Strategies of marine dinoflagellate survival and some rules of assembly

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Abstract

Dinoflagellate ecology is based on multiple adaptive strategies and species having diverse habitat preferences. Nine types of mixing-irradiance-nutrient habitats selecting for specific marine dinoflagellate life-form types are recognised, with five rules of assembly proposed to govern bloom-species selection and community organisation within these habitats. Assembly is moulded around an abiotic template of light energy, nutrient supply and physical mixing in permutative combinations. Species selected will have one of three basic (*C-, S-, R-*) strategies: colonist species (*C-*) which predominate in chemically disturbed habitats; nutrient stress tolerant species (*S-*), and species (*R-*) tolerant of shear/stress forces in physically disturbed water masses. This organisational plan of three major habitat variables and three major adaptive strategies is termed the 3-3 plan. The bloom behaviour and habitat specialisation of dinoflagellates and diatoms are compared. Dinoflagellates behave as annual species, bloom soloists, are ecophysiologically diverse, and habitat specialists whose blooms tend to be monospecific. Diatoms behave as perennial species, guild members, are habitat cosmopolites, have a relatively uniform bloom strategy based on species-rich pools and exhibit limited habitat specialisation. Dinoflagellate bloom-species selection follows a taxonomic hierarchical pathway which progresses from phylogenetic to generic to species selection, and in that sequence. Each hierarchical taxonomic level has its own adaptive requirements subject to rules of assembly. Dinoflagellates would appear to be well suited to exploit marine habitats and to be competitive with other phylogenetic groups, yet fail to do so.
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1. Introduction

Phytoplankton ecology traditionally has focused on primary production and its regulation, but the global increase in harmful algal blooms (HABs) and red tides has reawakened interest in phylogenetic and species-level responses, particularly that of dinoflagellates. A census of harmful and red tide bloom-species found among ten phylogenetic classes shows that dinoflagellates, evolutionarily and numerically, are the principal phytoplanktonic group to have incorporated toxicity or other harmful modes into their strategies (Table 1; Smayda, 1997a; Sournia, 1995). [Since new taxonomic and bloom species

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Table 1
Distribution of harmful (HAB) and benign 'red tide' (RT) bloom species among phylogenetic groups in the marine phytoplankton (modified from Sournia, 1995)

Class	Species Number		% HAB + RT in
	Total	ΣHAB + RT	Total Species
Raphidophyceae	12	9 (6)	75 (50)
Cyanophyceae	10	6 (2)	60 (20)
Euglenophyceae	37	9 (1)	24 (3)
Cryptophyceae	73	8 (0)	11 (0)
Dinophyceae	1880	184 (57)	10 (3)
Diatomophyceae	1300	89 (4)	7 (<1)
Chrysophyceae	126	7 (1)	6 (<1)
Chlorophyceae	122	6 (0)	5 (0)
Prymnesiophyceae	303	14 (5)	5 (2)
Prasinophyceae	136	5 (0)	4 (0)
Σ	3999	337 (76)	8 (2)

( ) = number, or percent of harmful species in total for phylogenetic group.

continue to be reported, the number (percent of total) of harmful species within each phylogenetic group (Table 1) subject to damage]. Phylogenetic groups that evolved prior (chlorophytes, prasinophytes, cryptophytes) and subsequently (coccolithophorids, diatoms) to the dinoflagellates have muted toxic capacities. Raphidophytes and cyanophytes have a higher frequency of harmful species, but their low biodiversity limits their contribution to the overall bloom-species pool dominated by dinoflagellates. About 200 dinoflagellate species, or 10% of the total number ($\sim$ 2000), achieve toxic blooms or benign red tides. Of these, approximately 3% (ca. 60 species) are reported to be harmful. Relative to other phylogenetic groups, dinoflagellates account for 75% of all harmful phytoplankton species, with four genera pre-eminent: *Alexandrium*, *Dinophysis*, *Gymnodinium* and *Prorocentrum*. The toxic capacity (specialisation) of the dinoflagellates is further revealed by the diversity of their phycotoxins (Hallegraeff, 1993) and their multiple modes of harmful impact (Smayda, 1997a).

Of the approximately 200 dinoflagellate species reported to produce HABs (n = $\sim$ 60) and red tides (n = $\sim$ 130), about 75% (n = 141) occur in two of the five major lineages that characterise dinoflagellate evolution (see Frontispiece in Taylor, 1987), with species from two Orders – Peridiniales and Gymnodiniales-particularly prominent. The distribu-

tion of benign (BEN) and harmful (HAB) bloom taxa in these Orders is as follows (Sournia, 1995):

	BEN	HAB
Peridiniales	53/788 = 7%	22/788 = 3%
Gymnodiniales	52/529 = 10%	14/529 = 3%
• of total	105/130 = 81%	36/60 = 60%

All phylogenetic groups have species whose blooms (red tides) periodically discolour the sea surface, but are not harmful (Table 1). Dinoflagellate species, once again, are prominent in such blooms.

The ecological traits and adaptive strategies that dinoflagellates have acquired evolutionarily, and how they facilitate their increasingly successful exploitation of, and blooms in global coastal waters are poorly understood. These aspects are the focus of this paper, and will be evaluated from the perspectives of dinoflagellate biodiversity, community organisation and assembly, and bloom features. Enquiry into the adaptive specialisms and the clusters of dinoflagellate species that have them is also relevant to the ongoing effort to define phytoplankton functional groups (see Reynolds et al., 2002).

2. Dinoflagellate morphological and species diversity

Among phytoplanktonic groups, dinoflagellates stand out for their species richness (Table 1), morphological diversity, and adaptive radiation in colonising the diverse habitats found in the sea. The approximately 2000 species recognised (Table 1; Sournia, 1995) include species organised along morphological lines reminiscent of the invertebrate kingdom, with helminth-like (*Haplozoon*), jellyfish-like (*Kofoidinium*), parasitic (*Blastodinium*) and ocelloid (= have rudimentary visual capacity (*Nematodinium*) morphotypes accompanying the more classical dinoflagellate morphotypes (see Frontispiece in Taylor, 1987). In addition to a pelagic life-mode, dinoflagellates colonise tidal pools, sediment (psammic) and sea-ice environments, and have also established endophytic, symbiotic and parasitic associations (see Taylor, 1987). Broad nutritional diversity accompanies their morphological and habitat diversity. Obligate auto-

trophy is the exception, rather than the rule; heterotrophs outnumber autotrophs, and have evolved various mechanisms to ingest prey (Elbrächter, 1991); many species are capable of both photosynthesis and heterotrophy, while some, such as *Pfiesteria piscicida*, use predatory attack strategies (Burkholder and Glasgow, 1997). Efforts to characterise dinoflagellate bloom-species behaviour must consider the convergent and divergent features of their cellular, population and community behaviour.

The morphological, nutritional and habitat diversity of the dinoflagellates, notwithstanding, a reasonable assumption is that species having similar features and behaviour have similar ecologies, while species that differ significantly in morphology and nutritionally have different ecologies and adaptive strategies.

3. Assembly and organisation of dinoflagellate communities

Dinoflagellates, as all pelagic microalgae, must be able to survive and grow under conditions of high physical disturbance and the intense stress of light and nutrient limitation to achieve a planktonic life-mode. The critical stage in their life history, whether seasonally, interannually or regionally, is not exposure to optimal habitat conditions for growth, which are rare, but enduring the more prolonged periods of sub-optimal conditions. Phytoplankton must have strategies to survive sub-optimal conditions. This axiom led Reynolds (1988) to hypothesise that freshwater phytoplankton species collectively have evolved three types of adaptive strategies to survive the permutations of habitat disturbance and stress that they experience: they are good competitors, stress-tolerant and disturbance-tolerant — adaptations expected also to affect community organisation. Reynolds suggested that their adaptations for competition allow phytoplankton to exploit habitats and environments saturated by light and in nutrients needed for photosynthesis and growth. Physiological investment in rapid growth and reproduction, with an ability to do so before other species, would enhance their competitive ability. Tolerance of stress would allow species to survive and function under conditions of severe nutrient depletion. Disturbance-tolerance would allow species to withstand frequent or continuous turbulent transport

through the light gradient and advective translocations. The strength of these adaptations was expected to vary among species.

Reynolds generally confirmed his concept of adaptive strategies. He established that freshwater phytoplankton species distributed over a variety of habitats formed distinct associations independent of phylogeny, and indicative of particular environments (see Reynolds, 1997). These taxonomic associations, when mapped against the accompanying distributions of habitat nutrients, irradiance and the degree of physical turbulence, revealed that the indicator species could be subgrouped into the three primary adaptive strategies anticipated by Reynolds. These groups of species were classified as having *C*-(= competitors, opportunistic colonists), *S*-(stress-tolerant) and *R*-(disturbance-tolerant, or ruderal) strategies (Reynolds, 1988, 1997). The morphological, physiological and distributional features of the species within each of the *C*-, *S*- and *R*-strategies are coherent.

Smayda and Reynolds (2001) recently established that marine species share the adaptive strategies of freshwater phytoplankton. These adaptive strategies appear to be basic features of the evolutionary ecology of phytoplankton, and transcend the selective effect that differences in habitat salinity (and other limnetic and marine distinctions) have on species selection and community organisation. Smayda and Reynolds were led to evaluate whether marine dinoflagellate bloom-species have similar strategies, after their application of Margalef's Mandala (Margalef, 1978; Margalef et al., 1979) to describe habitat selection of bloom-species was marginally successful. The Mandala positions red tide blooms in the ecological space of high nutrient levels and low turbulence, and groups all red tides as similar phenomena independent of the bloom-species or bloom-habitat. The nutrient-turbulence interaction in the Mandala requires external input to provide the high nutrient levels called for, since the dampened mixing intrinsic to low turbulence is a poor nutrient-pump. This restriction would confine red tide blooms to periods (habitats) of high nutrient levels supplied from terrestrial sources. [The high nutrient levels associated with upwellings accompany physical conditions that the Mandala depicts as antagonistic to red tide blooms.] Yet, newer data compromise this notion of red tide singularity, with numerous exceptions to this paradigm, including occurrences of major

harmful blooms in oligotrophic seas, e.g. *Karenia brevis* in the Gulf of Mexico (Steidinger et al., 1998), and blooms that develop during the relatively turbulent, intermittent upwelling relaxations (Smayda, 2000, 2002a).

Field observations indicate that dinoflagellate bloom-species have neither a monotonous habitat preference, nor uniform response. Smayda and Reynolds (2001) recognised nine different pelagic habitats in which dinoflagellates bloom (Figs. 1 and 2). Ordinated along an onshore–offshore gradient of decreasing nutrient, reduced mixing and deepened euphotic zone (= diminished irradiance), each of the nine types of mixing-irradiance-nutrient habitats is characterised by a specific dinoflagellate life-form Type having both a distinctive morphotype and habitat preference. Dinoflagellate bloom-species do not cluster into, nor depend upon a single, basic ecological zone of high irradiance, low turbulence and elevated nutrients in order to bloom. Bloom-species have diverse, rather than uniform habitat preferences. The multiple life-form Types found indicate that dinoflagellates have evolved multiple adaptive strategies, rather than an ecology based on a common strategy. Of special interest, and similar to freshwater species, Smayda and Reynolds (2001) were able to classify marine dinoflagellate bloom-species as *C*-, *S*- and *R*-strategists based on their habitat match-ups.

The successful application to the marine phytoplankton of the life-form concept and associated adaptive strategies developed by Reynolds for freshwater species seemingly describes a basic feature of the phytoplanktonic life-mode. It suggests that phytoplankton organise into communities moulded around an abiotic template of light energy, nutrient

- **Type I** (= *Gymndinioids*)

  Gymnodinium spp., *Gyrodinium instriatum, Heterocapsa rotundata*
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- **Type II** (= *Peridinians / Prorocentroids*)

  Heterocapsa triquetra, Scrippsiella trochoidea, Prorocentrum micans, Prorocentrum minimum
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- **Type III** *(= Ceratians)*

  Ceratium tripos, Ceratium fusus, Ceratium lineatum
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- **Type IV** *(= Frontal Zone Taxa)*

  Karenia mikimotoi, Alexandrium tamarense
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- **Type V** *(= Upwelling Relaxation Taxa)*

  Gymnodinium catenatum, Lingulodinium polyedrum
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- **Type VI** *(= Coastal Current Entrained Taxa)*

  Karenia brevis, Ceratium spp., *Pyrodinium bahamense* var. *compressum*
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- **Type VII** *(= Dinophysoids)*

  Dinophysis acuta, Dinophysis acuminata
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- **Type VIII** *(= Tropical Oceanic Flora)*

  Amphisolenia, Histioneis, Ornithocercus, Ceratium spp.
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- **Type IX** *(= Tropical Shade Flora)*

  Pyrocystis noctiluca, Pyrocystis pyriformis

Fig. 1. Dinoflagellate bloom and vegetation life-form Types, and representative species along an onshore–offshore gradient of decreasing nutrients, reduced mixing and deepened euphotic zone (modified from Smayda and Reynolds, 2001).
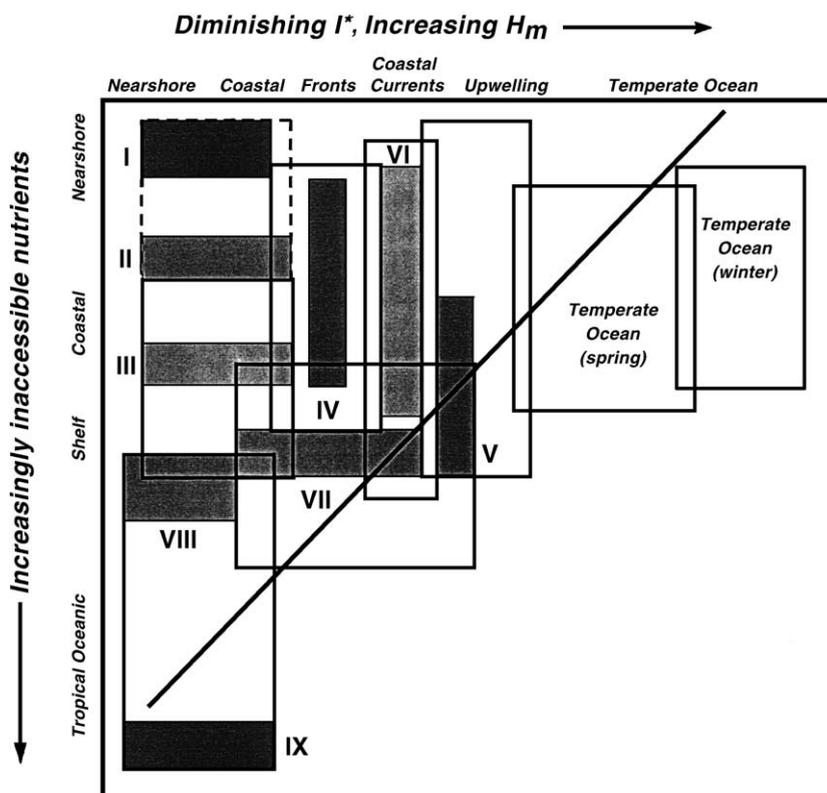
Fig. 2. Predominant dinoflagellate life-form Types associated with the turbulence-nutrient matrix along an onshore–offshore continuum characterizing pelagic habitats. Type I = gymnodinioids; Type II = peridinioids and prorocentroids; Type III = ceratians; Type IV = frontal zone species; Type V = upwelling relaxation taxa; Type VI = coastal current entrained taxa; Type VII = dinophysoids; Type VIII = tropical oceanic flora; Type IX = tropical shade flora. 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. (1979). Consult Fig. 1 for Type species (from Smayda and Reynolds, 2001).

supply and physical mixing in permutative combinations, with the species selected to fill the accompanying niche structure having one of the three basic (*C-, S-, R-*) strategies recognised. This relatively simple organisational plan of three major habitat variables and three major adaptive strategies, termed the 3-3 plan, on which phytoplankton behaviour is based simplifies efforts to quantify the mechanisms of species selection and community assembly. The present contribution represents our initial steps towards establishing the rules of assembly by which marine dinoflagellate communities are organised; in this, we build upon the life-form and adaptive strategy Types recognised in our previous publication (Smayda and Reynolds, 2001). It is also offered as a contribution to the development of a functional group classification of phytoplankton called for by Reynolds et al. (2002).

4. Rules of assembly of dinoflagellate communities and selection of species

The basic abiotic habitat template of permutative combinations of mixing-irradiance-nutrients around which phytoplankton communities, both freshwater and marine, are organised, also selects for, and assembles dinoflagellate species into communities (Figs. 1 and 2). The tightness of the life-form associations suggests that their assembly occurs in accordance with specific rules. Five basic rules of assembly are evident, with additional ones likely.

4.1. Assembly Rule I: Specific habitat conditions select for specific life-forms

The first rule of assembly derives from a notable characteristic of phytoplankton community organisation, and termed the *axiom of distinct associations.* Just as Reynolds (1997) and Reynolds et al. (2002), found that freshwater species formed distinct associations indicative of particular habitat types, marine phytoplankton communities likewise have predictable species-pairings, vegetative and life-form associations, 'plankton types' and 'plankton regions' that are associated with specific habitats and occur on temporal and spatial scales, and successively (Figs. 1 and 2; Braarud et al., 1953; Ramsfjell, 1960; Smayda, 1980; Smayda and Reynolds, 2001). This leads to the First Rule of Assembly: The composition and assembly of dinoflagellate communities are habitat dependent, with specific habitat conditions (factors) selecting for the life-forms assembled. The corollary of this rule is that dinoflagellates are not free-ranging, eurytolerant cosmopolites, but have specific habitat requirements.

4.2. Assembly Rule II: Life-forms are selected primarily on a physical–chemical habitat template of turbulence-irradiance-nutrients

The chaotic assembly of life-forms expected to occur in response to habitat variability and the large number of potential regulatory factors, and because of species richness, is not evident. Rather, the habitat component of the 3-3 plan of community assembly, discussed earlier, is operative and the basis of Assembly Rule 2: Life-form selection is primarily the result of abiotic factor selection, and specifically in response to the physical–chemical habitat template combinations of turbulence-irradiance-nutrients. In addition to being congruent with the axiom of distinct associations, the rule of abiotic assembly is supported by two major lines of evidence. It is consistent with the nine Types of dinoflagellate life-forms detectable along the onshore–offshore continuum of variable mixing-irradiance-nutrient conditions (Figs. 1 and 2; Smayda and Reynolds, 2001). Bloom-species of Type I life-forms, for example, which thrive in nutrient-enriched coastal waters, do not bloom in oceanic, oligotrophic Type IX habitats, nor do Type IX life-forms occur and bloom

in Type I habitats. Assembly Rule 2 is also consistent with the basic principles of community assembly established by Margalef's classical Mandala (Margalef, 1978; Margalef et al., 1979). That is, the selection and succession of phytoplankton life-forms are related to the turbulence-nutrient axes which describe the seasonal excursions and regional differences in water mass physico-chemical properties.

4.3. Assembly Rule III: Dinoflagellates employ three basic life-form strategies, C-, S- and R- strategies, to exploit abiotic habitat conditions, with r-and K-selected species found within each strategy

Permutations in the habitat mixing-irradiance-nutrient components underlying Assembly Rule II rule out a common dinoflagellate life-form strategy. Planktonic algae are adapted to exploit undisturbed, resource-replete habitats, or to survive in resource-depleted habitats, or to function under the high-frequency light fluctuations of well-mixed water columns (Reynolds, 1997). These adaptations, the adaptive strategy component of the 3-3 plan of community assembly discussed earlier, and based primarily on distributional and bloom behaviour observations, form the basis of Assembly Rule 3: Dinoflagellates use three basic strategies, the **C-**, **S-** and **R-**strategies, to exploit permutations in habitat mixing-irradiance-nutrient conditions, and within each strategy classical **r-**and **K-**strategist species occur.

C-, **S-** and **R-**strategist species are clearly recognisable among the dinoflagellate life-form Types distributed along the onshore–offshore gradient in habitat mixing-irradiance-nutrient features (Figs. 1 and 2; Smayda and Reynolds, 2001). In chemically disturbed (= nutrient-enriched through anthropogenic activities), near-shore habitats, Types I and II, which are relatively shallow and water mass stratification is seasonally intense, the predominant bloom-species are typically **C-**strategist (= colonist) species (Fig. 1). These species are invasive, small (have a high cell surface area to volume ratio), competitive, fast growing, proliferate after a period of nutrient elevation, achieve great abundance, and when toxic are primarily ichthyotoxic. Blooms of **C-**strategist *Gymnodinium* species, *Heterocapsa rotundata*, *Heterocapsa triquetra*, *Scrippsiella trochoidea* and several *Prorocentrum* species are common in Type I and II habitats.

In the oligotrophic, highly stratified, deep euphotic habitats, including sub-tropical and tropical oceanic provinces (Types VII, VIII, IX), a nutrient stress-tolerant ensemble of *S*-strategist species predominates (Figs. 1 and 2). Primarily *acquisitive*, *S*-strategists are typically very large species, often highly ornamented, and capable of depth-keeping by means of motility or auto-regulated buoyancy (i.e. *Noctiluca*, *Pyrocystis*). Slow growing, they achieve modest, but persistent abundance, often possess endosymbionts, or supplement their photo-autotrophy by mixotrophy. Fluctuations in their abundance may be driven more by physical accumulation and dispersion than by active growth, with toxic effects occurring at very low population levels (see Smayda, 1997a).

In physically disturbed water masses, habitat Types IV, V, VI, tolerance of the shear/stress forces and the ability to capture sufficient light energy for photosynthesis are more important than adaptations to circumvent the stress of nutrient over-enrichment (*C*-strategists) and oligonutrification (*S*-strategists). This requirement selects for *R*-strategist (= ruderal) species, which are mixing-drift adapted, disturbance-tolerant and primarily *attuning* or *acclimating* strategists (Figs. 1 and 2). Their light-harvesting pigments, cellular shape, strong phototaxic capability and auto-regulated, motility-based behaviour, sometimes facilitated by chain formation (*Gymnodinium catenatum*, *Pyrodinium bahamense* var. *compressum*), permit them to become light-saturated and to grow at lower aggregate light levels than *C*-and *S*-strategists. *R*-strategists are anticipated to have slightly higher growth rates than other dinoflagellates (excluding life-form Types I, II) to counterbalance population losses because of washout and shear/stress damage accompanying occurrence in mixing-drift habitats.

Within each of the *C*-, *S*-, *R*-strategies of Assembly Rule 3, species-specific differences, manifested as differences in response rates to environmental changes and in intrinsic growth rates, are expected. These differences correspond to the classical distinction made between *r*-species and *K*-species, with *r*-species capable of developing relatively rapid rates of growth (*r*) in situ and having quicker response times than *K*-species, which are obligately slower growing, saturate at lower levels of resource, and can better tolerate or accommodate to periods of resource stress (Reynolds, 1988; Smayda and Reynolds, 2001). This invocation of *C*-, *S*-, *R*-based adaptive strategies differs from the traditional view that bloom species selection follows exclusively an *r*-versus *K*-pathway (see Margalef et al., 1979; Smayda, 2000). It should be pointed out that not all species fit comfortably within a specific *C*-, *S*-, *R*-category, and show intermediate characters between them (Smayda and Reynolds, 2001). Ceratian species (Type III) particularly intergrade between *C*-, *S*-, *R*-strategies. The ecophysiology and species-specific requirements of species provisionally assigned as representative of the various life-forms and *C*-, *S*-, *R*-strategies are being evaluated to determine whether they are consistent with their apparent habitat preferences and adaptive strategies recognised by us. The results obtained would also help to establish whether the species comprising the life-form groupings recognised respond similarly to the sets of environmental conditions accompanying their assigned habitat preferences (see Reynolds et al., (2002), and particularly those associated with Assembly Rule III.

4.4. Assembly Rule IV: Bloom-species selection follows a taxonomic hierarchical pathway which progresses from phylogenetic to generic to species selection, and in that sequence

The selection of bloom-species in accordance with Assembly Rules I to III is the terminal result of a multiple selection process formalised as Assembly Rule IV: bloom-species selection follows a taxonomic hierarchical pathway, progressing from phylogenetic to generic to species selection, and in that sequence. Appropriate phylogenetic and generic selections are required for, and must precede selection of the bloom-species. While failure of a given species to bloom may result from unfavourable niche structure, it may also be the result of unfavourable conditions which select against its phylogenetic group or genus.

Assembly Rule IV derives from the 'open niche' concept introduced by Smayda and Villareal (1989) to deal with the unpredictable species blooms which occur during summer in Narragansett Bay. The conceptual basis of the open niche is outlined in Fig. 3, with the principle considered to be generally applicable to bloom-species selection. Unlike winter–spring diatom blooms, the phylogenetic groups and affiliated species selected to bloom during the summer
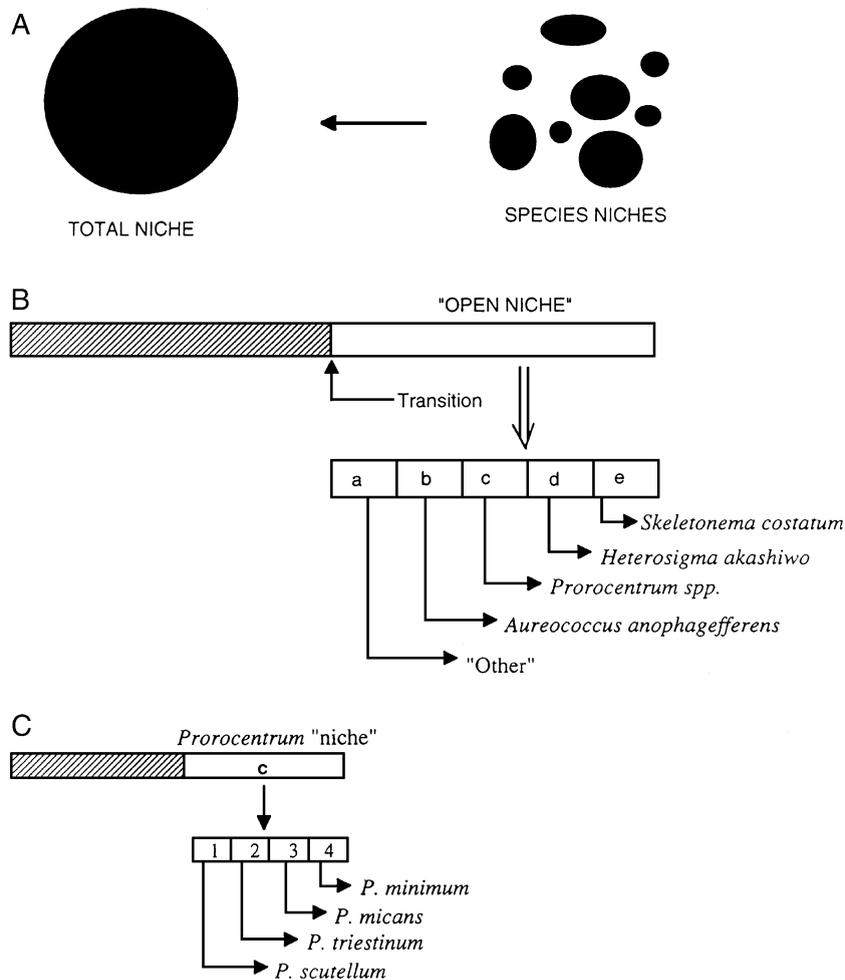
Fig. 3. A. Conceptualisation of phytoplankton niche space as the total niche size equalling the sum of the individual species niches. B. Niche transitions in Narragansett Bay between winter–spring bloom period (hatched area) and open niche period (open area) developing during late spring–summer. The phylogenetic group then selected to bloom is unpredictable, but has included pelagophytes (b), dinoflagellates (c), raphidophytes (d), diatoms (e) and other phylogenetic groups (a). The species indicated are important bloom-taxa in Narragansett Bay. C. The four candidate bloom species of *Prorocentrum* which will potentially bloom, should that dinoflagellate genus (C–c) be selected to bloom during the open niche period. The hatched area in C represents other dinoflagellate genera available to bloom. See text for further details.

open niche period in Narragansett Bay are unpredictable. It is unpredictable whether a diatom (usually *Skeletonema costatum*) or flagellate will then bloom and, if the latter, equally unpredictable whether the species will be a dinoflagellate, raphidophyte, pelagophyte, or from another phylogenetic group. All have bloomed. This uncertainty over phylogenetic bloom group selection is followed by another uncertainty-the bloom genus selected from within the chosen phylogeny. When the dinoflagellate niche is selected for, *Heterocapsa*, *Prorocentrum* and *Scrippsiella* are among the candidate bloom genera (Fig. 3-Bc). If the genus selected for is species-rich, there is yet another unpredictable selection- which of the candidate species will bloom. Selection for the dinoflagellate phylogenetic niche in Narragansett Bay often leads to selection of *Prorocentrum* over *Heterocapsa* and *Scrippsiella*. Which of the four *Prorocentrum* candidate species then blooms is unpredictable: *Prorocentrum micans*, *P. minimum*, *P. scutellum* and

P. triestinum—all have bloomed (Smayda, unpublished; Fig. 3-Cc).

It is important to recognise that each taxonomic level has its own adaptive requirements, if not strategy, subject to rules of assembly. Phylogenetically, for example, diatoms require Si to bloom, dinoflagellates do not. Among genera, marine *Ceratium* species do not form resting stages, toxic *Alexandrium* species do. We suggest that the critical hierarchical niche/adaptive strategy occurs at the generic level. This conclusion is prompted by the high degree of generic restriction found among the nine dinoflagellate life-forms recognised (Figs. 1 and 2). The dinoflagellate HAB expansion problem might therefore be viewed ecologically as primarily an issue of harmful genus selection, and secondarily one of species selection (Smayda, 2002b). The proposed importance of generic selection partly underpins Assembly Rule V.

4.5. Assembly Rule V: Selection of species within a given life-form is stochastic

Although bloom-species selection is the terminal stage in the hierarchical selection process in Assembly Rule IV, which of the candidate species suited to the habitat niche structure will be selected to bloom is usually unpredictable (Smayda, 1997b; Smayda and Reynolds, 2001). This unpredictability is such a major feature of the ca. 200 known HAB and red tide dinoflagellate species (Table 1), and in such stark contrast to the much greater predictability of diatom bloom periods and species successions, that it prompts Assembly Rule V: The selection of species within a given life-form is stochastic. That is, as Smayda and Reynolds (2001) have phrased it: the selection of species possessing the mandated life-form attributes is the stochastic result of being 'in the right place at the right time', and at suitable inoculum levels. Assembly Rule V is consistent with the principle of chaotic behaviour that Huisman and Weissing (2001) recently derived after demonstrating through modelling that the outcome of phytoplankton multispecies competitions for limiting resources is fundamentally unpredictable. They conclude (p. 492 in Huisman and Weissing, 2001) that 'even with full knowledge of all species traits, it may be fundamentally impossible to forecast the dominance of toxic species'.

Unlike species selections, *C*-, *S*-, *R*-life-form selections are not stochastic. They are under tight regulation by the life-form defining abiotic template of mixing-irradiance-nutrients, with predictable *C*-, *S*-*R*-strategist responses (Figs. 1 and 2), as stipulated by Assembly Rule III. Nor does Assembly Rule V contradict the other rules of assembly. For a species to be selected, it must be available in the local species-pool, a presence that is variable. Species-pools are continuously restructured through recruitment of species from diverse sources: seedings of indigenous and allochthonous species; of holoplanktonic species, of meroplanktonic species aperiodically seeded via excystment of resting stages deposited in seed banks, etc. The dispersal of species, including mixing- drift life-form Types IV, V, VI (Figs. 1 and 2), resulting from wind-induced mixing, frontal zone movements, and larger circulation patterns inoculates recipient habitats and modifies local species pools (Pitcher and Boyd, 1996). Life-cycle features may also be a factor. Type II peridinians generally have a resting stage, unlike Type I gymnodinioids (Fig. 1). This may contribute to differences in their recruitment (seeding) behaviour. Grazing susceptibility and the allelopathic ability of the species to thwart predation by stunning, repelling or killing grazers is another variable attribute of dinoflagellate species (Smayda, 1992), and may contribute to unpredictability by favouring selection of certain species over others. Allelochemical competitive ability may favour still other species (Smayda, 1997b) and influence species selection outcomes. Given these abiotic and biotic aspects, the stochastic selection of bloom species and, hence, their low predictability of occurrence are not difficult to comprehend.

5. Contrasting bloom behaviour and habitat specialisation of dinoflagellates and diatoms

Adaptive strategies overlap among phylogenies. The degree of overlap influences the extent to which the different phylogenies (and species) can co-exist (Assembly Rule IV). Blooms and distributional characteristics provide informative windows into adaptive strategies and the extent of phylogenetic adaptive overlap, since bloom behaviour integrates the adaptive strategies that a phylogenetic group has. In the

hierarchical taxonomic progression leading to bloom species selection (Assembly Rule IV), the degree to which the three taxonomic entities involved (phylogenetic, genus, species) are intrinsically preadapted to overcome habitat resistance to selection is of interest. For example, can an algal species develop adaptive strategies or are they an intrinsic, inflexible part of the species? Strain variability is a well-documented characteristic of phytoplankton species, both among regionally separated populations and co-occurring cells within a given population. This suggests that individual species indeed have an engrained adaptive flexibility. But one might argue that adaptive flexibility is greatest at the phylogenetic level (and least at the species level?) since considerable taxonomic and ecophysiological diversity is available within phylogenies to achieve successful niche filling and matchup. However, this might be the default outcome accruing to the winner(s) of a more rigorous phylogenetically based competition and/or ecophysiology. For example, consider the contrasting bloom behaviour of dinoflagellates and diatoms. Diatom blooms (independent of their species composition) have five major features: coastal (including upwelling systems) diatom blooms are annually recurrent, predictable, prolonged, of high species diversity, and a species succession occurs (Guillard and Kilham, 1977; Smayda, 1980). Dinoflagellate blooms, in contrast, usually are unpredictable, ephemeral, have low species diversity, and exhibit a rudimentary species succession, if any. During the annually recurrent, prolonged diatom blooms, multiple generations (2^n) of the bloom-species are produced. These population waves provide multiple opportunities for dispersal, range maintenance and, for species with resting stages, frequent seed bank replenishment. Dinoflagellate blooms lack these advantages. Many species appear to have a 'boom and bust' bloom strategy and, based on this bloom behaviour, to behave as annual species irrespective of their life-form. Diatoms, in contrast, tend to behave as perennial species. High species diversity characterises diatom communities, which suggests that the assembled species and their successions represent ecological guilds having relatively low competition coefficients. Dinoflagellate blooms, in contrast, tend to be monospecific (see Smayda, 1997b). This feature together with their unpredictable, and brief blooms

and rudimentary species succession suggests that dinoflagellates lack the guild-oriented, communal strategies of diatoms. Rather, dinoflagellates appear to behave as 'soloists' in their exploitation habitat resources.

Diatoms conform more closely than dinoflagellates to the basic features of bloom behaviour, community biodiversity and species succession commonly attributed to phytoplankton. Diatoms display limited habitat specialisation in contrast to the diverse habitat preferences of dinoflagellates (Figs. 1 and 2; Guillard and Kilham, 1977; Smayda, 1980). Excluding latitudinal differences induced by temperature (i.e., Arctic, Boreal, Tropical species), diatom species typical of annual bloom cycles and successions tend to be similar along the onshore-offshore gradient in habitats (Figs. 1 and 2) to which dinoflagellates have specialised. Diatoms exhibit a high degree of cosmopolitanism. The diatom spring-bloom community, for example, is regionally similar in the open continental shelf waters, bays, estuaries and coastal lagoons off New England (Marshall, 1976). Unique fjordic, upwelling or mixing-drift diatom assemblages are likewise not evident (Skjoldal et al., 1995; Smayda, 2000). These distributional and bloom patterns reveal that diatoms are (ecophysiologically) eurytolerant of habitat diversity in contrast to the habitat specialisation of dinoflagellates (Figs. 1 and 2). These contrasts reveal another significant phylogenetic divergence: dinoflagellates exhibit high diversity in habitat preference, but low bloom-species diversity (behaviour) within these habitats. Diatoms have the opposite pattern: low habitat diversity, but high bloom-species diversity. The similar diatom bloom-species composition found across the dinoflagellate life-form habitats suggests that diatom bloom strategies are based on availability of a common species-pool, whereas dinoflagellates rely on unique species pools in their habitat specialisation and adaptive strategies, a trait which furthers the stochastic species selections codified in Assembly Rule V. Diatoms also appear to follow a strategy of saturating the habitat, i.e., have high species redundancy (diversity), whereas dinoflagellates in their habitat specialisation sacrifice redundancy (= have low diversity; monospecific blooms) for ecophysiological diversity (Fig. 1), i.e., they behave as soloists, rather than as members of a guild.

In summary, dinoflagellates exhibit unique differences from diatoms in their adaptive ecologies which may be aiding their increasingly successful exploitation of coastal waters and global bloom expansion. Dinoflagellates behave as annual species, bloom soloists, are ecophysiologically diverse, and habitat specialists, whereas diatoms behave as perennial species, guild members and are habitat cosmopolites. Diatoms have a relatively uniform bloom strategy based on species-rich pools and exhibit limited habitat specialisation. Dinoflagellates have multiple life-form strategies consistent with their diverse habitat specialisations, but rely on impoverished bloom species pools.

6. An unresolved aspect of dinoflagellate organisation, assembly and strategies

The unpredictable bloom and annual and regional occurrence patterns of the dinoflagellates are fundamental characteristics of the dinoflagellates irrespective of their life-form Types (Figs. 1 and 2), adaptive strategies and the rules of assembly. The opposite behaviour might be expected. They are biodiverse, have multiple habitat preferences, multiple strategies, habitat eurytolerance, are nutritionally versatile, and also biophysically competent to withstand the range of turbulent motion and the shear/stress accompanying physical advection (Smayda, 2002a). These traits would appear to make dinoflagellates particularly well suited to exploit marine habitats and to be competitive with other phylogenetic groups, yet they fail to do so. What is holding them in check? Dinoflagellates do not appear to bloom in the fashion of diatoms, nor otherwise conform to classical phytoplankton behaviour (see Smayda, 1997a,b). Should this exceptional ecology be confirmed, then some fundamental questions concerning the phytoplankton life-mode and evolution of its attributed behaviour would have to be addressed.

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