

Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms

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The habitat preferences of dinoflagellate bloom species along an onshore–offshore, mixing–nutrient gradient, their associated life-form (morphotype) characteristics and adaptive strategies were evaluated from the perspective of Margalef’s Mandala and Reynolds Intaglio. Nine different mixing–nutrient habitats and associated dinoflagellate life-form types having distinctive morphotype features and habitat preferences are distinguishable. Reynolds Intaglio provided greater fidelity to actual in situ dinoflagellate community assembly than the Mandala. We suggest that the correlation between degree of mixing and nutrient levels presumed in the Mandala is not the essential interaction in the selection of life forms and their succession. A more significant aspect of the turbulence axis is the degree of vertical, micro-habitat structural differentiation that it permits. Three primary adaptive strategies consistent with C–S–R strategies recognized among freshwater phytoplankton species characterize the component dinoflagellate species: invasive, small- to intermediate-sized colonist species (C) which often predominate in chemically-disturbed water bodies; acquisitive, larger-celled, nutrient stress-tolerant species (S); and disturbance-tolerant ruderal species (R) tolerant of shear/stress forces in physically-disturbed water masses (fronts, upwelling relaxations, current entrainment). It is suggested that harmful algal bloom community assembly and dynamics reflect two basic selection features—life-form and species-specific selection, that commonly held life-form properties override phylogenetic properties in bloom-species selection, and that the latter is often stochastic, rather than singular. The high degree of unpredictability of individual species blooms is consistent with stochastic selection, e.g. bloom species are often selected as a result of being in the right place at the right time at suitable inoculum levels. A focus on the life-form properties, habitat preference and stochastic selection of bloom species would appear to be more viable and realistic than current ecological investigative approaches.

INTRODUCTION

It is generally accepted that a global expansion and increasing frequency of nearshore blooms of benign, noxious and toxic flagellate species is in progress (Anderson, 1989; Smayda, 1989, 1990; Hallegraeff, 1993). Collectively termed ‘red tides’ in the older literature, these blooms are now generally referred to as harmful algal blooms (HAB), a characterization not without problems [see (Smayda, 1997a)]. However, for convenience, and without regard to actual trophodynamic or public health impacts, we will use the acronym HAB to refer to this increased flagellate bloom syndrome. HAB events are hardly recent phenomena, but whereas past blooms were often unpredictable rogue events, they are now seemingly

more commonplace in annual successional cycles. A notable feature of HAB events is that the bloom species are often novel in not having been previously detected, or found to be prolific at the bloom site (Smayda, 1998). The mechanisms of bloom-species selection, and the causes of the shifts in phytoplankton community structure favoring flagellate taxa and their blooms, are major unresolved HAB issues. We are particularly interested in the apparent changing character of the bloom species being selected and their blooms as expressions (indicators) of specific habitat conditions; we evaluate this aspect here. Our approach will apply a plankton assemblage perspective, rather than be physiologically based; this partly reflects the availability of data. We will not address the issues of why bloom events are increasing, or what factors regulate

the abundance and selection of HAB species. We are aware, however, of the arguable evidence that altered nutrient conditions may be important (Smayda, 1990; Reid, 1997), and that ballasted water introductions of novel species have in some cases led to their subsequent blooms (Hallegraeff and Bolch, 1992).

METHOD

Problem formulation

Indigenous phytoplankton communities are assembled from an extensive array of species of diverse size, shape and overlapping autecology, from among which bloom species are selected. Why do such diversity, redundancy and commonality co-occur? Is it because bloom taxa, at some deeper level, share common life-form properties which are more significant to their selection than their phylogenetic and autecological diversity? And embedded within this conundrum is the related issue: is selection primarily for a given species, or for a given life-form property common to many species? That is, is habitat selection of bloom species perchance not, as traditionally viewed, fundamentally that of selection for a given species of dinoflagellate, raphidophyte, euglenophyte, chrysophyte or silicoflagellate but, rather, selection for a specific life-form property commonly shared and associated with the phytoplanktonic life mode? Should life-form selection and not species selection be the norm, then the species (phylogeny) which fill the bloom niches should be viewed as being essentially stochastic selections. That is, the observed species' blooms result from that (those) species being in the right place at the right time, rather than occur as a response to a very unique habitat condition favoring only the bloom species. Confirmation of this alternative mode of species' selection would require significant revision of contemporary conceptual and experimental approaches which currently focus on species-specific responses, rather than on life-form properties, in seeking to quantify HAB dynamics. It would also simplify the search for mechanisms, since commonly shared life-form properties are more easily identified, more tractable and fewer in number than those characterizing the autecology of individual species. The latter complicates searches for unique, species-specific physiological and ecological traits in seeking to explain the unpredictable blooms of individual HAB species.

We suggest that the dynamics of any HAB event reflect two interwoven tiers of response: dynamics guided by shared and common ecophysiological traits independent of phylogeny, melded with the dynamics resulting from the distinctive attributes of the stochastically-selected bloom species, or more directed bloom-species selections.

That is, HAB dynamics reflect two basic selection features—life-form and species-specific selection. Our supposition is that life-form properties take precedence over phylogenetic properties in the selection of species responsible for a particular HAB event. We explore this eventuality, leaving for future consideration the issue of the proportionate contributions of life-form and species-specific traits to HAB dynamics.

Approach

In exploring our supposition, we will apply a plankton-vegetation perspective in seeking to identify common life-form characters found among HAB taxa. Numerous descriptions of marine phytoplankton assemblages convincingly support the axiom that special communities and species associations characterize water masses and current systems [see (Braarud *et al.*, 1953; Ramsfjell, 1960; Smayda, 1980)]. Among the earliest of these, Cleve's (Cleve, 1900) concept of 'plankton types' grouped phytoplankton assemblages into thermal units having centers of abundance within their respective thermal zones (seasons). Thus, the 'Tripos-plankton' was predominantly a dinoflagellate assemblage, especially *Ceratium tripos*. The 'Sira-plankton' was predominantly a chain-forming diatom assemblage dominated by the spring bloom species *Thalassiosira nordenskiöldii*; the 'Desmo-plankton', a tropical community dominated by the filamentous, N-fixing *Trichodesmium* and the 'Stylo-plankton', an oceanic diatom community dominated by large, attenuate *Rhizosolenia* species. The relevant feature of Cleve's (and others) findings of interest to us is that phytoplankton assemblages cluster taxa having shared features, and that one or several related members of this group are often pre-eminent in their concurrent abundance. Gran convincingly established that Cleve erred, however, in attributing seasonal successional cycles to invasions of 'plankton types' (Gran, 1902). He showed that autochthonous species are of greater importance in the organization of local phytoplankton communities and their successions. Gran also demonstrated more rigorously that the assembly of species into 'plankton elements' depended upon water-mass conditions.

A singular feature of Cleve and Gran's pioneering studies and subsequent, more quantitative descriptions of phytoplankton associations [see (Smayda, 1980)] is the high degree of redundancy of size, shape and motility/non-motility among the different taxonomic components within phytoplankton communities and associations. Thus, large *Rhizosolenia* species tend to co-occur; nanophytoplanktonic communities of different phylogenetic mixtures are commonplace; flagellate and diatom-dominated communities tend to be temporally and/or spatially segregated, etc. We attach great significance to such apparent

morphometric and behavioral selection, and it encourages us to look for HAB dinoflagellate life forms. Given the considerable influence of size and shape on phytoplankton processes (Reynolds, 1988, 1989), and the axiom that form follows function among phytoplankton (Sournia, 1982a), we view habitat selection of a given size or shape as also a selection favoring a given process (function), such as growth rate, suspension mode etc. Our analyses, therefore, will focus on the size and shape (= morphotype) and behavioral attributes of bloom taxa and secondarily, on their taxonomic status. We accept Gran's conclusion that bloom species within coastal successions are primarily selected from the local, indigenous flora. However, where invasive species are involved, we believe their potential selection as bloom taxa in competition with the local flora will also be based on life-form criteria.

Margalef's model

The best guide to the description of marine phytoplankton assemblages is Margalef's Mandala [Figures 1, 2; (Margalef, 1978; Margalef *et al.*, 1979)] and is one of the two models that we will apply. Margalef's elegant model combines the interactive effects of habitat mixing and nutrient conditions on selection of phylogenetic morphotypes and their seasonal succession, which he suggests occurs along a template of *r* versus *K* growth strategies. Margalef's use of these two variables as the main habitat axes in his model accommodates our view that the pelagic habitat is basically hostile to phytoplankton growth, given its nutritionally-dilute nature and the various dissipative effects of turbulent mixing. We consider these two habitat elements to be the principal, abiotic organizational determinants of HAB assemblages. The model's focus on phylogenetic morphotypes simplifies analysis of the complex taxonomy of phytoplankton assemblages, and we follow a similar approach to facilitate our search for common HAB life-form properties. Margalef's incorporation of succession into the model also accommodates our view that habitat factors identified as operative in regulating phytoplankton communities temporally (i.e. successions) can also be expected to regulate spatial differences in assemblages. This allows assessment of HAB events which cannot be identified as specific stages within local successional cycles; unfortunately, most HAB events fall into this category. Finally, the distinction between *r* versus *K* strategists in Margalef's model is also consistent with our view that the strategies adopted by the competing life forms must be considered (Reynolds, 1988).

There are some problematic aspects of this model, which Margalef confronted: the modeled association between nutrients, their source and degree of mixing; the positioning of the 'red tide' species in the successional model (Figure 2) and some presumed physiological adaptations of HAB

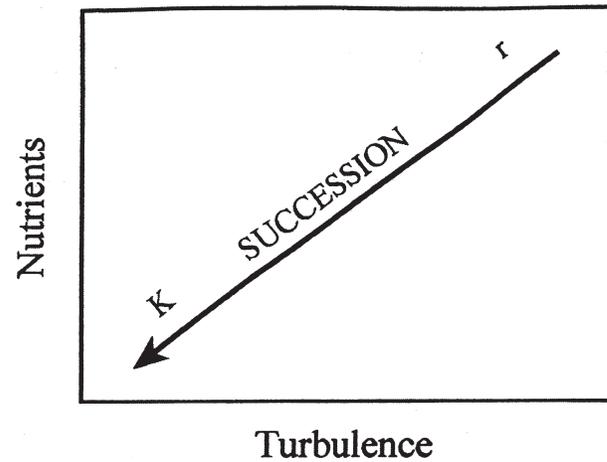


Fig. 1. Margalef's matrix summarizing the sequence of phytoplankton (the main sequence) as a function of diminishing 'turbulence' and nutrient availability. [From (Margalef, 1978).]

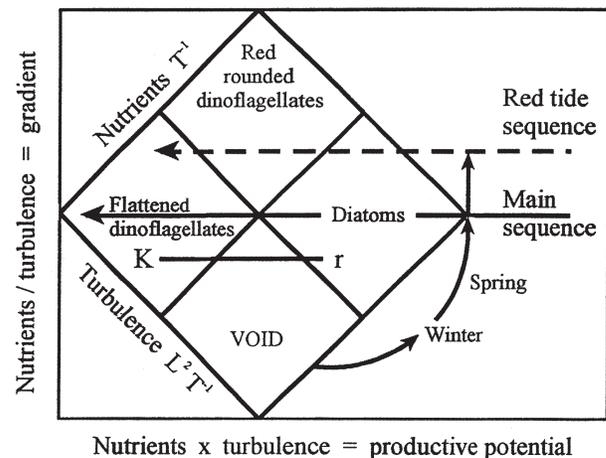


Fig. 2. Margalef's Mandala developed from Figure 1, and including a 'red tide' or HAB trajectory. [From (Margalef *et al.*, 1979).]

taxa. Margalef, pointedly, applied his model to 'red tide' outbreaks to predict that in nutrient-rich waters of low turbulence (conditions which disfavor diatoms), HAB species and their blooms would be selected. Since the model links nutrient input to the degree of turbulence (Figure 2), this HAB-stimulatory combination of relatively high nutrients and low turbulence is seemingly paradoxical. Margalef attributed this inversion in the model to nutrient accretion from terrestrial and anthropogenically-derived sources, but viewed the co-occurrence of high nutrients and low turbulence as anachronistic, and "as an unusual combination [which] might represent a sort of illness, not completely ironed out by evolution, since it produces the red tides that

may end in catastrophe” [p. 505 in (Margalef, 1978)]. While accepting that elevated nutrient levels favored ‘red tides’, he considered such blooms usually to “represent spectacular local accumulation rather than *in situ* growth [when] calculated by mass balance” [(p. 90 in (Margalef *et al.*, 1979)]. [More recent evaluations suggest *in situ* nutrient fluxes can indeed yield blooms (LeCorre *et al.*, 1993).] The well known prodigious blooms of ichthyotoxic *Gymnodinium breve* which occur in the highly oligotrophic Gulf of Mexico (Steidinger *et al.*, 1998) would appear to lie outside this extrapolation and challenge the model. (Other, similarly contradictory bloom events can also be cited.) There is also a physiological challenge. The paradoxically-low nutrient affinity constants characterizing the ~25 coastal HAB taxa for which data are available (Smayda, 1997b) deviate from the model’s projection that HAB taxa would have high nutrient affinity to accommodate their assumed preference for low nutrient waters (Figure 2). A similar dichotomy has been observed among the freshwater phytoplankton (Reynolds, 1993).

In the two decades since Margalef’s seminal publications, a considerably expanded database on bloom occurrences, associated habitat conditions, degree of nitrification and bloom-species’ autecology has accumulated. This allows these enigmatic aspects of the Mandala to be re-examined and also facilitates its use, together with Reynolds’ C-S-R model, in our analysis of the extent to which the observed taxonomic diversity of HAB events can be accounted for as habitat selections for dinoflagellate life forms, rather than for individual species.

Reynolds’ C-S-R model

The extrapolative difficulties with the nutrient–turbulence axes in Margalef’s model are partly the result of linking these two axes when they really are independent variables. The accepted concepts of high *in situ* nutrient turnover rates and surge uptake of nutrients by phytoplankton (Conway *et al.*, 1976; McCarthy and Goldman, 1979), supported by mass balance studies [see (LeCorre *et al.*, 1993)], also vitiate exacting life-form dependence on the putative nutrient–turbulence relationship, and in influencing whether HAB taxa will be selected. A subtle biological factor in the form of differences in competition strategies of the species vying for dominance may also be confounding the linkage between HAB events and specific combinations of the nutrient–turbulence axes. Our initial attempts (Reynolds and Smayda, 1998) to segregate HAB species into the classical r versus K groups were unsuccessful, analogous to the difficulties that Reynolds (Reynolds, 1987) encountered in his search for generic explanations for selection among the freshwater plankton. Thus, a more finely tuned, cryptic aspect of the nutrient–turbulence selectivity axis may be that the r versus K

strategy continuum in the model (Figure 1) only partially reveals the actual competition strategies of the life forms represented in the HAB species’ pools and potentially available for bloom selection. Reynolds’s solution to this conundrum in dealing with the freshwater phytoplankton was to map the distributions of distinct associations of phytoplankton genera against axes provisionally labelled ‘nutrients’ and ‘turbulence’ (Reynolds, 1987). These associations had been identified previously through the tendency of their component species to co-occur in a range of spatially- and temporally-differentiated circumstances (Reynolds, 1980, 1984). In this way, it became possible to distinguish among species which can thrive under conditions of deep, isothermal mixing, those which develop in late succession in strongly-stratified environments and, significantly, those found predominantly in shallow, nutrient-replete ponds and in newly-formed epilimnia of small eutrophic lakes at the start of summer. Further investigations of the adaptations of the key organisms making up the species’ associations demonstrated remarkable coherences among life form and morphology (i.e. small cells, large colonial structure, attenuated cells or filamentous coenobial), physiological performance (growth rate, temperature sensitivity, light harvesting, buoyancy, grazer resistance) and the ecologies which distinguished them in the first place (Reynolds, 1984, 1988, 1989).

Reynolds attached great importance to the convergence of morphological properties and the irrelevance of phylogenetic affinities in the circumscription of the broad evolutionary strategies represented. Influenced very much by the work of Grime [e.g. (Grime, 1979)], Reynolds (Reynolds, 1988, 1993, 1995) eventually was able to distinguish three primary adaptive strategies found among the freshwater phytoplankton: the invasive, r-selected, small, fast-growing, high surface-to-volume colonist (C) species; the acquisitive, large, slow-growing but biomass-conserving, K-selected, nutrient stress-tolerant (S) species; and the attuning, light-harvesting, attenuated, disturbance-tolerant ruderal (R) species. Within each of these primary adaptive strategies, both r- and K-selected species occur. Margalef’s axes were also refined further: the ‘turbulence’ axis became substituted by a vector conveying the vertical extent of mixing relative to an integral embracing light intensity and its attenuation with depth; the ‘nutrients’ axis became more one of the state of their depletion and the accessibility of the residual resource [see (Reynolds, 1987, 1996)]. What emerged was a sort of ‘habitat template’ (Southwood, 1977; Grime, 1979) to which a major part of the adaptive and compositional variability of the freshwater phytoplankton could be fitted, and in just two axes. Other factors are not ignored but, in most well-researched habitats, they appear to play

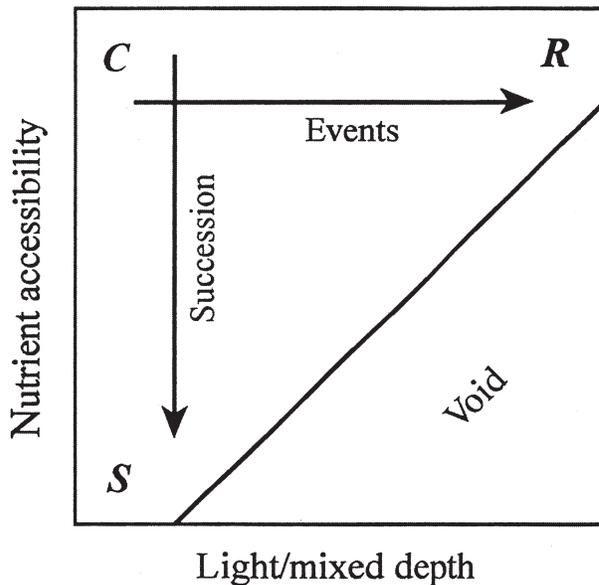


Fig. 3. Reynolds Intaglio which allows selection of species within a wide ecological space, save habitats where nutrients and light are both continuously deficient (the 'void'). [From (Reynolds, 1987).] For further details, see text.

a subordinate role. Thus, the template is not two-dimensional but, rather, its other dimensions impart a sort of low relief, like an intaglio, in fact. This freshwater phytoplankton template is the other model that we will use (Figure 3).

RESULTS

Test of supposition

Our first task was to see whether dinoflagellate bloom taxa ordinate morphometrically and on life-form characters along an onshore–offshore gradient of decreasing nutrient, reduced mixing and deepened euphotic zone. Comparison of the predominant dinoflagellate bloom taxa or vegetation element (in oceanic regions) reported for various representative marine habitats reveals a striking pattern (Figure 4). A gradient in life-form properties occurs along a continuum of progressively decreasing nutrient levels, increasing inertia of water masses against mixing (generally), and deepening of the stratified layer, i.e. along the abiotic axes of the Margalef (Figure 1) and Reynolds (Figure 3) models. In relatively shallow, highly nutrient-enriched habitats that are often mesohaline and have reduced water-mass exchange with offshore waters, the predominant dinoflagellate blooms tend to be those of small- to intermediate-sized gymnodinioid species (Type I in our classification). Given the well known taxonomic difficulties in distinguishing among *Gymnodinium* and its

many 'look-alike' species (Gentien, 1998; Chang, 1999) and between the genera *Gymnodinium* and *Gyrodinium* (Chang, 1996), we will use gymnodinioid as the life-form designation to refer collectively to the genera of 'unarmored' dinoflagellates whose blooms characterize Type I habitats. In addition to unidentified and 'look-alike' *Gymnodinium* spp., *Gyrodinium instriatum*, *Gyrodinium fissum* and *Katodinium rotundatum* are among the representative gymnodinioids reported to bloom in Type I nutrient-enriched habitats, using representative examples from Ecuador, Japan, Korea, and Norway (Iizuka and Irie, 1969; Iizuka, 1972; Tangen, 1979; Park, 1991; Jimenez, 1993). This prevalence of gymnodinioid blooms in Type I habitats does not preclude blooms of 'armored' species. *Alexandrium minutum* appears to be particularly capable of blooming at high nutrient levels in similar habitats (Halim, 1960; Marasović and Pucher-Petkovic, 1991).

In habitats where nutrient levels are somewhat lower, but still elevated, various intermediate sized peridiniids, including *Heterocapsa triquetra* and *Scrippsiella trochoidea*, and prorocentroids, including *Prorocentrum micans* and *Prorocentrum minimum*, become important summer bloom taxa (Type II). The eutrophic inner Oslofjord is a representative Type II site (Braarud, 1945; Tangen, 1979). Type III blooms of large, attenuate and morphologically complex ceratians commonly develop during late summer or autumn successional stages in temperate and boreal coastal habitats. This assemblage extends offshore into stratified coastal waters and remains responsive to nutrient loading. Increased bloom events of *Ceratium* spp., notably *C. tripos*, in the Kattegat have been attributed to increased nutrient loading (Edler, 1984). Type III ceratian blooms often culminate in anoxia or hypoxic events, as in the German Bight (Hickel *et al.*, 1989), Kattegat (Granéli *et al.*, 1989) and New York Bight (Falkowski *et al.*, 1980).

A particularly interesting group along the onshore–offshore gradient are the HAB dinoflagellates adapted to the increased velocities associated with frontal zones, to the dampened but still elevated vertical mixing during relaxations in coastal upwelling, or while entrained within coastal currents, i.e. the frontal zone (Type IV), upwelling relaxation (Type V) and coastally-entrained (Type VI) HAB assemblages. Nutrient levels during blooms of these coastal assemblages are intermediate between those at the opposing ends of the onshore–offshore gradient (Figure 4). The classical frontal zone (Type IV) species is *Gymnodinium mikimotoi*—frequently identified as *Gyrodinium aureolum*, its 'look-alike'—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). This apparent habitat preference contrasts with the tendency of North Sea diatoms to dominate in tidally-mixed water

nearshore habitats and leads to local blooms. Exposure of Type V taxa to the coupled physical processes characterizing the active and relaxation phases of upwelling suggests that this life form must also tolerate the predominant physical stresses confronting Type IV and Type VI life forms (Figure 4), and that Types IV, V and VI show intergrading adaptations.

The well known toxic species, *Alexandrium fundyense* (Franks and Anderson, 1992; Anderson, 1997), *Pyrodinium bahamense* var. *compressum* (Seliger, 1993) and *Gymnodinium breve* (Steidinger *et al.*, 1998) are notable examples of Type VI HAB dinoflagellates adapted for entrainment and dispersal within coastal currents. The apparent dispersal of *Pyrodinium* within the Indo-Pacific region, and accompanied by devastating blooms, is particularly noteworthy [see (Hallegraeff and Maclean, 1989)]. Dispersal of ichthyotoxic *G. breve* within the Gulf Stream transporting it from its 'natural' habitat in the Gulf of Mexico has led to seedings and blooms in far-field coastal embayments (Tester *et al.*, 1991). Similar novel bloom episodes of a closely-related species have accompanied El Niño disturbances in New Zealand waters (Chang *et al.*, 1995). Although *G. breve* may differ significantly from other Type VI species in certain autecological traits, its ability to tolerate the shear/stress forces of coastal current entrainment is evident. It may even be a relict coastal upwelling relaxation species (Type V) in the Gulf of Mexico where upwelling may have been more common during ancient periods (Emslie and Morgan, 1994).

These three distinct 'mixing-drift' Types recognized based on their association with elevated turbulence and current shear exhibit behavior antithetical to the general perception that HAB dinoflagellates require a high degree of stratification to bloom and dampened turbulence to survive. Whatever adaptations allow Types IV, V and VI species to tolerate high shear/stress, all are still vulnerable to turbulence which, if too intense, can inhibit their growth, as shown for *A. tamarense* (var. '*excavatum*') and *L. polyedra* (White, 1976; Carreto *et al.*, 1986; Thomas and Gibson, 1990). The frontal zone/upwelling relaxation/coastal current bloom taxa (life forms) eventually might be re-classified as one Type, since the different species assigned to a given Type within this mixing-drift group (Types IV–VI) can also survive and bloom in related habitats. Thus, *A. tamarense*, *G. breve* and *G. mikimotoi* not only readily survive dispersal and grow while entrained within coastal currents, they also bloom in frontal zones. (*Alexandrium tamarense* and *P. bahamense* var. *compressum* also flourish in nutrient-enriched habitats.) Notwithstanding the various overlapping and intergrading traits of the Type IV–VI species, we tentatively distinguish among them in this initial effort at a HAB life form Type classification pending completion of a more detailed

analysis of associated cellular features and kinetics currently in progress.

Excluding *G. breve*, whose extreme toxicity is its primary shared cellular feature, Type IV to VI dinoflagellates are generally characterized by strong phototactic capability, chain formation, a perennating stage in their life cycle, marked behavioral and auto-aggregative ability, toxin production and induce mortality. They also exhibit markedly flexible and controlled behavior associated with their motility, such as the pronounced vertical aggregation exhibited by Type IV *G. mikimotoi* in the North Sea (Bjørnsen and Nielsen, 1991) and Type VI *Ceratium furca* (Edler and Olsson, 1985). The auto-regulated behavior of toxic *G. catenatum* observed in Spanish upwelling rias (Fraga *et al.*, 1989) particularly illustrates this group trait. Following relaxation of upwelling, the period when it blooms, *G. catenatum* increases its swimming speed (Fraga *et al.*, 1989) by forming longer chains, which can reach 64 cells chain⁻¹ and 2.0 mm in length (Blackburn *et al.*, 1989). This increased motility facilitates its retention within the habitat and allows it to undertake diel, nutrient-retrieval migrations into the underlying nutrient reservoir, two behaviorisms which promote its blooms (Fraga *et al.*, 1989; Fraga and Bakun, 1993). During periods of nutrient deficiency, *G. catenatum* reduces its chain size, abandons its serpentine swimming motion, and the cells (now in stationary growth phase) then hang vertically within the water column (Blackburn *et al.*, 1989).

Various *Dinophysis* spp. also tolerate coastal upwelling sites where they achieve modest blooms during upwelling relaxations, based on field studies along the Iberian peninsula [see (Reguera *et al.*, 1995)]. These taxa, however, appear to represent a transitional life form (Type VII)—the dinophysoids—along the onshore-offshore, mixing-nutrient gradient in being more attuned to less pronounced, smaller-scale convective currents than typifying Type V (upwelling relaxation) bloom species (Figure 4). Relatively-large garlanded dinophysoids belonging to the genus *Dinophysis* are also common in offshore coastal waters of lower nutrient levels and more pronounced seasonal stratification, and during similar conditions within shallower regions. Within their apparent preferred habitats, *Dinophysis* spp. frequently become aggregated within the streamlines accompanying small-scale, Langmuir circulation cells. Hence, erstwhile blooms of this slow-growing HAB assemblage may often result primarily from physical accumulation, rather than active growth (Lassus *et al.*, 1993). *Dinophysis acuta* can achieve maxima in two distinct hydrographic regimes (Reguera *et al.*, 1995): a summer bloom located deep (15–20 m) within the stratified layer below the pycnocline and available for spatial redistribution by wind-induced upwelling or internal waves; and autumnal, upper surface-layer blooms

accompanying advection of shelf waters not affected by upwelling events. The fastidious growth requirements of the dinophysoids, which have stymied their laboratory cultivation, are a notable feature of Type VII species increasingly recognized to have a mixotrophic tendency (Granéli *et al.*, 1995). This exacting ecophysiology, reminiscent of the well known difficulties experienced in efforts to cultivate oceanic *Trichodesmium*, contrasts with the relative ease with which Types I–VI HAB dinoflagellates can be cultivated.

Farther offshore along the mixing-nutrient gradient, the bloom capacity (= strategy) of the character dinoflagellate flora appears to be even more truncated than that characterizing the coastal dinophysoids. At this segment along the gradient, the flora shifts from known (to date) HAB taxa to the characteristic dinoflagellate vegetation (life forms) prominent there. Two dinoflagellate life-form Types are recognized within the very oligotrophic, highly stratified and deepened trophogenic zone of the sub-tropical and tropical oceanic provinces: a tropical oceanic flora (Type VIII) and tropical shade flora (Type IX). The dinophysoid architecture is elaborated upon even further by the tropical oceanic flora (Figure 4) adapted to highly stratified, oligotrophic, sub-tropical and tropical oceanic waters. This morphotype is vividly evident in the very large (generally), highly-ornamented representatives of *Amphisolenia*, *Dinophysis*, *Histioneis* and *Ornithocercus*, genera common in such habitats. Large ceratians of flamboyant morphometry are also commonplace, with evidence for vertical distributional patterns ordinated along specific irradiance preferences (Stemann Nielsen, 1939). Within the deeper waters of such water masses, a permanent tropical shade flora (Sournia, 1982b) of extremely large, bladder-type cells of *Pyrocystis* spp., such as *P. noctiluca*, occurs near the base of the euphotic zone, with a population maximum generally at 60–100 m (Swift and Meunier, 1976; Ballek and Swift, 1986). *Pyrocystis* spp. are capable of depth-keeping through regulation of cellular buoyancy. Coupled with cellular division, *Pyrocystis* has a gymnodinioid stage within its life cycle, a curious atavism to the predominant HAB type (Type I) characterizing the first stage of the habitat nutrient-mixing HAB morphotype ordination (Figure 4).

Obviously, numerous other species of different phylogenetic origins, morphotype and physiological characteristics co-occur with the HAB species typifying the different habitats recognized along the nutrient-mixing gradient. Large species co-exist with smaller species, just as diatoms co-exist with dinoflagellates, and bloom taxa with non-bloom taxa having similar morphometry, phylogeny and physiology. However, our analyses reveal that in habitats where very high nutrient levels occur in combination with marked stratification and reduced advection, the pre-

dominant HAB dinoflagellate taxa frequently selected for are small- to intermediate-sized gymnodinioids (Type I). Blooms of larger and morphometrically more complex HAB taxa are much rarer in such habitats. One can reasonably predict that neither the Type V species, *G. catenatum* (Hallegraeff and Fraga, 1998), nor Type IX *Pyrocystis* (Ballek and Swift, 1986), will ordinarily bloom under such conditions and in such areas. At the other extreme of the habitat gradient, i.e. extremely low nutrient levels, pronounced stratification and deepened euphotic zone, the character forms of the predominant dinoflagellate vegetation assemblages will be very large, motile, depth-keeping taxa which are often highly ornamented (Type IX). Smaller, highly motile and morphometrically-simple life forms are less characteristic in such habitats and therefore, one can reasonably predict that blooms of the Type II peridinioid/prorocentroid life form will not occur in such offshore oligotrophic habitats.

Between these two extremes of the nutrient-mixing gradient, the life-form characteristics of the HAB taxa typifying the seven intermediate habitats intergrade with the Type I and Type IX features (Figure 4). Gradients in cellular-based features having significant ecophysiological impacts accompany the gradient in dinoflagellate life form. There is a general tendency for cell size to increase along the nutrient-mixing gradient, and for the dominant Type cell shape to shift from the 'classical' gymnodinioid and peridinioid/prorocentroid forms to attenuated filiforms (because of cell lengthening and/or chain formation) and ovoidal forms, with the latter becoming progressively more ornamented or elaborate farther offshore in the increasingly nutrient-depauperate and highly-stratified water masses. Along this shape template, there is a general progression in cell size from 'small' to 'larger' to 'colonies' to 'huge' cells. This size/shape sequence leads to a general decrease in the ratio of cell surface area-to-cell volume (μm^{-1}) along the gradient. This influences the rates of growth and other metabolic processes such as photon capture, motility and phototactic capacity, nutrient retrieval migrations (Smayda, 1997b) etc. This is treated in greater detail by Smayda and Reynolds (in review). An increase in generation time and reduction in maximal reported abundance also generally accompany this onshore-offshore gradient in life form, cell size and cell shape. Heightened mixotrophic tendencies and increased endosymbiosis in Type VII to Type IX life forms also seem likely.

DISCUSSION

Our basic supposition that life-form properties override phylogenetic properties in the selection of species for HAB events requires demonstration that HAB species

indeed can be sub-grouped into life forms based on morphotype and habitat preference. Our success in being able to distinguish nine Types of HAB bloom events reflecting an array of HAB species with distinct morphotype features and specific habitat preferences along an onshore–offshore mixing–nutrient gradient satisfies this first requirement. The degree to which these Type–habitat associations conform with the Margalef and Reynolds’ models can now be evaluated.

A schematic map of the continuum of pelagic marine habitats along the onshore–offshore gradient of progressive change in the degree of mixing, irradiance available for photosynthesis and accessible nutrients is shown in Figure 5a. Overlap of the depicted habitats does not imply contiguity, rather that the mixing/irradiance/nutrient features in that box (i.e. habitat) overlap those found in adjacent boxes (most likely, the phasing, frequency and intensity differ). The diagonal relates the layout to Margalef’s (Margalef, 1978) main *r* versus *K* successional sequence. When the nine dinoflagellate life-form Types are overlain onto this habitat template (Figure 5b), their clear separation into Type habitat preferences and transitions into new Type assemblages at new combinations of degree of mixing and nutrient availability are very evident (Figure 5a). Dinoflagellate life forms ‘avoid’ the energy-limited, temperate winter–spring and major upwelling conditions favored by diatoms and their blooms (upper right section of Figure 5a,b). The mixing–drift-adapted Types IV, V and VI appear and cluster in habitats of diminished, but still pronounced, vertical mixing and shear/stress effects. These Types, which show analogies to Reynolds’ (Reynolds, 1995) *R* type of acclimating species, and their habitats are intermediate between the diatom-dominated provinces and the other dinoflagellate life-form Types favored by more pronounced stratification. That is, Types IV, V and VI taxa are more light controlled and biophysically-impacted than Types I, II, III, VIII and IX encountered to the left of the habitat template (Figure 5a,b). The latter five Types, clustered in the energy-replete, stratified habitats of the template, show analogies to Reynolds’ (Reynolds, 1995) *C* and *S* types of acclimating species. Since the combination of high stratification and high seasonal irradiance provides energy sufficiency, the availability of nutrient resource now becomes significant. This nutrient control becomes progressively greater with the increasing depth of the stratified layer along the onshore/offshore gradient, progressing from eutrophic coastal waters to highly-stratified tropical oceanic conditions. This nutrient effect is magnified by the relative duration of the physical structure (what Margalef referred to as increasing vertical segregation of the environment).

Ordination of the life-form Types along this continuum shows not only a clear succession from *r* to *K*

strategies, but this succession also occurs along a vertical axis of nutrient control, a sequence of life forms consistent with Reynolds’ (Reynolds, 1987; 1995) findings for freshwater phytoplankton (Figure 3). This behavior represents a major departure from Margalef’s Mandala, which posits the main successional sequence occurs across turbulence/nutrient axes (i.e. along a diagonal; Figures 1, 5a). We believe that the presumed correlation between degree of mixing and nutrient levels in the Mandala is not the essential interaction in the selection of life forms and their succession. There is no demonstrable correlation between these parameters significant to this aspect of phytoplankton behavior. As pointed out by Reynolds (Reynolds, 1986) based on freshwater mesocosm experiments, the nutrient and turbulence axes are independent variables, and the degree of mixing selects for different characters. In our marine examples taken from field conditions, significant differences in the level and degree of nutrient control can accompany relatively similar conditions of energy availability (stratification degree). The marked sequence from life-form Type I → II → III → VII → VIII → IX is an outcome of increasing nutrient control under energy-replete conditions. We believe that the more significant aspect of the turbulence axis is the degree of vertical, micro-habitat structural differentiation that it permits. It is generally accepted that such structure allows flagellates to utilize their marked motility-based behavioral capacities [see (Edler and Olsson, 1985; Bjørnsen and Nielsen, 1991; Smayda, 1997a)] to exploit the nutrient resource gradient, including nutrient-retrieval migrations, pycnocline blooms and vertical depth-keeping.

The ordination of the various life-form Types on the habitat template (Figure 5a,b) suggests the component dinoflagellates have different strategies consistent with *C*-*S*-*R* strategies recognized among freshwater phytoplankton species (Reynolds, 1984, 1985, 1995) and terrestrial vegetation (Grime, 1979). We suggest Types IV, V and VI more readily fulfil the role of disturbance-tolerant ruderals (*R*), Types I and II that of invasive competitors (*C*), and Types VII, VIII and IX have evolved ways to deal with the stress of low nutrient accessibility (*S*). *R* species occur in physically-disturbed water masses and are primarily attuning or acclimating strategists tolerant of, or dependent upon, entrainment within actively-mixed or circulating water layers. Among their traits are: pre-adaptations to shear/stress effects; effective light-harvesting antennae and cellular shape; or related adaptive form achieved through chain formation. Their abiding attributes enable their growth to be light-saturated at lower aggregate light levels than apply to other types of phytoplankton. They are anticipated to have slightly higher growth rates (exclusive of Types I and

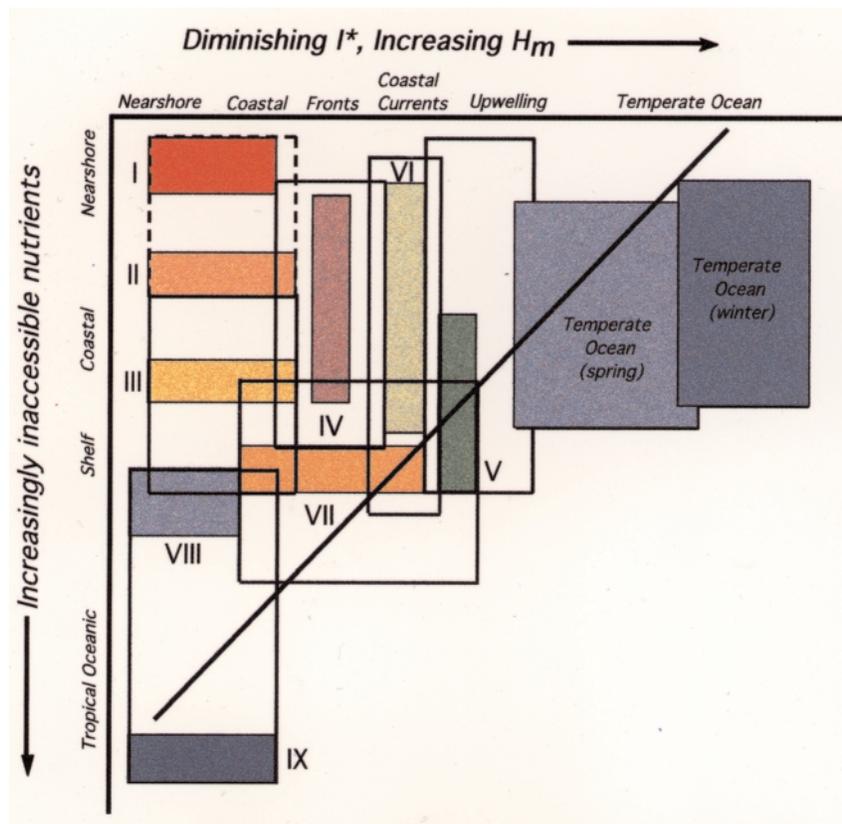
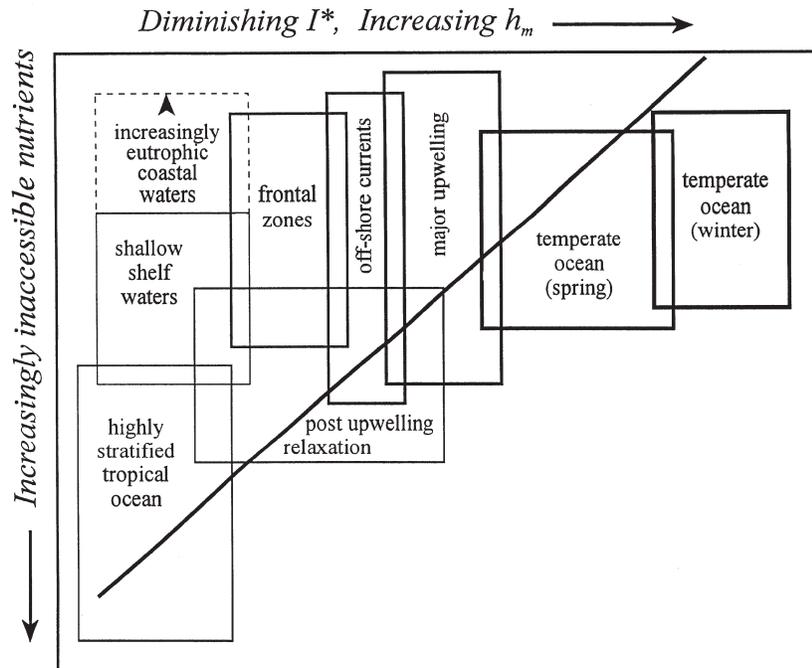


Fig. 5. a. Schematic matrix of pelagic marine habitats along an onshore–offshore gradient separating deep-mixed and well-stratified, but nutrient-deficient systems. I^* refers to irradiance level received by cells within water column; H_m represents depth of mixed-layer. Overlap of types within the habitat template schema does not always imply their contiguity. The diagonal approximates the main successional sequence depicted in Margalef *et al.* (Margalef *et al.*, 1979). **b.** Predominant dinoflagellate life-form Types (from Figure 4) associated with the turbulence–nutrient matrix (from Figure 5a) along an onshore–offshore continuum characterizing pelagic habitats. Type I = gymnodinioids; Type II = peridinioids and prorocentroids; Type III = ceratians; Type IV = frontal zone species; Type V = upwelling relaxation taxa; Type VI = coastal current entrained taxa; Type VII = dinophysoids; Type VIII = tropical oceanic flora; Type IX = tropical shade flora. Consult text for Type species.

II) than other dinoflagellates to counterbalance wind-induced washout. Their counterparts among diatoms are the spring-bloom species.

C species are primarily invasive species which often predominate following onset of elevated nutrient conditions, i.e. chemically-disturbed water bodies. They are generally smaller than R and S species, have faster growth rates and achieve greater abundances. When toxic, they are primarily ichthyotoxic. S species are primarily acquisitive species, typically very large, often highly ornamented, and capable of depth-keeping through motility alone or in combination with auto-regulated buoyancy. They are typically K-selected species which achieve modest but persistent abundance, and they often possess endosymbionts, or mixotrophically supplement their photo-autotrophy.

Not all species fit comfortably within a specific category; many show characters intermediate between them. This is particularly the case with our Type III, characterized by ceratians. *Ceratium* species are also represented among Type VI (coastal current entrainment) taxa (Franks *et al.*, 1989), Type V (upwelling relaxation) taxa, such as *C. furca* (Reguera *et al.*, 1995), and are commonplace Type VIII components. That is, the genus *Ceratium* appears to have C, S and R species' strategists. Taxa assigned to a specific Type in our classification are not necessarily restricted to that particular habitat or its growth conditions. *Gymnodinium catenatum*, a conspicuous component of Type V (upwelling relaxation blooms), is very successful in a shallow, relatively-small Tasmanian embayment where upwelling is not a factor. Its blooms there have been correlated with river run-off events in association with reductions in wind intensity (Hallegraeff *et al.*, 1995).

Margalef has suggested that the high resource and high energy portion of the Mandala (Figure 2) and, by implication, in Reynolds Intaglio (Figure 3), i.e. Type I and II habitats and C strategist bloom sites, is a habitat combination unresolved evolutionarily by phytoplankton, and contributes to catastrophic red tide outbreaks (Margalef, 1979). Contrary to the widespread notion that dinoflagellates prefer low nutrient conditions, we interpret some features of their physiology and bloom dynamics as indicative of their general preference for high nutrient levels. The K_s values for nutrient uptake of 14 dinoflagellates are considerably higher (usually $>2 \mu\text{M}$) than for diatoms of equivalent size, and generally (Smayda, 1997b). This has led Smayda (Smayda, 1997b) to suggest that dinoflagellates and flagellates generally have evolved four major adaptations to offset the ecological disadvantages of high K_s values: nutrient retrieval migrations, mixotrophic nutritional tendencies, allelochemically-enhanced interspecific competition, and allelopathic, anti-predation defense mechanisms. This low affinity indicates greater dependence on high nutrient levels. This is

reflected in the frequent associations of Types I, II and III life-form blooms with nutrient enrichment, and observations that introductions of life-form Types IV, V and VI into nutrient-enriched coastal areas can stimulate their blooms above those in their Type habitats (Blasco *et al.*, 1996; Lee and Kwak, 1986).

The use of a habitat template does not merely provide a scheme for classifying the phytoplankton on a functional basis; it also permits compositional changes to be tracked or predicted within the context of temporal changes affecting seasonal mixing, the development of vertical structure and nutrient partitioning. Thus, just as it is possible to represent much of the environmental variability by tracing the seasonally-changing Intaglio co-ordinates (see the simplified annual cycle in a Temperate stratifying lake sketched in Figure 6), the selective bias towards particular life-forms with advantageous adaptations also moves seasonally and, in turn, from R species to C species, then to S species and, with loss of vertical structure, back to R species. Different lakes with differing morphometries, stratification cycles and nutrient budgets can be distinguished in similar matrices (Reynolds, 1988). It is also possible to anticipate the compositional responses when the cycle is altered due to the intervention of external factors, such as storms or floods, or because there is some other change in the availability of critical nutrient resources.

We believe that this concept is readily transferable to the sea. However, referring to our recognition that large sections of the ocean are hostile to the support of an active phytoplankton, i.e. the 'void', on the grounds of poverty of

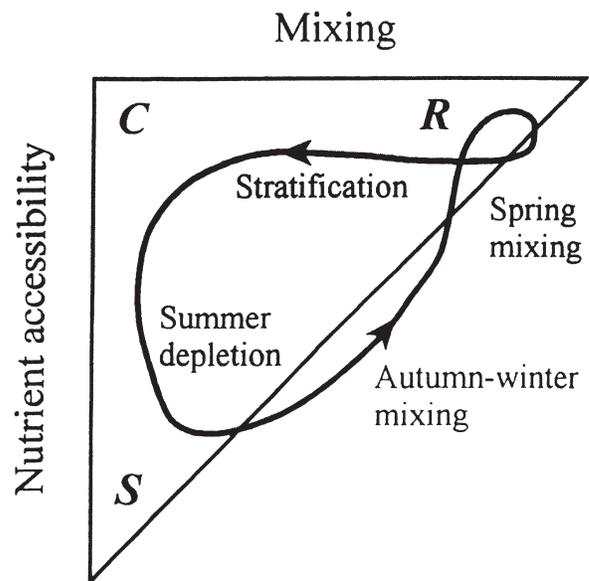


Fig. 6. Ideal year-long trace of the selective trajectory imposed by (temperate) seasonal habitat variability, and associated zones of C, S and R species' occurrences.

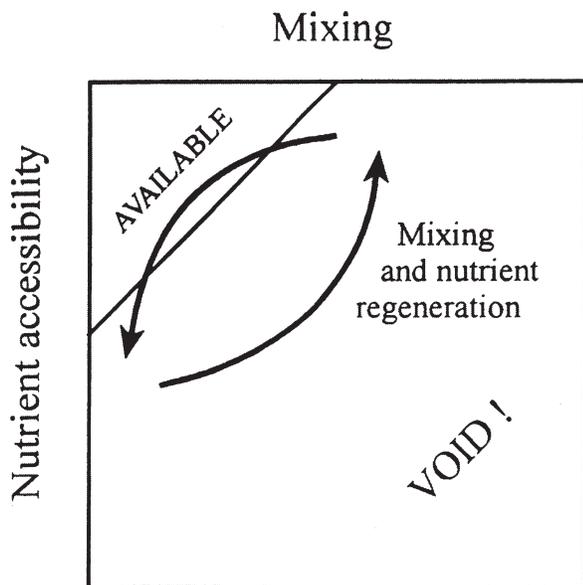


Fig. 7. Habitat suitable for phytoplankton growth in the sea is diminished (the 'void') mostly because it is too nutrient- and light-deficient to support phytoplankton growth. Region depicted in the upper left-hand corner and designated as 'available' shows the considerable restriction in habitat available with conditions suitable for phytoplankton exploitation.

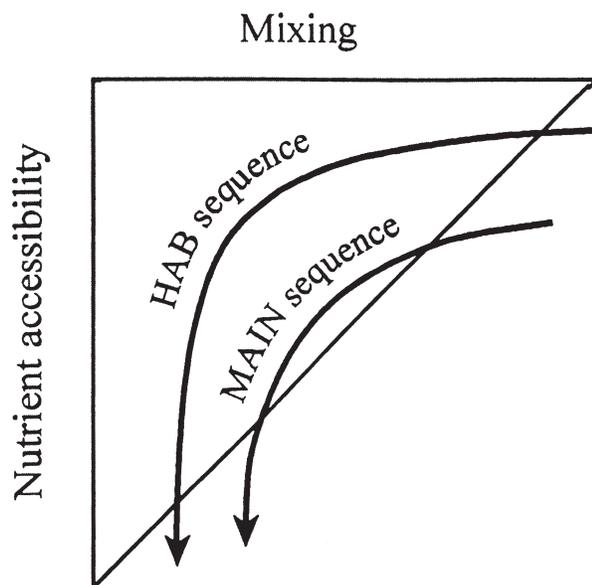


Fig. 8. Expansion of top left-hand corner of Figure 7 showing that the main phytoplankton sequence (literally) skirts the edge of the 'available' habitat, but, with more nutrients available, the trajectories pass deeper within the mixing-nutrient matrix selecting more strongly for C-strategist algae and HAB species.

both nutrients and harvestable light, a fair representation of the oceanic habitat template might come closer to the image depicted in Figure 7. In essence, the 'void' area dominates and the exploitable ('available') habitat occurs only in the top left-hand corner, where shallow depth or strong thermal stratification combine with an adequately supportive supply of crucially-limiting, regenerated nutrients. Phytoplankton development is confined to this area, with selection among the available species alternating predominantly between the most efficient light-harvesting (R) species and the most versatile nutrient scavengers (S). The trajectory, which closely parallels the hypotenuse of the triangle, indeed corresponds to the selection of the kinds of species picked up along Margalef's (Margalef, 1978; Margalef *et al.*, 1979) main sequence.

The Intaglio approach allows us to incorporate well-isolated habitats which, typically or temporally, are also replete with nutrients: those quiet estuaries and nutrient-rich lagoons that are home to C-strategist haptophytes (e.g. *Chrysochromulina*, *Isochrysis*), chlorophytes (e.g. *Dunaliella*, *Nannochloris*) and euglenophytes (*Eutreptia*), and also to those gymnodinioids, peridiniids and proocentroids highlighted in this account. The seasonal prevalence of such species among the assemblages of neritic and shelf waters would be representable by a mixing/nutrient-availability trajectory which intercepted the Intaglio higher with respect to the nutrient axis and which penetrated deeper

towards the apex before the deflection due to nutrient consumption (see Figure 8). The range of species able to exploit the conditions is thus widened and, all other factors being equal, these are most likely and most conspicuously to be the faster growing C species. We label this second trajectory 'HAB Sequence' because we think this model most readily conceptualizes the occurrence of harmful blooms of dinoflagellates and of other kinds of algae as the response to coastal enrichment of fast-growing species with invasive life-history strategies which, hitherto, have tended to confine species to limited ranges and somewhat specialized marine habitats.

In summary, our results suggest that for HAB dinoflagellates, distinctive associations occur between habitats ordinated along a resource and energy template and the composition of the communities. These communities can be described in terms of a life form, and these life forms have distinctive ecophysiological properties significant to their bloom dynamics, habitat selection and successions. This latter conclusion is based on extrapolations from Reynolds' (Reynolds, 1988, 1993, 1995) extensive studies on freshwater phytoplankton. Of the two models evaluated here, Reynolds Intaglio (Figure 3) provides greater fidelity to actual *in situ* HAB dinoflagellate community assembly than Margalef's Mandala (Figures 1, 2). The fact that Reynolds' model was based only on a consideration of freshwater phytoplankton species is particularly

significant. Its successful application to the marine phytoplankton indicates that the life-form Intaglio developed by him is not unique to either the freshwater or marine phytoplankton, but describes a basic feature of the phytoplanktonic life mode.

Even without, as yet, the full resolution on the attributes of individual species of the marine phytoplankton similar to that gained for freshwater species, or without precise information on specific events in the sea, we believe that the model helps us to explore and interpret, at least provisionally, the spatial and temporal occurrence of phytoplankton populations in the seas. In doing so, we emphasise again that the model is descriptive and not mechanistic. No area of the template is necessarily exclusive of species other than those said to be favored, nor do given habitat co-ordinates guarantee that the most advantaged species will dominate. For life-form selection has a stochastic aspect associated with which species conforming to the life form called for will be selected, and how this selection will take place. It is a statement about habitat disposition and growth opportunities for the species 'on site', where those with the most appropriate pre-adaptations and fielding the largest inocula are likely to gain the greatest advantage, i.e. being at the right place at the right time. In a related paper, we consider the rules of community assembly of harmful dinoflagellates from evolutionary and life-form perspectives (Smayda and Reynolds, in review).

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