

Review

Adaptive Ecology, Growth Strategies and the Global Bloom Expansion of Dinoflagellates

THEODORE J. SMAYDA*

Graduate School of Oceanography, University of Rhode Island, Kingston, RI 02881, U.S.A.

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Dinoflagellates exhibit unique differences from diatoms in their adaptive ecologies that may be favoring 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 specialization. Dinoflagellates have multiple life-form strategies consistent with their diverse habitat specializations, but rely on impoverished bloom species pools. Niche structure and dinoflagellate competition for niche space are considered. The “open niche period” formulated originally for Narragansett Bay is extrapolated as a general bloom paradigm. It is suggested that successful niche occupancy leading to blooms involves adaptive strategies at three hierarchical taxonomic elements: phylogenetic, generic and species-specific, and in that sequence. Transoceanic expatriation of emigrant species leading to indigenous status and blooms requires completion of a three-stage colonization process. Anthropogenic seedings are not, in themselves, bloom stimulation events; they are only the first phase of a multiple-step process. The organismal and niche features required for a hidden flora member to become a bloom species are considered, and the interplay between niche structure, habitat carrying capacity, colonization requirements and stochasticity as factors in the changing global bloom behavior of dinoflagellates discussed. The question is posed whether traditional perspectives of phytoplankton behavior apply completely to dinoflagellates.

Keywords:

- Harmful blooms,
- dinoflagellates,
- adaptive strategies,
- niche behavior,
- emigration and colonization,
- ballast water,
- diatom contrasts.

1. Introduction

The global increase in the frequency, intensity and geographic spread of harmful microalgal blooms (HABs) has attracted considerable attention, partly because of adverse effects on public health, seafood safety and aquaculture. These practical concerns have stimulated much research, including efforts to develop mitigation techniques (see Kim, 2000). Mitigation efforts are exercises in crisis control: they may abort or reduce the negative effects of a harmful bloom, but cannot prevent recurrences. Ultimate control requires identification of the factors which regulate HABs, followed by actions to relieve those conditions. This requires insight into the basic features of the HAB expansion, including the adap-

tive strategies of HAB species—the concern of this article. Dinoflagellate adaptive ecology will be focused upon because among the phylogenetic groups driving the global HAB expansion, dinoflagellates are the major contributor (Sournia, 1995; Smayda, 1997a). Given the apparent global stimulation in dinoflagellate blooms, it would appear that among the phylogenetic groups making up the phytoplankton their adaptations and niche requirements in particular are being favored in global coastal waters at present.

What is it, then, about the ecophysiology and growth strategies of dinoflagellates that has led to their increasingly successful exploitation of coastal waters globally, their altered bloom behavior, and their prominent role in the global HAB expansion? Four primary causation theories have been advanced (Hallegraeff, 1993): the effects of cultural eutrophication, aquaculture initiatives, unusual climatological conditions, and spreading of species

* E-mail address: tsmayda@gso.uri.edu

through dispersal of resting cysts in ballast water or in transplanted shellfish stocks. The first three of these mechanisms deal with habitat modification—regrouped here as the “changing environment” theory. The fourth mechanism—the “emigration” theory—addresses geographic range expansion. (The distinction between emigration and immigration is discussed below.) The merits of these mechanisms will not be evaluated, since population dynamics lie outside the scope of this article. Rather, the focus is on the adaptive ecologies that dinoflagellates may use to facilitate their exploitation of, and expansion in global coastal waters. The adaptive strategies that other phylogenetic groups may have will be considered primarily in order to contrast apparent dinoflagellate adaptations.

2. Dinoflagellate vs. Diatom Bloom Behavior as Phylogenetically Adaptive Responses

Adaptations have their origins in evolutionary history. Comparative phylogenetic analyses of the ecophysiological behavior exhibited by the different phylogenetic groups in meeting the common and vital requirements of their phytoplanktonic life mode provide insight into their adaptations. Diatoms and flagellates, for example, generally have similar nutrient requirements (excluding the need for silica), but diatoms, when nutrient-limited, seek to alleviate limitation through a sink-strategy, while flagellates use a swim-strategy (Smayda, 1997a). These different behavioral strategies to remedy nutrient limitation, in turn, require linked strategies to protect the cells against light-limitation as they sink or swim within the water column during their nutrient-gathering searches. The differing pigment signatures among phylogenetic groups (Jeffrey and Vesk, 1997) partly reveal the adaptations (=absorption and action spectra) evolved for photon capture and wavelength reception in a variable light environment, and needed for photosynthesis and in phototaxis. Adaptive strategies within a phylogenetic group are not only coupled; multiple strategies may be present to achieve a basic requirement or response. The use of mixotrophy by many dinoflagellates (Hansen, 1998) to supplement inorganic nutrient uptake during swim strategy behavior to reduce nutrient limitation is an example.

2.1 Contrasting bloom behavior of dinoflagellates and diatoms

Adaptive strategies overlap among phylogenies. The degree of overlap influences the extent to which the different phylogenies (and species) co-existent within communities compete for available niche space. Blooms provide useful windows into these strategies and the extent of phylogenetic adaptive overlap, since bloom behavior

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

Fig. 1. Dinoflagellate bloom and vegetation life-form types and representative species found along an onshore-offshore gradient of decreasing nutrients, reduced mixing, and deepened euphotic zone (from Smayda and Reynolds, 2001).

integrates a phylogenetic group's adaptive strategies. Consider the contrasting bloom behavior of dinoflagellates and diatoms. Diatom blooms (independent of 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, of low species diversity, and exhibit a rudimentary species succession, if any. During the annually recurrent, prolonged diatom blooms, multiple generations (2ⁿ) 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 their bloom behavior, to behave as annual species irrespective of their life-form (Fig. 1). Diatoms, in contrast, tend to behave as perennial species. High species diversity characterizes diatom communities, which suggests that the assembled species

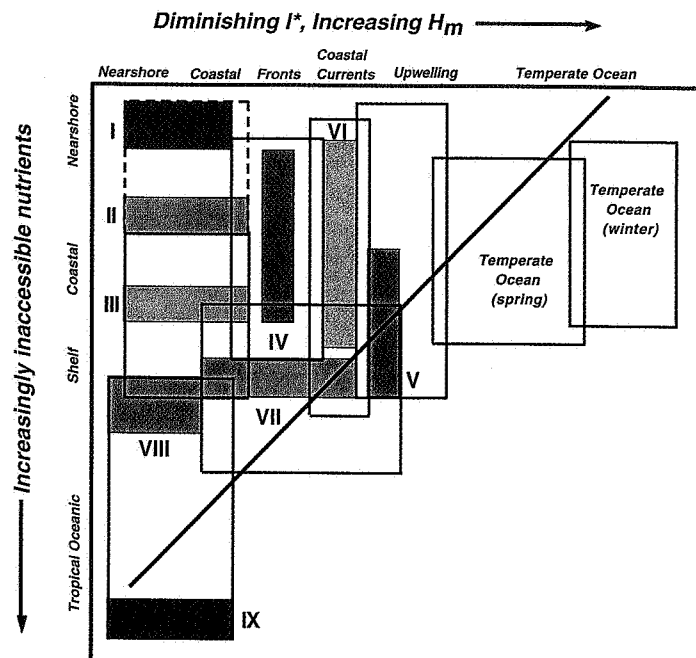


Fig. 2. Predominant dinoflagellate life-form Types associated with the turbulence-nutrient matrix along an onshore-offshore continuum characterizing pelagic habitats. Type I = gymnodinioids; Type II = peridinioids and proro-centroids; Type III = ceratians; Type IV = frontal zone species; Type V = upwelling 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.

and their successions represent ecological guilds having relatively low competition coefficients. Dinoflagellate blooms, in contrast, tend to be monospecific (see Smayda, 1997a). This feature, together with their unpredictable, brief blooms and relative absence of a species succession, suggests that dinoflagellates lack the guild-oriented, communal strategies of diatoms. Rather, dinoflagellates appear to behave as “soloists” in exploiting habitat resources.

This contrasting bloom behavior of diatoms and dinoflagellates is a major phylogenetic difference. Diatoms conform more closely than dinoflagellates to the basic features of bloom behavior, community biodiversity and species succession commonly attributed to phytoplankton. Discussion of the corollary that bloom behavior and community assembly properties are evolved traits, rather than equivalent and intrinsic among the phylogenies represented in the phytoplankton, lies beyond the scope of this paper. I suggest that the distinctive bloom behavior of dinoflagellates relative to diatoms reflects unique adaptive strategies currently favoring their increasingly successful exploitation of coastal waters and HAB expansion.

3. Dinoflagellate Life-Forms and Adaptive Strategies

3.1 Dinoflagellate habitat types and life-forms

A common view is that dinoflagellate blooms cluster into a single, basic red tide ecological zone of high irradiance, low turbulence and elevated nutrients, within which bloom species selection follows an *r*- versus *K*-pathway (Margalef *et al.*, 1979; Smayda, 2000). This paradigm and soloist bloom behavior, suggested to characterize dinoflagellate species, might be interpreted as evidence for a monotonous habitat preference and uniform response. Smayda and Reynolds (2001) have concluded otherwise—that dinoflagellates have diverse rather than uniform habitat preferences and adaptive strategies. They recognize nine distinct habitats in which dinoflagellates bloom, with each habitat characterized by a more or less specific bloom (life-form) assemblage. Three basic life-form strategies, termed *C*-, *S*- and *R*-strategies, were also recognized, within each of which the classic *r*- and *K*-species occur. The nine habitats and associated life-form types (Figs. 1 and 2) ordinate on a habitat-template of decreasing nutrient, reduced mixing and deepened euphotic zone (=diminished irradiance) along an onshore-

offshore gradient. Type I habitats are relatively shallow, nutrient-enriched, nearshore waters in which small gymnodinioid species tend to predominate. Type II habitats have lower, but still elevated nutrient levels; peridinioids and prorocentroids predominate. In more open coastal waters (Type III), ceratians dominate blooms. Progressing offshore, a "mixing-drift" group consisting of three habitat/bloom Types occurs: species adapted to the increased velocities associated with frontal zones (Type IV), and those which tolerate entrainment within coastal currents (Type VI), or exposure (Type V) to damped, but still high vertical mixing coefficients during upwelling relaxations. That dinoflagellates assemble into life-form types having specific habitat preferences is further evident from observations that Types I (nutrient-enriched) and V (upwelling relaxation) species, for example, are not found among the Tropical Oceanic Flora (Type VIII), nor are dinophysoids (Type VII) usual in Type I habitats.

Species representative of life-form Types I through VII are participating in the HAB expansion, with novel blooms of rare species from the "hidden flora" and newly described taxa prominent in habitat Types I, II and III. Although phycotoxin occurrence patterns are unevenly distributed among dinoflagellates, there is a high incidence of paralytic shellfish toxin occurrence among mixing-drift species (Types IV, V, VI), while species causing diarrhetic shellfish poisoning (DSP) are concentrated among dinophysoids (Type VII). Dieoffs induced by harmful blooms of Type I gymnodinioids and Type II peridinioids usually result from factors other than phycotoxins. The accompanying mortality is usually localized, whereas ichthyotoxic species in Types IV to VI often form large blooms and cause widespread damage. The adaptive value of phycotoxicity to dinoflagellates remains obscure.

In summary, the occurrence of multiple life-form types among dinoflagellates indicates that they have evolved multiple adaptive strategies rather than rely on a common strategy. This is contrary to dogma, and contrasts with the adaptive conservatism that seemingly characterizes diatoms.

3.2 Contrasting habitat specialization of dinoflagellates and diatoms

Diatoms display limited habitat specialization, in contrast to the diverse habitat preferences of dinoflagellates (Guillard and Kilham, 1997; 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 (Fig. 2) to which dinoflagellates have specialized (Fig. 1). 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 (ecophysiologicaly) eurytolerant of habitat diversity in contrast to the habitat specialization of dinoflagellates (Figs. 1 and 2). These contrasts also reveal another significant phylogenetic divergence: dinoflagellates exhibit high diversity in habitat preference, but low bloom species diversity (behavior) 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 specialization and adaptive strategies. Diatoms also appear to follow a strategy of saturating the habitat, i.e., high species redundancy (diversity), whereas dinoflagellates in their habitat specialization 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 the changing environment theory of the HAB expansion, the implicit habitat changes would be expected to alter diatom bloom behavior in parallel with that observed for dinoflagellates and other flagellates. This does not appear to be happening. The contrasting ecological and species pool strategies of dinoflagellates and diatoms, along with the habitat eurytolerance and cosmopolitanism of diatoms, may be factors in their differing global bloom responses, including the relative rarity of anomalous diatom blooms within the HAB phenomenon. The habitat specialization of dinoflagellates, seemingly, would make them particularly responsive to niche changes as they open, close and modify. What adaptive strategies accompany dinoflagellate habitat specialization, and how does niche structure select for bloom species?

3.3 C-, S- and R-strategies of dinoflagellate life-forms

The nine habitats to which dinoflagellates have specialized (Fig. 2) occur as a continuum of progressive change in degree of mixing, irradiance for photosynthesis, and accessible nutrients. In Fig. 2, overlap of adjacent habitats (i.e., boxes) indicates overlapping mixing/irradiance/nutrient features. Just as habitat conditions overlap, so do species requirements for nutrients, irradiance and watermass mixing/stratification; hence, dinoflagellates have evolved adaptive strategies to achieve their life-form and habitat specializations. Three primary adaptive strategies, termed C-, S- R-strategies, become

evident when the nine life-form Types are ordinated onto the habitat-template (Figs. 1 and 2). These strategies were first recognized among freshwater phytoplankton species (Reynolds, 1988; Smayda and Reynolds, 2001), which suggests that they are general attributes of phytoplankton.

Types I and II habitats are chemically disturbed (nutrient-enriched), relatively shallow, and watermass stratification is seasonally intense. The predominant bloom species in such habitats (Fig. 1) typically are *invasive*—*C*-strategist—colonist species. They are competitive, small (i.e., have a high cell surface area to volume ratio), fast growing, proliferate after a period of nutrient elevation, achieve great abundance and, when toxic, are primarily ichthyotoxic. At the other extreme of nutrient availability in the oligotrophic, highly stratified, deep euphotic zone of sub-tropical and tropical oceanic provinces, *S*-strategists predominate, such as life-form Types VII, VIII, IX (Fig. 1). Primarily *acquisitive*, *S*-species are nutrient-stress tolerant. Typically very large, they are often highly ornamented and capable of depth-keeping by means of motility, alone or in combination with 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. Among *S*-species, dinophysoids (Type VII) primarily are participating in the HAB expansion, but in this their population behavior may differ from that of *C*- and *R*-strategists. Oscillations in their abundance may be driven more by physical accumulation than by active growth, with toxic effects occurring at very low population levels (see Smayda, 1997b). Life-form Types VIII and IX have yet to be implicated in HAB events.

R-strategist species occur in, and tolerate the shear/stress forces of physically disturbed watermasses. These mixing-drift adapted and disturbance-tolerant species (Types IV, V, VI) are primarily *attuning* or *acclimating* strategists. Pre-adapted to withstand shear/stress effects, they are anticipated to have slightly higher growth rates than other dinoflagellates (excluding Types I, II) to counterbalance wind-induced washout. Their light-harvesting pigments, cellular shape, and auto-regulated behavior achieved through chain formation allow growth to become light-saturated at lower aggregate light levels than in the other dinoflagellate types. *R*-species are generally characterized by strong phototactic capability, chain formation, a perennating stage in their life cycle, marked behavioral and auto-aggregative ability, and produce toxins and/or induce mortality. The auto-regulated behavior of toxic *G. catenatum* in Spanish upwelling rias is a particularly elegant example of the motility-based behavior of *R*-strategists (Fraga *et al.*, 1989).

The habitat specializations and *C-S-R* strategies of dinoflagellates are tied to niche structure. The remarkable diversity, bloom unpredictability and stochasticity

characterizing dinoflagellate HAB events presumably have their foundation in similarly variable niche behavior.

4. Dinoflagellate Bloom Behavior and Niches

4.1 The niche perspective

Unusual blooms, geographic range extensions, newly achieved competitive dominance, and sudden appearances of new taxa (species, genera) characterize the HAB expansion. This behavior is symptomatic of an altered niche structure and community ecology, since species do not live in isolation, but in communities of species governed by rules of assembly. Niches are properties of species, with each species defining its own niche (Tokeshi, 1999). Accordingly, the HAB phenomenon must be analyzed from the ecological perspectives of species coexistence, community ecology, habitat space, and resource spectra. The following questions result: to what extent have HAB species acquired the ability to exploit new resources (niches), either not previously available to them or being utilized by existing species? Where adaptive occupancies (invasions) occur, have new adaptive zones (see Tokeshi, 1996), i.e., vacant niche space, become available for exploitation by emigrant and indigenous HAB species? Or is niche fragmentation more important, which allows more species or selected replacement species to share in the common resource pools within bloom habitats? Adaptive invasion and niche fragmentation are not mutually exclusive (Tokeshi, 1996); they can co-occur and even merge to influence phylogenetic, generic, species, and sibling species bloom-behavior.

This complexity and the limited ecophysiological data available make it difficult to link niche apportionment models and the adaptive strategies that HAB species may use in competing for niche space. However, it is essential to view the HAB phenomenon as an expression of altered niche availability and exploitation, rather than as a series of random bloom events resulting in changing collections of species within a community. This perspective is applied in addressing two basic features of the HAB expansion which the changing environment and emigration theories seek to explain. How does a hidden flora component become a major bloom species, and how does an emigrant bloom species enter a community? The issues of the “open niche” and niche diversification along taxonomic hierarchies are considered first.

4.2 The open niche period

The “open niche” concept was introduced (Smayda and Villareal, 1989a) to deal with the unpredictable species blooms in Narragansett Bay following the annual winter-spring diatom bloom. While the underlying taxa may be specific to that bay, the open niche principle is probably generally applicable to HAB species. Transition

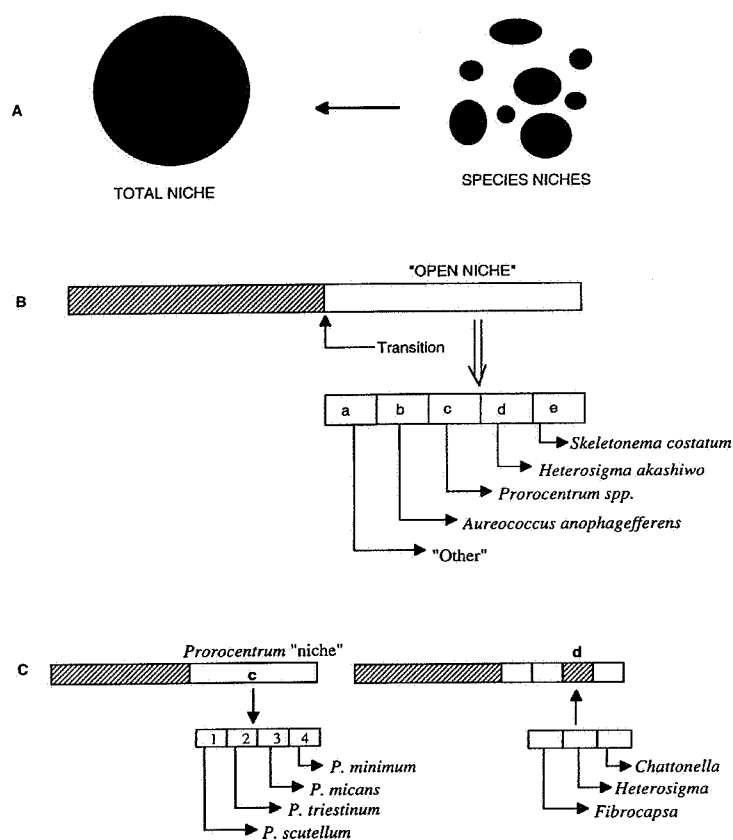


Fig. 3. A. Conceptualization of phytoplankton niche space showing total niche size to be the sum of the individual species niches having variable breadth. B. Niche transitions in Narragansett Bay between winter-spring bloom period (hatched area) and open niche period during late spring–summer (open area) when the phylogenetic group selected to bloom is unpredictable, but has included pelagophytes (b), dinoflagellates (c), raphidophytes (d), diatoms (e), and representatives of other phylogenetic groups (a). The species indicated are important bloom taxa in Narragansett Bay. Cc. The four candidate bloom species of *Prorocentrum* which will potentially bloom, should that dinoflagellate genus be selected to bloom during the open niche period in Narragansett Bay. Cd. Candidate raphidophyte genera available to bloom when the raphidophyte bloom niche is selected for in Narragansett Bay. See text for further details.

into the open niche period begins in May–June and persists through the summer. Unlike the annual diatom bloom, the phylogenetic groups and affiliated species selected to bloom are then unpredictable. Specifically, it is unpredictable whether a diatom (usually *Skeletonema costatum*) or flagellate will bloom during the open niche period, and if the latter, it is also unpredictable whether it will be a dinoflagellate, raphidophyte, or a species representing another phylogenetic group. The time of initiation, duration and magnitude of the bloom events and coexisting species selections are also unpredictable and variable (Karentz and Smayda, 1984; Smayda, 1998).

The conceptual basis of the open niche is outlined in Fig. 3; the bloom taxa behavior depicted is that found in Narragansett Bay. The total niche is divisible into individual species niches (Fig. 3-A). Total niche space may be neither seasonally constant, nor fully occupied (see Tokeshi, 1996, 1999). Since niches are inherently multi-

dimensional, i.e., incorporate all of the factors governing a species persistence, the actual niche structure and its variability are indeterminable. The term “open niche”, as used in the present context, therefore, is probably more appropriately designated the “open niche period” (Fig. 3-B). On a taxonomic hierarchical scale, three (major) unpredictable selections occur during the open niche period: the phylogenetic, genus and species bloom selections. Within this hierarchy, phylogenetic group selection determines whether the dominant bloom species will be a diatom, dinoflagellate, raphidophyte, pelagophyte, or some other phylogeny (Pratt, 1966; Karentz and Smayda, 1984; Smayda and Villareal, 1989a, b; Li and Smayda, 2000). Phylogenetic selection appears to be strong, since only one group (at a time) usually dominates the open niche period (=HAB season), such as the exceptional, five-month bloom in 1985 of the previously unknown, harmful pelagophyte *Aureococcus anophagefferens* (Smayda

and Villareal, 1989a, b). Phylogenetic selections are not exclusive; subdominant species blooms representing other phylogenies co-occur with the dominant phylogenetic bloom species. During the *A. anophagefferens* bloom, diatoms, dinoflagellates, raphidophytes and euglenid species achieved mini-blooms (Smayda and Villareal, 1989a). Selection for a given phylogeny can be rare; *Aureococcus* is predicted to have a bloom frequency in Narragansett Bay of twice per century based on long-term monitoring (Li and Smayda, 2000). Similar tendencies characterize genus and species bloom behavior.

Uncertainty as to which phylogenetic bloom-group will be selected is followed by another uncertainty—the bloom genus selected. When the raphidophyte niche is selected for, *Chattonella*, *Fibrocapsa* and *Heterosigma*, all of which occur in Narragansett Bay, become the candidate bloom genera (Fig. 3-Cd). *Heterosigma akashiwo* is usually selected (Pratt, 1966; Li and Smayda, 2000). If the genus selected for is species-rich, there is yet another unpredictable selection—which candidate species will bloom. Selection for the dinoflagellate phylogenetic niche 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 (Fig. 3-Cc).

4.3 Importance of genus selection and need for escape strategies

The open niche problem suggests that dinoflagellates need three hierarchically distinct adaptive strategies to achieve niche occupancy and bloom success: an overarching phylogenetic-level niche/strategy, within which genus level niches/strategies occur, and these, in turn, refined into species-specific niches/strategies. The latter may have a subspecies component wherein different gene complexes provide intraspecific (strain) variability in adaptive capability (see Tokeshi, 1999). Which of the three hierarchical taxonomic strategies is most determinative of the HAB expansion? Successful niche exploitation by HAB species clearly follows only after success at the phylogenetic and genus levels, i.e., taxonomic “gates” that must be passed through. Each taxonomic level has its own adaptive requirements, if not strategy. Considerable phylogenetic niche overlap probably occurs, given the shared and common needs of the phytoplankton life mode, as well as overlap among congeneric and sibling species. I suggest that the critical hierarchical niche/adaptive strategy occurs at the generic level, a tentative conclusion prompted by the high degree of generic restriction found among the nine dinoflagellate life-forms recognized (Fig. 1). While overlap of genera among life-form types occurs (some of this may be due to unresolved taxonomy), species habitat preferences and associated

ecophysiological specialization tend to segregate along generic lines (see Subsection 3.1). The dinoflagellate HAB expansion problem might therefore be viewed ecologically as primarily an issue of harmful genus selection, and secondarily one of species selection.

The unpredictable bloom taxa selections and bloom diversity during the open niche period in Narragansett Bay are, as pointed out, common features of HAB species (see also Smayda and Reynolds, 2001). Applying Tokeshi's (1996) principle that a species' abundance is directly related to niche space, i.e., a larger niche results in greater abundance, the temporally variable fluctuations in HAB species abundance, persistence and occurrence during the open niche period, and generally, can be linked to the underlying niche structure. The rare, five-month *A. anophagefferens* bloom; the *H. akashiwo* blooms when raphidophytes are selected for; the selection of *Prorocentrum* from among other dinoflagellate genera; and the variable selection of one of the four *Prorocentrum* bloom candidate species, all as noted for Narragansett Bay (Fig. 3), must reflect variable openings, closings, expansions and contractions of the respective niches. This behavior suggests that flagellate niche structure is intrinsically much more unstable than diatom niche structure. Accordingly, dinoflagellate species must include escape or survival mechanisms within their adaptive strategies to compensate for the low probability that the required niche space within their life-form habitat will persist interannually. Species which produce resting stages have such protection. In species lacking this life-cycle feature, adaptations along the line of the mixing-drift life forms (Figs. 1 and 2) may provide the escape option. A species may have both compensating adaptations to niche impermanence.

5. Emigration, Range Expansion and Dinoflagellates Adaptive Strategies

The high incidence of unique blooms of minor, rare and alien species is a puzzling feature of the HAB expansion. It is unlikely that these novel blooms have a common explanation. Successful colonization, attainment of competitive dominance, altered niche structure, and stochastic coincidence of species presence and favorable niche matchups (see Smayda and Reynolds, 2001) are undoubtedly contributory, but difficult to quantify. Nonetheless, this behavior has an explanation rooted in the same ecological principle: colonization and niche exploitation. Emigrant (invasive) species must complete a three-stage process before they can bloom (i.e., establish a metapopulation) within invaded habitats: regional translocation, colonization, and achievement of competitive dominance (no matter the duration or frequency of its blooms), and in that sequence. Within this sequence, the colonization phase has three stages.

For successful expatriation, bioinvasive species (emigrants) of transoceanic or distant interregional origin must first survive the large-scale dispersal and growth impediments along their emigration pathway. In contrast, some species are always available for local immigrations (seedlings), being members of regionally contiguous populations and communities, such as Type VI life-forms (Figs. 1 and 2). Immigrant species have already achieved colonization, but share with emigrant species the need for receptive niches to bloom in invaded habitats (refugia). In the case of minor and rare indigenous species exhibiting novel blooms, emigration/immigration is not an issue—it has already been achieved. But these species share the problem confronting third-stage emigrants and local immigrants: achievement of competitive dominance, a response dependent upon niche structure. How, then, does an alien species enter a community? How does a hidden flora component become a major bloom species? The requirements and strategies required of successful emigrants are discussed before novel bloom events of resident species.

5.1 Natural expatriation

Expatriations of dinoflagellates from source habitats while entrained within coastal currents are common (see Wyatt, 1995). In the western Atlantic, large-scale transport of *Alexandrium tamarense* occurs in south-flowing coastal currents having origins in the Gulf of Maine (see Anderson, 1997). From source waters in the Gulf of Mexico, *Karenia brevis* is transported into the South Atlantic Bight by the Florida Current and Gulf Stream (Tester and Steidinger, 1997). Dundas *et al.* (1989) have charted the progressive, harmful dispersion of the prymnesiophyte *Chrysochromulina polylepis* within the Baltic and Norwegian Coastal Currents during a novel bloom. In the Indo-Pacific, toxic *Pyrodinium bahamense* var. *compressum* has gradually spread northwards following an initial bloom off New Guinea (Maclean, 1989). The dinoflagellate species in these expatriations are recognizable as members of the mixing-drift life-form (Types IV, V, VI; Figs. 1 and 2). A common feature of these expatriations is that the dispersions are latitudinal. Species susceptible to latitudinal dispersion (because of coastal current orientation) probably encounter lower habitat hostility to survival and growth en route than species facing transoceanic (longitudinal) dispersions. The latitudinal range of the biogeographic (thermal) provinces tends to be broad, so that coastal currents in their on-shore-offshore meanderings provide entrained species with relatively easy access (seedlings into) to preferred habitats during dispersal. Longitudinal (transoceanic) dispersal of species between opposing coastal habitats requires transfer through oligotrophic seas, survival of water quality conditions in oceanic watermasses (see

Johnston, 1963) and, depending upon transit latitude(s), a wide temperature tolerance. Of the two emigration options, latitudinal expatriation would appear to be easier to achieve than transoceanic emigration. The pre-adaptations for successful emigration and the modes of expatriation (latitudinal vs. longitudinal) probably differ among life-form Types (Figs. 1 and 2). Types I to III might be more successful in latitudinal expatriation, and Types IV to VII better adapted for transoceanic expatriation.

5.2 Anthropogenically assisted expatriations

Although the species expatriations cited show that natural dispersal mechanisms occur, evidence that expatriations are important in the HAB expansion remains tenuous. There is molecular evidence that transoceanic displacements of HAB species away from genetically related sources have occurred (Scholin *et al.*, 1995). However, the extent to which reported genetic similarities of metapopulations have resulted from natural emigration over geological time or more recent anthropogenic vectoring is uncertain. Current systems can be viewed as expatriation corridors facilitating gene flow. However, flow velocities would appear to be too low and the required dispersal distances too far to account for the purported recent (i.e., ca. past three decades) geographic spreading and blooms of novel species. If such expatriations have occurred, then a means of accelerated emigration is required. Rapid transoceanic and transbiogeographic transport in ballast water and shellfish transplantation could override the adaptive strategies needed to survive naturally occurring advective dispersion through hostile, intervening watermasses. Ballast water dispersal of dinoflagellates has been championed by Hallegraeff and colleagues. Hallegraeff and Bolch (1992) demonstrated that the resting stages of dinoflagellates seemingly not endemic to a region can indeed survive ballast water transport and successfully germinate under laboratory conditions. This finding, combined with the novel blooms of three harmful dinoflagellate species newly reported from Australian waters, and their disjunct global distribution, led to their theory that ballast water vectoring of these dinoflagellates facilitated emigration and led to their local blooms (Hallegraeff *et al.*, 1988; Hallegraeff and Bolch, 1992). This suggestion has become inflated into the widely held view that ballast water vectoring of species into new growth areas is an important contributor to the global HAB expansion. This raises the question: what adaptive strategies and processes are needed for successful emigration of ballasted species introductions?

5.3 Colonization by emigrant species: Stage I

Assume that an emigrant species is ballasted into recipient waters while in its resting stage—the life cycle

stage most favorable initially to successful colonization upon translocation. Successful colonization is required if the seeding is not to become sterile. Should the required dormancy period, environmental excystment cues and/or habitat conditions prevent germination of the resting stages (propagules), they may deposit onto the sediments and lie dormant, ready for favorable excystment conditions. Dinoflagellate resting cysts may survive 10 or more years, with evidence for species-specific differences (Lewis *et al.*, 1999). The advantage of prolonged survival capacity contrasts with the plight of emigrant species that lack a resting stage. Growth conditions in the invaded habitat must immediately favor their colonization, otherwise the introduced population will become extinct.

Assume that germination of the resting stages occurs. The colonization hurdle then is whether the population level (carrying capacity) supported by the prevailing habitat conditions will reach or exceed the minimal viable population level, below which extinction is likely. Assuming that the finite growth rate is log-normally distributed with mean r and variance v , the expected time to population extinction is (Hanski, 1999):

$$T_e(n_o) = 1/sr[\exp(sk)(1 - \exp(-sn_o)) - sn_o], \quad (1)$$

where $s = 2r/v$ and n_o and k are the natural logarithms of the initial population size and carrying capacity, respectively. If $n_o = k$, and assuming further that $r > 0$ and sk is so large that the bracketed term in Eq. (1) is close to unity, the asymptotic scaling of time to extinction, T_e , with population carrying capacity is:

$$T_e(k) = K^3/sr. \quad (2)$$

T_e depends upon the habitat carrying capacity and the ratio of growth (r) to its variance (v), i.e., the s ratio which is a useful measure of environmental stochasticity. When s is large, habitat stochasticity (i.e., relative inconstancy of growth-supporting conditions) is weak, and the ratio of growth to its variance is then high which promotes population growth. When s is small, the stronger habitat stochasticity leads to high variance in growth, dampening population growth and abundance. This condition is generally representative of dinoflagellate growth behavior and growth conditions in their life-form habitats (see Smayda and Reynolds, 2001).

Solving Eq. (2) for various population ceiling (K) and propagule (seeding) levels (n_o) yields two responses of interest. When growth conditions are supportive and relatively constant, i.e., weak habitat stochasticity, s is large, and the time to extinction (T_e) increases linearly with K . That is, the larger the population produced during germination and the environmental carrying capacity for that species, the greater its resistance to extinction.

When the variance in growth rate is high because of high variability in growth conditions, i.e., s is small, population growth is damped, the carrying capacity lowered, and T_e increases roughly logarithmically (hyperbolically) with K (see also figure 2.5 in Hanski, 1999). Recasting this effect as the influence of propagule (n_o) size on colonization success, T_e is short for small initial seed populations (n_o), but increases rapidly to an asymptotic value as n_o increases towards K . The probable success of colonization at any given inoculum level is therefore a function of habitat stochasticity, s . For a given inoculum level, the population attained and its T_e will increase with s , a response which reduces the danger of extinction. When s decreases, extinction is threatened because of increased habitat resistance to colonization.

Colonization by emigrant species is therefore influenced by their propagule abundance, habitat receptivity, and the population carrying capacity during the critical initial phase (Stage I) of colonization. Specific adaptive strategies at this stage are not required of the species; these colonization conditions are common demographic requirements. Nor is there an ideal combination of the three colonizing requirements applicable to all life-form types and habitats (Figs. 1 and 2). The supportive combinations will vary even for a given species, since the probability of successful recruitment at a given propagule (inoculum) level varies with the degree of environmental stochasticity (Eq. (2)). If environmental stochasticity is strong, even large population seedings face a substantial risk of extinction. In the case of ballasted species, the question of whether enough cysts (propagules) are introduced to initiate successful colonization may be of minor relevance. Bulk introductions may be common; a single ballast tank contained >300 million viable *Alexandrium tamarense* cysts (Hallegraeff and Bolch, 1992). Given habitat stochasticity, the genetic makeup of the alien seed stock may be more important. Ballasted cysts are representative of the populations growing at the source sites of the ballast water; i.e., the excysted cells contain genetic material from past populations growing elsewhere. Successful germination in the invaded environment leading to Stage I colonization success requires compatible matchup of the cyst-encoded gene pool derived from blooms elsewhere with growth conditions in the new habitat. Dinoflagellate gene pools are very variable (Scholin *et al.*, 1995). Tokeshi (1999) has suggested that gene complexes exist as a series of adaptive peaks and valleys, with each peak represented by a constellation of genes. Species whose adaptive peaks match up with habitat conditions are favored. For ballasted cysts derived primarily from a single bloom and habitat site, habitat (invaded) matchup of this constricted gene pool may be tenuous. Serial introductions of cysts from a variety of source sites would increase gene pool diversity over single invasion

seedlings. High genetic diversity of the cysts in the seed bank increases the probability of successful germination and colonization.

Whatever the level of germination success of the resting stages during the initial colonization phase, the population must become self-sustaining. Colonization has not occurred, if it is dependent upon periodic, impermanent invasions: a "founder" population must be established. This requires that the cells germinated locally from the propagules complete their life cycle, culminating in their production of resting stages which are deposited in the local seed bed and become available for the subsequent germinations needed for colonization. Population persistence is the second stage of colonization.

5.4 Colonization of emigrant species: Stage II—persistence

The small, initial populations produced by successful first stage colonists face extinction because of limited genetic and demographic resilience against environmental stochasticity (see Eqs. (1) and (2)), even though the minimal population density that initially protects against extinction may have been reached. Recruitment beyond this threshold abundance is needed to mitigate habitat stochasticity; i.e., the founder population must achieve persistence—the second stage of colonization. Persistence is promoted by increases in the abundance and genetic diversity of the descendants of the founder population(s). The spatial and temporal stochasticity in dinoflagellate life-form occurrence, growth and habitats mandates another requirement. The colonizing population must disperse into the surrounding region and establish nearby satellite colonies. Both colonization and cohort expatriation are mandatory steps towards persistence.

In this struggle, the ratio of the colonization rate (c) to the extinction rate (e) is fundamental. If colonization is taken to be the rate of population growth, and extinction the rate of population loss through grazing, advection, mortality and other decrements, the ratio of colonization to extinction (c/e) is an important determinant of whether persistence is achieved. This can be formalized (Hanski, 1999):

$$dP/dt = cP(1 - P) - eP \quad (3)$$

where the changes in population size (P) per unit time (t) are functions of the colonization and extinction rate parameters, respectively, i.e., c and e . The equilibrium (persistent population) value of P is derived by setting the right hand term of Eq. (3) to zero:

$$\hat{P} = 1 - e/c. \quad (4)$$

When condition $e/c \leq 1$ occurs, the population goes ex-

tinct, $\hat{P} = 0$ (Eq. (4)). Equation (3) can be rewritten in the form:

$$\frac{dP}{dt} = (c - e)P \left(1 - \frac{P}{1 - e/c} \right). \quad (5)$$

There is a stable equilibrium point which allows persistence, and towards which P must move in time for successful colonization to take place, at which point the introduced species becomes indigenous. Stage II colonization may take many years, and initial success and subsequent year-class exploitation do not guarantee successful colonization. Boalch (1987) gives several examples of invader species disappearing some years after temporarily successful invasion.

Little can be said about the adaptive strategies that dinoflagellates need for successful, human assisted emigration, if any. Putative examples of ballasted emigrants are very limited, and primarily argued for Tasmanian outbreaks of *Gymnodinium catenatum* (Hallegraeff and Bolch, 1992), a Type V life-form (Fig. 1). The demographic determinants of emigration success (Eq. (3)) would seem to override specific organismal adaptations. The emigration potential of a species is probably linked more to its intrinsic growth rate and resting stage capabilities than to its specific pre-adaptations for emigration. Emigration potentials among life-forms may differ (Figs. 1 and 2). It is unclear whether colonization is linked to growth capability, and whether rarer species have poorer dispersal and colonization potential than species which achieve greater abundance.

Despite the growing invocation of ballasted assisted emigration as a factor in the global HAB expansion, there is little species-specific evidence in support of such colonization beyond the efforts of Hallegraeff and his colleagues. While it remains difficult to quantify the extent to which the global HAB expansion is being driven by emigration events, this contribution would appear to be relatively rare in comparison with other factors. Further discussion of the emigration theory lies beyond the present focus. One aspect needs comment, however. Although ballast water/shellfish stock transplant seedlings of dinoflagellates are often characterized as HAB stimulatory mechanisms, anthropogenically assisted seedlings are not, in of themselves, bloom stimulation events. They are but the first phase of a multiple step process that must be completed before blooms of invasive species occur. Successful colonization is not a guarantee of bloom success. The niche level barriers to bloom achievement which confront a potential colonist must be overcome, if it is to bloom rather than remain in a population maintenance (persistence) phase.

6. Niches, Blooms of Successful Colonists, and Hidden Flora Species

6.1 Colonization Stage III—community entry

An invading species always interacts with the resident species. Such competition affects Stages I and II colonization success, and continues as the species seeks to establish and maintain itself within the community. It must fit itself into a functional relationship with the resident species (Tokeshi, 1999), and in this it encounters resistance. The species must be competitively stronger than at least some of the resident species, unless an unoccupied niche is available. Since all indigenous species in the assemblage are subject to invasion and niche preemption by new species (Tokeshi, 1996), there is a collision of niche requirements because of niche overlap. The probability of successful invasion is influenced by the niche space (size) of the resident species being challenged (Tokeshi, 1996), and whose individual abundances vary from high to low to rare. The more species-rich a community, the more species that can be classified as rare (Gaston, 1994); hence, community biodiversity is an influential factor in Stage III colonization. Rarity, independent of whether it is indicative of a narrow niche (Tokeshi, 1999) or not (Gaston, 1994), is not an adaptive strategy. Rare, resident species are constrained relative to abundant species, either because of a narrower, more specialized niche breadth or the lack or scarcity of required conditions within the niche. Species having narrow niches are more likely to specialize and be more vulnerable to disruption of their unique requirements.

Consider the two extremes of potential niche conflict: niche competition between the invader and rarer species, and between emigrant and the most abundant species. In the case of rarer species, the niche features mentioned above and the high communal incidence of rare species provide invasive species with multiple opportunities to achieve community entry. Community entry can be achieved through successful invasion of the niche(s) of the least abundant species—niche preemption (see Tokeshi, 1996). In this, superior growth capability of the invading species and its indifference to the habitat constraints holding growth of the rare species in check, and whose niche space is partially or totally preempted, would be advantageous. Alternatively, the invading species may attack the most (more) abundant species, taking from it a proportion of its niche space (Tokeshi, 1999)—a more formidable colonization route. Species of high abundance are more likely than less abundant species (i.e., the specialists) to experience niche fragmentation, and remain dominant because of superior or sufficiently versatile (i.e., generalist) traits (Tokeshi, 1996). The invader species may carve out a segment of the dominant species niches (i.e., dominance decay) by having superior allelochemical and/

or grazer resistance (allelopathy) capabilities (see Smayda, 1997a).

In these examples, the invader species is the attacker seeking to carve out and fill niche space taken from existing species. A less competitive attack would be to exploit new resources, or those unused by existing species, i.e., the adaptive invasion discussed previously, or to occupy new and vacant niches created by habitat disturbance. The range of community entry options and the multiple species interactions that confront invader species suggest that there is not a uniform strategy among species for Stage III colonization.

6.2 Hidden flora and blooms: competitive maintenance vs. competitive dominance

Assume the species has achieved colonization Stage III—it is now a member of the community as one of the rare species. In losing its status as an emigrant species, it has become a member of the hidden flora whose novel blooms have been a major element of the HAB expansion. What adaptive and habitat features are required for a species to ascend from community rarity to community dominance (whatever the duration of dominance)? To remain as members of the hidden flora, species must be competitively persistent, but to bloom they must become competitively dominant. Community persistence follows the conditions of Eq. (3), even if the species population abundance places it among the hidden flora, and persists because of “silent growth”, the companion characteristic of hidden flora components. While not detectable as blooms, these subtle recruitments sustain the population. Motile cells of *Alexandrium ostenfeldii*, for example, are rarely found in the plankton, but its cysts are common in sediments (MacKenzie *et al.*, 1996). The reasons why planktonic stages of many dinoflagellates are rare when there appears to be an abundant and easily germinated seed source for bloom initiation in many areas are as provocative as their precipitous bloom events. Wyatt and Jenkinson (1997) have suggested that an important function of the brief pelagic phase of *Alexandrium* species is to maintain their cyst beds, but this may be more a consequence than a cause of bloom stimulation.

How does a hidden flora component become a major bloom species? Whatever the bloom stimulus, the species confronts the same hurdles as Stage III colonizers: the need to achieve competitive superiority; to benefit from niche fragmentation, dominance decay or niche preemption; and/or to occupy newly created niche space. The track from hidden flora status to bloom dominance may occur stepwise, in which case the species progressively increases its community importance from rare → to common → to abundant. At each step, the species competitively interacts with the entrenched species in the dominance hierarchy. The rate of successful upward in-

vasion will vary among species, habitats and growth conditions, but at each step and for each species colonization Stage III principles apply. When novel blooms of rare species occur, their niche has been favored, resulting in an increased growth rate, growth period and carrying capacity. Such bloom stimulation may result from changes in biotic control: altered grazing structure, or changes in competing species favoring its abundance, and/or changes in physical-chemical growth supporting variables. Genetic drift of the bloom species may have produced a local strain of "super-growers" or competitors, or perhaps resulted from hybridization (where previous emigrant species are involved) of serially introduced seed stock (see Scholin *et al.*, 1995). In this process the hidden flora species seemingly progresses from a **K**- to **r**-strategy within its basic **C**-, **S**- or **R**-strategy (Smayda and Reynolds, 2001).

A common feature within the HAB expansion are instances of taxonomically new species producing novel blooms, such as the recent appearance of *Heterocapsa circularisquama* in Japanese waters (Yamaguchi *et al.*, 1997) and the brown tide pelagophytes *A. anophagefferens* and *Aureoumbra lagunensis* in U.S. coastal waters (Smayda and Villareal, 1989a; Buskey *et al.*, 1998). Suggestions that blooms of taxonomically new genera and species reveal anthropogenically assisted emigration must be viewed skeptically. The required evolutionary time for speciation is expected to be considerably greater than the temporal opportunity provided by ballast water introductions and shellfish transplantations.

These considerations lead to the following tentative conclusions. Anthropogenic seedings are not, in themselves, bloom stimulation events; they are only the first phase of a multiple-step process. A newly vectored, non-indigenous species is initially pioneering; it must either find an open niche or displace a niche occupant as its first step towards successful accommodation within the community. Until colonization is achieved, alien species introduced into water masses that have been modified by cultural nutrient enrichment, water mass conditioning by aquaculture, or climatological disturbances, will not bloom. Successful colonization alone is not decisive, it usually must be accompanied at some point, or coincide with habitat disturbance—a pre-condition for many HAB occurrences.

7. Summary and Conclusions

Sournia's (1995) inventory revealed that dinoflagellate species account for about half (then known) of the total number of phytoplankton species reported ($n = 267$) to be red tide (i.e., benign) and toxic bloom species. This corresponded to about 7% of the dinoflagellate species pool. This high incidence is consistent with the well known morphological and ecophysiological diversity that characterizes the

dinoflagellates. The contradiction that is evident is that on the one hand dinoflagellates appear to be generalists—there is hardly an environmental condition that is not exploited by them. Within this generalist behavior, there is seemingly a very high degree of habitat specialization accompanied by multiple adaptive strategies. The enigma is that there is an extremely high degree of unpredictability in their bloom occurrences, bloom species selections and conditions under which their blooms occur. Stochasticity, rather than bloom regularity and predictability (in contrast to diatoms, for example), characterizes the expression of dinoflagellate ecologies and adaptive strategies. What attributes of the dinoflagellate life-form are we failing to recognize in our collective efforts to define their ecology and in applying traditional insights and biases? Dinoflagellates seemingly combine the swarming behavior of insects with the classical bloom behavior of phytoplankton in their ecology and adaptive strategies.

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