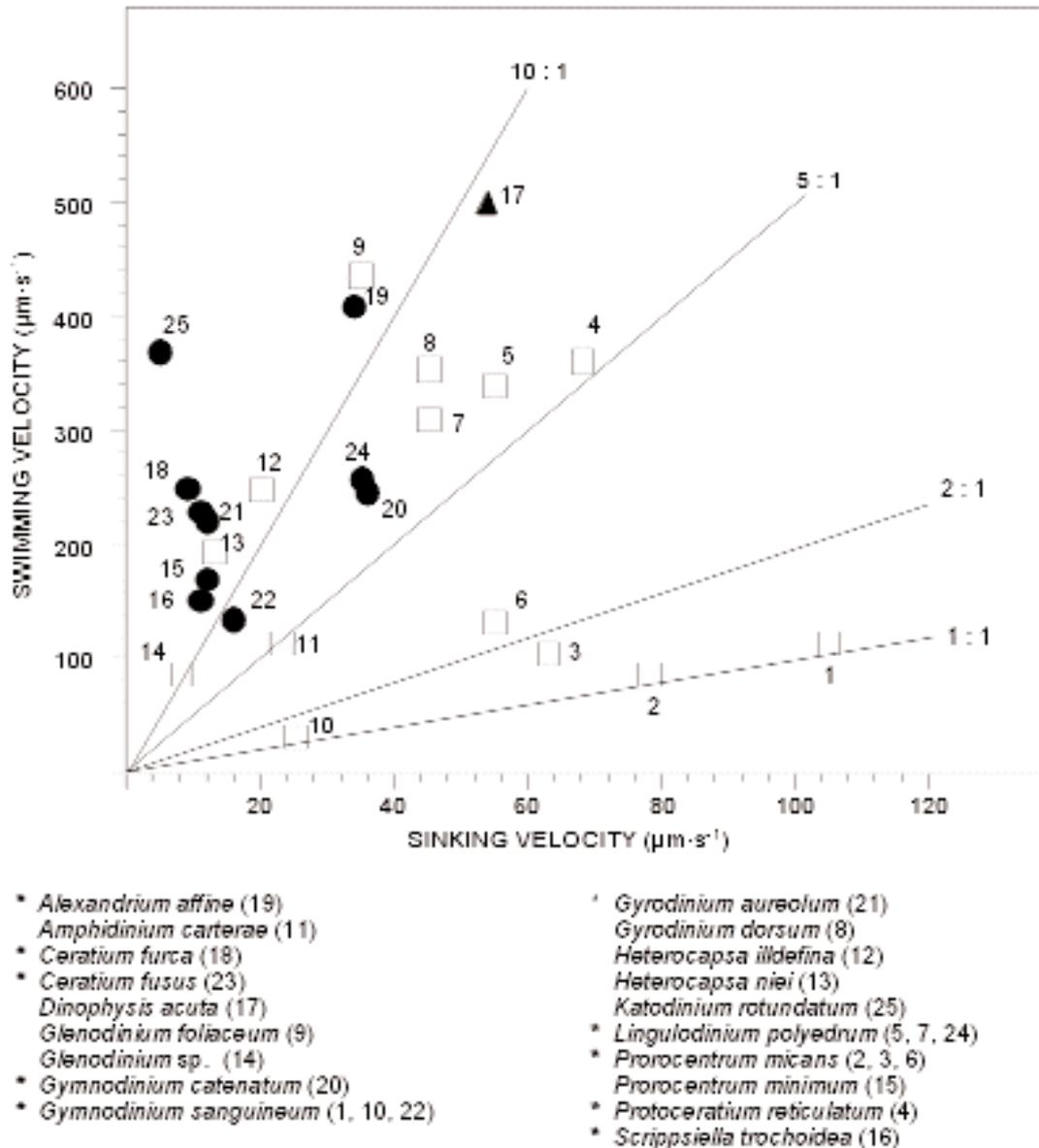


Fig. 7: Species-specific dinoflagellate swimming and sinking velocities, and their ratios. Open squares are data from Kamykowski *et al.* (1989); solid circles are newer data, as further explained in text. Species denoted by an asterisk produce red tides in upwelling regions and/or at fronts

S/V was calculated, where needed, from morphometric data available in taxonomic monographs dealing with the species in question.

Relative to sinking rates, both weak and strong swimmers occur among dinoflagellates, including

those producing red tides in upwelling regions (Fig. 7). *G. sanguineum*, a major bloom species in the Peruvian upwelling system, falls within the group having the lowest ratio of ascent to descent, c. 1:1. *G. sanguineum* can descend more readily than it can swim

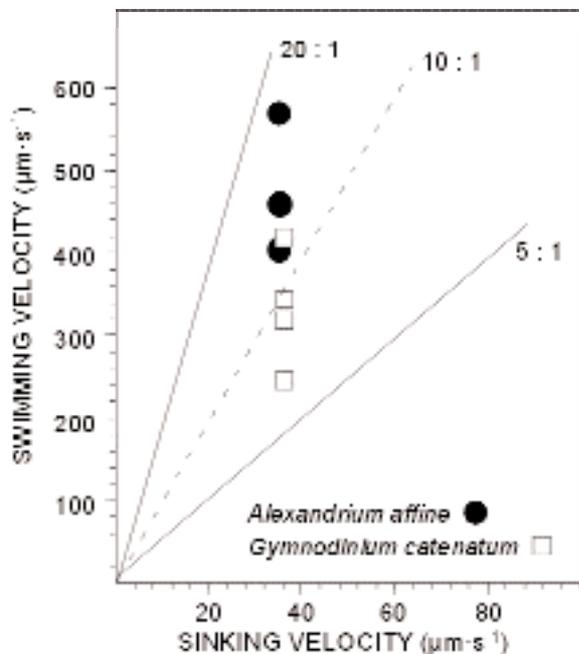


Fig. 8: Effect of colony size on the relationship between swimming and sinking velocities of *Alexandrium affine* and *Gymnodinium catenatum*. The progressively increasing swimming velocities depicted are for 1, 2 and 4-celled chains of *Alexandrium affine* and 1, 2, 4 and 8-celled chains of *Gymnodinium catenatum* respectively (data from Fraga *et al.* 1989)

upwards; *P. micans* shares this characteristic. *G. catenatum* (single cells) and *L. polyedrum* swim at rates about six times faster than they sink, revealing that they can readily ascend to overcome sinking. Many dinoflagellates have ratios of about 10:1. These include the relatively small species *P. minimum* and *Katodinium rotundatum*, which produce intense blooms in non-upwelling habitats, and the large, attenuate *C. fusus* and *C. furca*, which bloom in both upwelling regions and nutrient-enriched embayments. Smayda and Bienfang (1983) present related material on dinoflagellate swim:sink ratios. The importance of chain-formation in increasing swim:sink ratios is shown in Figure 8. For an eight-cell chain of *G. catenatum*, the ratio is nearly double that for solitary cells. The propulsion advantage that chain-formation confers is evident for *A. affine*: the ratio increases from about 12:1 for solitary cells to 17:1 for a four-cell chain. Chain formation clearly provides improved biophysical advantage to dinoflagellates seeking growth opportunities and vertical depth-keeping within physically

dynamic upwelling regions. Otherwise, red tide species that bloom in upwelling systems apparently do not have a unique swim:sink strategy compared to dinoflagellates generally. Both groups exhibit the wide range in ascent/descent capabilities characteristic of dinoflagellates collectively. Nonetheless, for a given upwelling or downwelling condition potentially supportive of dinoflagellate growth, some species would be more capable of survival than others during these conditions, if present or introduced into the perturbed water mass.

How do swimming speeds compare with the rates of vertical motion in coastal upwelling systems (Tables VIII, X)? In Figure 9, the swimming rates of 71 clones and species of dinoflagellates, other phytoplankton, and protoperidinin predators are compared to various field-based upwelling rates. The maximal frontal vertical motion of $17.3 \text{ m}\cdot\text{day}^{-1}$ expected (Franks 1992) is also shown in the figure. There is about a 25-fold range in swimming speeds, with maximal velocities *c.* $500 \mu\text{m}\cdot\text{s}^{-1}$. Protoperidinin grazers, as a group, tend to be fast swimmers and "naked" flagellates are generally slower than dinoflagellates. Thus, within the range of extreme stability and vertical mixing, there is a zone of vertical velocity rates at which, based on motility rates, dinoflagellates would survive and could bloom in coastal upwelling systems. Franks (1992) suggested that the maximal frontal zone speed of $200 \mu\text{m}\cdot\text{s}^{-1}$ is a threshold between strong and weak swimmers. Using this standard, both strong and weak swimming species form red tides in upwelling regions. Of the red tide dinoflagellates, the motility rate of 77% ($n = 13$) lies at or above $200 \mu\text{m}\cdot\text{s}^{-1}$, in contrast to only 15% ($n = 20$) of the other flagellates; 42% of all dinoflagellates ($n = 45$) exceeds this threshold. The conspicuous rarity of "naked" flagellate blooms in upwelling systems (Table I) was pointed out earlier.

These results reveal that dinoflagellate swimming speeds often potentially exceed vertical and horizontal water mass movements, even at the fairly high intensities representative of coastal upwelling and frontal zone systems. Biophysically, they may often escape the damaging effects of turbulence-induced shear through protective entrainment within Kolmogorov length-scale eddies (Fig. 5). At the population level, growth rates often exceed advective losses and lead to bloom events (Fig. 2, Kierstead and Slobodkin 1953). Dinoflagellate blooms are not restricted to stable, stratified water masses because of an inability to withstand higher velocity fields. Their motility rates suggest an ability to maintain populations during periods of turbulence, upwelling and downwelling in those habitats. If the tolerant species are then insignificant, other bloom control factors may then be

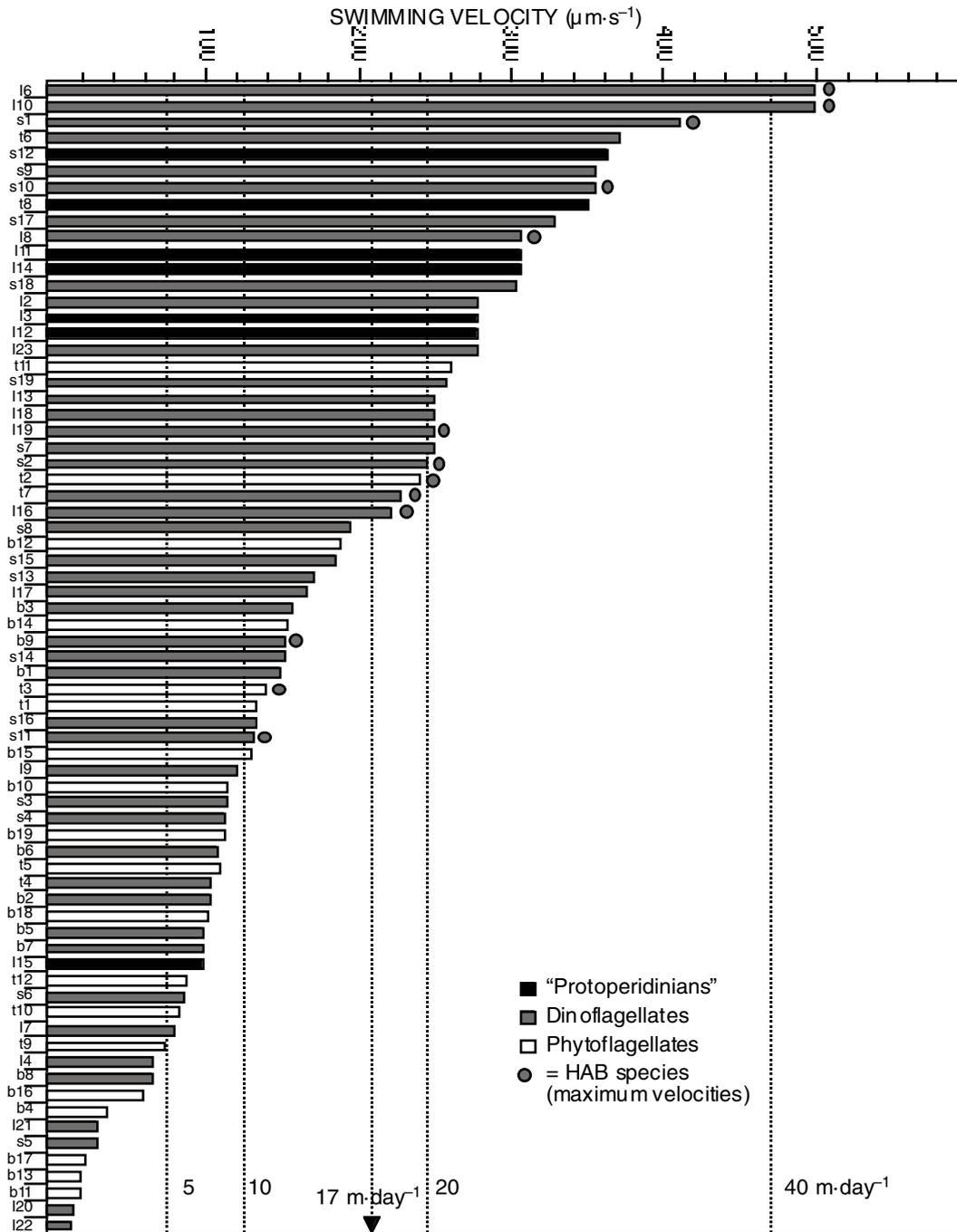


Fig. 9: Swimming velocities of 71 clones and species of dinoflagellate and other phytoflagellates reported in the literature. Coded entries on vertical scale identify taxa (see Appendix). Vertical lines represent upwelling rates reported for various systems; the rate of $17.3 \text{ m}\cdot\text{day}^{-1}$ represents maximal frontal, vertical velocities, according to Franks (1992)

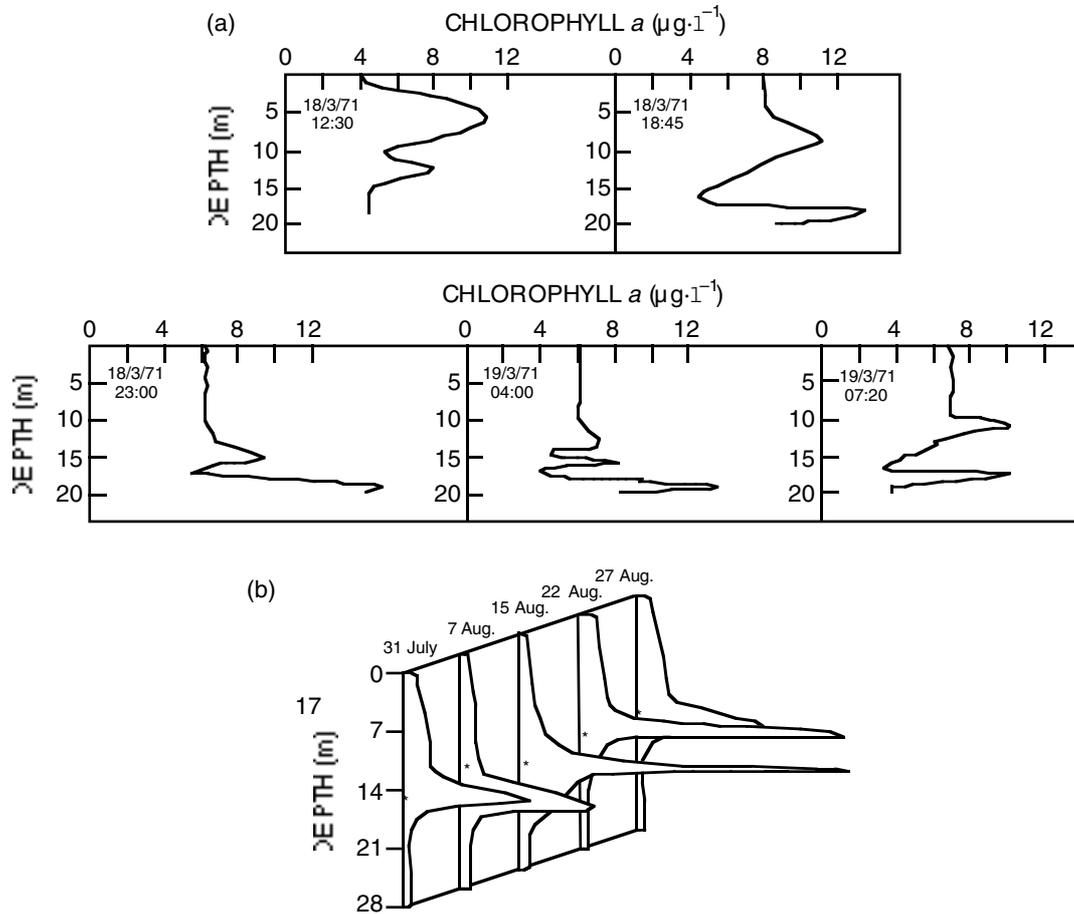


Fig. 10: Illustrations of dinoflagellate depth-keeping and accumulation into thin-layer strata within the water column, showing (a) the diel behaviour of *Gymnodinium sanguineum* (from Lasker and Zweifel 1978) and (b) the temporal behaviour of *Gyrodinium aureolum* (= *Gymnodinium mikimotoi*) (from Bjørnsen and Nielsen 1991). The asterisks indicate the position of the pycnocline

more important than the velocity field.

Kamykowski (1981) argued that, for dinoflagellate populations resident in shallow water columns, or at low turbidity, their migratory phases provide little selective advantage, unlike for deep-water populations, or those resident in highly turbid water. Field validation that dinoflagellates apply vertical positioning strategies within the water column during physically active periods is shown in Figure 10. Dinoflagellate growth at the base of the thermocline or at pycnoclines is characteristic of frontal boundaries (Holligan 1979). This capability, combined with behavioural depth-keeping, results in thin-layer accumulations on diel and longer time-scales. *G. aureolum* (= *G. mikimotoi*) blooms collected into sharp, 1-m thick layers at

depths below 10 m, and persisted for over a four-week period (Fig. 10, Bjørnsen and Nielsen 1991). *G. sanguineum* collected into layers 1–4 m thick in the California Current system (Kiefer and Lasker 1975, Lasker and Zweifel 1978) and *C. tripos* concentrated in thin layers below the seasonal thermocline at depths between 20 and 25 m (Mahoney and Steimle 1979). In developing vertical depth-keeping strategies, dinoflagellates exploit the low energy cost of motility, i.e. <0.1% of the total energy budget for growth (Holligan 1985). In this situation, they are aided by the low Reynolds Numbers ($Re = <0.05$), which characterize their motility (Levandowsky and Kaneta 1987). This allows dinoflagellates (cell size = 10–50 μm) swimming at rates from 300 to 600 $\mu\text{m}\cdot\text{s}^{-1}$ to stop

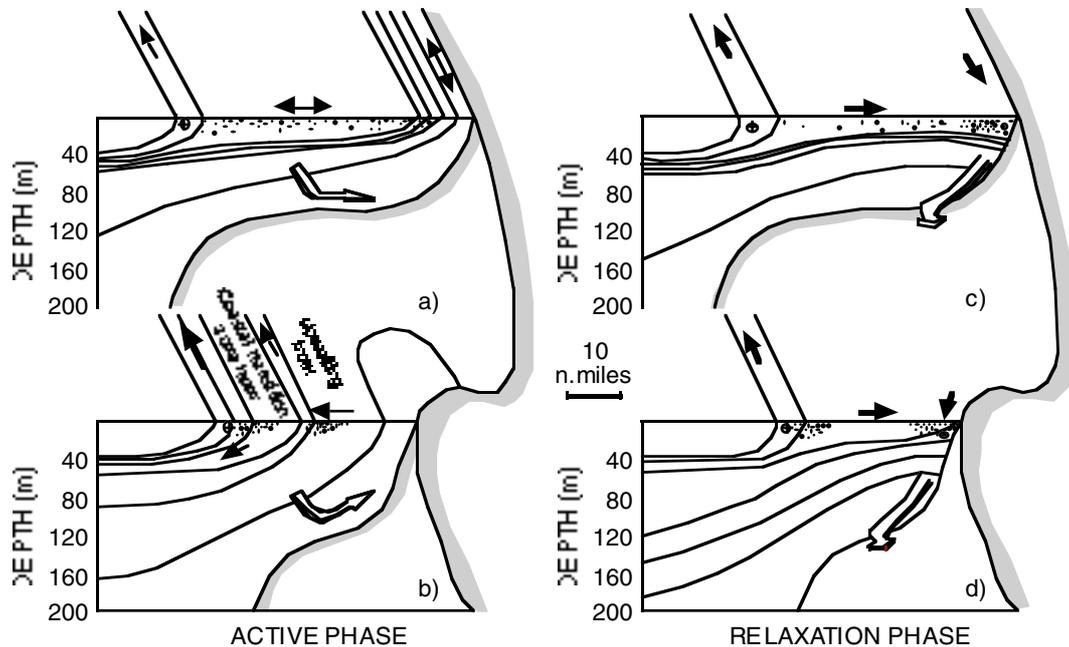


Fig. 11: Conceptual three-dimensional model of across-shelf and longshore circulation and the formation of red tides proposed for the southern Benguela upwelling system (from Pitcher and Boyd 1996)

moving abruptly upon entry into a suitable micro-habitat. The distance needed to accelerate from “rest” to full speed is also negligible relative to the size of the organism. This provides dinoflagellates with a fine-tuning capability, facilitating their volitional auto-aggregation into sharp, tightly banded, subsurface layers, whose thickness may be as little as a decimetre, or less (Fig. 10, Bjørnsen and Nielsen 1991). (It is not clear whether aggregations forced through physical accumulations at frontal zones confer similar ecological benefit.) The disruption and reformation of subsurface patches can also affect upper trophic levels. Northern anchovy *Engraulis mordax* in the California Current utilize remarkable behavioural patterns to search for, hunt out and remain within subsurface patches of its preferential prey, *G. sanguineum*, (Hunter and Thomas 1974, Lasker and Zweifel 1978). Mixing events, which break up the patches to below recognition, and grazing-threshold densities ($30 \text{ cells}\cdot\text{ml}^{-1}$), lead to starvation unless reformed soon thereafter. Given the importance of similar clupeoid fish in other upwelling regions (Longhurst 1971), and the nutritional dependence of first-feeding stages of larval fish, similar ecosystem consequences of the aggregation and breakup of subsurface dinoflagellate patches at frontal zones may occur in those systems.

DEVELOPMENT OF RED TIDE BLOOMS IN COASTAL UPWELLING SYSTEMS

What specifically triggers red tide blooms, particularly those with vast spatial scales and huge biomass levels that develop into anoxic events in coastal upwelling systems (Brongersma-Sanders 1957, Dugdale *et al.* 1977, Pitcher and Cockcroft 1998)? Small-scale analogues of these anoxic events are sometimes induced in non-upwelling regions by ceratium blooms (Granéli *et al.* 1989, Mahoney and Steimle 1979, Westernhagen *et al.* 1986). Pitcher and Boyd’s (1996) provocative, three-dimensional conceptual model relating longshore and across-shelf circulation patterns and red tide formation off the west coast of southern Africa (Fig. 11) is used as a template in seeking to identify red tide bloom control mechanisms. The essence of the Pitcher and Boyd model is that coupling among physical processes during active and relaxation phases of upwelling varies, and will either favour or repress red tide blooms. Their model, heavily rooted in field observations, basically addresses the critical, first phase of red tide bloom development: the source and role of seed stock in initiating blooms.

Table XI: Advected distances traversed and relative population increases of entrained dinoflagellates estimated for assumed combinations of current velocities and growth rates

Advective velocity (m·s ⁻¹)	Doubling rate (days)	Distance to complete first division (km)	Increase after 10 days	Distance travelled in 10 days (km)
0.5	1 ($\mu = 1.0$)	43	1 024-fold	430
0.5	2 ($\mu = 0.5$)	86	32-fold	
0.2	1	17	–	170
0.2	2	34	–	

During active upwelling, diatoms bloom in the narrow coastal upwelling zone shorewards of the offshore, coastal transition zone front, where dinoflagellates accumulate in this region of convergent flow (Fig. 11a). Where the shelf is broad, or when upwelling weakens, dinoflagellates are often redistributed across the width of the shelf. Seeded initially by populations from the coastal transition zone front (which persists throughout the upwelling season), they are dispersed while entrained in the onshore flow of across-shelf currents. In regions of narrow shelves, or during periods of strong or sustained upwelling, the upwelling front often moves offshore and augments the coastal transition front. Much of the shelf region then supports a diatom bloom, whereas the dinoflagellates, restricted to a narrow band in the offshore front, are transported longshore and equatorwards by a frontal jet (Fig. 11b). During upwelling relaxations, and independent of shelf width, weakened across-shelf currents flow onshore, seeding the region with dinoflagellates that frequently accumulate inshore under the influence of longshore currents (Figs 11c, d). Pitcher and Boyd (1996) connected the spatial distributions of various dinoflagellate species to the dynamics shown in Figure 11. A key element of the model, i.e. that dinoflagellates can be seeded from offshore frontal growth zones or refugia to form nearshore blooms, is consistent with observations elsewhere. Nearshore blooms of *C. tripos* (Mahoney and Steimle 1979) and *G. breve* (Haddad and Carder 1979) have been linked to seedings from offshore bloom sites. These are distinct from seedings of expatriate populations entrained in longshore currents (Tester *et al.* 1991, Wyatt 1995). Dinoflagellates can traverse considerable distances within relatively short time-scales when entrained within longshore and across-shelf currents (Table XI). The Pitcher and Boyd model accommodates rapid dispersion, facilitating dinoflagel-

late exploitation of growth opportunities opening during upwelling relaxations. However, once water masses are seeded, the factors triggering bloom formation are obscure, but three seem important: nutrient availability, phyto-stimulation and grazing pressure.

Nutrient limitation and excretion

Although coastal upwelling systems are nutrient-enriched, it is not the case that they are never nutrient-limited, or that remineralization and excretion are unimportant to primary production. A plume of newly upwelled water in the Peruvian system moving 40 km offshore over a 3.5-day period was nearly stripped of its initial nitrogen content (Whitledge 1981). There is experimental evidence for nitrogen and silicate limitation in the major upwelling systems (Harrison *et al.* 1981, Packard *et al.* 1978b, Shannon and Pillar 1986, Nelson *et al.* 1981). Progressive nutrient depletion of upwelling plumes moving offshore led to biochemical differences and reduced productivity in the Benguela system (Barlow 1982a, b). Margalef *et al.* (1979) reasoned that red tide blooms are primarily physical accumulations, because mass balance calculations would show that *in situ* nutrient fluxes from remineralization are lower than the supply rates needed to produce these blooms. Holligan (1985) and LeCorre *et al.* (1993) showed that this did not apply to frontal zone blooms of *G. aureolum* (= *G. mikimotoi*) nor appears to apply to upwelling ecosystems.

Upwelled nutrients alone do not explain coastal upwelling fertility and bloom events; nutrient recycling is important. The percentage of primary production in different upwelling systems attributable to nitrogen excretion, and the trophic sources of recycled nitrogen are compared in Table XII. Excreted nitrogen accounts for 47–72% of the measured production, similar to that in some non-upwelling, coastal areas and oceanic gyres. The relative importance of zooplankton and nekton excretion varies among upwelling systems, as does benthic excretion and sedimentary release. Zooplankton excretion rates per unit mass exceed rates for sardine and anchovy (Whitledge 1981), which may account for the surprising importance of zooplankton in nutrient excretion. The conspicuously high micronekton excretion in the Baja California system reflects the great abundance of the pelagic galatheid crab *Pleuroncodes planipes* (Walsh 1976). Following the Peruvian anchovy decline, nekton excretion rates became similar to those in the North-West Africa upwelling system (Whitledge 1981). The author concluded that, once upwelling stabilizes following its initiation, zooplankton excretion then accounts for about 20–30% of the productivity.

Table XII: Excretion and grazing by zooplankton and nekton in upwelling ecosystems

Region	Percentages of primary production resulting from excreted nitrogen and its trophic sources (Whitledge 1981)				
	Production	Zooplankton	Nekton	Micronekton	Benthos + sediments
North-West Africa	72	33	15	–	24
Cape Blanc	61	24	29	–	8
Peru	56	19	18	–	13–19
Baja California (March)	47	3	1	32	11
Baja California (April)	52	16	1	23	12
Coastal areas	55–75	43–66	–	–	–
North Pacific gyre	44–83	44–83	–	–	–
	Percentages of daily phytoplankton nitrogen grazed, and proportional ingestion by zooplankton and nekton				
	Ingested	Zooplankton	Nekton	Source	
North-West Africa	71	69	31	Whitledge (1981)	
Peru	61	47	53	Whitledge (1981)	
Baja California	60	40	60	Whitledge (1981)	
Benguela	48	35	13	Shannon and Field (1985)	

Microzooplankton and microbial loop excretion (not budgeted in Table XII) would provide some of the 17–56% of the missing nitrogen needed to meet primary production estimates.

Biological conditioning and an aquacultural analogue of red tide stimulation

Biological conditioning of upwelled deep-water stimulates phytoplankton growth, particularly in newly upwelled waters (Harrison *et al.* 1981, Huntsman and Barber 1977). The initial growth repression of upwelling source-waters appears to be caused by trace metal-organic ligand interactions, which can be overcome by addition of biogenic ligands (Barber and Ryther 1969, Barber *et al.* 1971). Elimination of trace metal toxicity, particularly important for red tide species (Boyer and Brand 1998), appears to be a major aspect of this conditioning. However, the need for conditioning is variable, influenced by the degree to which newly upwelled water admixes with nearshore waters that have already supported phytoplankton growth. Natural chelators appear to be secreted during growth and/or excreted by grazers; exposure to this conditioning improves growth and production rates (Barber *et al.* 1971, Huntsman and Barber 1977). Phyto-stimulation of another type may also help to generate red tides during upwelling relaxations. Growth rates of natural populations of *L. polyedrum* averaged 1.0·day⁻¹, but in culture were only 0.25·day⁻¹ (Harrison 1976), unless enriched with nutrients and

soil extract that stimulates higher growth rates (1.0–1.5·day⁻¹; Sweeney and Hasfings 1958). Culture media prepared with seawater collected from within red-water patches of *P. micans* stimulated growth over that in media prepared with seawater from outside the patches (Sweeney 1975). This led Harrison (1976) to conclude that dinoflagellates respond to a “growth factor” that is produced *in situ*, but lacking in culture media.

The chemical nature of the phyto-stimulants, if they occur, is obscure, unlike their potential sources: the grazing community. The behaviour of clupeoids in aggregating into dense (up to hundreds of thousands of fish), and large schools (>100 tons in some cases) in upwelling systems is notable (Longhurst 1971). This feature and the enormous abundance of upwelling stocks suggest an analogue to the putative relationship between fish farming and harmful red tides that is postulated by some investigators. In that instance, particularly after initiation of salmonid culture, harmful and often novel red tides at some point seemingly occur with increased frequency (Smayda 1998). Excretion of nutrients and growth-promoting substances by the caged fish stocks are suspected factors. There are nutrient buildups within naturally occurring dense schools, such as for the clupeoid *Brevoortia tyrannus* (Oviatt *et al.* 1972). Whitledge (1981) estimated that, in the Peruvian system, a school of 100 anchovy·m⁻³ would excrete in about two hours a quantity of NH₄ equivalent to the daily phytoplankton needs within the water column. Fish excretion is not restricted to inorganic and organic nutrients

that affect phytoplankton yield; excreted effluent is a rich mixture of various organic compounds (Whitledge 1981), which may have phyto-stimulatory properties. An ability to use dissolved organic nutrients has been demonstrated for the upwelling red tide species *P. micans* and *H. akashiwo* (Table I) and the robust, nearshore bloom species *K. rotundatum* (Mahoney and McLaughlin 1977). Low concentrations of guanylic acid stimulated growth of *G. sanguineum* (Ueno *et al.* 1977). Zooplankton excretion (Table XII) supplements the fish-derived nutrient flux.

It is suggested here that nutrients and growth-promoting substances excreted by migrating shoals and "boils" of upwelling clupeoid stocks may selectively stimulate red tide-producing species, particularly during upwelling relaxation phases when the biologically conditioned, near-surface waters are less constrained by upwelling processes and begin to flux back onshore (Fig. 11). This proposed stimulation is viewed as a two-step process, the first effect being stimulation of local growth of dinoflagellates within their various spatial heterogeneities. The subsequent step is seeding from these growth refugia into new areas (Pitcher and Boyd's 1996 model – Fig. 11), and facilitated by the altered physical structure that allows access to, and growth within, new areas. The well known bloom-induced discolouration loci of "brown" and "red water" patches, as distinguished from "blue water" patches, which characterize upwelling systems (Beers *et al.* 1971), may reflect this proposed mechanism of bloom stimulation. Coalescence of these growth patches or large-scale entrainments enhances the prospects that a considerable red tide bloom will develop.

Grazing and red tides in upwelling systems

Despite the potential importance of nutrient recycling in influencing yield, species' selection and localized blooms, the limited data provide no convincing evidence that nutrients or biological conditioning are important in triggering and sustaining the more massive red tide blooms that lead to anoxia and die offs (Brongersma-Sanders 1957), and for which upwelling systems are famous. This turns attention to the potential effect of grazers. Many of the dinoflagellate species that form red tides in upwelling systems (Table I) have been tested as prey in zooplankton grazing experiments, including *A. catenella*, *A. tamarensis*, *G. sanguineum*, *H. triquetra*, *L. polyedrum*, *P. micans*, *Protoceratium reticulatum* and *S. trochoidea* (Huntley *et al.* 1986, Uye and Takamatsu 1990). Each species was either nutritionally accepted or rejected by one or more of the experimental copepods; some dinoflagellates re-

pressed grazing or caused physiological stress. Thus, the extent to which zooplankton grazing is a factor moulding dinoflagellate behaviour at any given time or place in upwelling habitats depends on the match between dinoflagellate (prey) and zooplankton (predator). Available data do not support the view that dinoflagellates in upwelling region are relatively free from predation by zooplankton. Blasco (1977) concluded that a red tide bloom in the Baja California system was controlled by copepod grazing, and that *Calanus helgolandicus* ingested *G. sanguineum* at a mean rate of about one cell every 30 seconds.

Dietary diversity is a characteristic feature of clupeoids: in each upwelling system, these stocks employ an herbivorous-omnivorous feeding strategy during their life cycle. In the Baja Californian system, the pelagic galatheid crab *P. planipes* replaces the phytophagous and zooplanktivorous niche of the absent clupeoids (Walsh 1976). This complex feeding behaviour, which varies with stage in life cycle and involves prey-switching, has led to conflicting views as to the normal diet and prey preferences of various clupeoids (Davies 1957, King and MacLeod 1976, Cushing 1978), and whether prey-limitation occurs (Shannon and Field 1985). The basic conclusion is that upwelling system clupeoids achieve a mixed diet through direct or adventitious feeding. Selective grazing on mixed dinoflagellate assemblages also occurs (Scura and Jerde 1977, Lasker and Zweifel 1978), and prey-limitation can lead to switching to prey of poorer nutritional quality. Peruvian anchovy *Engraulis ringens* prey-switched to a *G. sanguineum* bloom and suffered reduced growth and recruitment (Rojas de Mendiola 1979). The impact of these diverse feeding preferences and behaviour on bloom species' selection is unknown.

Much more is known about grazer responses to coastal upwelling primary production. The percentage of daily phytoplankton production (as nitrogen) grazed by zooplankton and nekton in four upwelling systems (Table XII) varies from 48% (Benguela) to 71% (North-West Africa), with zooplankton grazing being three- and two-fold more important than clupeoid grazing respectively. Equivalent grazing takes place in the Peruvian system. In the Baja California system, grazing by the pelagic, red-crab-dominated nekton is 50% greater than zooplankton grazing. The Benguela budget differs appreciably from the other upwelling systems (Table XII): the finding that only 13% of primary production is probably utilized by the clupeoid stocks is particularly notable. Longhurst (1971) assumed that sardine/anchovy stocks in the southern Benguela were somehow in dynamic balance with plankton production, and that the combined biomass of these clupeoids equalled that which could

be supported by the plankton-based foodweb. The result of Shannon and Field (1985) suggests otherwise: in the Benguela, about 50% of primary production can escape pelagic zooplankton and nekton grazing, which, if not grazed by other, unbudgeted components, must sink and rot in bottom waters. During the 1976 Peruvian anoxic event, when anchovy stocks had declined, sedimentation of >12% of the primary production was calculated to be needed to trigger anoxia, with the input estimated to have been as much as 50% (Whitledge 1981). These circumstances suggest that a substantial collapse in grazing pressure by upwelling system clupeoids may be a major factor in anoxic developments. Whereas anoxic events appear to be basically bloom-collapse events, the mechanisms triggering and sustaining the causative blooms following seedings (Fig. 11) are obscure.

PALAEONTOLOGICAL AND GEOCHEMICAL ASPECTS

Do the periodic die-offs in upwelling systems induced by red tides have a biogeochemical homeostatic function? That is, do the die-offs serve to readjust the rates of energy flow and remineralization back to levels essential to "normal" upwelling ecosystem functioning? Flagellate blooms have been of major trophodynamic significance throughout their evolution. Prior to the evolutionary appearance of the diatoms, about 100 million years ago, the phylogenetically diverse flagellates had already evolved as the major primary producers. In fact, most of the grazing strategies and trophic pathways characterizing Recent seas have developed on a flagellate template. Evidence that flagellates achieved major blooms in ancient seas includes widespread occurrences of sedimentary deposits of dinosterol, a unique "molecular fossil" specifically derived from dinoflagellates (Withers 1987). The curious tendency for catastrophic blooms to develop in eastern boundary upwelling regions, as in the Benguela, North-West African, Peruvian and Chilean upwelling systems, has been well documented (Brongersma-Sanders 1957, Rojas de Mendiola 1979). The magnitude of the huge die-offs of fish, guano birds and benthic fauna attributed to bloom toxins or anoxia has trophodynamic significance. Brongersma-Sanders (1957) ascribed palaeontological implications to these catastrophic die-offs, linking fossilized deposits of belemnites to analogous mass mortalities of squids *Dosidicus gigas*, which occur in the Chilean upwelling zone during red tide outbreaks. Extensive fossil deposits also attributed to red tide induced mortalities include those of bivalves and gastropods

(Noe-Nygaard *et al.* 1987), cormorants and other marine birds, fish and marine mammals, including seals, dugongs and dolphins (Emslie and Morgan 1994). The latter authors have linked late Pliocene deposits ($2-2.5 \times 10^6$ MYA) along the Florida Gulf coast to reduced upwelling following emergence of the Panama land bridge. This association in the Gulf of Mexico and its linkage to altered upwelling patterns are notable. Blooms of the ichthyotoxic, "mixing-drift" (Type VI) life-form, *G. breve*, in this oligotrophic sea can cause enormous mass mortalities prompting the question of whether these ongoing occurrences are relict continuations from ancient seas. Between 1844 and 1946, nine major bloom events were recorded (Gunther *et al.* 1948), with evidence of mass mortalities extending back to 1648 (Brongersma-Sanders 1957). Between 1946 and 1979, there were 21 blooms of *G. breve* along the north-west Florida coast (Roberts *et al.* 1979). The magnitude and trophodynamic importance that these die-offs can achieve are evident from a nine-month (1946-47) bloom event: an estimated 0.5 billion fish from all trophic levels perished, accompanied by widespread benthic mortality (Gunther *et al.* 1948).

Geochemical signatures of mass mortalities, evident as sedimentary enrichments, reveal the trophodynamic importance of toxic blooms. The relatively sudden "pelagic" deaths and sinking of huge amounts of biomass, and/or the in-place die-offs of benthic fauna probably overload biochemically the normal trophodynamic capacity for nutrient recycling and remineralization, and lead to sedimentary burial of biogeochemical products. Fossil phosphorite deposits in upwelling zones have been attributed to repeated red-tide-induced mass mortalities of vertebrates (Brongersma-Sanders 1957, see Fig. 9 in Cushing 1975), and there is evidence that petroleum is a product of diagenetic reactions on sterols of dinoflagellate origin, such as dinosterol (Withers 1987). Brongersma-Sanders (1957) pointed out the coincidence of rich oil deposits in the Gulf of Mexico and the frequent, historic occurrences of mass mortalities accompanying red tide outbreaks (*G. breve* primarily) in the perimeter seas bordering the U.S., Mexico and the Yucatan. These huge, aperiodic carbon and nitrogen fluxes, with sedimentary burial in regionally recognizable depocenters (see Walsh, 1988), suggest another trophodynamic role of harmful blooms. Is it possible that such fluxes in the nutrient-enriched upwelling systems represent regional homeostatic mechanisms needed for periodic adjustments of carbon and nitrogen balance? These natural, mesoscale effects may be analogous to the increased incidences of antagonistic blooms and die-offs accompanying increased anthropogenic nutrient loadings of coastal waters, albeit on

a much smaller, but biogeochemically consistent, scale (Smayda 1990). The modelled results of Van Cappelin and Ingall (1995) suggest that global-scale anoxia-dysoxia events more efficiently recycle phosphorus, and lead to higher rates of primary production and carbon burial. The authors suggest that the redox-dependent sedimentary burial of phosphorus, and phosphorus-mediated coupling of oceanic productivity and atmospheric oxygen, may "provide effective safeguards against catastrophic depletion or buildup of atmospheric oxygen and irreversible eutrophication of the oceans". Because upwelling and its intermittent relaxations function as an oscillating nutrient pump, it has an eutrophication aspect seemingly interlinked in geochemical balance, with associated occurrences of anoxia and their causative red tide blooms. This, too, supports the evidence that red tides are a natural, major biotic feature of upwelling systems.

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APPENDIX

Identification of coded species entries in Figure 9

Code	Species	Source	Code	Species	Source
16	<i>Gonyaulax polygramma</i>	5	t1	<i>Eutreptiella</i> sp.	6
110	<i>Dinophysis acuta</i>	5	s16	<i>Gymnodinium sanguineum</i>	4
s1	<i>Alexandrium affine</i>	2	s11	<i>Prorocentrum micans</i>	3
t6	<i>Katodinium rotundatum</i>	6	b15	<i>Pavlova lutheri</i>	1
s12	<i>Protoceratium reticulatum</i>	3	19	<i>Amphidinium carterae</i>	5
s9	<i>Gyrodinium dorsum</i>	3	b10	<i>Brachiomonas submarina</i>	1
s10	<i>Lingulodinium polyedrum</i>	3	s3	<i>Amphidinium carterae</i>	3
t8	<i>Pyramimonas</i> cf. <i>disomata</i>	6	s4	<i>Gymnodinium splendens</i>	3
s17	<i>Gyrodinium dorsum</i>	4	b19	<i>Hymenomonas carterae</i>	1
18	<i>Gymnodinium sanguineum</i>	5	b6	<i>Peridinium cinctum</i>	1
111	<i>Protoperidinium pentagonum</i>	5	t5	<i>Apedinella spinifera</i>	6
114	<i>Protoperidinium claudicans</i>	5	t4	<i>Pseudopedinella pyriformis</i>	6
s18	<i>Gyrodinium dorsum</i>	4	b2	<i>Amphidinium brittanicum</i>	1
12	<i>Gyrodinium</i> sp.	5	b18	<i>Hymenomonas carterae</i>	1
13	<i>Ceratium furca</i>	5	b5	<i>Heterocapsa pygmaea</i>	1
112	<i>Protoperidinium subinermis</i>	5	b7	<i>Prorocentrum micans</i>	1
123	<i>Cachonina niei</i>	5	115	<i>Protoperidinium crassipes</i>	5
t11	<i>Hemiselmis simplex</i>	6	t12	<i>Micromonas pusilla</i>	6
s19	<i>Lingulodinium polyedrum</i>	4	s6	<i>Glenodinium</i> sp.	3
113	<i>Protoperidinium ovatum</i>	5	t10	<i>Heteromastix (Nephroselmis) pyriformis</i>	6
118	<i>Ceratium tripos</i>	5	17	<i>Prorocentrum minimum</i>	5
119	<i>Ceratium fusus</i>	5	t9	<i>Ochromonas minima</i>	6
s7	<i>Heterocapsa ildefina</i>	3	14	<i>Scrippsiella trochoidea</i>	5
s2	<i>Gymnodinium catenatum</i>	2	b8	<i>Prorocentrum minimum</i>	1
t2	<i>Eutreptiella gymnastica</i>	6	b16	<i>Pseudoscourfeldia marina</i>	1
t7	<i>Gyrodinium aureolum</i> (= <i>Gymnodinium mikimotoi</i>)	6	b4	<i>Gyrodinium aureolum</i> (= <i>Gymnodinium mikimotoi</i>)	1
116	<i>Ceratium furca</i>	5	121	<i>Ceratium horridum</i>	5
s8	<i>Heterocapsa niei</i>	3	s5	<i>Gymnodinium nelsonii</i>	3
b12	<i>Nephroselmis pyriformis</i>	1	b17	<i>Pyramimonas amyliifera</i>	1
s15	<i>Peridinium foliaceum</i>	4	b13	<i>Heterosigma akashiwo</i>	1
s13	<i>Prorocentrum minimum</i>	4	b11	<i>Micromonas pusilla</i>	1
117	<i>Ceratium furca</i> (chain)	5	120	<i>Ceratium longipes</i>	5
b3	<i>Ceratium tripos</i>	1	122	<i>Ceratium macroceros</i>	5
b14	<i>Phaeocystis pouchetii</i>	1			
b9	<i>Scrippsiella trochoidea</i>	1			
s14	<i>Scrippsiella trochoidea</i>	4			
b1	<i>Amphidinium carterae</i>	1			
t3	<i>Heterosigma akashiwo</i>	6			

(1) Bauerfeind *et al.* 1986; (2) Fraga *et al.* 1989; (3) Kamykowski *et al.* 1989; (4) Kamykowski *et al.* 1992; (5) Levandowsky and Kaneta 1987; (6) Throndsen 1973