

Reflections on the ballast water dispersal—harmful algal bloom paradigm

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Abstract

The ballast water dispersal—HAB paradigm, increasingly invoked circumstantially to explain puzzling and unaccountable HAB species outbreaks when lacking the multiple tests of confirmation recommended by Bolch and de Salas (2007), is evaluated. The types and examples of natural dispersions and taxon cycles are compared to exotic species bloom behavior linked to ballast water vectoring. The regional spreading, bloom behavior and disjunct distributions of the brown tide pelagophyte *Aureococcus anophagefferens* and the toxic dinoflagellate *Gymnodinium catenatum*, attributed to ballast water vectoring, are used as representative examples to evaluate the general application of the ballast water—HAB paradigm and associated interpretative problems. Human-aided emigration has a seeding and colonization ecology that differs from bloom ecology. For self-sustaining blooms to occur, these two ecologies must be accommodated by habitat growth conditions. The three stages that a non-native species must pass through (pioneering, persistence, community entry) to achieve colonization, community maintenance, and to bloom, and the niche-related factors and role of habitat disturbance are discussed. The relevance of cryptic occurrences, cyst deposits, dormancy periods and bloom rhythms of HAB species to their blooms attributed to ballast water-assisted introductions is also sketched. The different forms of HAB species rarity, their impact on the ballast water dispersal—HAB paradigm, and the dispersion and blooms of specialist and generalist HAB species are discussed. The remarkable novel and, often, monospecific blooms of dinoflagellate HAB species are being paralleled by similar eruptive bloom behavior cutting across phylogenetic lines, and being found also in raphidophytes, haptophytes, diatoms, silicoflagellates, etc. These blooms cannot be explained only as seeding events. An ecological release of ‘old barriers’ appears to be occurring generally at coastal bloom sites, i.e. something significant is happening ecologically and embedded within the ballast water—HAB paradigm. There may be a relationship between Life Form type [Smayda, T.J., Reynolds, C.S., 2001. Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. *J. Plankton Res.* 23, 447–461] and mode of expatriation; HAB dinoflagellate species commonly reported to produce ballast water-assisted toxic blooms invariably are members of cyst-producing Life Forms IV, V, VI. Ballast water vectoring of Life Forms I, II, III is rarely reported, even though many produce cysts, and where their novel introductions do occur they are more likely to be ichthyotoxic and vectored in shellfish stock consignments. The relevance of, and need to distinguish between morphospecies and their geographic/ribotype clades are discussed based on the *Alexandrium tamarense/catenella/fundyense* complex. Morphospecies-level ballast water dispersions are probably minor compared to the dispersal of the different ribotypes (toxic/non-toxic clades) making up HAB morphospecies; the redistribution and admixture of genotypes should be the focus. Ballast water-assisted expatriations impact the global occurrence of HABs through the direct transfer of previously absent species or introduction of genetic strains from the donor habitat that are ecologically favored over resident strains. The hybridization of species may be of potentially greater impact, resulting from the (1) mating of individuals from the donor and recipient habitats, or (2) through the interbreeding of strains introduced from two different donor sites into the recipient site, and whose progeny have greater ecological fitness than indigenous strains. Exceptional ecological changes of some sort appear to be occurring globally which, in combination with the genetically altered ecophysiological behavior of HAB species linked to ballast water dispersion and

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admixture, underpins the global HAB phenomenon. The impact of ballast water and shellfish transplantation on HABs and phytoplankton community ecology, generally, is considerably greater than the current focus on HAB species distributions, vectoring, and blooms. The methodological, investigative and conceptual potential of the ballast water—HAB paradigm should be exploited by developing a GEOHAB type initiative to advance quantification of global HAB ecology.

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1. Introduction

The eruption of blooms of rare and novel harmful species within and beyond their recognized geographic ranges, and blooms of previously undescribed species are common features of the global increase in harmful algal blooms (HABs). The planetary scale of the HAB phenomenon suggests a common ecological driver is operative, but if there is one the specific mechanism is obscure. There is, as yet, no general theory adequate to explain the global HAB phenomenon. Three well-documented long-term global trends and patterns in progress have attracted attention as the mechanisms potentially underlying the HAB phenomenon: increasing nutrient enrichment of global coastal waters and epicontinental seas; global warming and associated climatic perturbations (North Atlantic Oscillation and El Niño-ENSO events); global dispersal and redistribution of bloom species in ballast water. Each has been hypothesized to provide the ecological change or disturbance driving the global HAB phenomenon (Hallegraeff, 1993; Smayda, 2002), but the mechanisms would differ fundamentally. Ecologically significant changes in nutrients, temperature and related climatically induced changes in watermass behavior are habitat modifications—their proposed HAB impacts, therefore, are ‘changing environment’ hypotheses (Smayda, 2002). Anthropogenic dispersal and redistribution of HAB species in ballast water and shellfish stock transplantation are propagule seedings facilitating geographic range expansions—the proposed impacts of this broadcasting on HAB events, therefore, are ‘emigration’ hypotheses (Smayda, 2002).

Our quantitative understanding and the scientific underpinning of the ballast water dispersal—HAB paradigm are based primarily on the work of Hallegraeff and his colleagues. The supporting evidence mustered by them includes: the enormous volumes and high frequency of ballast water and trans-oceanic movements involved; the great abundance and survival of viable cells in ballast water; successful excystment of vegetative cells from (ballasted) resting stages; floristic evidence of recent colonization by emigrant HAB

species; molecular and toxicological evidence; parallel vectoring in shellfish transplantation, etc. This evidence has attracted much attention, and investigators unable to explain bloom behavior from the data available (invariably incomplete) increasingly have attributed puzzling and unaccountable HAB species outbreaks, dispersions, range expansions and morphospecies distributions to ballast water vectoring. In essence, the “emigration hypothesis” has become transformed into a “global spreading hypothesis”, a unifying concept of great appeal to investigators hard-pressed to explain the global HAB phenomenon.

I share the view that ballast water/shellfish stock vectoring is a factor in the HAB phenomenon, but am less certain about its relative, overall importance. As Bolch and de Salas (2007) demonstrate, attribution of a novel bloom-species out-sourced from a far-field donor region to a local bloom-site requires multiple tests of evidence, including: molecular data, toxin profiles, sediment dating studies, biogeographical data and mating studies, to which time series data should be added. Ecological factors and processes also must be considered since seedings of alien bloom-species are not, in of themselves, bloom stimulation events. Their introductions are but the first step of a multiple process that embeds two ecologies, which combined, determine whether an introduction will be successful and lead to a bloom – the pioneer (invasion) and colonization phase – followed by the bloom phase (Smayda, 2002). Investigators commonly overlook this two-ecology feature when invoking the ballast water hypothesis, application of which almost always is uncritical, speculative and unwarranted, being rooted in circumstantial evidence and lacking the data and ecological rigor needed to establish the proposed bioinvasion. This can (and has) lead to ecological error and even alarmist views, such as the prediction that ballast water seedings will probably increase HABs in the North Sea as a result of climate change (Peperzak, 2005). van den Bergh et al. (2002) promulgate HAB mitigation policies based on the premise “HABs are generated by micro-algae [which] are primarily introduced through ballast water of ships and, to a lesser extent through import of living fish, in particular shellfish”.

The common and indiscriminate application of the “emigration hypothesis”, with its focus on propagule seedings, may be deflecting ecological attention away from more important and pervasive consequences of the ballast water/shellfish stock dispersal—HAB paradigm. For example, it is unresolved whether the global HAB phenomenon is the singular result of a global spreading, a global synchrony (Smayda, 2006a), the coincidence of globally unconnected and unrelated blooms – spatially or ecologically – or varying combinations of these processes. Each carries its own set of ecologies, investigative approaches, and mitigation efforts. My concern is that the popular, problematic application of ballast water—HAB paradigm may be tilting the collective view towards a global spreading bias to the neglect of the “changing environment” hypotheses.

This special issue of HARMFUL ALGAE, edited by Gustaaf Hallegraeff, is therefore welcomed for the new information that it provides on the ballast water—HAB paradigm (Hallegraeff, 2007). This paradigm is a major HAB hypothesis now sufficiently mature to warrant its evaluation. The ecological concerns sketched above are amplified in the following analysis, its preparation stimulated by this special issue of HARMFUL ALGAE and the kind invitation of Gustaaf Hallegraeff. The term emigration is used preferentially over immigration in this article because focus will be on the processes that affect the dispersal of species from their donor sites over those factors that regulate colonization and blooming at the recipient site. Reference to ballast water vectoring will apply to shellfish stock transplantations as well, unless stated otherwise.

2. Natural dispersion of HAB species

2.1. Taxon cycles

The geographic distributions of species are not fixed. On a historical scale geological and ecological barriers appear, disappear and change location. The species, in response, go through phases of geographical expansion and contraction, moving (over geological time) towards extinction. This dynamic – termed the “taxon cycle” – occurs naturally in response to changes in ecological conditions as geographical barriers to dispersal are overcome, eliminated or imposed (Ricklefs and Bermingham, 2002). A corollary of taxon cycles is that species disperse naturally between geographically and ecologically separated habitats and biotas. The regional extinctions, expansions and contractions of toxic *Gymnodinium catenatum/nolleri* and *Lingulodinium polyedrum* described by Mudie et al. (2002) and

Dale and Nordberg (1993) are examples of HAB taxon cycles.

2.2. Latitudinal dispersions

Although regional dispersion is not a bloom prerequisite for HAB species, natural dispersions leading to blooms are commonplace. In fact, certain HAB dinoflagellate species appear to be adapted for mixing-drift dispersal; interestingly, most of these species produce paralytic shellfish poisons (PSP) (Smayda and Reynolds, 2001). This prompts the question—what is the relative importance of natural dispersal versus human-assisted dispersal in contributing to the HAB phenomenon?

Plankton habitats are open systems—all species confront entrainment within currents resulting in cellular outwash from their growth sites. Advection that exceeds the growth rate impedes local growth—the population wanes and collapses; advection into ecologically more favorable habitats promotes growth. Two primary types of regional spreading occur—short- and long-distance dispersal. Near-field (infra-regional) dispersions are characterized by propagule diffusion from a population epicenter, from which the cells spread regionally and serially inoculate habitats along the dispersion route resulting in localized blooms—a spreading pattern Wyatt (1995) has termed neighbourhood diffusion. Examples include: *Alexandrium tamarense* in the Gulf of Maine and the eastern coast of the U.K. (Franks and Anderson, 1982; Brown et al., 2001); the across-shelf and alongshore movements of dinoflagellates in the Benguela upwelling system (Pitcher and Boyd, 1996); the regional, colonizing dispersion of *Karenia mikimotoi* in the North Sea (Partensky and Sournia, 1986); the progressive spreading of various flagellate bloom species over 7° of latitude along the Scandinavian coast (Johnsen et al., 1997). Of historical and ecological interest, the regional dispersion pattern of the diatom *Odontella (Biddulphia) sinensis* recorded a century ago (Ostenfeld, 1909), following its apparent vectoring into northern European waters from the Indo-Pacific in ship’s ballast water, matched the regional distribution patterns of *Chrysochromulina polylepis* (a haptophyte) during its devastating 1988 bloom in this region 80-years later (Lindahl and Dahl, 1990), and subsequently during blooms of other microalgal species (Johnsen et al., 1997).

Long-range dispersals also occur leading to far-field blooms along advection routes that can exceed 1000 km—a spreading Wyatt (1995) has termed hierarchical diffusion. An example is the unusual

bloom of toxic *Karenia brevis* that developed off the North Carolina coast (eastern U.S.) accessed through its far-field transport from the Gulf of Mexico in the Gulf of Mexico Loop Current and Florida Current—Gulf Stream system (Tester et al., 1993). Toxic *Pyrodinium bahamense* var. *compressum*, previously unknown in the western Pacific, spread northwards over 25° of latitude, from 10°S to 15°N, over a 15-year period following its 1972 bloom near Papua New Guinea (MacLean, 1989). Its progressive spread through the Indonesian archipelago to the Philippines appeared to be saltatory, its advance facilitated by local blooms which compensated for dilution losses, and which Seliger (1989) attributed to a combination of coastal nutrient enrichments and stepwise alongshore transport in the prevailing current systems.

An important feature of natural dispersions, whether neighbourhood or hierarchical, is that they are primarily latitudinal, irrespective of the HAB species involved, geographical location, or dispersal distance. For the species cited above, *A. tamarense* disperses to the south along both the New England coast (Franks and Anderson, 1982) and the North Sea side of the U.K. coast (Brown et al., 2001). For *K. brevis*, drift is southerly along the Florida coast on the Gulf of Mexico side, and to the north on the Atlantic side (see Fig. 3 in Tester et al., 1993), while *P. bahamense* var. *compressum*, in the western Pacific region, primarily dispersed northwards (see Fig. 1 in MacLean, 1989). The biogeographical consequence of latitudinal spreading to HAB species has been the general emergence of cosmopolitan distributions aligned along latitudinal corridors (see Dodge and Marshall, 1994; Okolodkov, 2005; Wyatt, 1995). The broad latitudinal expanse of biogeographical (thermal) provinces (see Longhurst, 1998) provides species relatively easy access to preferred habitats during their dispersal within the meandering alongshore and onshore-offshore coastal currents.

2.3. Longitudinal dispersion

During neighbourhood and hierarchical dispersal continuous advective loss displaces cells into hostile open sea habitats beyond their natural geographical range. The distributional patterns of the 240 coastal species mapped by the Continuous Plankton Recorder Survey Team (2004) reveal offshore translocation is common. When irreversibly advected offshore, the cells of these species must survive trans-oceanic (longitudinal) passage to re-enter suitable nearshore habitats. However, the vast spreading distances and intense

habitat resistance to survival and growth *en route* are major ecological impediments to successful, natural trans-oceanic expatriations of coastal species. *Alexandrium tamiyavanichi* may have accomplished a successful, natural trans-oceanic dispersal, spreading from the western Pacific to East Africa within equatorial currents, then on to southern Africa via the Agulhas current (Ruiz Sebastián et al., 2005).

Latitudinal expatriations are easier to achieve than trans-oceanic expatriation along longitudinal corridors, but wide latitudinal swaths of hostile ecological conditions also occur to disrupt and restrain, if not thwart, the latitudinal dispersion of some species to suitable far-field habitats. The abrupt Iberian, Tasmanian and New Zealand blooms of *Gymnodinium catenatum* (see Sections 3.4–3.6) are examples of latitudinally impeded dispersions (Hallegraeff et al., 1988; Hallegraeff and Bolch, 1992). It is exactly such “geographical jumps”, whether latitudinal or trans-oceanic, that a species must accomplish to achieve novel far-field blooms that attracts interest in “emigration hypotheses” and, specifically, in the ballast water—HAB paradigm. The relative importance of natural versus human-assisted dispersal in disjunct regional blooms is assessed from the perspective of enigmatic and exotic HAB species behavior.

2.4. Enigmatic and exotic blooms

The bloom behavior of some HAB species differs markedly from species that routinely undergo neighbourhood and hierarchical dispersion. Their blooms are usually precipitous, abundant, ephemeral, often recorded as “first events”, and the source (allochthonous or autochthonous) of the propagules seeding the bloom is usually unknown. Adding to the special interest in these species, the bloom dominants are often previously undescribed and rare species. Blooms of such species appear to be increasing, putative examples include: the brown tide, pelagophyte species *Aureococcus anophagefferens* and *Aureoumbra lagunensis*; the dinoflagellates *Heterocapsa circularisquama* and (in the North Sea) *Karenia mikimotoi*.

Aureococcus anophagefferens – appearing as a new genus and species – bloomed synchronously in 1985 in Narragansett Bay and Long Island coastal bays, its annual blooms have become persistent in the latter location (Nuzzi and Waters, 2004). *Aureoumbra lagunensis* – also as a new genus and species – appeared precipitously in Laguna Madre, Texas, in 1990, and bloomed for 7 consecutive years—the longest, continuous HAB event recorded to date

(Buskey et al., 1998). *Aureoumbra* has not been reported elsewhere. The dinoflagellate *Heterocapsa circularisquama*, which survives vectoring in pearl oyster spat (Honjo et al., 1998), was not recorded in Japanese waters prior to 1988. During the period of aquacultural consignments of pearl oyster (*Pinctata fucata*) and short-necked clam (*Tapes philippinarum*) from south-east Asia to Japan, *H. circularisquama* bloomed suddenly (1988) in the Seto Inland Sea. It has since spread in Japanese coastal waters where its blooms cause extensive shellfish mortality (Matsuyama et al., 2003). *Karenia mikimotoi* suddenly appeared in 1966 off the southern Norwegian coast, then spread throughout the North Sea to become one of the most common toxic dinoflagellates in northern European waters (Dahl and Tangen, 1993; Partensky and Sournia, 1986). Transplantations of Japanese oyster to France from 1966 onwards may have aided its bioinvasion (van den Bergh et al., 2002).

These four representative (putative) exotic species, to use Elbrächter's (1999) descriptor, appear to have become incorporated into the communities contributing to the local bloom and successional cycles. Other exotic HAB species do not persist (see Smayda, 1998) or rarely recur after their initial bloom event – these taxa behave more like vagrant species. Exotic species, independent of their bloom dynamics, share a distinct feature relative to species that exhibit neighbourhood and hierarchical spreadings (see Section 2.2)—the absence of a detectable latitudinal dispersion. This thwarts field investigators from locating the population epicenters of exotic species to track their regional excursion and monitor their bloom behavior *en route*. Circumstantially, exotic species exhibit exactly the type of bloom behavior implicating the ballast water—HAB paradigm. Their sudden blooms and unknown propagule source fit a key premise of the anthropically assisted “emigration hypothesis”—such blooms must start from allochthonous inocula released at the bloom site during deballasting, or from transplanted shellfish. The embedded inference in this bias is that neighbourhood or hierarchical diffusion of propagules, or growth of indigenous cryptic (“hidden flora”) species are considered unlikely sources. The complexities associated with proving the presumed role of ballast water in triggering such blooms are considered in the following section.

3. Applying the “emigration hypothesis” to exotic blooms

Investigators who invoke the ballast water—HAB paradigm (or shellfish stock vectoring) to explain novel

and exotic HAB events invariably lack the data to carry out the multiple tests of confirmation proscribed by Bolch and de Salas (2007). The diminished analytical power that results is burdened and biased by the inferences embedded in the ballast water—HAB paradigm, and can lead to ecological error. This can be illustrated by the behavior of two representative species whose dispersal and exotic blooms have been attributed to ballast water vectoring—*Aureococcus anophagefferens*, a harmful non-motile, picoplanktonic pelagophyte, and the chain-forming, toxic dinoflagellate *Gymnodinium catenatum*. Their selection is not to be construed as a critique of those studies; they are selected because they elucidate the strengths and weaknesses of the ballast water—HAB paradigm.

3.1. *Aureococcus anophagefferens*—inferential evidence of ballast water-assisted behavior

Since its first recorded bloom in 1985, the brown tide species *A. anophagefferens* has been detected along the eastern U.S. coast, from New Hampshire to Florida, and also in ballast- and bilge-water (see Doblin et al., 2004). Its 1997 bloom in Saldanha Bay, South Africa, its only other known location, has been taken to indicate a disjunct distribution (Probyn et al., 2001). The bloom persistence and apparent regional spreading of *A. anophagefferens* have been interpreted as the behavior of an introduced species that has become indigenous at its new bloom sites and has expanded its range. Doblin et al. (2004) has linked its apparent disjunct distribution, first reported occurrence and bloom in 1985 in southern New England and Long Island Sound embayments, and subsequent regional spreading to ballast water vectoring. This proposed linkage is underpinned by having found viable *Aureococcus* cells in the ballast water of two commercial vessels and in the bilge-water of local, small craft, sampled 16 years later (in 2001). In attributing these three bloom properties of *A. anophagefferens* to ballast water-driven behavior, the problems of undersampling and reliance on demographic data make both the inferences and interpretations tenuous. Habitats are always undersampled; undersampling can distort a species' biogeography, i.e. give the illusion of a disjunct distribution; undersampling distorts bloom behavior—time series data are needed, particularly for rhythmic blooming; and sampling can prove presence, but not absence. The bloom ecology of exotic species cannot be reconstructed from data based only on the presence or absence of cells in ballast water, or their apparent pre-bloom absence at the bloom site. The presence or absence of a species – detection of which is

both sampling dependent and related to abundance – is phenomenological, not an ecological process. It is the residual abundance remaining after growth, grazing, advection, etc. Demographic data cannot demonstrate failed or successful invasions, distributional processes, or prove the absence of species. The ballast water presence of a species (whether its vegetative or resting stage) indicates only that it was present at its capture sight; its presence does not mean that it will grow at its release site. Yet this ecological over-reach, within which successful immigration is inferred, is common.

3.2. *Aureococcus anophagefferens*—evidence against ballast water-assisted behavior

The limitations and consequential ecological error that undersampling and reliance on demographic data impose on applying the “emigration hypothesis” cannot be exaggerated. In the case of *A. anophagefferens*, chemotaxonomic evidence demonstrates that it was indeed present – cryptically – at the original bloom site. A rare marine sterol produced by *A. anophagefferens* was detected in dated marine sediments (Giner et al., 2004). This led to the conclusion that *A. anophagefferens* has been present in Long Island waters (Great South Bay) “for at least a century”. This prolonged presence does not preclude ballast water introductions of *Aureococcus*, but it does seriously challenge the conclusion that it was the source of the original (1985) bloom (Doblin et al., 2004). The presumed post-1985 spreading of *Aureococcus* in eastern U.S. coastal waters, also attributed to ballast water conveyance, rather than to natural spreading or local blooms of resident populations, was based on *Aureococcus* having been found in the bilge water of small craft (Doblin et al., 2004). However, this conclusion is also challenged by the evidence that this presumed vectoring is an artifact of undersampling, furthering the illusion of its pre-bloom regional absence. *Aureococcus anophagefferens* was not reported in the contiguous waters off Delaware, Maryland and Virginia prior to 1998. However, a chemotaxonomic marker for pelagophytes such as *Aureococcus*, the accessory pigment 19'-butanolyoxyfucoxanthin, was found in the sediments of those coastal bays. This strongly suggests *A. anophagefferens* was present as early as 1993, the first year of available HPLC data (Trice et al., 2004).

The biochemical (sterol; pigment) signatures of *A. anophagefferens* found in the sediments indicate that it is probably indigenous in eastern U.S. coastal waters, and not a recent, ballast water-aided immigrant. This

finding reinforces the well-recognized and methodologically utilized fact that the sedimentary record must be evaluated in assessing whether an exotic HAB event originates in a ballast water/shellfish stock introduction, or is the bloom of a cryptic, indigenous species. There is a more important insight—non-traditional biochemical analyses of a species sedimentary record may be required to test ballast water origination hypotheses, particularly if resting stages are unknown or life cycle stages are difficult to recognize among the sedimentary debris. *Aureococcus anophagefferens* cells, for example, are only 2–4 μm and easily camouflaged among the sedimentary debris.

3.3. *Aureococcus anophagefferens*—evidence for and against a disjunct distribution

Claims that the blooms, geographic range expansions, and disjunct distributions of exotic HAB species are ballast water-aided dispersal events based only on demographic data are not unusual. This was advocated for *A. anophagefferens* as follows (Doblin et al., 2004): “the disjunct global distribution of *Aureococcus* may suggest that there was relatively recent introduction to South Africa and the evidence provided here indicates that ships’ ballast water could be a transport vector.” And, the “distribution of brown tide seems to be rapidly increasing both within and outside the United States, suggesting there is an anthropogenic dispersal vector”. The primary evidence proffered for this behavior is circumstantial—viable *Aureococcus* cells found in the ballast water of two ships which had ballasted in Venezuelan, Belgian and/or Dutch coastal waters! This ballasting history supports an alternative, and equally unverified, conclusion—the ballast water occurrences of *Aureococcus* reveal its unreported occurrence in European and Venezuelan waters. And this, together with its documented presence in South African waters (Probyn et al., 2001), indicates *A. anophagefferens* has a broader distribution than its purported disjunct distribution. This reinterpretation of the ballast water presence of *A. anophagefferens* casts doubt on its alleged disjunct distribution, and the need to invoke a ballast water explanation for its occurrence. Nor can it be discounted that the presumed disjunct distribution is a sampling artifact, further nullifying its occurrence and the need for ballast water expatriation. At best, then, both interpretations are qualitative, if not anecdotal; they have minimal ecological value, and reflect the great uncertainty associated with application of the ballast water—HAB paradigm. More relevant—a species entrained in ballast water is in conveyance away from

its donor site, and the ecological conditions there, to the recipient site(s), and probably differing ecologically and in the stage of the bloom and successional cycles influencing receptivity to the introduced populations. Traditionally, the deballasting site is focused on—the origination site and its ecology are invariably ignored. Failure to recognize that ballast water populations indicate both presence (at the donor sites) and the potential presence (at the deballasting site(s)) can weaken efforts to evaluate exotic HAB events as ballast water-driven behavior.

The *Aureococcus* analysis focused on the physical aspect of the ballast water—HAB paradigm – the conveyance and seeding of viable propagules. The ballast water—HAB paradigm has an important biological aspect that must also be kept in focus – the sources and role of resting cysts in exotic species blooms. This is evaluated using blooms of the PSP species *Gymnodinium catenatum* as a representative model.

3.4. *Gymnodinium catenatum*—the Tasmanian blooms and the case for resting cyst introductions

Toxic *Gymnodinium catenatum*, a previously obscure species that was known only from the Gulf of California and Argentinian waters prior to 1970, has since been recorded at 16 global sites—it is an emergent cosmopolitan species (Irwin et al., 2003). Holmes et al. (2002) found a lack of genetic diversity among broadly distributed populations of *G. catenatum* which they concluded was consistent with the hypothesis of a relatively recent global spreading. The required spreading rate for this dispersion considerably exceeds that expected from natural diffusion, if even achievable, given the trans-oceanic barriers and latitudinal barriers (see Section 2.3) to such spreading. An alternative mechanism of accelerated spreading therefore seems probable, assuming *G. catenatum* was not indigenous at its new bloom locations. The precipitous, first recorded appearance of *G. catenatum* in bloom proportions in Tasmanian waters in 1980 provided the clue to the mechanism—cysts of this species found in ships' ballast water could provide the required seeding and redistribution mechanism (see Hallegraeff and Bolch, 1992). This insight was bolstered by the discovery of *G. catenatum* resting stages in ^{210}Pb and ^{137}Cs dated sediments collected near the bloom site, and of specific interest was their sudden appearance around 1972 coincident with commencement of woodchip shipments in cargo ships plying between Tasmania and Japan (McMinn et al., 1997; Hallegraeff, 1998). There was a

gap of ca. 8 years between the first recorded sedimentary appearance and pelagic bloom of *G. catenatum*, with no evidence of cysts being present back to ca. 1865 (McMinn, 1997). [The presence of cysts in a layer dated to 1937 ± 6 years was attributed to bioturbation.] Following the 1980 outbreak, major blooms occurred in 1986, 1991 and 1993 (McMinn, 1997). Since these pioneering studies, ballast water vectoring has become the explanation of choice to explain the spreading behavior of *G. catenatum* and other HAB species, such as *A. anophagefferens* already discussed. Application of the ballast water—HAB paradigm to two other *G. catenatum* blooms, one in Spain and the other in New Zealand, from the perspective of resting stage behavior will now be considered.

3.5. *Gymnodinium catenatum*—the 1976 Iberian bloom

Prior to the 1980 Tasmanian bloom an eruptive bloom of *G. catenatum* occurred in 1976 off north-western Spain, the first record of its pelagic occurrence in European waters. Two retrospective hypotheses stimulated by the Tasmanian bloom (Hallegraeff and Bolch, 1992) were advanced to explain this event: trans-Atlantic transfer of *G. catenatum* in ballast water from Argentinian/Uruguayan waters, where it was previously recorded, by Spanish fishing vessels operative in those waters (Wyatt, 1992). The other explanation—natural dispersal of *G. catenatum* from its known growth region off Morocco to Portugal and Spain, entering Galician fjords during upwelling relaxations (see Blackburn et al., 1989). Both hypotheses are predicated on *G. catenatum* not being indigenous along the Iberian peninsula. Recent analyses of dated sediment cores collected off Portugal however, revealed the presence of *G. catenatum* cysts back to the turn of the 20th century (ca. 1898). This led Amorim and Dale (2006) to conclude that “plausibly” *G. catenatum* was ship-ballasted to the area at that time, the tentative “most likely origin [being] natural populations [in] the North-East Pacific”. Assuming that blooms of *G. catenatum* along the Iberian peninsula prior to 1976 were not overlooked, an interval of about 75 years elapsed between its first recorded regional appearance and the 1976 bloom. Amorim and Dale (2006) emphasized that this introduction appears to have coincided with a major environmental change, specifically cultural eutrophication. They did not discuss the 1976 *G. catenatum* bloom.

The inferential bias inherent within the ballast water hypothesis is evident in the interpretation of the *G.*

catenatum cyst record in Portuguese sediment cores (Amorim and Dale, 2006). Its abrupt sedimentary appearance at the turn of the century was attributed to human-aided introduction, i.e. relatively soon after the regular use of seawater as ballast beginning in the late 1870s and 1880s (see Ruiz Sebastián et al., 2005). This origin was promulgated without having considered, or having eliminated that the colonizing population was supplied by natural dispersal accompanying range expansions and contractions during a *G. catenatum* taxon cycle (Ricklefs and Bermingham, 2002), or through natural bioinvasion. This alternative explanation, however, is just as tenuous as the ballast water origin claimed. Both rely on demographic data and pose the interpretative problems discussed in dealing with *A. anophagefferens* (Section 3.1). They also lack the multiple tests of confirmation recommended by Bolch and de Salas (2007). Ruiz Sebastián et al. (2005) confronted a similar problem when seeking to explain the presence of *Alexandrium catenella* along the west coast of South Africa, and found to be genetically related to the North American clade. A ballast water translocation seems tenuous given an 1888 PSP event in these waters attributed to *A. catenella*.

Based on the Portuguese sediment core data, it can be argued that the 1976 *G. catenatum* bloom event did not require a coincident ballast water-aided seeding—the excystment of resting stages pre-positioned in the sediments could have provided the bloom inoculum. This interpretation, however, introduces other complexities—the cause of the historical delay of the 1976 bloom event, given that cysts have been present since 1898; and the cause of the eruptive bloom in 1976. These enigmas prompt the question of whether there may be bloom rhythms which contribute to the extremely variable temporal and regional bloom behavior that characterizes HAB species generally, and which create the illusion of disjunctive spatial and temporal HAB behavior that elicits the ballast water hypothesis. This prospect will be returned to after consideration of a *G. catenatum* bloom event in New Zealand waters.

3.6. *Gymnodinium catenatum*—the 2000–2001 New Zealand bloom

The first reported *G. catenatum* bloom in New Zealand coastal waters – in 2000–2001 along a 1,500 km coastline – presents the same uncertainties as the Iberian *G. catenatum* bloom, i.e. whether it had an indigenous origin or was an allochthonous seeding and, if the latter, the source and mechanism of delivery (Irwin et al., 2003). The New Zealand bloom further

exposes the interpretative problems that confront ballast water-based explanations of HABs. Dated sediment cores from one of the bloom sites revealed the presence of *G. catenatum* cysts back to, at least, year 1937 (the bottom of the core). [Note the similar year of cyst occurrence in the Tasmanian sediment cores, but attributed to bioturbations, discussed earlier (Hallegraeff, 1998).] Yet prior to its 2000 PSP outbreak *G. catenatum* had never been identified from New Zealand waters despite an intense, national biotoxin monitoring program at 60–70 sites, and in operation since 1993. This effort was described as having “completely failed to detect *G. catenatum* in routine phytoplankton samples” despite strong sedimentary evidence that active blooms were occurring since 1980–1981 (Irwin et al., 2003). Thus, beginning from the 1937 date line, there was a lag of either 63 years (until the 2000 pelagic bloom year) or 43 years (until the 1980 sediment core bloom year). This multidecadal, cryptic hiatus is similar to that found for the Iberian *G. catenatum* population. And there is another similarity—an environmental change occurred, described as “broad scale”, and accompanied by changes in dinoflagellate cyst composition and abundance in the sediment seed bank (Irwin et al., 2003). Those changes were attributed to changes in water quality thought to accompany watershed deforestation and dairy farming initiatives. In addition, the 2000 bloom coincided with a La Nina event.

The novel Iberian and New Zealand *G. catenatum* blooms have three common features relevant to the ballast water—HAB paradigm. Cyst deposits indicate *G. catenatum* was present at both locations for decades prior to its first recorded bloom; routine pelagic monitoring failed to detect *G. catenatum* presence prior to this bloom; and an environmental disturbance partly overlapped its period of origination and/or initial bloom.

3.7. Cyst deposits, dormancy periods, bloom rhythms and the ballast water—HAB paradigm

The pre-bloom sedimentary deposits of *G. catenatum* cysts discovered after its first recorded Iberian and New Zealand pelagic blooms illustrate the interpretive problems that cryptic populations and cyst seed banks pose to the ballast water—HAB paradigm. Their undetected (unsampled) presence biases the analysis towards a vectoring explanation, and can obscure rhythmic bloom behavior that might occur at decadal or greater intervals. Both undersampling artifacts can give the illusion that rhythmic blooms and exotic species presence reflect propagule introductions, either through

natural dispersal or ballast water vectoring. Dinoflagellate resting stages can remain viable for decades before germinating to start blooms. The cysts of some dinoflagellate species present in ^{210}Pb -dated sediment cores collected from a Swedish coastal fjord remained viable for 37–55 years (McQuoid et al., 2002), considerably beyond the 10-year upper limit suggested by Lewis et al. (1999). This longevity reinforces the importance of carrying out dated sediment analyses to evaluate species invasion histories demonstrated by McMinn et al. (1997) in their analysis of the Tasmanian *G. catenatum* blooms. The long retention of resting cyst viability shows how difficult it is to detect blooms, particularly if rare or rhythmic, without a suitable long-term monitoring program. Cyst abundance can be enormous, with germination of a very small percentage adequate to seed a bloom. Consider the cyst population of *Lingulodinium polyedrum* in Loch Creran, Scotland, a relatively small ($183 \times 10^6 \text{ m}^3$; Lewis et al., 1985) fjordic habitat, where Lewis (1988) reported a population density of 250×10^9 cysts in the upper 1 cm sediment layer of the loch ($= 2136 \text{ cysts cm}^{-3}$). Of this population, about 0.6% (ca. 13 cysts cm^{-3}) of the cyst population had to germinate to provide the inoculum in support of a 1983 bloom. Cyst production at the bloom maximum reached $6400 \text{ cysts cm}^{-2} \text{ day}^{-1}$, an exceptionally high rate. Lewis concluded that a bloom every five years or less would be adequate to maintain sediment cyst abundance at the levels observed.

Some HAB species form highly episodic, if not erratic, blooms—*Lingulodinium polyedrum* is a particularly good example (Allen, 1933, 1943). In Portuguese waters, *L. polyedrum* and *Prorocentrum micans* each produced two blooms recorded between 1944 and 1987, with an interval of 23 and 22 years between these blooms, respectively (Sampayo, 1989). In the Bay of Fundy region, shellfish toxicity trends and peaks, reflecting the abundance of the *Alexandrium tamarense* complex, coincided with the 18.6 year lunar cycle during the 52-year period between 1943 and 1994 (White, 1987; Martin and Richard, 1996). Reports of rhythmic bloom behavior are very limited, but emerging patterns suggest bloom cycles, perhaps partly in response both to changing and cyclical environmental conditions, may be a factor in the highly episodic and largely unpredictable blooms characteristic of HAB species.

3.8. Sampling difficulties and the ballast water—HAB paradigm

The presence of species and their blooms frequently escape detection by sampling programs, whether the

occasional blooms of rare and hidden flora members or, even, common species. This methodological limitation impacts application of the *ballast water—HAB paradigm*. Long-term monitoring programs do not necessarily provide improved detection capability; this is evident from the failure of the intensive New Zealand monitoring program to detect *G. catenatum*, as mentioned previously. Godhe et al. (2001) recorded a number of dinoflagellate species from a sediment trap that were not detected in the water column sampling, including the first reported occurrences of several species in the Kattegat. Throndsen's (1970) use of the serial dilution culture method revealed that 21 of the 30 flagellate species that grew up in the cultures were previously unrecorded. Aquaculture is also providing bioassay evidence for blooms of species that were always present, but not recorded. For example, novel blooms of ichthyotoxic *Heterosigma akashiwo* developed soon after initiation of salmon fish farming or shellfish cultivation in Chile, China, Japan, New Zealand and South Korea (see Smayda, 2006b). And blooms of previously insignificant populations of *H. akashiwo* have been stimulated at aquaculturally conditioned growth sites in British Columbia and Puget Sound (U.S.).

The common tendency of the microflora to escape detection exacerbates the problem of applying ballast water explanations. It is remarkable how difficult the detection of a species can be, requiring the need to apply non-traditional techniques, as demonstrated by the *Aureococcus* results (Section 3.1), and revealing also the inadequacy of classical sampling methods. There is probably no correlation between a species' initial population density and its capacity to produce a bloom, partly because even rare species can reach an astronomically high abundance. Consider Narragansett Bay, the region with which I am most familiar. This relatively well-mixed estuary has a mean depth of ca. 10 m, occupies an area of 264 km^2 and has a volume of $2.6 \times 10^9 \text{ m}^3$. At a population density of only 1 cell/10 m, i.e. 1 cell in 10,000 L, far below standard detection procedures, ca 260 million propagules are available to start a bloom.

3.9. Habitat disturbance, alien species blooms and the ballast water—HAB paradigm

The Iberian and New Zealand blooms of *G. catenatum* were stated to be associated with an environmental change—eutrophication at the apparent time of first invasion into Portuguese waters (Amorim and Dale, 2006), and altered watershed use practises

that impacted water quality and, separately, a La Nina event coincident with the bloom outburst in New Zealand waters (Irwin et al., 2003). These disturbances are consistent with the conclusion that alien species introduced into a new habitat may eventually bloom only if accompanied at some point, or coincident with a habitat disturbance or altered ecology (Smayda, 2002). The interplay between environmental disturbance, niche structure, colonization by introduced species, and bloom development is discussed in a later section.

4. Rarity, HAB species vectoring, Life Forms and blooms

4.1. Equating rarity with HABs, and the ballast water—HAB paradigm

The ballast water—HAB paradigm has been influenced by novelty, i.e. rarity – species spring from nowhere, suddenly, to bloom. Many HAB species whose blooms have been attributed to ballast water vectoring are rare, or newly discovered species. This coincidence is too frequent to ignore and requires evaluation. Blooms of rare and exotic species raise the question of what is rarity, and does it affect emigration behavior and strategies? Do common and rare species differ in their intrinsic capacity for expatriation, whether natural or human-assisted? If affirmative, does this set limits to their range size, range maintenance strategies, bloom frequencies, rhythms and intensity required to prevent extinction? Is rarity adaptive?

Rarity is a complex natural phenomenon; it is also a relative term definable in different ways—in terms of a species geographical range size (wide or narrow); local and overall abundance (high or low); distribution within its geographic range (uniform or fragmented), and in the occurrence of “hot spots” (Gaston and Lawton, 1990). A HAB species can be rare in abundance over much of its geographical range (e.g. *Alexandrium ostenfeldii*; MacKenzie et al., 1996); of high overall abundance throughout its range (e.g. *Prorocentrum minimum*); rare or common within given segments of its range (e.g. *Heterosigma akashiwo*), and its presence within a biographical province can vary—*Pyrodinium bahamense* var. *compressum* is rare on a global scale, but not in the western Pacific Ocean. Rarity also has a temporal dimension—bloom events of a species at a given location may be annual, perennial or less frequent, its abundance then ranging from low to high. Rarity, therefore, is not a specific condition, it has multiple variants expressible in terms of presence, distribution, abundance, bloom frequency, etc. A species may be rare

in one context, but not in others. These features suggest common species are more likely to be captured, entrained, dispersed, and far-field released in ballast water than rarer species. Their capture is also expected to be more fortuitous, and their expatriate blooms less probable. Yet blooms of rare and other exotic species attributed to expatriation are becoming more frequent—in terms of species, frequency, and geographically. This raises the ecological issue of why blooms of this type are becoming more common, even increasing. Is this apparent progression up from rarity a function of the expanding global reach and volume of maritime shipping, increasingly accessing the habitats of rarer species and dispersing their propagules to ecologically favorable deballasting sites? Alternatively, is this behavior more in line with the changing environment hypotheses discussed earlier?

4.2. Dispersion and blooms of specialist and generalist HAB species

The “characteristic” bloom behavior of many exotic HAB species, as pointed out earlier, is similar to that of vagrant species—after flourishing initially, they collapse, disappear and “return” to rarity. Such ephemeral, non-recurrent appearances do not preclude achievement of range expansion—the species may have become resident as a cryptic species. The eruptive bloom-disappearance sequence that characterizes many rare and exotic species suggests they have weak colonization capacity, which raises several important ecological questions: are the growth requirements of rare HAB species more specialized than common HAB species? Are their competitive capacities weaker? Are these attributes – similar to the irreducible pairing between physical convexity and concavity – both a cause and a consequence of a species’ geographical and population rarity? If affirmative, the success of human-assisted expatriations may be species-specific, and influenced by the life-form class of the species being dispersed. Rarity *per se* does not appear to be an adaptive strategy, nor intrinsically limiting to expatriation. This is suggested by the bloom persistence some exotic species achieve at their new bloom sites, and the successful expatriation of common species to previously unexploited habitats (Hallegraeff et al., 1988; Hallegraeff and Bolch, 1992).

Finlay has pointed out that although a species’ abundance and range size are usually treated separately, they are not independent properties (Finlay, 2002; Finlay et al., 2002). Based partly on species-area data, he has argued that microbial eukaryote species that are rare are probably also ecological specialists with

fastidious ecological requirements, and therefore are suppressed in abundance. The result is they rarely form large populations, intrinsically are relatively difficult to detect, and will be recorded infrequently. These ecotypic features decrease the rate and scale of their dispersion and restrict their geographical distribution. The corollary is that widely distributed species are also globally abundant, and species that are narrowly distributed are less abundant. The likelihood of successful expatriation of a rare, i.e. specialist, species captured within ballast water and released into new habitats is probably diminished relative to generalist species, the other group recognized by Finlay. Generalist species appear to have broad ecological tolerance, plentiful habitats, high local abundance, are easily detectable, and tend to be “dominant” species.

4.3. Expatriation and dinoflagellate Life Forms

Should generalist (common) and specialist (rare) species occur among HAB taxa, their expatriation potential and emigration ecology are expected to differ. A provocative pattern (if not an artifact) relevant to this is evident among the HAB dinoflagellates most frequently cited as having achieved human-aided expatriation. Viewed from the perspective of the C–S–R and Life Form strategies recognized by Smayda and Reynolds (2001), ballast water-assisted expatriate blooms rarely are reported for species belonging to Life Forms I, II, III—members of the prorocentroid, peridinioid, gymnodinioid and ceratian branches of the phylogenetic tree (see frontispiece in Taylor, 1987). This group is made up mainly of C-strategists (i.e. small, fast growing, competitive and opportunistic colonist species), whose natural dispersal capacity is evident from the fact that almost all are cosmopolitan and common red tide or HAB species. When expatriation of harmful or nuisance species of Life Form types I, II, III are reported, shellfish stock vectoring may be more involved, e.g. *Heterocapsa circularisquama* in Japanese coastal waters (discussed in Section 2.3) and (less convincingly) *Karenia mikimotoi* to the North Sea. In contrast, HAB dinoflagellate species commonly cited to produce ballast water-assisted blooms invariably are members of Life Form types IV, V, VI—recognized as the “mixing-drift” group (Smayda and Reynolds, 2001), and which include *Alexandrium catenella*, *Alexandrium minutum*, *Alexandrium tamarense*, *Gymnodinium catenatum*. These species are R-strategists (i.e. fast swimming, disturbance and stress tolerant). The spreading of toxic *Pyrodinium bahmense* var. *compressum* over 25° of latitude in the Pacific

commented on earlier, and which MacLean (1989) partly attributed to ballast water dispersal, is also a “mixing-drift” species. Interestingly, all of these species produce paralytic shellfish poisons (PSP)—a capacity rare or absent among Life Forms I, II, III, which are more likely to be ichthyotoxic than PSP toxic. This striking coincidence raises the issue of whether the ability of a dinoflagellate to produce PSP is a component (or by-product) of its pre-adaptive capacity for successful expatriation? Conversely, does PSP synthesis capacity reflect a species’ resistance (intolerance) to natural dispersal (unlike Life Forms I, II, III) which ballast water vectoring overcomes because of its accelerated mode of dispersal? [Hallegraeff (pers. commun.) has suggested the explanation “lies in the fact that all PSP species make cysts”.] In this, the toxin is considered to be only a proxy, and not the specific adaptation. This prompts the following speculation: Life Form types differ in their pre-adaptive capacity for natural dispersal (emigration) and in the predominant mode of their expatriation. Life Form types I, II, III – C-strategists – may be more successful in achieving latitudinal dispersal. Life Form types IV, V, VI – R-strategists – may be better adapted for trans-oceanic expatriation, but are then more dependent on ballast water conveyance. Perhaps the vectoring mechanism selects for, and influences which Life Form and toxin type is favored. Thus ballast water dispersal may favor PSP and R-strategist species, while shellfish stock transplantation favors C-strategist species, which tend (as a group) to be more ichthyotoxic than PSP toxic.

5. “Everything is everywhere”, neutral dispersal, geographic clades

5.1. “Everything is everywhere”; neutral dispersal

The global spreading hypothesis, based primarily on exotic species blooms, premises that toxic microalgae are not uniformly distributed, and their trans-oceanic dispersions leading to HABs and range extensions require anthropic assistance. This premise is counter to the provocative and controversial conclusion, based on species-area curves, that microbial eukaryote species are not geographically restricted – “they have no biogeographies” – whether abundant, rare or cryptic (Finlay, 2002; Finlay et al., 2002). Supportive evidence that physical barriers are not a significant impediment restricting the large scale dispersal of microbial eukaryotes – “everything is everywhere” – comes from the distributions of various protistan groups (see Finlay et al. (2002). Finlay and co-workers suggest, as a

consequence (or reflection) of the above features, there is continuous worldwide dispersal – “*ubiquitous dispersal*” – of species (Finlay, 2002; Finlay et al., 2002). The descriptors, ubiquitous and cosmopolitan, as used by them are not synonymous, nor refer to an organism’s widespread distribution. Ubiquitous is distinguished from cosmopolitan in being the continuous dispersion of a given species—it is a process. Cosmopolitan is used to indicate the individuals of a species are capable of population growth in many different localities, worldwide—it is a potential distribution. The species may not be present in those localities but, if accessed, growth is expected.

An important element of the linked view that “*everything is everywhere*” and undergoing “*ubiquitous dispersal*” is that physical conveyance, i.e. current-driven neighbourhood or hierarchical dispersions, or latitudinal or longitudinal dispersions, are not the dispersal mechanism of interest, or to be focused on. Rather, the population density – a biological mechanism – is believed to govern the diffusion rate and general dispersal of microbial eukaryotes, and their capacity for geographic range expansion (Finlay, 2002). Of the several Laws of Dispersion that Finlay and co-workers considered to be operative, a species’ absolute abundance is considered to be of major importance. High abundance – considered to be high (derived from the species-area curve) regardless of whether the species is common, rare or cryptic – is believed to be the principal driver of the continuous and random dispersions of species, acting as a population pressure wave. Over geological time this relentless population-driven dispersal has overcome geographic barriers resulting in a collective cosmopolitanism. Finlay has termed this process “*neutral dispersal*”, in which the rate and dispersal of a species are principally a function of its absolute abundance. In this, random dispersal is the dominant force driving large-scale distributions of species, and the rate and scale of this dispersal are largely determined by the global population size. Of course, neutral dispersal does not obviate the multiple mechanisms available for other natural geographic redistributions of species—neighbourhood and hierarchical dispersions, latitudinal and longitudinal dispersions. Nor does the neutral dispersal hypothesis exclude the occurrence or impact of ballast water-aided dispersions of HABs. Elements of the “*everything is everywhere*” hypothesis would appear to apply to HAB species. Most HAB outbreaks occur in nearshore and coastal waters and in epicontinental seas, with a high degree of cosmopolitanism within individual biogeographical zones evident for both toxic and benign

species based on various species checklists. However, it must be emphasized that while cosmopolitanism may well apply to many morphospecies, molecular evidence is increasingly challenging sole reliance on this taxonomic level. There is strong and growing evidence that disjunct distributions of genotypes occur, such as the geographic/ribotype clades of *Alexandrium* discussed in Section 5.3. This suggests that at the morphospecies level ballast water invasions are of minor concern. More significant is the ballast water dispersal of the different ribotypes making up morphospecies. This not only facilitates the spatial redistribution and spreading of HABs, but enhances hybridization opportunities which contribute to the HAB phenomenon (see Section 7.2).

5.2. Vicariance, jump dispersal and ballast water vectoring

Accepting the various modes of natural dispersion that redistribute HAB species; that ballast water dispersal supplements natural dispersion and may speed up both access to and the frequency of seed stock delivery to remote areas, the question emerges whether ballast water and shellfish stock dispersal has altered the biogeographical patterns of HAB species and their bloom behavior, bearing in mind the distinction between emigration that leads to range expansion versus emigration that leads to novel blooms. The extent to which communities resist ballast-aided bioinvasion, ballast-aided bloom stimulation and colonization by alien species influences this impact. The limited quantitative evidence available suggests human-aided emigration has not significantly altered morphospecies biogeographical patterns. The direct evidence for this includes the occurrence of neighbourhood and hierarchical dispersions, geographic/ribotype clades, and the neutral dispersal phenomenon. The indirect evidence includes: the disjunct distributions of morphospecies appear to be more apparent than real, and largely a consequence of their rarity and/or undersampling, which compromises discovery that these hidden species are indigenous. Viewed from this perspective, the primary effect of ballast water dispersal might be to supplement natural dispersion, speeding up the frequency of seed stock delivery, its regional exchange, and providing access to remote areas, but all with relatively modest effect on extant morphospecies distributions.

The occurrence of ribotypes (Scholin et al., 1994, 1995) and neighbourhood and hierarchical dispersions suggest the current biogeographies of HAB morphospecies are long standing. Scholin et al. (1995) show the

potential natural, circumpolar dispersal routes between the Atlantic and Pacific Oceans available to the *Alexandrium* species complex. These oceanic dispersions would be facilitated by the geological history of the dinoflagellates, with pre-vicariant, uniform distributions also expected given that the dinoflagellate lineage dates back to the late Proterozoic (545 MYA), with the earliest fossils from about 240 MYA (see John et al., 2003). The mixing times, scope and patterns of ocean circulation since that epoch, and the opportunities for genetic exchange, seemingly favor uniform rather than discontinuous distributions initially that become available for geographical partitioning by vicariant events. In fact, cosmopolitan distributions are expected to be commonplace. As discussed earlier, the apparent disjunct distributions of some species may largely be sampling artifacts, and in which introduced ribotypes can be superimposed on indigenous ribotypes, as in the Mediterranean *Alexandrium catenella* blooms (see Section 5.3). Nonetheless, the idea that HAB species commonly exhibit discontinuous distributions, and that ballast water vectoring contributes to this disjunct occurrence is pervasive and must be addressed.

Terrestrial biogeographers have advanced two primary explanations for discontinuous distributions (Cox and Moore, 2005). Adherents of the dispersal hypothesis view such species as originally having been confined to a single area, from which they dispersed across intervening regional barriers to colonize other areas. The source and satellite populations became genetically isolated from each other, leading to speciation and a blurring of past separation events. The vicariance view contends disjunct distributions are not the result of impeded dispersal; rather, the species once enjoyed a continuous range of distribution that fragmented when barriers arose and geographically isolated the species, this resulting in a discontinuous distribution. Cox and Moore (2005) point out that gaps in the distribution of a species prior to awareness of vicariant events were considered to represent inhospitable areas that existed before the species evolved. This view is partially embedded in the ballast water – HAB paradigm, evident in the syllogism usually applied – that when a HAB species exhibiting an apparent disjunct distribution blooms in a new region, this must be the result of an emigration event. This inference, tightly embedded within the ballast water—HAB paradigm, presents a major teleological impediment to rigorous application and testing of the paradigm. This is evident in the explanation advanced that human-assisted dispersal from the Pacific accounted for the turn-of-the century appearance of *G. catenatum* in

Portuguese waters (see Section 3.5; Amorim and Dale, 2006). And it is also evident in the claim that the source of the population of *Fibrocapsa japonica* appearing in western European waters was the Pacific based on the chronology of its regional appearance, i.e. it was first reported from Pacific waters (Kooistra et al., 2001).

Vicariance and dispersal events are relevant to ballast water and shellfish stock vectoring of propagules, but differ from natural range extensions in which species gradually and continuously spread. The latter not only leads to range management and range expansion, it facilitates physiological and genetic differentiation along the distributional continuum, such as the geographic/ribotype clades found for the *A. tamarense* complex (see Section 5.3) (Scholin et al., 1994, 1995). Range extensions are evident even in the paleoceanographic dispersals of toxic *Alexandrium* species that occurred in response to tectonics, changing ocean configurations and current systems, and climatic fluctuations in the interval from 5 to 45 MYA (John et al., 2003). Human-aided dispersals, in contrast, are different—they skip over, rather than pass through pre-existing barriers (eventually) by eliminating the need to exploit ecologically favorable gaps within, or around the intervening barriers to achieve successful dispersion to favorable habitats beyond. To apply a phrase from Cox and Moore (2005), ballast water and shellfish stock transfers are “jump dispersals”, and may pose greater ecophysiological difficulties to successful colonization than natural dispersion. Organisms undergoing natural spreading must disperse actively across barriers. Ballast water/shellfish stock vectoring does not challenge a cell’s ecophysiology during dispersal, as much as its survival capacity and resistance while in ballast—those cells are in passive dispersal. Cells undergoing natural dispersal benefit, perhaps, from selective genetic adaptations (strain selection) that develop *en route*, and needed to facilitate survival during transit. A consequence is the strains may become better pre-conditioned for successful expatriation than “jump dispersal” species not experiencing this time-dependent, environmentally stimulated preconditioning, and operative generationally.

Molecular data and molecular clock analyses, particularly for PSP-producing taxa in the genus *Alexandrium* (Scholin et al., 1994, 1995; John et al., 2003), suggest vicariant events have been important over geological time in establishing the biogeographical patterns of HAB dinoflagellates. Accepting this vicariance and Finlay’s concept of ubiquitous dispersal (Section 5.1), are the present, ballast water-aided “jump dispersals” of HAB species into new habitats an

ecological return of the taxa (now genetically diverged) to historically equivalent habitats in which the ecological resistance to invasion and blooms may be less than that for new species ancestrally removed and less cosmopolitan? That is, blooms of *Alexandrium* species may be more favored by such dispersal than the less cosmopolitan, more fragile *Karenia* species which lack resting cysts. This is not an esoteric issue, but may provide the linkage between the ballast water—HAB paradigm and the global efflorescence of HABs. The global HAB phenomenon has the behavioral elements of both a global synchrony and rhythmicity, and an occurrence at a time when the ecology of global coastal water is changing, i.e. the “changing environment” hypotheses mentioned in the Introduction to this article.

5.3. Geographic clades

Focusing on morphospecies only when evaluating the role of ballast water/shellfish stock dispersal in HAB species dynamics carries risk. Hidden within morphospecies are strain differences that must be considered. Both toxic and non-toxic strains occur, as shown for the *Alexandrium tamarense* complex (*A. tamarense/catenella/fundyense*), with geography, not morphology, paramount in influencing whether a given isolate of this HAB morphospecies complex is toxic or not (Scholin et al., 1994, 1995). Strain differences cannot be ignored when evaluating ballast water/shellfish stock dispersals of HAB species because the distributional patterns of the toxic/non-toxic strains and their morphotype can differ. This is very evident for the *A. tamarense* complex. Three geographic clades occur that consist only of toxic strains—North American, temperate Asian, and tropical Asian; three other clades are exclusively non-toxic (western European, Mediterranean, Tasmanian) (Scholin et al., 1994, 1995; John et al., 2003). A recent spreading event of *Alexandrium catenella* in the NW Mediterranean Sea along the Catalan coast (Vila et al., 2001a, 2001b) and its blooms in Thau Lagoon, France (Lilly et al., 2002), both novel, are consistent with a human-assisted introduction. DNA and toxin analysis reveal the Thau Lagoon strains are not related to the western Europe and Mediterranean clades, but to *A. catenella* populations found in temperate Asia, specifically the Japanese Temperate Asian ribotype of the *A. tamarense/catenella/fundyense* species complex—the first report of a western Pacific strain of *A. catenella* found outside that region (Lilly et al., 2002). The cysts of this strain are believed to have been introduced by a ship arriving from either Japanese

or Australian waters and deballasting at a port nearby Thau Lagoon.

The six different ribotypes/geographical clades intergrade in morphology and distribution—there is phenotypic overlap between the genetically distinct sub-populations (e.g. North American and western European *Alexandrium tamarense*); there is genetic plasticity within regional populations (e.g. western North American *A. tamarense/catenella/fundyense*), and unique combinations of morphotypes and genotypes occur within the different ribotypes/geographic clades (Scholin et al., 1994, 1995; Higman et al., 2001; John et al., 2003). The diverse and varying assemblages of morphotype and genotypes within, and among the clades indicate strain-mixing also occurs, probably both through natural dispersion and human-aided dispersal. Hence geographic/ribotype clades are not fully reproductively isolated and probably can interbreed when in contact (see John et al., 2003). Thus, while the *A. tamarense* morphospecies complex is cosmopolitan in distribution, within the morphological kinship of the sub-populations there is a toxic discontinuity and heterogeneity along their overlapping, geographic distribution. Consequently, the potential toxic impact of the ballast water or shellfish stock broadcasting of *A. tamarense* complex propagules depends on the geographical source of the propagules. If *A. tamarense* from the North American clade is translocated, a toxic inoculum is being delivered; if the propagules are from the western European clade, the inoculation is not toxic. This reinforces the view that ballast water invasions of morphospecies are of minor concern; it is the redistribution of genotypes that is important (see Section 5.1).

6. Ecological extinction, ecological dormancy, ecological release

Assuming the exotic species discussed in Section 2.3 (*Aureococcus anophagefferens*, *Aureoumbra lagunensis*, *Heterocapsa circularisquama* and *Karenia mikimotoi*) were introduced in ballast water or shellfish stocks, a singular feature emerges—their bloom abundances at their novel bloom sites were the maxima recorded for those species. [Note: the genetic evidence does not support a link between the European and Japanese populations of *K. mikimotoi* (Hansen et al., 2000).] These species precipitously elevated from being rare (three of the species were previously unknown) to becoming very abundant; there are no prior recordings of their being common, abundant or

bloom-forming. There are two ways of viewing their explosive bloom behavior, and that of exotic species generally. At their donor sites, these species were reduced to such low abundance that they no longer interacted significantly with other species within the community. This behavior has been termed ecological extinction (Estes et al., 1989), and may be behavior *en route* to evolutionary extinction. A more likely situation suggested by their prior rarity and novel blooms is these species were ecologically dormant at their donor sites. Those sites are possibly ‘refugia’, to which the species retracted, where they survive, and from which their fortuitous capture in ballast water and release into a more favorable habitat led to their unique blooms, and possibly expanded their range, i.e. a process rescuing the species and breaking their ecological dormancy. The opposing view is that these species are cryptic members of the indigenous flora and their blooms give the perception of bioinvasion, not its reality. Ignoring that prospect, the more major feature of this aspect of the ballast water—HAB paradigm is the transfer of an exotic species from its donor site to the recipient site, in some way, releases the growth suppression active at the donor site – the species blooms! That is, there has been an ecological release. This, in my judgement, is the singular feature of the global HAB phenomenon, irrespective of the species, their rarity, their biogeography, their ecology, or bloom behavior. Ecological release is a broad spectrum HAB feature, it is not restricted to a given group of species—it cuts across phylogenetic lines. Some examples—it is represented among the raphidophytes in the form of novel blooms of *Heterosigma akashiwo* that have developed following initiation of salmon farming (Chang et al., 1990; Whyte et al., 1999; see also Section 3.8); among the haptophytes by the devastating 1988 bloom of *Chrysochromulina polylepis* in Scandinavian waters (Gjøsaeter et al., 2000); among the pelagophytes by the *Aureococcus anophagefferens* and *Aureoumbra lagunensis* blooms discussed in Section 2.4; among the dinoflagellates by *Heterocapsa circularisquama* and *Gymnodinium catenatum* blooms, also discussed earlier; among the silicoflagellates by the remarkable 1983 bloom of *Dictyocha speculum* in the western Baltic (Jochem and Babenerd, 1989; Moestrup and Thomsen, 1990); among the diatoms by the *Coscinodiscus wailesii* blooms in the North Sea (Edwards et al., 2001). This remarkable and perplexing behavior suggests that coastal bloom sites are experiencing the release of “old barriers” – that something significant is happening ecologically that is hidden within the ballast water – HAB paradigm.

7. Colonization, hybridization and the ballast water—HAB paradigm

7.1. Colonization and the ballast water—HAB paradigm

Colonization leading to HAB events is a complex process, and has been considered in detail by Smayda (2002). A newly vectored, non-indigenous species is pioneering initially: it must find an open niche or displace an occupant as its first step (Stage 1) towards colonization, then pass through a persistence phase (Stage 2) *en route* to community entry (Stage 3). On achieving residence, it must be successful at competitive maintenance, and to bloom it must rise to competitive dominance. Colonization during the critical, initial phase (Stage I) is influenced by propagule abundance, habitat receptivity, the degree of genetic matchup of the introduced cells with that ecologically imposed for successful exploitation of the invaded habitat, and the habitat population carrying capacity. Colonization has not occurred if periodic invasions are required to maintain the population. A self-sustaining ‘founder’ population must become established, and species that form resting cysts must be able to complete their life cycle and germinate anew. The founder population must also grow to a level that exceeds the threshold needed to counter environmental stochasticity, advective loss, and other processes that favor extinction, i.e. the species must achieve persistence, the second stage of colonization.

Stage II colonization may take many years; initial success and subsequent year-class exploitation do not guarantee successful invasion. There are virtually no data on how long it takes an introduced species to become bloom-prominent. Comparison of sediment core first records of *G. catenatum* cyst appearance and subsequent pelagic bloom in Tasmanian waters suggests an interval of 8 years (Hallegraeff and Bolch, 1991). The intervals based on first-records of its sediment/pelagic occurrence in Iberian and New Zealand waters are multidecadal (see Sections 3.2–3.3)—are they unrealistic? Lilly et al. (2002) discuss the problems of dating the exact time and source of a species introduction and subsequent recording of its first bloom in connection with a belatedly recognized *Alexandrium catenella* appearance in a French coastal lagoon. Bolch (1987) gives several examples of invader species disappearing some years after temporarily achieving successful invasion.

The third stage of colonization – community entry – confronts a fundamental HAB issue shared with the

enigmatic hidden flora bloom-species – how does an immigrant (exotic) species, which has successfully achieved colonization Stages I and II, emerge from within the community to become a HAB species? This involves a complex set of niche-related issues such as open niche availability, niche preemption, niche fragmentation and decay, etc., also considered in detail by Smayda (2002). Invading species always interact with the resident species, beginning with Stage I and continuing through Stage III, during which the major hurdle for the species is to establish and maintain itself within the community. It must fit into a functional relationship with the resident species and achieve competitive superiority in order to bloom, and encounters resistance in this process. The track from hidden flora status, or from modest abundance, to bloom dominance may be stepwise, in which 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 invasion will vary among species, habitats and growth conditions.

Most microalgae vectored in ballast water do not survive the voyage, or fail to establish viable populations when deballasted (Gregg and Hallegraeff, 2007). It is virtually impossible to prove that an introduction has occurred. This is because of undersampling, the species are overlooked, or their resting cysts do not fossilize, such as with *Alexandrium* species (Hallegraeff and Bolch, 1991). Nonetheless, some exotic species succeed (see Section 2.1) and bloom in great abundance. These novel species appear to be “robust” and raise the issue whether they are indeed “superior species”. There are virtually no data to examine this. But there is no evidence that the recently recognized appearance in the northwestern Mediterranean of the well known species, *Alexandrium catenella*, reflects its superior physiology over the indigenous population with regard to growth, nutrient uptake, allelochemical defense, etc. (Lilly et al., 2002; Vila et al., 2001a,b; Collos et al., 2004). The colonization and bloom enhancement processes of exotic HAB species seem to be primarily habitat-assisted. In the case of *Alexandrium catenella*, the construction of sheltered harbor areas along the Spanish Mediterranean coast serving as refugial sites may have aided blooms and dispersal (Garcés et al., 2000). A more likely factor enhancing colonization and blooms of such species is that a habitat disturbance or an ecological change (“changing environment” hypotheses) has upset the natural equilibrium of the host community, weakening its

intrinsic resistance to bioinvasion. This relaxation would appear to have two elements—altered niche structure, and a nutrient supply adequate to support the bloom. Successful colonization, alone, is not decisive. I have argued elsewhere that colonization leading to eruptive blooms usually must have been preceded by, or accompanied at some point, or coincident with habitat disturbance—a pre-condition for many HAB occurrences (Smayda, 2002). Whatever the mechanism of bloom stimulation, transfer of an exotic HAB species from the donor site to the recipient site releases its growth suppression at the donor site, and it blooms. The impression gained from such events is that an exceptional ecological change of some sort is occurring globally and/or the altered HAB behavior in recent decades has its origins in genetically altered ecophysiological behavior that is operative across phylogenetic lines (see Section 6).

The preceding assessment assumed a Case I type of colonization—the HAB species was not previously found at its novel bloom site. An alternative explanation, but not negating Case I, is that the bloom species was already present in the hidden flora, but ecologically dormant (see Section 6) or mal-adapted to local growth conditions. The ballast water transfer introduced a strain(s) of that species from the donor population better adapted recipient habitat conditions leading to its eruptive bloom (Case II).

7.2. Hybridization and the ballast water—HAB paradigm

The volume of ballast water being carried around the world annually in ships’ ballast water is enormous—10 billion m³ (Paterson, 2001). [This volume has since been reduced to 2–3 billion m³ by the International Maritime Organization (IMO) (G. Hallegraeff, pers. commun.)]. Not only is the volume of ballast water huge, the frequency, magnitude and diversity of species introductions are equally staggering. An estimated 300 million cysts of *Alexandrium tamarense* were present in a ballast tank filled during a toxic bloom in Japan, and when sampled at a New South Wales port its cysts were successfully germinated into viable cultures (Hallegraeff and Bolch, 1991). Introductions via shellfish transplantations also can be significant. Dijkema (1992) calculated 2.5 million viable dinoflagellate cysts can be transferred per tonne of mussels imported into Dutch coastal waters from “red tide” areas, yielding an annual introduction of ca 10¹⁰ dinoflagellates. In an importation of Pacific oyster, *Crassostrea gigas*, to Ireland from France, 67 phytoplankton species were recorded from

the gut contents and sediments of the consignment, including 15 dinoflagellate cyst producing species, three of which were harmful (O'Mahony, 1993). Hence an important feature of ballast water dispersals differing from natural dispersion is that the recipient deballasting sites and indigenous communities have become open to the global genetic bank and metapopulation characteristics of the microalgal morphospecies—a massive bioinvasion and interbreeding event is underway, with potentially profound ecological and evolutionary consequences. For example, Paterson (2001) reports >11,000 vessels arriving from >600 overseas locations reach 65 Australian ports annually. Multiple, allochthonous delivery of genetically diverse and geographic clades of HAB and other microalgal species to recipient deballasting sites has become the rule. And it must be remembered that ballast water introductions generally occur in both directions, i.e. donor ↔ recipient sites. Thus the tendency to view the ballast water—HAB paradigm parochially, i.e. as primarily of local interest, and only in terms of geographic displacement, needs to be enlarged to incorporate these larger scale features of ballast water-aided mixing of the global microalgal populations.

Habitat disturbances and ballast water-aided disruptions of phytoplankton community structure are not the only types of disequilibrating changes contributing to the HAB phenomenon. Genetic disruptions and amendments of indigenous communities are also resulting from ballast water dispersals (e.g. Scholin et al., 1994, 1995; Nagai et al., 2007). These introductions probably induce hybridization, giving rise to “robust” ecophysiological strains (i.e. “hybrid vigor”) that are driving the HAB phenomenon. Species introduced in ballast water are genetic samples of the donor population(s). Species captured while in bloom will be over-represented, but the less abundant species and overall genetic diversity under-represented. As the sample size of the population shrinks, the rarer species and genes will be culled. Consequently, the hybridization potential during admixture of donor and recipient populations of the same species, but of different lineages, is variable, influenced by the volume of the deballasted water and the time/place(s) of its capture. The result will be not only multiple hybridization events of the same species, but also the emergence, over time, of different strains leading to greater, local genetic diversity. Kooistra et al. (2001), based on strain differences in ITS markers, have suggested hybridization events have accompanied the putative range expansion of the toxic raphidophyte *Fibrocapsa japonica*, facilitated by ballast water-mediated mixing

of formerly isolated populations. Various interbreeding options are evident, including the following. The emergence of a strain better suited to growth from crossings of the donor (D) and recipient (R) populations (Case III) is conceivable: $D + R \Rightarrow DR$. Also expected (Case IV), is interbreeding between two strains of a species from different donor sites at a common recipient site, and also leading to robust bloom behavior: $D_1 + D_2 \Rightarrow D_1D_2$. There are several potential variations of Case IV mating, including crossing between the new hybrid and the resident strain: $D_1D_2 + R \Rightarrow D_1D_2R$.

The mating capacity for the proposed hybridization of HAB species is well developed. Sexual reproduction by oogamy, anisogamy, or isogamy through heterothallism and homothallism occurs (see Nagai et al., 2007), and successful mating experiments have been carried out (e.g. Blackburn et al., 2001; Figueroa and Bravo, 2005; Sako et al., 1995; Yoshimatsu, 1981, 1984). This does not mean, however, that mating is relatively simple or produces uniform progeny behavior irrespective of the strain crossings, that the interbreeding outcome is independent of the strain's geographical source, or that the specific mating behavior and its results can be extrapolated to all morphospecies. Mating experiments carried out by Blackburn et al. (2001) using strains of *G. catenatum* isolated from four global populations revealed a complex heterothallic, multi-group mating system, with varying levels of compatibility occurring between mating groups. Significant progeny differences in gamete production, cyst production, and cyst dormancy occurred between interpopulation crosses, as well as mating diversity at the intrapopulation level among the geographic populations. Hence the reproductive compatibility of strains within and among geographical metapopulations is highly variable. In closely related *G. nolleri*, resting cysts were produced both in crosses of clonal strains and in cultures established from cyst germination (inbreeding) (Figueroa and Bravo, 2005). For *G. catenatum*, outbreeding appears to be necessary for cyst formation since cultures started from a single cyst are rarely self-compatible (Blackburn et al., 2001). Clearly, interbreeding affects sexual life history, an ecologically important factor that influences colonization (see Section 7.1).

The idea that hybridization will lead to the emergence of highly toxic and ecologically competitive, new HAB ribotypes is based on the premise that the fitness of the progeny is higher than that of the parental taxa. This prompts the question: Is the high frequency of monospecific blooms of HAB species (unlike the species-diverse diatom blooms), which require multiple

ecological strategies to be operative simultaneously (growth, competition coefficients, grazer deterrence, etc.), a reflection of a newly acquired fitness? This capacity would not appear to be an unreasonable hybrid vigor trait resulting in “super strains” given the broad-based physiological and biochemical differences in strain behavior that occur (see review of Wood and Leatham, 1992). Conversely, when these species eventually become accommodated within the community, and are no longer distinctive, does this indicate that their fitness was diminished through genetic drift or introgression (see Wares et al., 2005)? It is easier to accept decreasing fitness as the cause of a hybrid’s “competitive deterioration”, rather than the community, as a whole, reacting adaptively to draw down, i.e. rectify, the hybrid’s emergence. A paradox may be embedded within this. The lack of genetic diversity found in the global populations of the raphidophytes *F. japonica* (Kooistra et al., 2001) and *H. akashiwo* (Connell (2000), and the dinoflagellate *G. catenatum* (Holmes et al., 2002) has been widely interpreted as evidence for their relatively recent global spread. But does this reduced genetic variability primarily reflect past disasters (catastrophes) that led to range retractions, but are now expanding, i.e. taxon cycles? Such (? disaster) species may represent a special class, or functional group, different from the invigorated HAB hybrid species discussed above. That is, their reduced genetic diversity limits their capacity for hybridization with the result, perhaps, that genetic drift is more decisive than hybridization in contributing to their bloom success.

Clearly, the present superficial treatment does not do justice to the extreme complexity involved, but it does expose the need for revisionist conceptual and methodological approaches to quantifying the distributional and bloom ecology of HABs. This need is also suggested by the surprising evidence that phytoplankton communities are not saturated, i.e. have their full complement of species. There is no evidence that when exotic species become indigenous they displace local species. This apparent absence of competitive exclusion/extinction, particularly surprising given the prevalence of monospecific blooms, is evident in the case of *Odontella sinensis* (Ostenfeld, 1909) and *Coscinodiscus wailesii* (Edwards et al., 2001) in the North Sea where the indigenous flora appears to persist (Boalch, 1987). Such invasions are additive, as also found for *Aureococcus anophagefferens* in the Peconic Bay (Nuzzi and Waters, 2004) and in the Seto Inland Sea (Imai et al., 2006), where the dominant HAB species have been shown to vary, but not eliminated upon the appearance of the exotic species *Heterocapsa circularisquama*.

Finally, evaluation of the role of ballast water/shellfish stock vectoring as a driver of the HAB phenomenon should not be limited to HAB species (or only to microalgae). The delivery of other microbial loop components is expected to be enormous, given the huge ballast volumes captured and delivered, including viruses, algicidal bacteria, and microbial loop grazers such as protoperidinians, ciliates and other protists (Hallegraeff and Bolch, 1992; Pierce et al., 1997; Galil and Hülsmann, 1997). These inoculations undoubtedly affect HAB population dynamics, and one can even visualize a situation in which a virus or algicidal bacterium attacks a member of the indigenous community, reducing its competitive ability which then provides a previously out-competed cryptic species with the opportunity to bloom. This ecological release might be falsely perceived as a bioinvasion.

8. Perspectives

The ballast water—HAB paradigm not only is providing valuable insights into the HAB phenomenon, it has unutilized methodological and conceptual potential. The various characteristics of the ballast water—HAB paradigm, particularly the human-aided global homogenization of the microalgal gene pool, make it an ideal tool for asking questions and designing testable hypotheses on the interplay between the ecophysiology, toxicology, bloom dynamics, etc. of the various HAB Life Forms and the diverse habitat properties and drivers known to regulate distribution, growth, community assembly and blooms. The ballast water—HAB paradigm offers opportunities to examine and to test ecological hypotheses. Invasions of exotic (alien) species allow studies of species interactions influenced by contemporary ecological processes, and therefore provide natural experiments in the absence of long-term time series data. I am not suggesting this approach is a panacea. However, while important insights into natural population bloom ecology are being obtained, the comparative field ecological approaches being applied at present have not significantly advanced knowledge of global HAB ecology. Annual studies of suitable sampling frequency and quantitative measurement of relevant physical, chemical and biological parameters are virtually non-existent. There is a lack of basic information on community assembly, bloom species selection and regulation, successional and trophic processes. The prevailing approach is to limit field studies to certain time periods, and then, usually, to exclude whole community and relevant habitat variable measurements. A decade or more of refocused research on natural population

dynamics would appear to be required to make significant advances in quantifying the causes, regulation and trophic dynamics of HABs, going beyond the limited regional insights and, usually, species-specific insights. The global scale of the ballast water—HAB paradigm and extant knowledge on this relationship, I suggest, provide the opportunity to carry out natural experiments beyond the current focus on distribution and vectoring. It would seem appropriate to develop an international program along the lines of the GEOHAB Core Research Project: HABs in Upwelling systems (GEOHAB, 2005).

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