Turbulence, watermass stratification and harmful algal blooms: an alternative view and frontal zones as "pelagic seed banks"

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Abstract

Watermass stratification has been considered the essential physical condition that dinoflagellates require to bloom because of their relative inability, unlike diatoms, to tolerate the elevated shear-stress associated with water-column mixing, turbulence and high velocity, coastal currents. The swimming speeds of 71 flagellate taxa, with a focus on dinoflagellates, are compared to the turbulence fields and vertical velocities that develop during representative wind conditions, upwelling and at frontal zones. The results suggest that the classical stratification–dinoflagellate bloom paradigm needs revision. Tolerance of turbulence, growth within well-mixed watermasses and survival and dispersal while entrained within current systems are well developed capacities among dinoflagellates. Their secretion of mucous, often copious during blooms, is suggested to be an environmental engineering strategy to dampen turbulence. Biophysical tolerance of turbulence by dinoflagellates is often accompanied by high swimming speeds. Motility speeds of many species exceed in situ vertical current velocities; this also allows diel migrational patterns and other motility-based behavior to persist. Species belonging to "mixing-drift" life-form assemblages can increase their swimming speeds through chain formation, which helps to compensate for the increased turbulence and vertical water-column velocities of their habitats. The ability of dinoflagellate species to tolerate the vertical velocities of offshore, frontal zones, where abundant populations often develop, suggests that fronts may serve as "pelagic seed banks", occurring as pelagic analogues of nearshore seed beds, from which seed stock is dispersed. The different ecologies associated with the hypothesized, "pelagic seed banks" of vegetative cells and the "seed beds" of resting stage cells deposited onto sediments are discussed. There is a contradiction in the stratification–HAB paradigm: the quiescent conditions of a stratified watermass, with its characteristic nutrient-poor conditions are expected to promote stasis of the population, rather than growth and blooms. The analyses suggest that dinoflagellate blooms do not preponderate in stratified watermasses because the bloom species are biophysically intolerant of the higher velocities and turbulence of more mixed watermasses. The watermass stratification that often accompanies flagellate blooms is probably a secondary, parallel event and less essential than some other factor(s) in triggering the observed bloom. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Dinoflagellates; Motility; Stratification; Frontal zones; Harmful blooms

1. Introduction

A basic premise of flagellate bloom ecology is that watermass stratification is essential for their blooms to occur. This classical view has its origins in field observations, experimental simulations and theory (Smayda, 1997). Field observations show that seasonal and regional blooms of flagellates are often associated with, even await, development of a stratified watermass. Experimental studies suggest that flagellates are more sensitive than diatoms to turbulence and

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associated shear-stress and rates of strain, resulting in physiological impairment and loss of cellular integrity (Estrada and Berdalet, 1998). Kierstead and Slobodkin (1953) showed theoretically that stratified waters have a "critical patch size", below which the rate of horizontal diffusion will exceed growth rates and thwart bloom development. This combination of observations underlies the view that reduced turbulence is the critical feature of watermass stratification favoring flagellate blooms and is codified by Margalef (Margalef, 1978; Margalef et al., 1979) in his classical Mandala. In this conceptual model, the selection of harmful algal and benign red tide bloom species is viewed as being abiotically regulated by interactions between turbulence and nutrients (Smayda and Reynolds, 2001).

Several weaknesses compromise the evidence used to support the watermass stratification–HAB paradigm. There is virtually no quantitative information on whether observed in situ associations between blooms and watermass stratification reflect cause-and-effect responses or are simply parallel tendencies. Experimental simulations of in situ turbulence and its effects on cellular processes extrapolated to natural populations are compromised because of problems of scaling, methodology and in distinguishing experimental artifacts. For example, Thomas and Gibson's (1990) experimentally derived prediction that near-surface blooms of the upwelling species *Lingulodinium polyedrum* will become inhibited at wind speeds >2.1 m s^{-1} is inconsistent with its observed behavior in the Californian upwelling system (Walsh et al., 1974). The terms turbulence, watermass stability and stratification are generally used interchangeably when relating phytoplankton dynamics to watermass mixing characteristics. This creates another problem. Turbulence and stratification differ both as physical processes and in their effects on phytoplankton (Smayda, 1997). Turbulence is primarily a biophysical stressor capable of impairing individual cells. Stratification, including microstratification, primarily influences population dynamics through interactions with the vertical irradiance and nutrient gradients. There is also a bloom support problem. Stratification is accompanied by reduced mixing, the latter functioning to pump nutrients upward into the euphotic zone from deeper layers and an important source of nutrients needed for bloom events. The contradiction becomes obvious: watermass stratification is the physical condition least likely to provide nutrients needed for the observed blooms. Such concerns have prompted this re-evaluation of the stratification–HAB paradigm. It is undertaken primarily from the perspective of the bloom organisms; i.e. as a cellular problem, rather than from the perspective of population dynamics, the traditional approach followed in the development and application of this paradigm.

2. Paradigm evaluation

2.1. Life-form types among dinoflagellate bloom species

The watermass stratification–HAB paradigm, in its simplest form, recognizes two distinct habitat states—watermasses are either stratified or more vigorously mixed. Embedded within this is the reductionism that flagellates, collectively, require a well-stratified watermass to bloom and that the component species are similar in this requirement. This has led to the perception that dinoflagellates have a monotonous habitat requirement and are ecophysiological uniform. To evaluate these assumptions, consider the onshore–offshore, mixing-nutrient gradient that generally characterizes the global ocean (Fig. 1) (overlap of the depicted habitats in Fig. 1 does not imply contiguity, only that the mixing/irradiance/nutrient features in that box (i.e. habitat) overlap those found in adjacent boxes). Nine distinct physical habitats are evident, ranging from turbulent, deep-mixed, winter watermasses to highly stratified (seasonally or permanently) nearshore embayments. Intermediate habitats occur within these extremes of the mixing gradient and include upwelling zones, offshore currents and frontal zones. Three distinct, highly stratified habitats also are aligned along the onshore–offshore nutrient gradient: eutrophic coastal waters, which gradate into the shallow, shelf waters and, farther offshore, into highly stratified, oligotrophic tropical waters.

The predominant dinoflagellate bloom taxa or vegetation element reported for these representative marine habitats reveals a striking pattern (Fig. 2): nine distinct bloom types are distinguishable (Smayda and Reynolds, 2001). There is a gradient in life-form properties along the offshore trajectory of increasing watermass inertia against mixing (generally), deepening
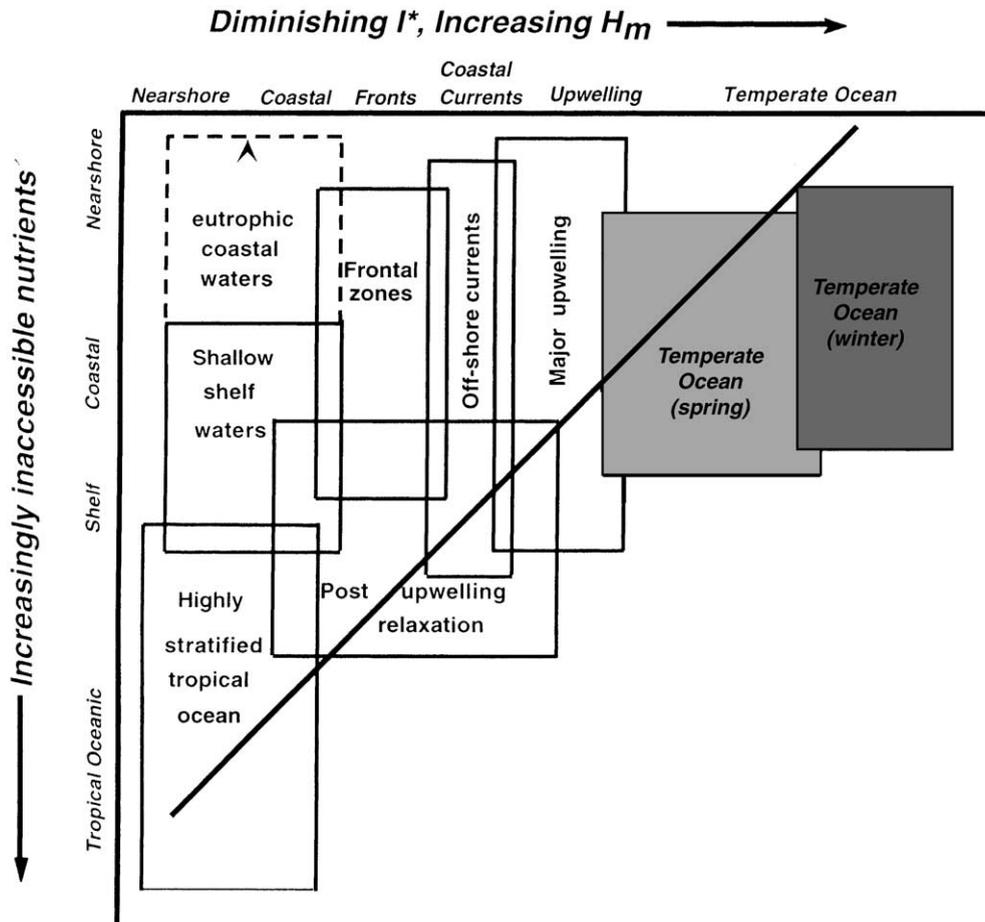
Fig. 1. Schematic matrix of pelagic marine habitats along an onshore–offshore gradient separating deep-mixed and well-stratified, nutrient-enriched and -deficient systems. Overlap of habitat types within the habitat template schema does not always imply their contiguity. The diagonal approximates to Margalef's main successional sequence (Margalef et al., 1979) (source: Smayda and Reynolds, 2001).

of the stratified layer and a progressive decrease in nutrient levels. When overlain onto the habitat template (Fig. 1), the nine dinoflagellate life-form types separate into type habitat preferences, with transitions into new type assemblages occurring at new combinations of mixing and nutrient availability (Fig. 3). Dinoflagellate life-forms "avoid" the energy-limited, temperate winter–spring and major upwelling conditions favored by diatoms and their blooms (upper right section of Figs. 1 and 3). Of particular interest are the mixing-drift adapted life-form types IV, V and VI, which appear and cluster in habitats of diminished, but still pronounced vertical mixing and shear/stress

effects. These HAB dinoflagellates are adapted to the increased velocities associated with frontal zones; to the damped, but still elevated vertical mixing during relaxations in coastal upwelling and during their entrainment within alongshore and across-shelf coastal currents, i.e. the frontal zone (type IV), upwelling relaxation (type V) and coastal current entrained (type VI) HAB assemblages.

The classical frontal zone (type IV) species is *Karenia mikimotoi*—frequently identified as *Gyrodinium aureolum*, its "look-alike"—which blooms along frontal zones within the English Channel, North Sea, Skagerrak and Gulf of St. Lawrence (Le Févre,

- **Type I** (= *Gymnodinioids*)

   Gymnodinium spp. , Gyrodinium instriatum, Heterocapsa rotundata
   \

 - **Type II** *(= Peridinians / Prorocentroids)*

    Heterocapsa triquetra, Scrippsiella trochoidea, Prorocentrum micans, Prorocentrum minimum
    \

  - **Type III** *(= Ceratians)*

     Ceratium tripos, Ceratium fusus, Ceratium lineatum
     \

   - **Type IV** *(= Frontal Zone Taxa)*

      Karenia mikimotoi , Alexandrium excavata
      \

    - **Type V** *(= Upwelling Relaxation Taxa)*

       Gymnodinium catenatum, Lingulodinium polyedrum
       \

     - **Type VI** *(= Coastal Current Entrained Taxa)*

        Karenia brevis, Ceratium spp., *Pyrodinium bahamense* var. *compressum*
        \

      - **Type VII** *(= Dinophysoids)*

         Dinophysis acuta, Dinophysis acuminata
         \

       - **Type VIII** *(= Tropical Oceanic Flora)*

          Amphisolenia, Histioneis, Ornithocercus, Ceratium spp.
          \

        - **Type IX**   *(= Tropical Shade Flora)*

           Pyrocystis noctiluca, Pyrocystis pyriformis

Fig. 2. Dinoflagellate bloom and vegetation life-form types, and representative species, found along an onshore–offshore gradient of decreasing nutrients, reduced mixing and deepened euphotic zone.

1986; Dahl and Tangen, 1993; Blasco et al., 1996). *K. mikimotoi* is also highly adapted for entrainment within coastal currents (Lindahl, 1986) and has spread throughout the North Sea and contiguous waters since first recorded in the 1960s (Partensky and Sournia, 1986). *Alexandrium tamarense* (var. "*excavatum*") occurs as a type IV species in the Argentine Sea, where its frontal zone blooms are well known occurrences (Carreto et al., 1986). Among HAB dinoflagellates adapted to bloom during upwelling relaxations (type V), and therefore able to survive within upwelling habitats, are *Lingulodinium* (*Gonyaulax*) *polyedrum* (Blasco, 1977) and *Gymnodinium catenatum* (Fraga et al., 1988, 1990). Pitcher and Boyd (1996) and Smayda (2000) have discussed the rigors of dinoflagellate survival in wind-driven, coastal upwelling habitats, including responses to oscillations in active

and quiescent upwelling phases. During active upwelling, dinoflagellates often accumulate offshore in regions of upwelling fronts, while during upwelling relaxations these frontal populations become entrained in weakened, across-shelf currents directed onshore, a dispersion which seeds nearshore habitats and leads to local blooms. In their exposure to the coupled physical processes which characterize the active and relaxation phases of upwelling, type V life-forms must also tolerate the predominant physical stresses which confront type IV and VI (coastal current entrained) life-forms (Fig. 4). Hence, the "mixing-drift" adapted type IV, V and VI species intergrade in their adaptations. Notable type VI HAB dinoflagellates adapted for entrainment and dispersal within coastal currents include the highly toxic species *A. tamarense*, *Pyrodinium bahamense* var. *compressum* and *Karenia* (*Gymnodinium*) *brevis*
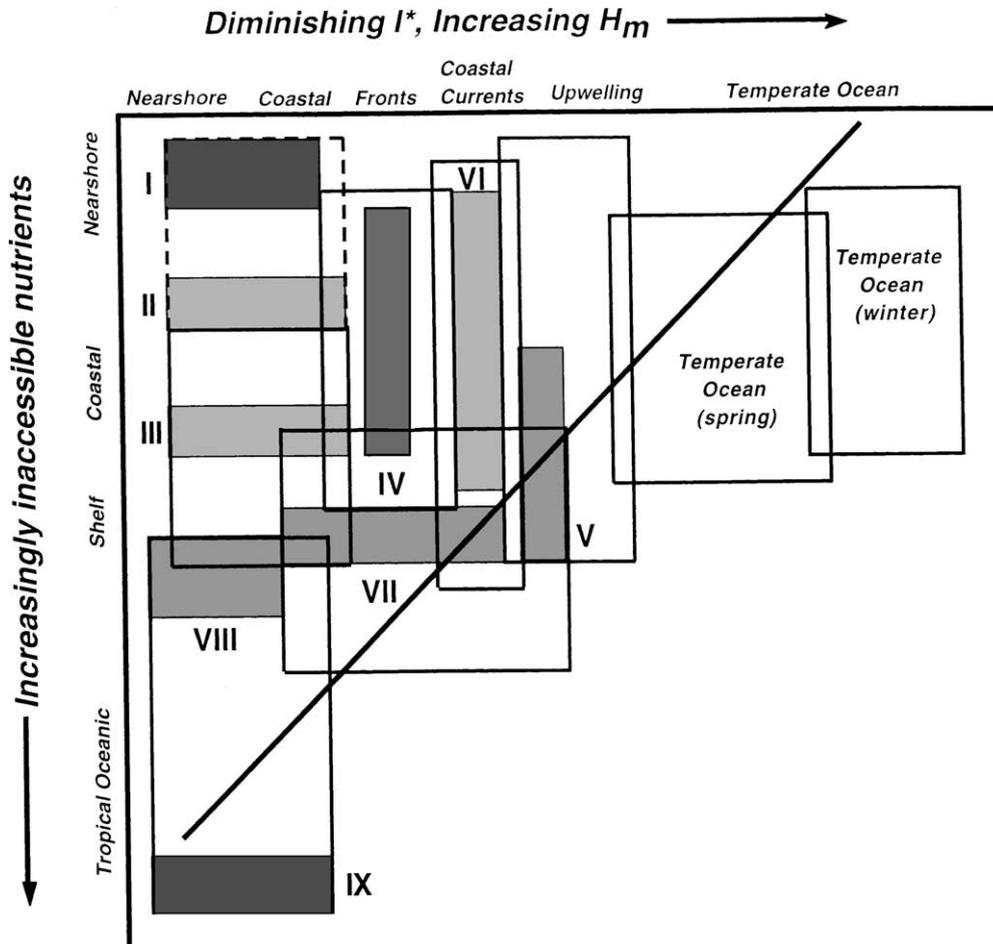
Fig. 3. Predominant dinoflagellate life-form types (Fig. 2) associated with the turbulence-nutrient matrix (Fig. 1) along the onshore–offshore continuum characterizing pelagic habitats. Type I = gymnodinioids; type II = peridinioids and prorocentroids; type III = ceratians; type IV = frontal zone species; type V = upwelling relaxation taxa; type VI = coastal current entrained taxa; type VII = dinophysoids; type VIII = tropical oceanic flora; type IX = tropical shade flora (source: Smayda and Reynolds, 2001).

(Franks and Anderson, 1992; Seliger, 1993; Steidinger et al., 1998; Tester et al., 1991). A more detailed treatment of the nine life-form types and adaptive strategies of the component species is found in Smayda and Reynolds (2001), with dinoflagellate bloom ecology in upwelling systems treated by Smayda (2000).

2.2. Turbulence and dinoflagellate behavior

If some dinoflagellates are adapted to the physically dynamic conditions associated with upwelling, fronts and the velocities of coastal currents—the

"mixing-drift" life-form types (Figs. 2 and 3)—are they unique in this capacity compared to other dinoflagellates? Wind-induced habitat structuring creates an extraordinarily complex and variable physical habitat in which there is frequent habitat destruction and exposure of phytoplankton to turbulence, physical divergences, frontal zone downwelling and entrainment within alongshore and onshore–offshore currents; physical processes whose velocities and spatial heterogeneity vary. Laboratory experiments have shown that excessive turbulence can negatively impact dinoflagellate cells by three mechanisms: physical
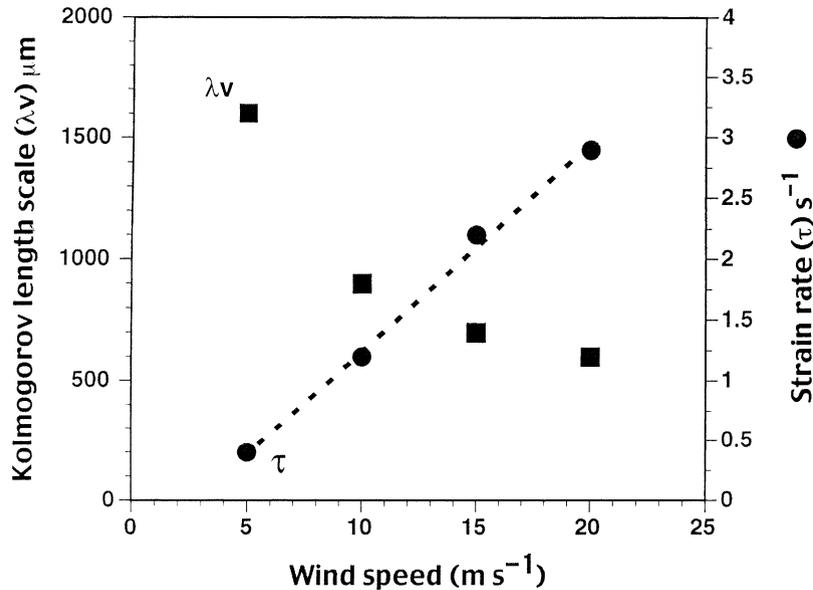
Fig. 4. Relationship between wind speed, Kolmogorov length scale and associated strain rates (data from Table 1 in Estrada and Berdalet, 1998; the units of the λ_v values given as mm by Estrada and Berdalet have been corrected to cm).

damage, physiological impairment and behavioral modification (Berdalet and Estrada, 1993; Thomas and Gibson, 1990; White, 1976), with dinoflagellates varying interspecifically in their vulnerability to turbulent shear and strain (Berdalet and Estrada, 1993).

Turbulent kinetic energy introduced into the watermass by the prevailing winds induces vertical mixing leading to turbulence (Mann and Lazier, 1996). The energy of this turbulent motion, the intensity of which pulsates with variations in wind stress, is continuously transferred from large to ever-smaller eddies which progressively and, ultimately, completely dissipate. The rate of turbulent energy dissipation (ε; $W\,kg^{-1}$) during this energy cascade is the twisting or shearing force in the turbulence, the feature that makes turbulence so biophysically threatening to phytoplankton. The potential for negative effects on the entrained phytoplankton, at least theoretically, increases when there is a significant mismatch between the size–shape characteristics of cells captured by the eddies and the scale and velocity of the eddies (Margalef, 1978). With increasing wind stress, the size of the smallest eddies, i.e. Kolmogorov length scale (λ_v), formed during the eddy cascade decreases. A decrease in eddy size is accompanied by increases in the velocity gradient and the rate of strain (Mann and Lazier, 1996; Estrada and Berdalet, 1998) (Fig. 4). Cells (life-forms, colonies) whose maximum linear dimensions exceed eddy widths are theoretically more likely to be damaged or selected against than smaller cells captured and entrained within larger eddies (Margalef, 1978). At wind speeds between 5 and $20\,m\,s^{-1}$, calculated Kolmogorov length scales range from 600 to $1600\,\mu m$ (Fig. 4). To put the depicted windspeeds and accompanying minimal eddy sizes into perspective, average longshore wind speeds in the Peruvian ($15°S$), Baja California and northwest African upwelling systems ranged from 4.6 to $5.5\,m\,s^{-1}$ (Walsh, 1976) and reached $7.0\,m\,s^{-1}$ during an intense event off northwest Africa (Codispoti, 1981). At these upwelling-inducing wind speeds, which are at the lower end of the Kolmogorov length scale–wind speed relationship (Fig. 4), the accompanying eddy sizes are estimated to vary from about 1200 to $1600\,\mu m$. Some of the fastest dissipation rates found accompany tidal mixing of estuaries and coastal embayments: the size of the smaller eddies can then be only $200–400\,\mu m$ (Reynolds, 1997).

The minimal Kolmogorov eddy sizes and associated rates of strain anticipated to be induced by the wind

speeds shown in Fig. 4, seemingly would not select against many dinoflagellate bloom species when exposed to such turbulence. Many HAB species have a cell diameter of ≤50 μm, i.e. one to two orders of magnitude smaller than eddy size diameters. Their cell size would allow them to survive entrainment without biophysical damage within the micro-eddy cascade generated at wind speeds from 5 to 20 m s^{-1}. At wind speeds >20 m s^{-1}, as found in the Benguela region (Bailey and Chapman, 1991), the turbulence regime set up would then have stronger selective pressure against dinoflagellates (Fig. 4). Blooms of large ceratians, such as *Ceratium fusus*, which can reach 600 μm in length, might be selected against at wind speeds >15 m s^{-1}, particularly in regions of intense tidal mixing. It seems likely, then, that an ability to survive the turbulence spectrum (at least most of the time) not only characterizes the mixing-drift life-forms (types IV, V and VI; Figs. 2 and 3), but dinoflagellates generally. The issue of interest here is not whether reduced turbulence induces blooms; that is a separate issue. Rather, can dinoflagellate species survive the turbulence spectrum, which develops during intensified watermass mixing and withstand the entrainment and dispersal velocities within coastal currents to seed potential bloom events during periods or in habitats of reduced turbulence?

2.3. Mucous secretion during dinoflagellate blooms: an environmental engineering strategy to dampen turbulence?

Although mucilage production is a general phytoplanktonic trait, dinoflagellates often secrete exceptional amounts of mucous during blooms, during which the watermass has been variously described as viscous, slimy, ropy, etc. Gunther et al.'s (1948, p. 315) description of this effect during a *K. brevis* bloom is representative: the watermass "was viscid like a thin oil... felt very slimy... and ran off the hands and fingers in gelatinous-like streams". In red tide patches developed in the Peruvian upwelling system, Gunther (1936) described the bubbled sea surface as an "oily scum resembling a surface film of fuel oil". During a *K. mikimotoi* (*aureolum*) bloom, the viscous seawater "frothed upon SCUBA (diver) exhalations" (Potts and Edwards, 1987), with the viscid microlayers sometimes trapping small bubbles of photosynthetically derived oxygen (Jenkinson, 1989).

This species has been reported to secrete 10% of its fixed carbon (Dixon and Holligan, 1989). Copious mucous secretion during a *Cochlodinium catenatum* bloom produced a "viscous foam" (Guzman et al., 1990) and significant exudation occurred during blooms of *Gonyaulax polygramma* (Lam and Yip, 1989), *G. catenatum* (La Barbera-Sanchez et al., 1993) and *Noctiluca miliaris* (Subramanian, 1985; Jenkinson and Biddanda, 1995). In La Jolla Bay, dissolved organic matter levels increased two–five-fold during blooms of *L. polyedrum* (Holmes et al., 1967), a species which can secrete at least 25% of its photosynthate (Thomas et al., 1995). Stationary phase cultures of *Akashiwo* (*Gymnodinium*) *sanguineum* and *Scrippsiella trochoidea* secreted >50% of their photosynthate (Hellebust, 1965) and media in which *Prorocentrum minimum* was cultured became viscous (Sakshaug et al., 1984). Thus, many notable dinoflagellate bloom species are capable of copious mucous secretion.

The high levels of organic matter secreted during dinoflagellate blooms increases the viscosity of bloom waters (Jenkinson, 1989, 1993). I suggest that mucous secretion may be an environmental engineering strategy that dinoflagellates use to dampen the turbulence spectrum and thereby create a more favorable physical habitat. The basis of this strategy lies in the smoothing effect that organic exudates have in limiting the size of the smallest turbulent eddies which, following the Kolmogorov length scale (λ_v) can be estimated from the equation (Mann and Lazier, 1996):

$$\lambda_v = 2\pi \left(\frac{\nu^3}{\varepsilon} \right)^{1/4}$$

where ν is the kinematic viscosity (m^2 s^{-1}) and ε the rate of turbulent energy dissipation (m^2 s^{-3}). A turbulence damping strategy is probably not unique to dinoflagellates (other flagellate groups may have this capacity) and would be consistent with the swim strategy that flagellates collectively share (diatoms have a sink strategy).

2.4. Dinoflagellate swimming behavior

Vertical mixing and turbulence may significantly impact the degree of vertical, microhabitat structural differentiation present and determine whether

the extant turbulence field allows dinoflagellates to exploit this microstructure. Motility-based behavior, such as nutrient-retrieval migrations, depth-keeping and pycnocline blooms, allows flagellates to exploit the nutrient resource gradient and other microhabitat features (Smayda, 1997). Dinoflagellates, whether type IV (Figs. 2 and 3) or of other habitat preference, commonly bloom along frontal boundaries despite the sharp horizontal and vertical velocity gradients present (Carreto et al., 1986; Pitcher and Boyd, 1996; Pitcher et al., 1998). Sub-surface thermocline and pycnocline ("thin-layer") blooms are also characteristic features (Holligan, 1979). These thin-layer accumulations, which occur on diel and longer time scales, reveal that dinoflagellates can effectively apply vertical positioning strategies even during physically dynamic periods. *K. mikimotoi* (*aureolum*) bloomed continuously over a 4-week period within sharp, 1 m thick layers at depths below 10 m (Bjørnsen and Nielsen, 1991). *Akashiwo* (*Gymnodinium*) *sanguineum* collected into layers 1–4 m thick within the California current system (Kiefer and Lasker, 1975; Lasker and Zweifel, 1978). *Ceratium tripos* occurred in thin-layers below the seasonal thermocline at depths between 20 and 25 m (Mahoney and Steimle Jr., 1979). In these strategies of vertical depth-keeping, dinoflagellates exploit the low energy cost of motility, <0.1% of the total energy budget for growth (Holligan, 1985) and further aided by the low Reynolds numbers ($Re \leq 0.05$) that characterize their motility (Levandowsky and Kaneta, 1987). Dinoflagellates ($\emptyset = 10$–$50\,\mu m$) swimming at rates from 300 to $600\,\mu m\,s^{-1}$ can abruptly cease swimming upon entry into a suitable microhabitat. Similarly, the distance needed to accelerate from "rest" to full speed is negligible, being on the scale of organism size (Levandowsky and Kaneta, 1987). These conspicuous fine-tuning features of motility allow dinoflagellates to auto-aggregate volitionally into sharp, tightly banded, sub-surface layers whose thickness may be as little as a decimeter, or less (Bjørnsen and Nielsen, 1991). The analogy of "hovering hummingbirds" comes to mind in envisioning the plight of dinoflagellates seeking to achieve depth-keeping within preferred microhabitats when threatened with vertical niche displacement by watermass movements.

At what vertical velocities of up- and downwelling will the motility speeds of dinoflagellates become inadequate and prevent behavioral migration, depth-keeping, retention within the euphotic zone or thin-layer accumulation? Table 1 lists the swimming speeds of some taxa reported to bloom in frontal zones and during upwelling. Their swimming speeds range about 265-fold, from $32\,\mu m\,s^{-1}$ (*Akashiwo*

Table 1
Swimming speeds of single-celled dinoflagellates and other motile species reported to bloom in type IV and V habitats

Species	Swimming speed ($\mu m\,s^{-1}$)	Source
A. sanguineum	300	Cullen and Horrigan (1981)
A. sanguineum	278	Blasco (1977)
A. sanguineum	135	Kamykowski et al. (1992)
A. sanguineum	115	Kamykowski et al. (1989)
A. sanguineum "nelsoni"	32	Kamykowski et al. (1989)
A. sanguineum[a]	410	Fraga et al. (1989)
C. furca	278	Levandowsky and Kaneta (1987)
C. furca	222	Levandowsky and Kaneta (1987)
C. furca	206	Edler and Olsson (1985)
D. acuta	500	Levandowsky and Kaneta (1987)
G. polygramma	500	Levandowsky and Kaneta (1987)
G. catenatum[b]	247	Fraga et al. (1989)
G. aureolum (*mikimotoi*)	230	Throndsen (1973)
H. akashiwo	140	Throndsen (1973)
L. polyedra	400	Jeong (1994)
L. polyedra	355	Kamykowski et al. (1989)
L. polyedra	278	Levandowsky and Kaneta (1987)
L. polyedrum	258	Kamykowski et al. (1992)
M. rubrum	8500	Crawford and Lindholm (1997)
M. rubrum	2217	Barber and Smith Jr. (1981)
P. micans	236	Edler and Olsson (1985)
P. micans	133	Kamykowski et al. (1989)
P. micans	100	Bauerfeind et al. (1986)
P. micans	87	Kamykowski et al. (1989)
Protoceratium reticulatum	362	Kamykowski et al. (1989)
S. trochoidea	153	Kamykowski et al. (1992)
S. trochoidea	82	Bauerfeind et al. (1986)
S. trochoidea	69	Levandowsky and Kaneta (1987)

[a] Four-cell chain, rate $580\,\mu m\,s^{-1}$.
[b] Eight-cell chain, rate $440\,\mu m\,s^{-1}$.

(*Gymnodinium*) *sanguineum*) to 8500 µm s^{-1} (*Mesodinium rubrum*). Excluding the exceptional rate for *Mesodinium*, the range drops to 15-fold, with minimum and maximum migrational rates about 10 cm h^{-1} and 1.8 m h^{-1}, respectively. Thus, flagellates vary considerably in their intrinsic motility to offset physical displacement through mixing, advection and turbulence: *Mesodinium* (functional as a phytoplankter) is extremely fast; *Noctiluca* is positively buoyant; while other dinoflagellate taxa exhibit intermediate to sluggish rates of motility. Swimming rates are variable, rather than fixed, as shown in Table 1 for *A. sanguineum*, *Prorocentrum micans* and *S. trochoidea*. Since motility is influenced by temperature, nutrients and irradiance (Kamykowski and Yamazaki, 1997) and the ascent and descent velocities differ for a given species (Bauerfeind et al., 1986), reports of intra-specific variability in motility are not surprising.

Fig. 5 examines the question of whether the mixing-drift, life-form types (IV, V and VI) are more energetic swimmers than other life-form types (Figs. 2 and 3). The ratio of swimming to sinking velocity is a useful index of the relative ease of migrational return to a preferred depth by a species following its vertical displacement by vertical watermass movement. The ascent and descent velocities of a species differ (Bauerfeind et al., 1986); sinking rates add to descent rates, but subtract from ascent rates (this finer point can not be incorporated into the analysis). The sources of the species data used in Fig. 5 are as identified in Table 1 and based also on data in Smayda and Bienfang (1983). Where sinking rates were not found, they were calculated using the Kamykowski et al. (1992) equation:

$$V_i = -22.90 \left(\frac{S}{V} \right) + 7.50$$

where V_i is the sinking velocity (m per day) as a function of the cell surface area/volume ratio (S/V; µm^{-1}). S/V was calculated, where needed, from morphometric data available in taxonomic monographs dealing with the species in question.

Relative to their sinking rates, both weak and strong swimmers occur among dinoflagellates (Fig. 5). *A. sanguineum*, a major bloom species in the Peruvian upwelling system (Smayda, 2000), falls within the group having the lowest ratio of ascent to descent, ca. 1:1. It can descend more readily than it can swim

upward. *P. micans* also has this characteristic. The type V (upwelling relaxation) life-forms, *G. catenatum* (single cells) and *L. polyedrum*, swim at rates about six times faster than they sink, and can readily ascend to overcome sinking. Many dinoflagellates have swim/sink ratios of about 10:1, including the relatively small species *Katodinium rotundatum* and *P. minimum*, which produce intense type I and II blooms, respectively and the large, attenuate ceratians, *C. fusus* and *Ceratium furca*, both of which bloom in upwelling regions and nutrient enriched embayments (type III). Smayda and Bienfang (1983) present related material on dinoflagellate swim/sink ratios.

2.5. Chain formation and swimming behavior

Most dinoflagellates exist as solitary cells, but at least four mixing-drift life-form species (types IV, V and VI) form chains: *Alexandrium affine*, *Alexandrium catenella*, *G. catenatum* and *P. bahamense*. The chains produced by *G. catenatum* can include up to 64 cells and reach lengths of 2 mm (Blackburn et al., 1989). *A. tamarense* (type VI) has also been reported to form chains of up to four cells during blooms in Walvis Bay (Grindley and Sapeika, 1969). (Chain formation also occurs in *Alexandrium cohorticula*—up to 64 cells per chain (Ogata et al., 1990), *Alexandrium fraterculum*—≥25 cells per chain (Plates 1–7 in Fukuyo et al., 1988), *Alexandrium monilatum*—at least 8 cells per chain (Walker and Steidinger, 1979) and *Cochlodinium* cf. *polykrikoides*, species whose life-forms have not been typified). The habitat preference of the "mixing-drift" community is enhanced by their formation of fast-moving chains. This allows them to navigate the sometimes intense vertical and horizontal watermass velocities that can characterize their habitats, since their swimming rates generally increase with chain formation (Fraga et al., 1989). In culture, eight-cell chains of *G. catenatum* increased their swimming speed above solitary cell rates by about 70%, from 247 to 440 µm s^{-1}; for four-celled chains of *A. affine*, the rate increased about 45%, from 410 to 580 µm s^{-1} (Fig. 6). In natural populations of *A. catenella*, the ascending migration velocities of four–eight-cell chains were 461 µm s^{-1} (Takeuchi, 1988) (this rate is 2.5-fold lower than reported by Karp-Boss et al. (2000) for *A. catenella* chains in culture). Downward migrational speeds
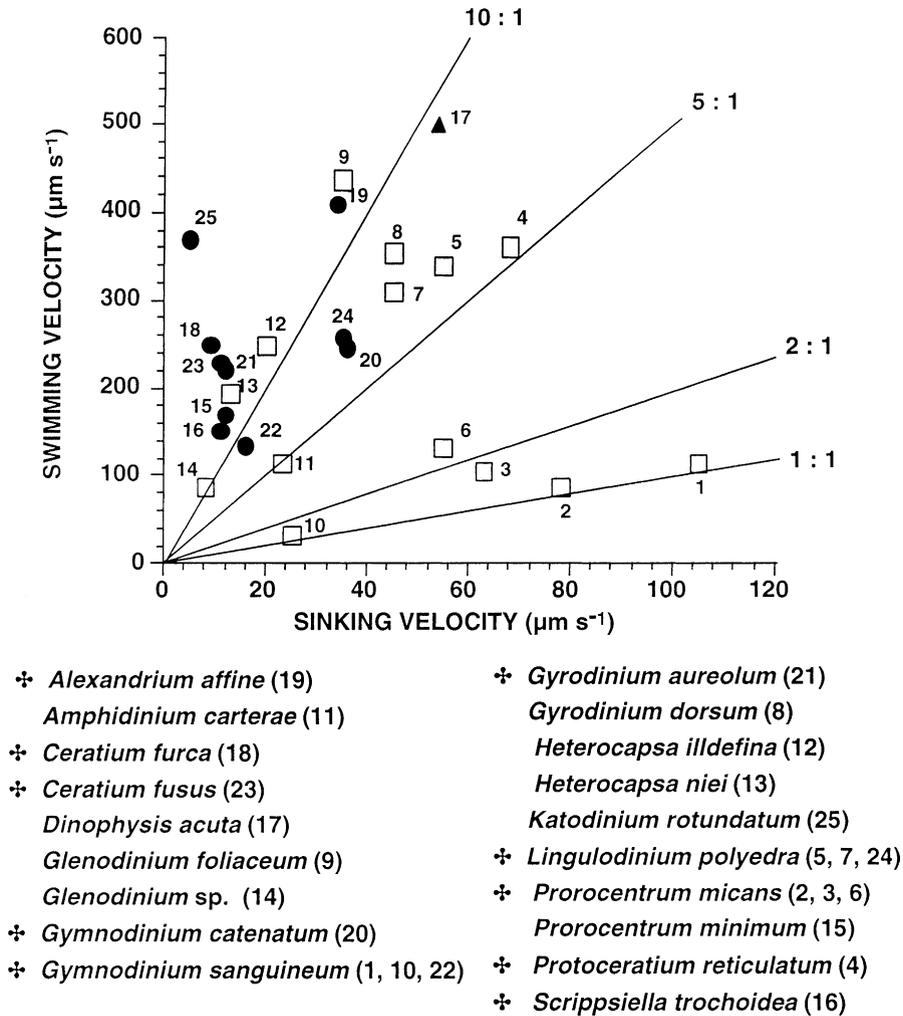
Fig. 5. Dinoflagellate species swimming and sinking velocities, and their swim/sink ratios. Open squares are data from Kamykowski et al. (1989); solid circles are for species identified in Table 1 and based on data in Smayda and Bienfang (1983); see Section 2.4 for further details. Species with cruciform notation produce red tides in upwelling regions and/or at fronts.

were $694\,\mu m\,s^{-1}$, with chain-forming cells reported to have migrated to deeper layers than solitary cells. The maximal rates reported for these three chain forming species (440–$694\,\mu m\,s^{-1}$) are among the highest motility rates reported for flagellates (Figs. 6–8).

Chain formation increases the swim/sink ratio (Fig. 7): the ratio for an eight-cell chain of *G. catenatum* is nearly twice that for solitary cells and also confers a propulsion advantage: for *A. affine*, the swim/sink ratio (17:1) for a four-cell chain increases by about 50% above that (12:1) for solitary cells.

Fraga et al. (1989) concluded that the increased swimming speeds that accompany modest chain formation of these type V species are specific adaptations that favor their retention within the euphotic zone during downwelling and at local divergences. Field populations of *G. catenatum* survived downwelling velocities of ca. 10 m per day and remained within the euphotic zone (Figueras et al., 1995). While chain formation provides biophysical advantages to dinoflagellates for growth and vertical depth-keeping within physically dynamic watermasses, the swim/sink strategies of the
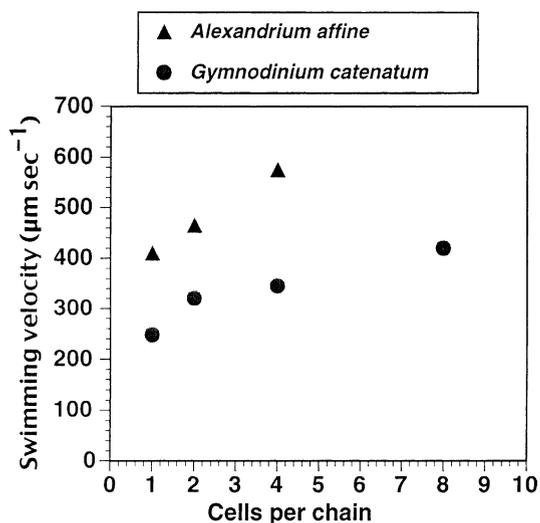
Fig. 6. Effect of colony size on the swimming velocity of *A. affine* and *G. catenatum*. Data from Fraga et al. (1989).
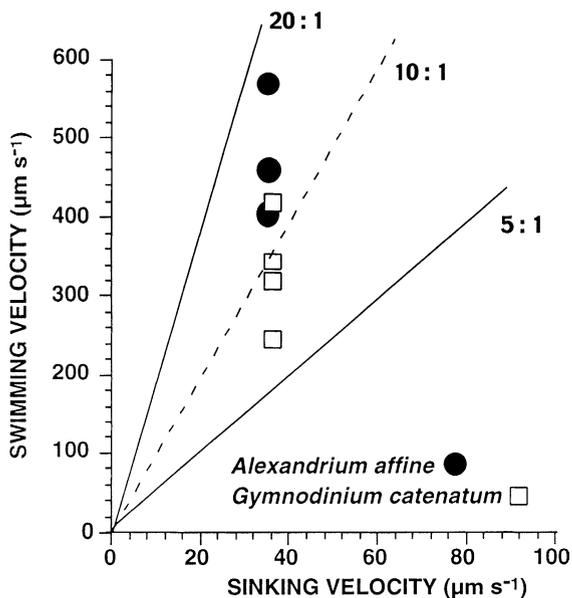

Fig. 7. Effect of colony size on the relationship between swimming and sinking velocities of *A. affine* and *G. catenatum*. For each species, the progressive increase in swimming velocity shown for *A. affine* is for one-, two- and four-cell chains, respectively, and for *G. catenatum*: one-, two-, four- and eight-cell chains. Data from Fraga et al. (1989).

mixing-drift, life-form types are not unique. Dinoflagellates, collectively, have a wide range of ascent/descent capabilities to supplement their biophysical tolerance to turbulence (Fig. 5).

2.6. Swimming speeds and watermass velocities

How do flagellate swimming speeds compare with the rates of vertical and horizontal watermass velocities in coastal systems? Fig. 8 depicts (for solitary cells) the swimming rates of 71 clones and species of dinoflagellates, phytoflagellates and protoperidinian predators, and some field-based measurements of watermass vertical velocities. The 71 clones exhibit a 25-fold range in swimming speeds, with maximal velocities of ca. $500\,\mu m\,s^{-1}$ (*Dinophysis acuta*). Fig. 8 does not include the swimming rates for three protoperidinian grazers, which exceed $1000\,\mu m\,s^{-1}$: *Protoperidinium gregarium* ($1800\,\mu m\,s^{-1}$; Lombard and Capon, 1971), *Protoperidinium* cf. *quinquecorne* ($1500\,\mu m\,s^{-1}$; Levandowsky and Kaneta, 1987) and *Protoperidinium* cf. *divergens* ($1260\,\mu m\,s^{-1}$; Jeong, 1994). Rates for seven other protoperidinians are shown in Fig. 8. The rapid swimming speeds of protoperidinians, predatory on many of the dinoflagellates included in Fig. 8, are not surprising; high motility rates are consistent with a predatory nature. This also applies to highly motile, ichthyotoxic *Pfiesteria piscicida* which, in chemotaxic response to fish exudates, can swim towards its fish prey at a median swimming speed of $670\,\mu m\,s^{-1}$ (Burkholder and Glasgow Jr., 1997), a rate that exceeds the highest rate shown in Fig. 8. "Naked" flagellates are generally slower than dinoflagellates, their swimming speeds fall mostly below $150\,\mu m\,s^{-1}$.

Within the ecological space falling between the extremes of intense watermass stability and vertical mixing (Fig. 1), there are ranges (zones) of vertical velocity rates at which, based on their motility, dinoflagellates would survive and could bloom. Upwelling rates, for example, generally range from about 1–25 m per day ($289\,\mu m\,s^{-1}$) (Guillén and Calienes, 1981; Walsh et al., 1977), with a rate of 40 m per day ($463\,\mu m\,s^{-1}$) also reported (Brink et al., 1981). The majority of dinoflagellates swim at rates which exceed an upwelling velocity of 10 m per day ($125\,\mu m\,s^{-1}$) and 33% of the dinoflagellates swim at rates which would equal or exceed an upwelling rate of 20 m per

Fig. 8. Swimming speeds of solitary cells of 71 clones and species of dinoflagellates and other phytoflagellates, as reported in the literature. Vertical bars represent upwelling rates reported for various systems and the rate of 17.3 m per day is the theoretical maximum frontal vertical velocity (Franks, 1992). Identification of coded species entries are given in Appendix table in Smayda (2000).

day ($250 \, \mu \text{m} \, \text{s}^{-1}$) (Fig. 8). Vertical velocities of the intensified motion and mixing within frontal zones are difficult to measure, but maximal velocities of ca. $200 \, \mu \text{m} \, \text{s}^{-1}$ (17.3 m per day) have been theorized (Franks, 1992). Applying Franks' (1992) suggestion that the maximal frontal zone speed of $200 \, \mu \text{m} \, \text{s}^{-1}$

is the threshold between strong and weak swimmers, species from both categories could survive and bloom in well-mixed, turbulent watermasses (Fig. 8). Of the 13 HAB dinoflagellates in Fig. 8, 10 species (77%) have a motility rate $\geq 200 \, \mu \text{m} \, \text{s}^{-1}$, a speed achieved by 42% of all dinoflagellates in the comparison. In

contrast, only 15% ($n = 20$) of the other flagellates exceed this threshold. The conspicuous rarity of "naked" flagellate blooms in upwelling systems has been pointed out by Smayda (2000).

2.7. Frontal zones as pelagic seed banks

A starter population (inoculum) must be present for blooms to develop; their course and successional events influenced thereafter by the cellular growth and population dispersion rates (Kierstead and Slobodkin, 1953). For meroplanktonic species, seed populations are often vegetative cells newly excysted from resting stages deposited in high abundance on bottom sediments, where they accumulate as "seed beds" (Anderson and Morel, 1979; Ishikawa and Taniguchi, 1997; Wyatt and Jenkinson, 1997). Holoplanktonic species must rely on other seeding sources. In the case of flagellate species, their motility and biophysical capacity will determine whether they survive the turbulence and vertical velocity fields encountered during their seeding. If their recruitment is successful, then whether a bloom develops or not is determined by the rates of cellular growth and advective "washout" rates of the seed population. As formulated in Margalef's Mandala (Margalef, 1978; Margalef et al., 1979), alongshore and across-shelf currents, and minor current filaments represent a "diffusion velocity" ("production potential"), which is the tendency of a population patch to expand into the surrounding environment. In the vertical plane, the diffusion velocity ("vertical diffusivity") is the minimum swimming speed (or sinking rate for diatoms) that a population of cells must have to remain at preferred microhabitats within the euphotic zone. Margalef (1978) suggested that a mean coefficient of eddy diffusivity of $0.4 \, \text{cm}^2 \, \text{s}^{-1}$ is the transition state between diatom and dinoflagellate predominance, with diatoms occurring in regions of high turbulence (2–$100 \, \text{cm}^2 \, \text{s}^{-1}$) and dinoflagellates at lower turbulence (0.02–$1 \, \text{cm}^2 \, \text{s}^{-1}$). The coefficient of eddy diffusivity reached $190 \, \text{cm}^2 \, \text{s}^{-1}$ during an upwelling event in the southern Benguela current (Boyd, 1982), an intensity considerably beyond flagellate capacity.

Dinoflagellate swimming rates are fundamental in coping with the problems that physical diffusion poses to cellular growth and blooms. Their swimming velocities must be adequate to offset diffusion losses in two planes. Within the vertical (i.e. turbulent) plane, they must swim faster than up- or downwelling velocities to avoid displacement from their preferred or growth-supportive microhabitats within the euphotic zone and to carry out other motility-based behavior important to their ecology (Smayda, 1997). Within the horizontal plane, their swimming speeds must be at escape velocity levels, if they are to disentrain from the dispersing current (or to entrain!) and continue local growth. Obviously, advective washout will influence population growth, but it is equally true that advective losses or population thinning, also provide seeding opportunities and therefore, can function as seeding mechanisms. It is this aspect of advective diffusion that is of interest here. The following treatment focuses on vertical and horizontal diffusion relative to dinoflagellate motility and turbulence tolerance; not as population growth issues, but their role in the development of "pelagic seed banks" that are hypothesized to occur and which serve to provide inocula for bloom events elsewhere.

Dinoflagellates exploit the mosaic of physical conditions to which they are exposed by two linked, and spatially and temporally operative strategies: one affects cellular growth; the other population blooms. The cellular strategy provides seed stock; the population strategy advects the seed stock to supportive bloom sites. Frontal systems, common oceanographic features, provide the physical setting facilitating these strategies, i.e. serve as the proposed sites and sources of pelagic seeding of dinoflagellates. This is the essence of the hypothesized "pelagic seed bank" and perceived as a pelagic analogue of the "seed beds" deposited onto sediments, with two major distinctions. Vegetative cells make up the "pelagic seed bank" populations and resting stage cells make up "seed beds". Seedings from the latter, unlike seed stock derived from "pelagic seed banks", usually require an antecedent life cycle transformation step in which vegetative, motile cells are germinated from their resting stage (blooms of tychopelagic diatom species do not). Epibenthic, palmelloid vegetative stages, such as reported for *Heterosigma akashiwo* (Tomas, 1978) also occur and seed overlying watermasses through release of pelagic, motile cells. The seeding ecology of the two types of seed banks differs also in the predominant diffusion plane involved. Seed stocks derived from "pelagic seed banks" must survive the

hazards of horizontal dispersion during their far-field dispersal. In contrast, "seed bed" excystments must meet relatively simple dispersal requirements to be effective, their seedings being primarily operative on near-field scales. These seedings are usually local events; require suitable growth conditions in the overlying watermass for recruitment success; and which the newly excysted cells can usually access through relatively short vertical migrations. In all of this, seeding success is facilitated by excystment cues transmitted through and from the overlying watermass which will tend to synchronize germination with the occurrence of favorable growth conditions in the overlying watermass needed for successful seeding by the germinated flagellates (Anderson, 1998; and references therein). The need for horizontal dispersion is minimal. In the case of type VI species (Fig. 2), a combined life cycle and diffusion ecology applies: seeding of the overlying watermass by vegetative cells excysted from seed beds, is followed by their entrainment and dispersal in coastal currents to seed far-field habitats, as shown for *A. tamarense* (Franks and Anderson, 1992).

What is the evidence for the hypothesized pelagic seed banks of dinoflagellates? Three conditions are required: that the species tolerate the turbulent fields and velocities in frontal systems, develop frontal zone populations and their successful advective transfer from these sites leads to blooms elsewhere. These conditions are satisfied. The capacity of dinoflagellates to tolerate the turbulence spectrum and velocities accompanying vertical mixing, coastal upwelling behavior and frontal zone dynamics was shown to be considerably greater than traditionally assumed. Dinoflagellate swimming speeds will often potentially exceed vertical and horizontal watermass movement rates, even at the fairly high intensities representative of coastal upwelling and frontal zone systems (Fig. 8). Experimentally derived motility rates (Fig. 8) and field observations suggest that dinoflagellates have the common ability to maintain populations and to undertake migrational behavior at the turbulence and ascending and descending watermass velocity features that characterize fronts (motility rates may be more important than sensitivity to extant watermass instabilities in selecting frontal zone tolerant species). Thirty dinoflagellate species have been reported to produce red tides or harmful blooms in coastal upwelling systems

(Smayda, 2000). Most dinoflagellate size classes and particularly of bloom species, are smaller than the smallest eddy sizes by one or two orders of magnitude, even in the most turbulent and fastest energy dissipating systems among planktonic habitats (Fig. 4).

Fronts serve multiple roles: as barriers to offshore displacement of advected populations; as concentration sites; as refugia; as ecotones (Sournia, 1994); attain impressive spatial scales and can support high dinoflagellate population densities. The Benguela shelf-break front can be 10–20 km wide and locate 10–25 km offshore (Summerhayes et al., 1995). A Chilean frontal system located 100 km offshore supported a *P. micans* bloom (Avaria, 1979) and a 300 km long patch of *L. polyedrum* ranging in width from several to 40 km developed in the California current (Lasker and Zweifel, 1978). A frontal zone bloom of *A. sanguineum* (up to 280 mg chl m^{-3}) stretched 2000 km within the Peru current (Packard et al., 1978; Lasker and Zweifel, 1978). Frontal zone physical processes supply nutrients and aggregate and disperse populations entrained in down- and upwelling divergences (Franks, 1992). These aggregations are not only passively accumulated. Dinoflagellates can actively grow along fronts, especially life-form types IV and V (Fig. 2), despite sharp horizontal and vertical velocity gradients (Carreto et al., 1986; Holligan, 1985; Pingree et al., 1978; Pitcher and Boyd, 1996; Pitcher et al., 1998). Blasco et al. (1996) linked blooms of cf. *G. aureolum* in frontal regions of the Gaspé current to high nitrogen recycling rates. The "pelagic seed bank" hypothesis does not require that the aggregated populations result from active, local growth. Passive, frontal zone accumulation of viable cells aggregated through physical processes and available for dispersal (horizontal diffusion), the next step in the strategy, will also serve.

While horizontal displacement ("wash out") may often pose a greater threat to population growth (i.e. the bloom) than cellular exposure to the turbulence field, they favor seedings from "seed banks". Alongshore current velocities are generally much greater than the onshore–offshore flow rates of across-shelf currents: velocities of ≥ 30 and $5 \, \text{cm s}^{-1}$, respectively, are common (Smayda, 2000). At such high current speeds, escape of entrained dinoflagellates to avoid dispersion away from preferred life-form habitats, or growth zones, is beyond their motile capacity,

but such entrainments would provide convenient dispersal corridors for seed bank populations at elevated dispersal rates. Horizontal diffusion is many orders of magnitude greater than vertical diffusion. For example, *K. mikimotoi* and *C. fusus*, which have swimming velocities of about $200\,\mu m\,s^{-1}$ (Fig. 5), if entrained within alongshore currents moving at $30\,cm\,s^{-1}$ would confront a horizontal displacement rate (26 km per day) that is 1500-fold greater than its vertical swimming velocity; for *D. acuta*, the difference is 600-fold. Dinoflagellates can traverse significant distances within relatively short time scales while entrained within alongshore and across-shelf currents. The more significant problem that frontal zone populations dinoflagellates confront would appear to be advective dispersions into less desirable habitats. Frontal zones are not stationary. The model developed by Pitcher and Boyd (1996) showing the formation and onshore–offshore movements of fronts in response to wind conditions provides another mechanism of "pelagic seed bank" delivery of seed stock (Fig. 3). Where upwelling occurs (no matter its strength), frontal systems and alongshore and across-shelf currents also develop. This accommodates rapid dispersion and facilitates dinoflagellate exploitation of regional growth opportunities. Frontal zone formation and dynamics of the type reported by Pitcher and Boyd are not unique events. At least a dozen types of fronts of different physical origin have been described, including tidal, estuarine, coastal, upwelling relaxation and shelf-break fronts, located both near- and offshore, with each type characterized by heightened phytoplankton growth (Le Févre, 1986).

A key element of the model—that dinoflagellates can be seeded from offshore frontal growth zones, or refugia to form nearshore blooms—is consistent with field observations. Pitcher and Boyd (1996) showed onshore delivery and blooming of *Prorocentrum rostratum*, *Prorocentrum gracile* and *Ceratium lineatum* seeded from offshore frontal sites. Nearshore blooms of *C. tripos* (Mahoney and Steimle Jr., 1979) and *Karenia brevis* (Haddad and Carder, 1979; Tester and Steidinger, 1997) have been linked to seedings from offshore bloom sites. These events are distinct from seedings of expatriate populations entrained in alongshore currents (Tester et al., 1991; Wyatt, 1995). The numerous occurrences of red tide outbreaks in the frontal systems of northwest European shelf seas reviewed by Le Févre, 1986) are consistent with the "pelagic seed bank" hypothesis. While there is supporting evidence for the "pelagic seed bank" hypothesis, it is not to be inferred that the resultant seedings will lead to blooms. The factors triggering bloom formation are complicated and seasonally and regionally variable, with the consequence that sterile seedings are probably commonplace. Whatever the bloom control factors, the watermass stratification that often accompanies flagellate blooms is probably a secondary, parallel event and less essential than some other factor(s) in triggering the observed bloom. Dinoflagellates generally may have evolved a biophysical tolerance to frequent, growth-promoting, water-column disturbances, rather than depend exclusively upon the quiescent conditions of a stratified water-column whose characteristic nutrient-poor conditions would promote stasis of the population, rather than promote growth and blooms.

A key conclusion of the analyses is that dinoflagellates tolerate turbulence and advective diffusion to a much greater extent than suggested by the classical stratification–HAB paradigm. Other supporting evidence for this comes from the numerical model developed by Yamamoto and Okai (2000), who, based on their field study, concluded (p. 378) "that flagellates would form red tides even in severe diffusive conditions". Karp-Boss et al. (2000), based on their experimental study of the effects of shear-flow on the motility of *A. catenella* and *Glenodinium foliaceum*, concluded (p. 1602) "in nature strong turbulence would be required to overwhelm (their) swimming efforts".

Acknowledgements

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