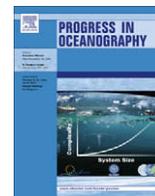




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Dinoflagellate blooms in upwelling systems: Seeding, variability, and contrasts with diatom bloom behaviour

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ABSTRACT

The influence of diatom bloom behaviour, dinoflagellate life cycles, propagule type and upwelling bloom cycles on the seeding of dinoflagellate blooms in eastern boundary current upwelling systems is evaluated. Winter–spring diatom bloom behaviour is contrasted with upwelling bloom behaviour because their phenology impacts dinoflagellate blooms. The winter–spring diatom bloom is usually sustained, whereas the classical upwelling diatom bloom occurs as a series of separate, recurrent mini-blooms intercalated by upwelling–relaxation periods, during which dinoflagellates often bloom. Four sequential wind-regulated phases characterize upwelling cycles, with each phase having different effects on diatom and dinoflagellate bloom behaviour: bloom “spin up”, bloom maximum, bloom “spin down”, and upwelling relaxation. The spin up – bloom maximum is the period of heightened diatom growth; the spin down – upwelling–relaxation phases are the periods when dinoflagellates often bloom. The duration, intensity and ratio of the upwelling and relaxation periods making up upwelling cycles determine the potential for dinoflagellate blooms to develop within a given upwelling cycle and prior to the subsequent “spin up” of upwelling that favours diatom blooms. Upwelling diatoms and meroplanktonic dinoflagellates have three types of propagules available to seed blooms: vegetative cells, resting cells and resting cysts. However, most upwelling dinoflagellates are holoplanktonic, which indicates that the capacity to form resting cysts is not an absolute requirement for growth and survival in upwelling systems. The long-term (decadal) gaps in bloom behaviour of *Gymnodinium catenatum* and *Lingulodinium polyedrum*, and the unpredictable bloom behaviour of dinoflagellates generally, are examined from the perspective of seeding strategies. Mismatches between observed and expected *in situ* bloom behaviour and resting cyst dynamics are common among upwelling dinoflagellates. This disassociation suggests unrecognized upwelling system factors that fall within the physical–chemical–biological domain are more important than life cycle in selecting dinoflagellates species having the survival-seeding strategies and ecophysiological adaptations required for growth in physically robust upwelling systems. It is conjectured that diatom life cycles, as a group, are geared towards exploiting seeding opportunities, whereas dinoflagellates have evolved life-cycle behaviour more attuned to survival. The role of ecological dormancy and ecological release from bloom inhibition underlying dinoflagellate bloom irregularity is considered. The expectation that the dinoflagellate species selected to bloom from among the common upwelling flora would be the same in all eastern boundary upwelling systems is not realized.

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1. Introduction

Biological oceanographers historically have focused on the winter–spring and coastal upwelling diatom blooms – the two classical blooms in the sea that are recurrent, predictable and trophically important. The annual winter–spring diatom bloom occurs generally in coastal waters, whereas upwelling blooms are regionally restricted; grouped into major and minor systems (Cushing, 1971); seasonal or year-round, and are particularly dynamic in eastern

boundary upwelling systems (Trainer et al., this issue). A phenological feature common to the winter–spring and upwelling blooms is the predominance of diatoms whose selection over flagellates is favoured by the accompanying well-mixed, nutrient-enriched waters. Dinoflagellate blooms, species composition and succession following the diatom bloom period in the annual cycle are less predictable and recurrent, and vary within and among bloom sites. Coastal dinoflagellate blooms are usually restricted to periods when the watermass is warmer, more stratified and nutrient poorer than during the winter–spring diatom bloom period, although there is evidence that nutrient enriched waters can stimulate dinoflagellate blooms (Glibert et al., 2008). When dinoflagellate blooms recur in

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eastern boundary upwelling systems, they tend to reappear at upwelling fronts, or at the downwelling-convergence cells that form during upwelling-relaxation periods (e.g., Figueiras et al., 2006; Pitcher and Boyd, 1996).

Upwelling systems have not escaped the global increase and expansion in harmful algal blooms (HABs) (Figueiras et al., 2006; GEOHAB, 2005). Because dinoflagellates are prominent in this phenomenon, they are focused on here. However, the upwelling dinoflagellate flora includes prominent species that are not harmful, some of which form benign red tides, such as *Scrippsiella trochoidea* and *Heterocapsa triquetra*. Harmful species that bloom in upwelling systems include the ichthyotoxic raphidophyte *Heterosigma akashiwo*, and *Alexandrium catenella*, *Dinophysis* spp., *Gymnodinium catenatum*, *Lingulodinium polyedrum*, *Protoceratium reticulatum*, among others, which synthesize toxins harmful to human health (Trainer et al., this issue). Consequently, hereafter the descriptors red tides and HABs are used to distinguish benign dinoflagellate blooms and taxa (red tides) from harmful blooms and species (HABs). This distinction is made to circumvent the problems (inaccuracies) that would result from use of the term HAB when considering the upwelling dinoflagellates collectively. The term “upwelling dinoflagellates” is also used in place of their cumbersome referral as “dinoflagellates in upwelling systems”.

Dinoflagellate species exhibit salient ecophysiological differences from diatoms, independent of whether they are red tide or HAB taxa (Smayda, 1997). The differences in dinoflagellate bloom behaviour at upwelling vs. winter-spring sites possibly are linked to the contrasting features of diatom bloom dynamics and successional dynamics at those sites. Consequently, this paper evaluates the impact of diatom bloom behaviour on dinoflagellate blooms in upwelling systems and the linked survival, seeding and bloom strategies of dinoflagellates vs. diatoms during the upwelling and relaxation phases of upwelling cycles. The first stage in the development of diatom and dinoflagellate blooms in upwelling systems – the seeding stage – will be emphasized. Given that focus, several terms will be used that require definition. Meroplanktonic and holoplanktonic are used in the classical sense of the terms – the species produces a resting cyst (mero-) or it does not (holo-). The resting cyst is a non-motile zygote formed by sexual reproduction, morphologically distinct from the vegetative cells, with a mandatory resting period needed (often) for its germination into a vegetative cell (Matsuoka and Fukuyo, 2000). Dinoflagellate life cycles are still being established, but the upwelling taxa that form true resting cysts are fairly well established. Holoplanktonic species, similar to meroplanktonic species, can also form non-motile, asexual temporary cysts that remain pelagic and have a quick recovery, i.e. germination capacity. Such behaviour is still being elucidated, but in an ecological sense it represents a different adaptive trait than the “overwintering” capacity resting cyst formation provides. *Ceratium* and *Prorocentrum* spp. are among the holoplanktonic upwelling dinoflagellates; *A. catenella*, *G. catenatum*, *L. polyedrum* and *Scrippsiella trochoidea* are some meroplanktonic species. The origin of the populations and the life-history stage of the cells that inoculate the dinoflagellate blooms that develop are usually unknown. Blooms can result from active cellular growth, physical accumulations of populations from far-field sources, local movements (re-seedings) of the same population, and a combination of these sources. The term seeding is used here to describe a generic inoculation process in which all of the above sources are imbedded. The term functional group is used in a general sense to refer either to dinoflagellates and diatoms collectively, or when contrasting their group behaviour. Finally, the long-term bloom behaviour of two representative HAB species, *G. catenatum* and *L. polyedrum*, is considered in detail from the perspective of dinoflagellate seeding-survival strategies.

2. Diatom upwelling blooms: contrasts with winter-spring diatom blooms and impacts on dinoflagellate blooms

The annual phytoplankton bloom and successional cycle in coastal waters classically begins with a winter-spring diatom bloom that is seasonally replaced by summer communities dominated by flagellates. The winter-spring bloom is usually sustained following its initiation and progresses sequentially through 3–4 stages, from initiation (in fairly well-mixed waters), once critical depth (irradiance) requirements are met, to a bloom maximum. Thereafter, the population decreases progressively because of nutrient depletion and increased grazing, and the bloom often terminates prior to the summer stratification period. A species succession accompanies this progression (Smayda, 1980). Red tides and HABs that develop usually appear during the stratified, nutrient-poorer summer season, i.e. as post winter-spring bloom events.

In contrast, the classical diatom upwelling bloom is neither continuous, a single event, nor sustained. It is composed of a series of mini-blooms whose individual continuance is interrupted by wind-induced, upwelling relaxation events that vary in intensity and duration. The mini-blooms appear, progress, disappear and recur – in start-stop fashion – varying in intensity and duration as an oscillating series modulated by the time-varying wind conditions and wind-driven advective processes (Fig. 1). Unlike dinoflagellate behaviour in coastal systems having a winter-spring bloom, dinoflagellate upwelling blooms are not seasonally displaced to a summer stratification period. Red tides and HABs in eastern boundary upwelling systems often develop as short-lived population bursts during the upwelling-relaxation phases that intercalate the upwelling mini-bloom cycle, rather than being restricted to a post-upwelling season (Fig. 1). However, in the Benguela system, red tide frequency is highest towards the end of the upwelling season when transitions in synoptic weather patterns diminish upwelling activity and increase thermal stratification (Pitcher et al., 1998, this issue). Crespo et al. (2007) recognized seven phases in the development of dinoflagellate blooms in response to meteorological-hydrographic forcing in the northwestern Iberian upwelling system, and Probyn et al. (2000) distinguished five phases in blooms forming in Saldanha Bay, South Africa. In the Gulf of Panama, dinoflagellates proliferate during the rainy season following seasonal upwelling (Smayda, 1966).

The regulation of upwelling and winter-spring diatom blooms differs. Diatom blooms in upwelling systems are regulated primarily by variable physical oceanographic conditions, with an increase in nutrients, coupled with advective reseeded of propagules that spins up each mini-upwelling bloom, the primary factor. In contrast, an irradiance-nutrient-grazing sequence gates progression of the winter-spring diatom bloom along a trajectory from initiation to termination; the initial step in this progression is the reduction in the mixed-layer depth which alleviates light-limitation – the critical irradiance depth (Sverdrup, 1953). Upwelling mini-blooms terminate primarily because of a reduced nutrient supply and the sinking and advective dispersal of the diatom population that accompanies diminished upwelling intensity. The winter-spring bloom terminates usually because of the combined effects of nutrient limitation and excessive grazing. Diatom succession during the winter-spring bloom is well documented, and has also been reported during the diatom phase of the seasonal upwelling cycle in the Gulf of Panama (Smayda, 1966). The annual successional pattern in the northwestern rias in the Iberian upwelling system is characterized by well-defined floristic transitions between the upwelling and stratified seasons, and within the regional and temporal upwelling-downwelling patterns (Figueiras and Niell, 1987; Figueiras and Rios, 1993). The occurrence of a diatom species succession in upwelling systems,

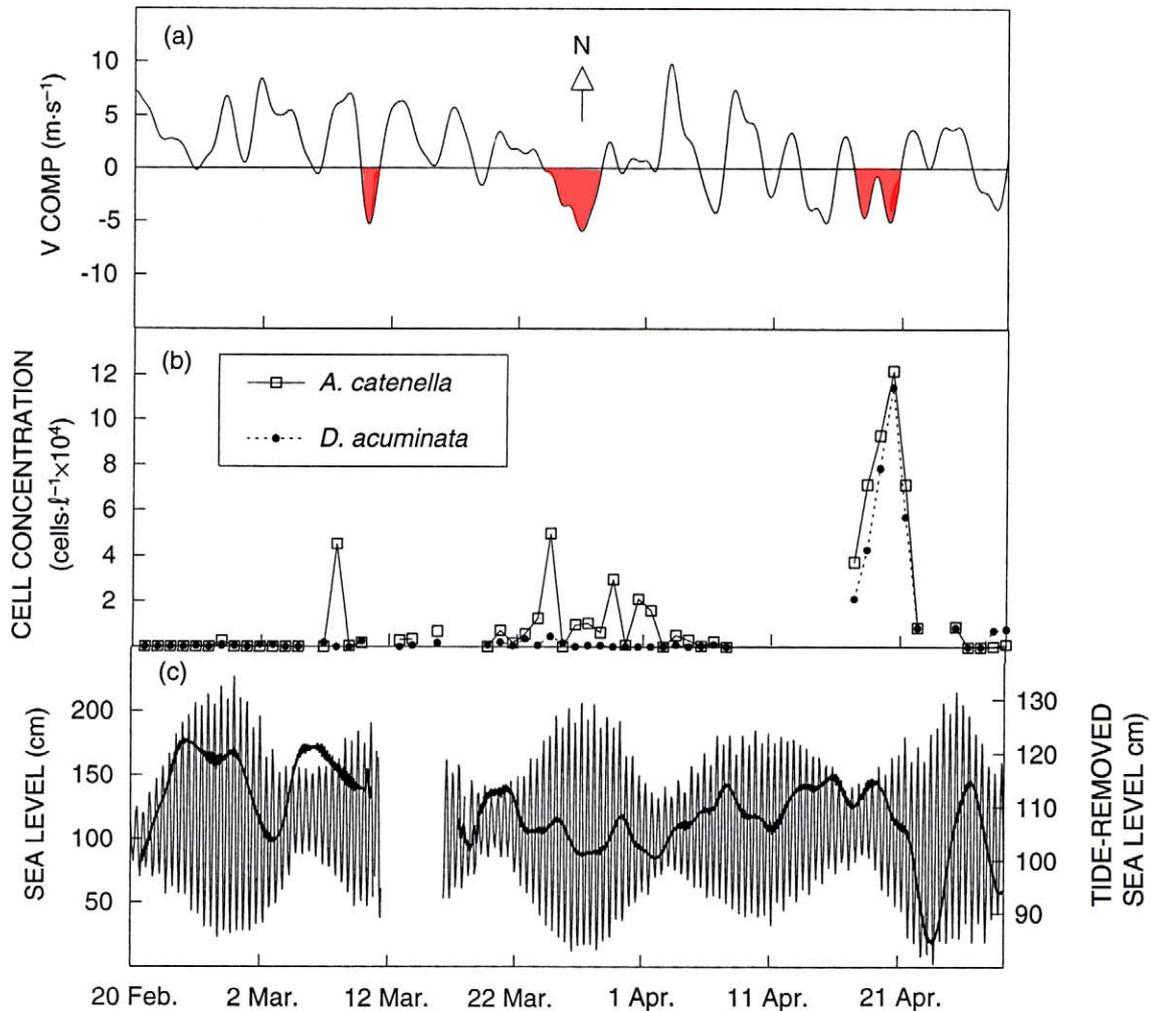


Fig. 1. Relationship between (a) relaxation of upwelling-favourable winds at Cape Columbine, South Africa; (b) the occurrence of *Alexandrium catenella* and *Dinophysis acuminata*, and (c) tidal and subtidal sea level variations in Saldanha Bay during a late summer upwelling cycle (from Probyn et al., 2000).

similar to winter–spring bloom behaviour, is contrary to expectations given the habitat disturbances induced by wind-driven upwelling intrusions and retractions (see Smayda, 1966, 1980). This demonstrates the extent to which succession is a basic attribute of diatom blooms, whereas dinoflagellate succession appears to be rudimentary in both types of coastal ecosystems.

In summary, the spatial and temporal behaviour and regulation of red tides and HABs in eastern boundary upwelling systems are distinct from that in coastal waters, generally and in relationship to diatom blooms. Diatom blooms reflect an overall sink strategy; dinoflagellate blooms are swim strategy events (Smayda, 1997). Diatom and dinoflagellate blooms rarely coincide in coastal systems where upwelling is not a factor. It is unknown whether this temporal separation occurs because the habitat conditions that select for sink or swim strategy behaviour select against the opposing strategists, or whether functional group competition, i.e. diatoms vs. dinoflagellates, based on growth rate, grazing or allelochemicals (singly or in combination) is more important. In contrast, dinoflagellate and diatom blooms are often contemporaneous in upwelling systems, but are then spatially segregated within the three-dimensional habitat structure that characterizes upwelling systems (Pitcher and Boyd, 1996; Pitcher et al., 1998). There is also temporal separation of diatom and dinoflagellate blooms. Dinoflagellate blooms develop sequentially to diatoms during upwelling-relaxation periods seeded by propagules advected from spatially separated bloom sites that

developed during the previous upwelling cycle (Fig. 1; Pitcher and Nelson, 2006; Figueiras et al., 2006; Crespo et al., 2007). Dinoflagellate red tides and HABs at winter–spring bloom sites tend to be restricted to the summer stratification period, and depend primarily on recycled nutrients because of their depletion by the winter–spring bloom. Dinoflagellate upwelling blooms are influenced more by reversible, dispersion-advection-seeding impacts of the wind-modified circulation, which terminates diatom blooms and seeds dinoflagellate blooms, than by the extent to which nutrients are depleted during the diatom bloom.

3. Upwelling cycles, relaxation periods and dinoflagellate blooms

3.1. Upwelling cycles

Upwelling, whether seasonal or annually persistent, is intermittent, cyclical and embedded within bloom cycles as event-scale physical intrusions (Fig. 1). The hallmark, diatom upwelling bloom is actually a series of separate, recurrent upwelling bloom events (intrusions) intercalated by upwelling relaxations of variable duration. Upwelling bloom cycles have four wind-regulated phases: “spin up”, bloom maximum, “spin down”, upwelling relaxation, occurring in that sequence (Fig. 2). The spin up – bloom maximum sequence in the cycle is the period of heightened diatom growth.

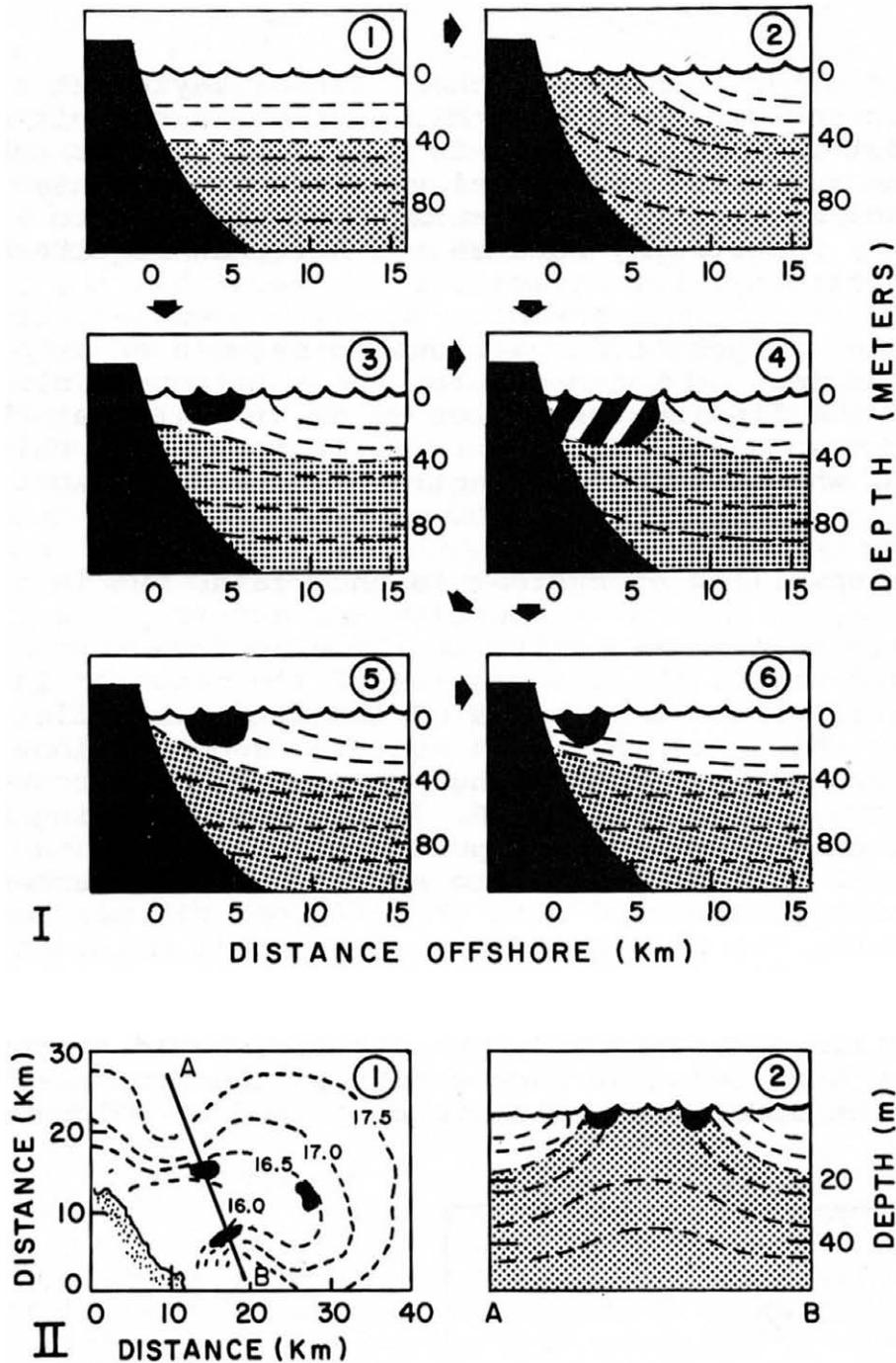


Fig. 2. Conceptual model of the sequential development of dinoflagellate blooms during various stages of the upwelling-relaxation cycle. Dashed lines represent isopycnals; stippled zones represent nutrient-rich water; solid black patches delineate blooms of dinoflagellates; black and white striped patch delineates bloom of diatoms and/or dinoflagellates. Panel 1 – illustrates the stratified vertical watermass before the onset of upwelling; Panel 2 – the upwelling spin up phase; it remains a pre-bloom condition if upwelling is excessive; Panel 3 – the spin up phase if the Panel 2 condition does not develop; cells seeded into the upwelling incursion are now able to exploit the nutrient-rich water, which does not upwell to the surface, and a diatom bloom begins; in some instances, fast-swimming dinoflagellates can exploit this condition by undertaking diel nutrient migrations; Panel 4 – upwelling intensifies and the diatom bloom maximum develops; Panel 5 – upwelling begins to weaken – spin down – with reduction in winds; diatom abundance decreases; nutrients in near-surface layer stripped by previous bloom (Panel 4) and also lower because of retraction of upwelled water; dinoflagellates may begin to bloom together with diatoms; Panel 6 – a deeper relaxation phase; across-shelf incursion of the warm, nutrient-poor upper surface layer to inshore overrides the previously upwelled water and favours dinoflagellate blooms. If relaxation period is sufficiently prolonged, it can proceed to pronounced stratification depicted in Panel 1. The progression depicted in Panels 1–6 constitutes the upwelling cycle; the duration of each stage within the cycle varies with wind conditions, and its direction is reversed when winds favouring upwelling intensify. Panel II-1 shows the plume-like shape of the isotherms as they intersect the sea surface and Panel II-2 illustrates the frontal zones favourable to dinoflagellate accumulations and blooms along the A–B transect in Panel II-1 (modified from the bloom development sequence of *Myrionecta rubra* in the Northwest African upwelling system proposed by Packard et al. (1978)).

The spin down – relaxation sequence in the cycle defines the post-diatom bloom period when wind-induced quelling of upwelling interrupts the diatom bloom in progress. Dinoflagellates may then

become prominent and bloom until upwelling resumes because of favourable winds – “spin up” phase – and a new diatom bloom develops (Figs. 1 and 2). The cellular adaptations dinoflagellates

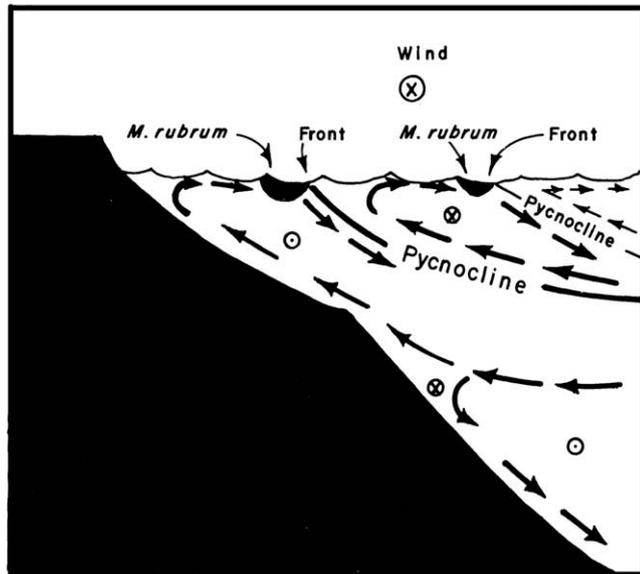


Fig. 3. Vertical section of upwelling and downwelling dynamics along an onshore-offshore gradient illustrating the development of fronts, at which dinoflagellate bloom (blackened patches), that develop during upwelling. During upwelling relaxations, the fronts spatially reorganize and the dinoflagellate cells are dispersed by the altered across-shelf circulation pattern responding to slackened winds, and become available as inocula seeding the habitats that open up depicted in Fig. 2 (modified from Packard et al., 1978).

require to become indigenous in upwelling systems are discussed by Smayda (this issue a,b). Adaptations at the population level, which impact seeding and growth behaviour, are also required to exploit the spatial and temporal “bloom-windows” that open and close during upwelling cycles. Brown and Hutchings (1987) used chlorophyll as a bloom index to follow the growth and decline of diatoms in several drogue studies of upwelled waters in the Benguela system. The bloom cycle was completed within 6–7 days, during which chlorophyll increased from $<1 \text{ mg m}^{-3}$ to $10\text{--}20 \text{ mg m}^{-3}$ at the bloom maximum, then decreased to $1\text{--}3 \text{ mg m}^{-3}$ during bloom decay and termination.

The following sections focus on dinoflagellate seeding and bloom behaviour during the upwelling relaxation phase (Figs. 1–3), applying four simplifying notions: the relaxation period resets the upwelling bloom cycle; this phase of the bloom cycle favours dinoflagellate blooms; dinoflagellates are then in their growth advective-accumulation phase (Pitcher and Boyd, 1996); and the diatom bloom is in its lag phase. (The converse applies: the dinoflagellate lag phase occurs during the upwelling (diatom) phase of the bloom cycle) In discussing seeding and bloom behaviour during upwelling cycles, the term upwelling phase will connote the diatom bloom period. The relaxation phase will be considered the dinoflagellate bloom period, although a red tide or harmful bloom may not develop then (see Section 3.2). Whereas our analysis focuses on the cyclical and intermittent occurrences of red tides and HABs within upwelling cycles, there can also be a seasonal dimension.

3.2. Upwelling-relaxation periods and dinoflagellate blooms

The duration of the bloom and relaxation phases vary within and among upwelling cycles (Fig. 1). For example, in the Benguela system, the first of two consecutive upwelling cycles tracked at a fixed station lasted 22 days (Mitchell-Innes and Walker, 1991; Pitcher et al., 1991). That cycle consisted of 2 days of upwelling followed by a 21-day relaxation period. The second upwelling cycle

lasted only 4 days – an upwelling intrusion that lasted 1 day was followed by a 3-day quiescent period. Upwelling cycles lasting 8–10 and 15–20 days have also been reported (Bailey and Chapman, 1991). The duration of the upwelling (diatom bloom) phase in an anchor station study in the Benguela system was relatively short (1–2 days); upwelling periods that persisted 16 days in the Benguela system and 8–10 days in the Peruvian system have been reported (Mitchell-Innes and Walker, 1991). These representative examples reveal the wide range that occurs in the duration of the upwelling cycles (4–20 days) and in the bloom (1–16 days) and relaxation (1–21 days) phases of the cycles. This variability in growth (bloom) opportunity – the ratio of the duration of the upwelling to relaxation periods, for both diatoms and dinoflagellates – and the variance in the intensity of the respective upwelling and relaxation periods within the cycle undoubtedly influence functional group selection and bloom behaviour (Fig. 2). Two types of bloom-windows potentially open during upwelling cycles – a diatom and a dinoflagellate bloom-window. Which functional group is selected to bloom, and its bloom intensity, are functions of the duration, intensity and ratio of the upwelling and relaxation phases. High ratios in the duration of the upwelling:relaxation periods are expected to favour diatoms and disfavour dinoflagellates. However, dinoflagellate blooms are not necessarily favoured at low upwelling:relaxation ratios. If the ratio is below the threshold required for the arrival of a sufficient seed population, or is unsuitable to allow a population increase – dinoflagellates relative to diatoms are generally slow growing (Tang, 1995, 1996) – dinoflagellate blooms will not develop.

Relaxation events have multiple effects: they disrupt diatom blooms and succession; favour dinoflagellate growth and physical accumulation; reorganize diatom and dinoflagellate communities; impact the diatom species selected to bloom and the seeding of diatoms and dinoflagellates when blooms spin up; and disperse seed dinoflagellates (propagules) into the reorganized physical structure (eddies, fronts, across-shelf currents, etc.). The offshore frontal systems that develop during upwelling can become active dinoflagellate growth zones, with the populations that accumulate available for dispersion or advection as propagules during the subsequent relaxation period (Fig. 3; Pitcher and Boyd, 1996; Pitcher et al., 1998; Crespo et al., 2006, 2007). Relaxation periods that lead to dinoflagellate blooms might facilitate life-cycle behaviour – mating behaviour in particular – essential to the maintenance of indigenous dinoflagellate populations. Upwelling is physically robust and stressful to dinoflagellate cellular integrity and swimming-based behaviour, both of which are turbulence-sensitive (Smayda, this issue b). Adaptive counter-measures to offset stress-induced life-cycle transitions are required, such as “small cell” induction (Berdalet, 1992; Silva and Faust, 1995), to promote survival, including sexual mating, and to allow the cells to metamorphose into the life cycle stage adaptive to the stress being imposed (Garcés et al., 2002). Water column mixing and advection rates during upwelling can challenge the ability of dinoflagellates to detect and swim towards mating partners. This impediment may be a lesser problem for a heterothallic, chain-forming upwelling species such as *A. catenella*, in which both the (–) and (+) cell types required for mating occur within the same chain (Yoshimatsu, 1981, 1984; Smayda, this issue a,b). However, in *G. catenatum*, two distinct, compatible chains are required for mating (Blackburn et al., 1989a). Most upwelling dinoflagellates, however, do not form chains. For example, *L. polyedrum*, does not form chains, but is heterothallic. The individual +/- gametes produced must detect and swim greater distances to achieve pairing than the gametes produced by chain-forming *A. catenella* (see Smayda, this issue a,b). Figueroa and Bravo (2005) suggested that mating behaviour in *L. polyedrum* may be facilitated by a sexual chemotaxis in response to pheromone release. Wyatt and Jenkinson (1997) have

considered, from a more theoretical perspective, the dependence of gamete encounter on threshold population densities and the influence of shear field on both gametic encounter and possible signalling between the +/- monads through pheromone release. The impediments to successful mating might be alleviated by the increase in population abundance that often occurs at the downwelling and frontal zone sites that form during upwelling relaxations (see Figueiras et al., 2006; Pitcher and Boyd, 1996).

4. Seeding of diatom upwelling blooms

4.1. General aspects

The seeding of diatom blooms is considered first to place dinoflagellate seeding behaviour into perspective, and to assess parallel and divergent behaviour. Because upwelling cycles are in series, each new diatom bloom – spin up – is started from cells that survived the preceding relaxation period (Fig. 2). Three types of propagules can seed diatom blooms: vegetative cells, resting cells, and (in meroplanktonic species) germinated resting cysts. Which propagule primarily seeds a given diatom bloom is probably influenced by the duration of the relaxation period. As noted earlier, the relaxation period in the Benguela system can be as short as 1 day or sustained for at least 3 weeks, during which the primary physiological and life-history character of the potential seed stock pool can transition from vegetative cells to resting cells and/or resting cysts. The propagule type that predominates and seeds the interrupted diatom bloom is probably related to the duration of the relaxation phase.

Transitions from the diatom bloom to the relaxation period, and reciprocally, can be abrupt, as shown for *L. polyedrum* bloom patterns in the California Current system (Walsh et al., 1974, 1977). Diatom upwelling blooms often terminate abruptly because of physical disruptions, not nutrient limitation. Vegetative cells from this bloom disperse within the altered current system and enter the relaxation period (Fig. 2) more or less as nutrient-sufficient cells. When the relaxation period is short (days), vegetative cells from the preceding bloom most likely will seed the bloom that newly spins up. During brief relaxation periods prior to an upwelling spin up, the loss of diatom physiological vigour and depletion of cellular nutrient quotas are probably insignificant. The longer the relaxation phase, the more likely relic vegetative cells from the source diatom bloom will become nutrient-limited and form resting cysts. Vegetative cells are then less likely to seed the ensuing bloom. Field studies are needed to confirm this conjectured behaviour.

4.2. Vegetative cells as propagules

Diatom populations followed during a drogue study in the Benguela system descended to deeper layers when upwelling relaxed and the upper layer stratified. Olivieri et al. (1985) postulated this behaviour functions as a reseeded mechanism in which the diatoms descend into and seed the inflowing upwelling source water as “pre-conditioned” vegetative cells capable of immediate, rapid growth when upwelled into the euphotic zone (Figs. 2 and 3). The capacity of pre-conditioned vegetative cells to accelerate blooms during upwelling spin up presumably diminishes the longer the relaxation interval separating the upwelling incursions. The facilitative role of cellular pre-conditioning in bloom formation proposed by Olivieri et al. (1985) is supported by experimental studies. A cellular physiological shift-up of the diatom seed population induced by the biological–chemical conditioning (“seasoning”) of newly upwelled water was needed for growth to commence in newly upwelled Peruvian water (Barber and Ryther,

1969; Barber et al., 1971). The potential role of biological conditioning of newly upwelled waters and experimental evidence for growth stimulation of red tide and HAB species segregated in bloom patches (Sweeney, 1975) are discussed by Smayda (2000).

4.3. Resting cyst based seeding strategy

During long (weeks) relaxation periods, resting cells and/or germinating resting spores are the most likely diatom propagules (Fig. 2). Some species form resting cells that are morphologically similar to vegetative cells, but physiologically and cytologically differentiated (McQuoid and Hobson, 1996). Resting cells can be produced at very low silica concentrations, whereas resting spore formation requires sufficient silica to form the thickened, protective frustule (Kuwata et al., 1993). Some diatoms form resting cells and resting spores; resting cells form when the severity of nutrient limitation falls below the threshold concentration that induces sporulation (McQuoid and Hobson, 1996). Resting cells can respond more quickly than resting spores to favourable growth conditions, and have been considered more effective than resting spores in seeding diatom blooms in upwelling areas off Japan (Kuwata and Takahashi, 1990; McQuoid and Hobson, 1996), but little is known about their importance in the eastern boundary upwelling blooms.

Numerous physical and chemical factors can induce formation of resting spores (McQuoid and Hobson, 1996), which is considered the primary survival-seeding adaptation that diatoms have to survive unfavourable growth conditions and to seed blooms. Most diatom species are meroplanktonic, i.e. produce a resting spore stage (Smayda, this issue a). In contrast, upwelling dinoflagellates are predominantly holoplanktonic (see Section 5.2). Based on water column and sediment trap data, Pitcher et al. (1991) found the bloom cycles of meroplanktonic diatoms in newly upwelled waters of the Benguela – mostly *Chaetoceros* spp., an important genus in upwelling systems (and also in spring blooms) – correlated with the production, vertical distribution and advective transport of resting spores. Resting spore production and reseeded rates were high throughout the *Chaetoceros* blooms, particularly during the population maximum. Sporulation was not restricted to suboptimal growth periods, which indicates that sporulation is not induced only by environmental stress, particularly low nutrient concentrations (McQuoid and Hobson, 1996), or that a prolonged dormancy period necessarily precedes germination.

The *Chaetoceros* dynamics reported by Pitcher et al. (1991) suggest that resting spore formation in some upwelling diatom species may be serial and anticipatory. An upwelling species that combines continuous sporulation with rapid germination of its spores would benefit in several ways. It could more rapidly exploit the bloom opportunities that open and close during upwelling cycles. Serial production of resting spores during blooms would diminish the ecological risks associated with exclusive reliance on specific and harsh environmental signals, such as nutrient limitation, to trigger sporulation. A rapid germination capacity would enhance timely responses to favourable growth conditions. Species that restrict their resting spore formation to extreme conditions in progressively deteriorating environments may have an overwintering strategy better suited to the winter–spring diatom bloom cycle. Those species often confront long-term gaps in bloom opportunities. However, species with such seasonally based survival-seeding strategies would appear to be disadvantaged and selected against for growth in the recurrent upwelling intrusions during bloom cycles (Figs. 1 and 2). Species with reduced dormancy requirements and high sporulation rates are expected to be better adapted.

The *in situ* sinking and ascent behaviour of resting spores (Pitcher et al., 1991) and vegetative cells (Olivieri et al., 1985) suggests that meroplanktonic diatoms survive, reseed and grow

during the oscillations in the upwelling-relaxation phases, employing a survival-seeding strategy that exploits the chemostatic-like pulsing and withdrawal of nutrient-rich upwelled water during upwelling cycles (Figs. 1 and 2). In effect, this bloom-seeding mechanism is similar to the nutrient-gathering migrations that some dinoflagellates undertake. During upwelling relaxations, vegetative cells and resting spores sink from the upper, stratified layer into the nutrient-richer bottom layer, which ascends during the subsequent upwelling spin up (Figs. 2 and 3). Resting spores germinate during this conveyance and seed the bloom that develops. The vertical and advective features of this seeding mechanism approximate the two-layer physical circulation model often applied to upwelling systems. Resting spores can form and germinate rapidly in response to environmental cues, with the parentage of the resting spores, in some species, physiologically determined one-cell division before sporulation. Resting spores can form in 6 to 48 h, and germinate (i.e. dormancy is broken) 1 day after they form (McQuoid and Hobson, 1996). Hollibaugh et al. (1981) reported that resting spore germination in three *Chaetoceros* spp. was optimal at the combinations of temperature and irradiance present during sporulation.

The capacity of diatoms to form resting cells and resting spores, and their growth and germination characteristics, vary among species. However, irrespective of whether the propagules seeding blooms are pre-conditioned vegetative cells (Olivieri et al., 1985), resting cells that have become reinvigorated by the new growth conditions, or germination-ready resting spores, i.e. the dormancy requirement has been met, the growth and seeding characteristics reported for representative upwelling diatoms support the reseeded hypothesis of Pitcher et al. (1991). Such cellular metamorphoses are also adaptive mechanisms facilitating short-term survival between the intermittent upwelling blooms and reseeded of the latter.

5. Seeding of dinoflagellate upwelling blooms

5.1. General aspects

Two prominent features characterize dinoflagellate upwelling blooms: the short-term – cycle to cycle – unpredictability in which species from among the low density populations of dinoflagellates that precede the relaxation period will bloom, if any, during upwelling relaxation; and the erratic, long-term irregularity and decadal scale gaps in blooms. The remarkable, long-term bloom irregularity of indigenous *L. polyedrum* and *G. catenatum* in the California Current and Iberian upwelling systems are illustrative (Allen, 1933, 1943; Gregorio and Pieper, 2000; Amorim et al., 2001, 2002, 2004; Margalef, 1956; Arévalo et al., 2006). Major *L. polyedrum* blooms occurred in the California Current system in 1901, 1907 and 1917; thereafter, *L. polyedrum* reached red tide abundance in only 3 years (1932, 1938 and 1942) of a 25-year time-series (1917–1942), and was absent or rare during many of those years, unlike the upwelling red tide species *Prorocentrum micans* (Allen, 1933, 1943). A 19-year bloom hiatus, from 1976 through 1994, then followed, after which extensive *L. polyedrum* blooms developed during 1995–1997 (Gregorio and Pieper, 2000). Along the western Iberian coasts, *L. polyedrum* formed conspicuous blooms in the Ria de Vigo in the 1950s (Margalef, 1956), but it is now rare and its blooms discolouring the watermass are only formed in the Northern Rias (Arévalo et al., 2006). Off the Portuguese coast, *L. polyedrum* bloomed in 1996 after a 22-year hiatus (Amorim et al., 2001). *Gymnodinium catenatum* produces massive blooms in the Iberian upwelling system at intervals ranging from 1 to >6 years (Amorim et al., 2002). Bloom irregularity is further considered in Sections 8 and 9.

Dinoflagellate bloom irregularity in upwelling systems contrasts markedly with the predictable, recurrent upwelling blooms of the indigenous diatom flora. This behaviour poses several fundamental questions: what constrains blooms in years when dinoflagellate blooms fail to develop, and what is the stimulus during bloom years? Does bloom failure reflect failed seeding behaviour, i.e. are propagules not seeded regularly in those systems to exploit favourable growth conditions? When the matchup leads to blooms, is it stochastic or are the apparent gaps in blooms due to sustained, inhospitable growth conditions? From a different perspective, does bloom irregularity reflect a cryptic, long-term rhythmicity under unrecognized habitat and biotic control? Each process subsumed within these queries at one time or another probably contributes to the short-term – cycle to cycle – irregularity in dinoflagellate blooms observed during upwelling relaxations. Blooms are processes, of which the changes in population density are only the outcome, that progress sequentially from an initiation (seeding) phase to active growth, to a declining population, and then to a bloom termination stage. That is, blooms require a seed, i.e. a starter population and a favourable environment to develop. Because seeding and survival strategies are shared fitness traits, the potential role of seeding – the critical first stage in the bloom cycle – in the short- and long-term variability in upwelling dinoflagellate blooms is examined in the following sections.

5.2. Relaxation period “bloom window”

During upwelling relaxations (Fig. 2), the watermass becomes warmer, mixing is less intense, the nutricline deepens, as does the euphotic layer (usually) because of lower biomass, and there is a residual pool of “fossil nutrients” from the prior upwelling intrusion. The diatom population dissipates: it displaces to deeper layers (Olivieri et al., 1985; Pitcher et al., 1991), “thinned” through advection and dispersed by the altered circulation. Flagellates reappear and sometimes progress to dominance within a few days (Pitcher et al., 1991). Floristic replacement and community reassembly alter the competition between diatoms and dinoflagellates for the now more limited nutrient supply. Dinoflagellates have a greater capacity than diatoms to exploit such conditions because of their motility – the reduced vertical mixing rates are less likely to impede their nutrient-gathering migrations and other motility-based behaviour (Smayda, this issue b). The dinoflagellate bloom window that opens during relaxation periods is time dependent – a spin up of upwelling that favours renewed diatom growth and leads to a dinoflagellate decline is inevitable (Figs. 1 and 2). Three interactive conditions must be satisfied for dinoflagellates to bloom during upwelling relaxations prior to the upwelling intrusions that favour diatoms: a seed population must be present; habitat conditions must favour net population growth; and the individual and ratioed duration of the upwelling:relaxation periods must be favourable (Figs. 1 and 2). The upwelling:relaxation ratio determines whether the “growth window” will be open long enough for seed stock to arrive in sufficient numbers to initiate a bloom, and then whether the relaxation period will be long enough for the bloom to develop. This dependency is also influenced by dinoflagellate cell division rates. The long-term, punctuated blooms of *L. polyedrum* and *G. catenatum* in the California Current and Iberian upwelling systems, discussed earlier, and the dinoflagellate blooms that develop during the brief upwelling-relaxation periods (Section 3.2.) suggest upwelling dinoflagellates have specific seeding-growth strategies to exploit ephemeral bloom window opportunities, and that these strategies differ from those of the diatoms. The following sections consider this further, recognizing that seeding and survival are linked strategies evolved to overwinter inhospitable environments and to renew vegetative growth when conditions are once again favourable.

5.3. Holoplanktonic dinoflagellates and bloom seeding

Seeding strategies have cellular and population-based components. At the cellular level, dinoflagellates, similar to diatoms, can be seeded as vegetative cells, resting cells, ecdysal (temporary) cysts, or resting cysts. These options are not equally shared among species; most upwelling dinoflagellates, unlike diatoms, do not form resting cysts – they are holoplanktonic. During active upwelling when diatoms are in bloom, holoplanktonic *Ceratium*, *Dinophysis*, *Karenia* and *Prorocentrum* species are often abundant at offshore growth sites at fronts (Fig. 3; Pitcher and Boyd, 1996; Pitcher et al., 1998) and in currents on the outer continental shelf (Crespo et al., 2007). They may also accumulate vertically within the water column in thin layers (Moita et al., 2006; Velo-Suárez et al., 2008), including the HAB diatom genus *Pseudo-nitzschia* (Deksheniaks et al., 2001; Rines et al., 2002). These sanctuaries function as “pelagic seed banks”, population maintenance centres (refugia) and sources of inocula during upwelling-relaxation periods (Smayda, 2002). Their propagules are available for onshore advection and seeding of nearshore blooms at downwelling sites during upwelling-relaxation periods (Figs. 2 and 3; Figueiras et al., 2006). Of the adaptations required by indigenous, holoplanktonic dinoflagellate species to grow in upwelling systems, their ability to survive the robust physical conditions and to access favourable growth sites are foremost. The combinations of cellular and population adaptations that provide this capacity undoubtedly vary among species, beyond the shared requirements that all upwelling dinoflagellates must meet – tolerance of high turbulent kinetic energy dissipation rates, and swimming rates that exceed vertical mixing velocities to allow phototactic and nutrient migration behaviour (Smayda, this issue b). The adaptations must also allow periodic access to favourable growth sites to meet-life history requirements.

5.4. “Small cells” as propagules

At some point during the bloom cycle of a species, vegetative cells experience unfavourable conditions. Cellular resistance and population counter-strategies are required for the cells to survive these hostile periods. Holoplanktonic species lack the protection that resting cysts provide – a cellular resistance strategy – and rely on other survival mechanisms. The “pelagic seed banks” that develop in regions of dampened turbulent kinetic energy – a population-based strategy – elaborated on in Smayda (2002, this issue b), appear to provide holoplanktonic dinoflagellates with a common survival-seeding option. This strategy relies on vegetative-cell survival. Based on field observations, Reguera (2002) proposed that *Dinophysis* species in the Iberian upwelling system produce “small cells” to survive adverse conditions. The small cells aggregate in thin layers where, in eventual response to more favourable growth conditions, they rejuvenate their cell size, restore normal swimming behaviour, and reseed the populations. Reguera hypothesized that the *Dinophysis* small-cell strategy incorporated into its life cycle allows the cells to “rejoin the vegetative population without wasting energy in cyst formation”, and to avoid sedimentation losses and vulnerable dependency on suitable germination conditions.

The formation of small cells, which are often morphologically indistinguishable from smaller, normal vegetative cells (Silva and Faust, 1995), is common in dinoflagellate life cycles, particularly when nutrients are exhausted. Holoplanktonic upwelling dinoflagellates reported to produce small cells include *Akashiwo sanguinea*, *Karenia mikimotoi*, *Prorocentrum micans*, *Prorocentrum minimum*, and meroplanktonic *Cochlodinium polykrikoides*, *L. polyedrum* and *Scrippsiella trochoidea* (Silva and Faust, 1995). These small cells have several functions. As vegetative cells that result from successive size diminution during cell divisions, they may be capable of

accelerated growth and increased population levels. The small cells produced by the upwelling species listed above proliferated and increased their cell size to normal levels when nutrients were replenished (Silva and Faust, 1995). Partensky and Vault (1989) found that *K. mikimotoi* formed two subpopulations regularly in culture and in natural populations – small cells and large (normal) cells – the former produced by budding of the latter, and the latter by enlargement of small cells when they ceased to divide. Partensky and Vault (1989) concluded that the high proliferative power of the asexual small cells relative to large cells could play a significant role in the red tides of *K. mikimotoi* that develop in northern European waters. Some small cells formed by meroplanktonic species are functional gametes that fuse during swarming to produce resting cysts (Silva and Faust, 1995; Nagai et al., 2003), and there is recent evidence that small cells produced by *G. catenatum* (Figueroa et al., 2008) and *Dinophysis* spp. (Escalera and Reguera, 2008) can directly divide and produce vegetative cells, thereby bypassing encystment. *Akashiwo sanguinea* possibly uses cell depauperation to survive high turbulent kinetic energy dissipation rates. When exposed to excessive turbulence (in culture), *A. sanguinea* produced small cells whose size and growth rate immediately increased when turbulence was quenched (Berdalet, 1992). Wyatt and Jenkinson (1997) discuss the behaviour of non-motile, ecdysal cells that develop in response to turbulence and sink into less turbulent, deeper waters, where they remain as quiescent, pelagic cysts.

Small-cell formation in response to turbulence is another example that survival-seeding is a linked strategy. The cytological nature, life cycle and survival-seeding roles of small cells are obscure. It is uncertain whether they are analogues of the holoplanktonic life-cycle strategy proposed for *Dinophysis* by Reguera (2002). Notwithstanding the evidence that holoplanktonic, upwelling dinoflagellates employ a small cell survival and seeding strategy, available field evidence points to “pelagic seed beds”, in combination with advective seeding mechanisms, as a more likely turbulence avoidance option and seeding pathway (see Figueiras et al., 2006).

5.5. Dinoflagellate resting cells as propagules

Some dinoflagellate species form non-motile ecdysal cysts, also termed pellicle cysts, which appear to function as cysts, but lack the morphological characteristics of resting cysts (Garcés, 2002). Current knowledge of resting cyst behaviour is based primarily on laboratory studies, hence their role in natural population dynamics is speculative. Wyatt and Jenkinson (1997) suggested that the naked, non-motile ecdysal cysts produced during impaired vegetative growth remain pelagic, and are the life cycle stage most likely to disperse. This potential propagule role of ecdysal cells is based on the rapidity with which they can hatch (within 24–48 h) when external conditions become favourable, and their ability to remain viable for long periods (months). Kim et al. (2002) described the formation of “hyaline”, non-motile resting cells by the upwelling species *C. polykrikoides*. These modified vegetative cells produced an enveloping, transparent membrane without an intervening sexual phase, and after 6 months in darkness morphed into motile cells. This suggests that *C. polykrikoides* resting cells enable an overwintering survival strategy similar to that provided by the zygotic resting cysts produced by meroplanktonic dinoflagellates. Upwelling dinoflagellates reported to form ecdysal cysts include *A. catenella*, *G. catenatum*, *Heterocapsa triquetra*, *L. polyedrum* and *P. minimum* (Garcés, 2002). The possible osmotrophic utilization of organic substances by resting cells is suggested by the study by Manoharan et al. (1999) who reported the red tide species *P. minimum* survived 10 days of darkness through its osmotrophic use of triacylglycerides and galactolipids.

5.6. Dinoflagellate resting cysts and seeding

5.6.1. Encystment rates and frequency

Resting cyst formation and germination are complex life-cycle transitions under tight cellular and ecological control. Encystment and excystment behaviour varies among species and geographical strains of a given species (Garcés et al., 2002; Lewis, 2002; Itakura and Yamaguchi, 2005); it is also under multifactorial regulation. Temperature, salinity, irradiance, daylength, macro- and micro-nutrient deficiency, bacteria and population density can induce cyst formation in dinoflagellates (see Lewis, 2002); nutrient deficiency is particularly important. Some species can produce cysts continuously or intermittently during population growth, a capacity designated as multivoltine. In other species, cyst formation is restricted to a narrow, specific period – an “encystment window” – within the bloom cycle (Nuzzo and Montresor, 1999). Upwelling dinoflagellates reported to be multivoltine (both in natural populations and in experimental culture) include the red tide species *S. trochoidea* (Wall et al., 1970; Montresor et al., 1998; Nuzzo and Montresor, 1999) and toxic *G. catenatum* (Bravo and Anderson, 1994; Moita and Amorim, 2002). Viewed from the perspective of bloom-seeding potential, the encystment behaviour of meroplanktonic dinoflagellates suggests there are two major cyst production strategies – serial and episodic production. The limited data preclude classifying the individual meroplanktonic, upwelling dinoflagellates as either serial or episodic resting cyst producers. However, the serial production capacity reported for *S. trochoidea* and *G. catenatum*, and the temporal and spatial variations in growth conditions that accompany upwelling perturbations suggest that serial cyst producers are favoured.

The rate and frequency of resting cyst production differ among species, traits that may be genetically determined and distinct from the influence of external factors on cyst production (see Lewis, 2002). The relative capacity of species to produce cysts within their serial or episodic strategy may influence which meroplanktonic species are selected for growth in upwelling systems. Experimental data suggest a maximum encystment frequency of 10–20% of the population (see Olli, 2002). This relatively low frequency contrasts with the 100% encystment reported for *Scrippsiella cf. lachrymosa* in culture (Olli, 2002). *Scrippsiella lachrymosa* is not an upwelling dinoflagellate, but its exceptionally high encystment frequency poses the question: can meroplanktonic species, within their serial and episodic cyst production strategies, be further grouped as a high vs. low frequency cyst producing species? Matsuoka and Takeuchi (1995) termed the encystment frequency the “index of cyst production”. Because cyst formation is under multiple physical and chemical control, the reported differences in cyst production among species may reflect more the degree and type of exogenous control (applied in experimental cultures) than reveal the intrinsic capacity of a species to form resting cysts. Cyst production *in situ* can be a very low percentage of total abundance, yet sufficient to seed future blooms. The index of cyst production by the upwelling species *A. catenella* in Tanabe Bay, based on cyst deposition into sediment traps, was only 1.2–2.1% of the total vegetative cell abundance. Most vegetative cells, planozygotes and resting cysts were produced during a 10-day bloom during the annual cycle (Matsuoka and Takeuchi, 1995). Despite this low production rate, it corresponded to a total annual cyst production rate of 5700 cysts cm⁻² of sea floor – a very high density of potential bloom propagules. Related aspects of the cyst production and excystment dynamics during blooms of *L. polyedrum* are considered in Section 6.1.

5.6.2. Excystment and seeding

The role of resting cysts in seeding meroplanktonic blooms during relaxation periods, whether locally produced or advected from

far-field seed banks, is not determined by whether cyst formation is multivoltine or episodic, nor whether the cyst production frequency is high or low. The time required for encystment, once induced, and to germinate, once the cysts have matured after passing through a mandatory dormancy period, are more important. Following their environmental induction, the planozygotes, sexually formed from vegetative cells, usually require one or more weeks to complete encystment (see Lewis, 2002), although *Protoceratium reticulatum* has been reported to encyst quickly and spontaneously in culture (Ellegaard et al., 2003). In contrast, diatom resting spores form and germinate more quickly. Spores can form in 6 to 48 h and germinate 1 day after formation (McQuoid and Hobson, 1996). This accelerated life-cycle behaviour facilitates *Chaetoceros* upwelling blooms seeded by germinated resting spores (Pitcher et al., 1991). In dinoflagellates, this strategy is dampened because of the time required for encystment and the mandatory dormancy period (often required) prior to excystment.

Resting cysts must germinate into vegetative cells to serve as propagules. In some species, this metamorphosis requires completion of a mandatory dormancy period that generally lasts 2 weeks to 6 months (Bolch, 2001). There is a broad range in the mandatory dormancy time reported for upwelling dinoflagellates, both within and among species: *A. catenella* (4–55 days), *G. catenatum* (0–12 days), *L. polyedrum* (several months), *S. trochoidea* (25 days) (Binder and Anderson, 1987; Bravo and Anderson, 1994; Figueroa and Bravo, 2005; Hallegraeff et al., 1998; Itakura and Yamaguchi, 2005). The mandatory dormancy period is a property of the cell; once the dormancy requirement is satisfied, the resting cyst is mature and ready to germinate, which is under external control (Anderson, 1998). Excystment can also be rhythmic, regulated by an endogenous clock under cellular control that restricts germination to a specific time (Anderson, 1998; Perez et al., 1998; Amorim et al., 2002). If environmental conditions do not favour germination, the resting cyst remains quiescent without loss of viability, although its age may affect germination success (Lewis, 2002). Germination can be continuous when conditions favour excystment, or discontinuous, occurring sequentially as a coupled series of germination-quiescent episodes when the external conditions that favour excystment fluctuate (see Anderson, 1998). Hence, delivery of germinated cells as propagules varies with the excystment environment and dispersal conditions (Fig. 2). The external conditions that trigger germination – “germination windows” – vary among species. Light and temperature are important, with two general types of light-dependent germination behaviour reported. The upwelling species *L. polyedrum* and *S. trochoidea* cannot germinate in darkness; light is required for their excystment (Nuzzo and Montresor, 1999; Blanco, 1990). *Gymnodinium catenatum* can germinate in the dark, but it is retarded (Bravo and Anderson, 1994). Temperature plays a key role in breaking dormancy (Anderson, 1998). In *A. catenella*, temperature influences the duration of the dormancy period and germination success (Hallegraeff et al., 1998; Itakura and Yamaguchi, 2005). The conditions that favour the excystment of a given species and its metapopulations vary with time, including daily changes and bloom site location. The combined effect of light and temperature on encystment and germination of *G. catenatum* has been evaluated by Bravo and Anderson (1994).

Dinoflagellate encystment and excystment times are probably, generally too long to auto-seed blooms through repetitive germination during upwelling-relaxation periods. Local excystments may trigger blooms, but their continuance depends on vegetative cell behaviour of the species, and not by resting cyst reseeded of the type reported for *Chaetoceros* (Pitcher et al., 1991). This expectation is consistent with the conclusion reached by Anderson et al. (1985) who measured the sinking rates (6–11 m d⁻¹) of the resting cysts produced by three coastal dinoflagellate species, including *S.*

trochoidea and *Alexandrium tamarense*. Despite their rapid sinking rates, in the absence of vertical mixing it would take up to 2 weeks for the cysts to deposit onto the sediment bed, which led Anderson et al. (1985) to conclude: “in general, the disparity between sinking rates and mandatory dormancy intervals makes it likely that many coastal and estuarine dinoflagellate cysts would not germinate before being deposited in nearshore sediments”.

In summary, meroplanktonic dinoflagellate blooms that develop during relaxation periods most likely are seeded by propagules dispersed from far-field sources as vegetative cells (essential for holoplanktonic species) or newly germinated from resting cysts while *en route*. Propagules excysted from local seed banks during the brief relaxation periods seem less likely sources given the limited time available prior to the disruptive upwelling intrusion that follows. This contributes to the irregularity in dinoflagellate outbreaks in upwelling systems. The bloom window – the time available for propagule delivery to threshold levels, and the duration of the upwelling relaxation period – determines whether a bloom develops and by which species. If neither temporal condition is adequate, the seeding will be sterile or lead to modest population growth. The complex encystment-excystment processes and the limited data available for meroplanktonic upwelling dinoflagellates obscure insight into the role and importance of germinated propagules in seeding their blooms. The collective evidence suggests meroplanktonic species selected for growth in upwelling systems have fitness traits that are not readily distinguishable, nor evident from those meroplanktonic dinoflagellates selected against (see also Smayda, this issue b). The success of the holoplanktonic upwelling dinoflagellates confounds the enigmatic role of resting cysts as propagules seeding upwelling dinoflagellate blooms.

5.6.3. Multiple seeding behaviour as an adaptive strategy

The types of propagules a species has within its life cycle should not be viewed as leading to primary, or exclusive reliance, on a specific propagule type to maintain its population and to seed its blooms and dispersions. A meroplanktonic species does not rely exclusively on propagules germinated from resting cysts, whereas holoplanktonic species seedings do not rely exclusively on vegetative propagules. More likely, a species opportunistically exploits the multiple seeding options its life cycle confers, rather than depends on a single and/or a specific seeding mode. *Lingulodinium polyedrum* provides an example of this versatility. Four different propagule options are available in its seeding strategy: vegetative cells, asexual ecdysal cells, asexual ecdysal cysts and resting cysts (see Figueroa and Bravo, 2005). These survival-seeding options, when applied, are not passive selections. There is evidence that the propagule option invoked is autoregulated through a complex relationship between environmental conditions and cellular programming, and more than one type of propagule can be active at the same time. Asexual ecdysal cysts produced by some vegetative cells in the population can be induced by turbulence (see Section 5.4). These naked, size-diminished vegetative cells lose their motility and sink to deeper layers, where they remain viable in a pelagic, quasi-dormant state for extended periods. Their temporary stasis ends with the release of turbulence inhibition or nutrient limitation (if the ecdysal stimulus); the ecdysed cells are then capable of rapid cell growth and cell size rejuvenation that can lead to, or sustain a bloom (see Section 5.4).

Lingulodinium polyedrum also has an alternative sexually based mechanism of survival and subsequent rapid germination – the formation of sexual ecdysal cysts. Similar to the asexual ecdysal cysts produced, they do not require a mandatory dormancy period. The short-living, ecdysed sexual cysts can form during nutrient-replete conditions and germinate <24–72 h after encystment (Figueroa and Bravo, 2005). The environmental conditions that stimulate the formation of ecdysal sexual stages (propagules) are

unknown; nutrient limitation does not appear to be a factor. *Lingulodinium polyedrum* has yet another cyst option. When limited by nutrients, specifically phosphorus, it forms resting cysts (in laboratory culture) that must pass through a long mandatory dormancy period prior to germination. This sexual cyst is the classical resting cyst produced by *L. polyedrum* (Lewis and Hallett, 1997). Figueroa and Bravo (2005) characterize sexual ecdysal cyst formation as the shorter survival-seeding route of the two sexually based encystment strategies that *L. polyedrum* has. The authors suggest that *L. polyedrum* chooses, based on the prevailing environmental conditions, which of the two sexual encystment strategies to follow in adjusting its life-cycle behaviour to compensate for, and to exploit, niche disturbances.

Extrapolating from the evidence available for *L. polyedrum*, it seems likely that dinoflagellates generally employ a variety of life-cycle options to survive, seed, sustain and otherwise support their population dynamics, rather than apply the narrow-propagule strategy suggested by their classification as mero- and holoplanktonic species. Such autoregulated behaviour, in which the adaptive survival-seeding options available to them are switched on and off, either singly or in combination, would be particularly helpful in upwelling systems subjected to the vagaries of the wind-induced temporal and spatial disruptions in growth conditions. This disruption is exacerbated by the thinning, dispersion, aggregation and restructuring of the populations that accompany the complex and robust circulation patterns that physically define upwelling systems (see Figueiras et al., 2006; Pitcher et al., this issue). In the comparison between the winter-spring and upwelling blooms and their impacts on dinoflagellate blooms (Section 2), survival-seeding behaviour was not considered. It would appear that dinoflagellate species through their unique (relative to diatoms) and additional capacity to form asexual small cells and ecdysed sexual cysts may have evolved more survival-seeding options than diatoms, yet their bloom success in upwelling systems is more limited. This suggests that dinoflagellates are more fastidious in their growth requirements than diatoms; are particularly well adapted to survive harsh conditions through long-term resistance strategies; and bloom opportunistically when growth conditions allow – evident in the long-term bloom behaviour of *G. catenatum* and *L. polyedrum* (see Sections 8 and 9). A conspicuous difference between diatoms and dinoflagellates relevant to this distinction is the much higher growth rates of the diatoms (Tang, 1995, 1996). This suggests the life cycles of diatoms, as a group, are geared towards exploiting seeding opportunities, whereas dinoflagellate life cycles are more attuned to survival. When dinoflagellates do bloom, their allelochemical potential (see Granéli and Hansen, 2006) may then compensate for their intrinsically low growth rates (Tang, 1995, 1996) and enhance the bloom component aspect of their survival-seeding strategy.

6. Resting cysts: long-term survival and episodic blooms

6.1. Viability, encystment:excystment ratios and blooms

Dinoflagellate resting cysts can remain viable for long periods. Lewis et al. (1999) suggested a minimum period of 10 years based on the induced excystment of resting cysts present in stored sediments. The estimated longevity times (in months) of the resting cysts of upwelling species that germinated in their experiments were: *G. catenatum* (12), *H. triquetra* (27), *P. reticulatum* (66) and *L. polyedrum* (122). *Chaetoceros* resting spores, important in seeding diatom blooms (Pitcher et al., 1991), survived equally long (96 months). Lewis (2002) emphasized that survival times *in situ* may differ. Viable resting cysts were found 37–55 years after their formation in ²¹⁰Pb-dated sediment cores collected from a Swedish

coastal fjord (McQuoid et al., 2002). Resting cysts of *S. trochoidea* assimilated phosphorus, which helped to remedy the phosphorus deficiency that triggered their formation (Rengefors et al., 1996). This suggests that it is unlikely that resting cysts are metabolically inert while dormant in seed beds prior to excystment. More likely, resting cysts have an active metabolism beyond the slow respiration of their biochemical reserves, perhaps linked to the nutritional behaviour of the type reported by Rengefors et al. (1996) – that helps to protect their viability and foster post-excystment success.

The general features of the production, excystment and benthic accumulation of resting cysts produced by *L. polyedrum* during blooms in Loch Creran, Scotland, a relatively small ($183 \times 10^6 \text{ m}^3$) fjordic habitat (Lewis et al., 1985), are relevant to dinoflagellate upwelling blooms. The decadal gaps between blooms of *L. polyedrum* in the California Current and Iberian upwelling systems were described in Section 5 and are further considered in Section 8. Two important insights into resting cyst dynamics are evident from the field studies of Lewis et al. (1985) and Lewis (1988): resting cyst abundance can be enormous, but the germination of a very small percentage of cysts is sufficient to seed blooms. Total cyst abundance in the upper 1-cm sediment layer of the loch was 250×10^9 cysts – equivalent to $2136 \text{ cysts cm}^{-2}$ (Lewis, 1988). *Lingulodinium polyedrum* cyst production reached $6400 \text{ cysts cm}^{-2} \text{ day}^{-1}$ during the bloom maximum, which Lewis characterized as exceptionally high. The author concluded that *L. polyedrum* blooms at 5-year intervals were adequate to maintain the cyst population density found in the sediment deposits. She also estimated that germination of only 0.6% (ca. 13 cysts cm^{-2}) of the cyst population would have provided the inoculum that initiated a bloom in 1983. The considerable surplus in the number of resting cysts produced by *L. polyedrum* above that germinated to seed the bloom – a high encystment:excystment ratio – suggests a seed bank maintenance function is incorporated into meroplanktonic dinoflagellate survival-seeding strategies. The historical accumulations and long survival times of sedimented cysts, the products of vintage blooms, mitigate the importance of the instantaneous capacity of a dinoflagellate species to produce and excyst resting cysts – whether continuous or episodic, high or low – in seeding blooms. This may not be the case for blooms sustained by an autoseeding capacity, such as attributed to *Chaetoceros* blooms (Pitcher et al., 1991).

6.2. Resting cysts and bloom behaviour – contradictions

A survival-seeding strategy based on resting cyst formation is an appealing concept, but its role in dinoflagellate upwelling blooms, and generally, has been difficult to quantify, and is enigmatic. Montresor et al. (1998) concluded that the population dynamics of dinoflagellate species cannot be inferred from resting cyst presence, or abundance. The numerous contradictions between resting cyst and vegetative cell dynamics reported during field studies support their general conclusion (e.g., Joyce and Pitcher, 2006; Pitcher and Joyce, 2009). Further, the predominance of holoplanktonic dinoflagellates in the upwelling flora indicates a resting cyst stage is not mandatory for growth in upwelling systems. Joyce and Pitcher (2006), based on surveys of *A. catenella* cysts on the southern Namaqua shelf on the west coast of South Africa and germination studies, concluded that cyst populations do not necessarily serve as an overwintering strategy, but may rather permit rapid cycling between benthic and pelagic stages. The blooms of meroplanktonic species in upwelling (and other) systems suggest niche separation occurs among dinoflagellates, based on a resting stage capacity. Neither the annual abundance nor seasonal succession of meroplanktonic dinoflagellates in the Gulf of Naples (non-upwelling) correlated with the resting cyst data from water column and sediment trap collections (Montresor et al., 1998). Seed banks of cryptic species found primarily in their

resting cyst stage occur, and are apparently maintained by aperiodic, low-density blooms that escape detection. The abundant, viable resting cyst populations of *Alexandrium ostenfeldii* found in seafloor sediments despite rare, local detection of its motile, vegetative cell stage is an example of vegetative cell rarity despite an abundant resting cyst population (Mackenzie et al., 1996). Sediment trap collections in the Gulf of Naples revealed high cyst production rates in *Alexandrium andersoni* and the upwelling species *G. catenatum*, even though neither species was detected in pelagic samples (Montresor et al., 1998). *Lingulodinium polyedrum* blooms have not been recorded in the Benguela upwelling system (Trainer et al., this issue), yet its cysts and those of *G. catenatum*, also not reported to bloom there (Trainer et al., this issue), are deposited in local sediments together with the cysts of *P. reticulatum*, which does bloom there (Bockelmann et al., 2007). The apparent failure of *L. polyedrum* to bloom in the Benguelan system is notable, given that its cysts remain viable for at least a decade (Lewis et al., 1999) and it is prominent in the Peruvian, California Current and Iberian upwelling systems (Trainer et al., this issue). Adding to the enigmatic bloom behavior of *L. polyedrum* is the deposition of its resting cysts into sediment traps deployed in the southern Benguela despite failure to detect its presence in the plankton (Joyce and Pitcher, 2006). The presence of *G. catenatum* resting cysts in the Benguela system, without evidence of pelagic blooms, is also notable, and differs from its behaviour in the Iberian upwelling system where it aperiodically produces massive blooms, similar to *L. polyedrum* (see Section 8). Pitcher and Joyce (2009) have considered the importance of having a resting cyst in the life cycle of upwelling dinoflagellate species, and concluded that mero- and holoplanktonic upwelling dinoflagellates have multiple life-cycle options to survive, seed, sustain, and otherwise support their population dynamics. They suggest that the greater issue is the extent to which cyst-forming dinoflagellate species utilize this capacity in combination with circulation patterns in moving between sedimented cyst depots and pelagic growth zones. Since the most abundant and seasonally recurrent dinoflagellates in upwelling systems are holoplanktonic (Trainer et al., this issue; Pitcher and Joyce, 2009), the absence of a resting cyst in their life cycle suggests their capacity to exploit the complex circulation patterns of upwelling systems is well developed and paramount to their other seeding and survival mechanisms.

7. Enigmatic bloom behaviour of meroplanktonic *Gymnodinium catenatum*

7.1. Blooms in the Iberian upwelling system

The difficulty encountered in quantifying the role of resting cysts in dinoflagellate upwelling blooms is more fully demonstrated by the enigmatic bloom dynamics of *G. catenatum* in the Iberian upwelling system – a species that may be expanding its geographical range (see Amorim and Dale, 2006; Smayda, 2007). A *G. catenatum* bloom erupted off northwestern Spain in 1976, the first pelagic record of its occurrence in European waters. The source of the propagules seeding that bloom is unresolved; both natural dispersion from Moroccan upwelling waters and ballast water inoculation have been invoked (see Blackburn et al., 1989b; Wyatt, 1992; Amorim and Dale, 2006). The key presumption in the debate over the ancestry of the propagules that seeded the 1976 bloom has been that *G. catenatum* was newly introduced (allochthonous), rather than indigenous. However, ^{210}Pb -dated sediment cores collected off the Tagus Estuary in central Portugal have since revealed that *G. catenatum* cysts are present in sediment layers dating back to ca. 1898 (Amorim and Dale, 2006). Prior to 1898, its cysts were not found, unlike for *L. polyedrum* and

P. reticulatum, which also occur in the Iberian upwelling system. Amorim and Dale (2006) attributed the appearance of *G. catenatum*, a century earlier, to ballast water inoculation during a period of cultural eutrophication.

It is unknown whether the 1976 (Estrada et al., 1984) and subsequent massive blooms of *G. catenatum* off the Portuguese coast – 1985 and 1995 (Amorim et al., 2004) – and in the Iberian upwelling system, generally, have a lineage linked to that “original” seed bed, or if the *G. catenatum* propagules seeding the more recent blooms were allochthonous. Of greater interest than the origin of the 1898 benthic seed bank, is that about 75 years have elapsed between the putative first European and Iberian upwelling appearance of *G. catenatum*, in 1976, and the formation of the Tagus Estuary seed bank. This historical gap in recorded bloom behaviour suggests *G. catenatum* did not bloom along the Iberian peninsula prior to 1976, but the sedimentary record suggests otherwise. Abundance of *G. catenatum* cysts in the sediment cores (Fig. 2 in Amorim and Dale, 2006) steadily increased to 25% of the total cyst assemblage in the six decades between ca. 1898 and 1960, then steadily declined to 10% of the total cyst population the following four decades (1960–2001). The historical record indicates undetected blooms of *G. catenatum* despite intensive, almost daily sampling in Ria de Vigo by Margalef in the 1950s (Reguera, personal communication), intercalated by periods of heightened activity that increased its relative cyst abundance, maintained the seed bank of *G. catenatum* for nearly eight decades prior to its 1976 bloom. That is, *G. catenatum* behaved as a cryptic bloom species prior to 1976, similar to the behaviour described earlier for *A. ostensfeldii* (MacKenzie et al., 1996). The sedimentary record of *G. catenatum* is also consistent with accumulating evidence (presented earlier) that aperiodic low-density blooms of meroplanktonic dinoflagellates that either escape detection, or which rarely produce detectable blooms, are common.

The cryptic presence of species primarily in their resting cyst stage demonstrates that seed stock availability is not sufficient alone to initiate a bloom. Whether a bloom then develops is determined by a population-based ecology. The factors that determine whether a seeding occurs differ from those that regulated population growth and bloom development. Failure of the *G. catenatum* population pulses, which maintained the seed bank prior to 1976, to develop into “full-fledged” blooms suggests there was a persistent, multidecadal ecological mismatch between the conditions that favoured bloom seeding (excystment) vs. those required for a bloom outbreak. The massive *G. catenatum* blooms that developed between 1985 and 1995 (Amorim et al., 2004) indicate a two-decade bloom window opened up for this species beginning with the 1976 bloom. This behaviour is symptomatic of a release from the unknown ecological condition(s) that restricted the pre-1976 blooms of *G. catenatum* to low-level pulses that maintained the seed bank.

7.2. Enigmatic *Gymnodinium catenatum* blooms elsewhere

The putative 75 years gap – from initial cyst presence to first bloom – of *G. catenatum* in the Iberian upwelling system has parallels at non-upwelling bloom sites in Tasmania and New Zealand. The first recorded bloom of *G. catenatum* in Tasmanian waters occurred in 1980, which Hallegraeff and Bolch (1992) attributed to ballast water seeding. Major blooms, i.e. opening of the bloom window, followed in 1986, 1991 and 1993 (Hallegraeff and Bolch, 1992; McMinn et al., 1997). Cysts were later found in a sediment layer deposited 43 years earlier (1937 ± 6 years) based on ²¹⁰Pb and ¹³⁷Cs dating, but McMinn et al. (1997) attributed that dated presence to be an artifact of bioturbation. In New Zealand coastal waters, the first recorded *G. catenatum* bloom occurred in 2000–2001 (Irwin et al., 2003). Dated sediment cores revealed its cysts

were present at least 63 years earlier – in 1937 (the year cysts were also found in the Tasmanian sediments). A sediment core “bloom year” also occurred in 1980, i.e. 43 years after the 1937 baseline. The symmetrical behaviour of the Iberian, Tasmanian and New Zealand blooms, each characterized by an extraordinary multi-decadal gap between first-bloom recordings of *G. catenatum* and initial seed bank appearance, is provocative. It suggests that the first blooms of *G. catenatum* detected at these sites were not recent bioinvasions, but were outbreaks following a prolonged delay in the ecological release of long-dormant endemic populations (see Smayda, 2007). In addition to the mandatory cellular dormancy prior to germination, there may be a population-based dormancy whose ecological release leading to blooms is regulated by external factors. The lags in the Iberian, Tasmanian and New Zealand systems suggest a similar lag is occurring in the Benguela system, and at some point the resting cyst deposits of *G. catenatum* in that system will seed the development of a major bloom. Presumably, at that time, the seeding and population growth ecologies will be in alignment and a bloom window will have opened.

8. *Gymnodinium catenatum* and *Lingulodinium polyedrum* blooms in upwelling systems: contrasts and commonalities of two meroplanktonic HAB species

Gymnodinium catenatum exemplifies the exceptionally long lag period that can occur between the first detected local bloom (or regional appearance) of a species and its initial cyst bank presence. The contradictions between observed bloom behaviour and that expected based on a resting cyst survival-seeding strategy – magnified by *G. catenatum* bloom behaviour – suggest meroplanktonic dinoflagellate species are not selected for growth in upwelling systems only, or even principally, because they form resting cysts. Resting cysts may have life history and ecological functions possibly even more important than a role in seeding blooms. *Gymnodinium catenatum* and other meroplanktonic dinoflagellates are not dependent on newly germinated cells from seed banks to initiate blooms. Vegetative cell propagules dispersed from pelagic seed banks in currents and upwelling plumes also seed blooms (Fig. 3). Both propagule types have been shown to seed the recurrent, but variable blooms of *G. catenatum* and its progression along the north–south axis of the Iberian upwelling system (Amorim et al., 2004). Inshore currents that developed following cessation of upwelling advected *G. catenatum* from off the northern Portuguese coast to bloom sites near the Galician Ria de Vigo in 6–7 days (Sordo et al., 2001), a transport distance of 130 km. The rapid bloom development of *L. polyedrum* in the Baja California sector of the California Current system during the relatively brief upwelling-relaxation periods also suggest that pelagic stocks of vegetative cells that survive the upwelling periods – not newly excysted cells – are the primary propagules that seed the relaxation period blooms of *L. polyedrum* that develop (Blasco, 1977, 1978). The physical dynamics during upwelling-relaxation periods (discussed in Section 3) mandate a rapid seeding to initiate blooms. This requirement is more readily accommodated by existent, pre-conditioned vegetative cells than by propagules that newly emerge through excystment.

The long-term gaps between blooms of *L. polyedrum* in the California Current system and along the Portuguese coast were described in Section 5. The punctuated, irregular multidecadal bloom behaviour of *G. catenatum* and *L. polyedrum* in the Iberian upwelling system, despite their contrasting life-cycle requirements and the different hydrodynamic and ecological conditions that elicit their blooms along the Portuguese coast, is remarkable. *Gymnodinium catenatum* and *L. polyedrum* exploit different niches: *L. polyedrum* exploits warm, stratified waters adjoined by upwelled

nutrient-rich plumes, whereas *G. catenatum* accumulates near-shore within upwelling plumes without significant advective loss (Amorim et al., 2004). The potential role of resting cysts in their bloom behaviour is also expected to differ. *Lingulodinium polyedrum* resting cysts require a long dormancy period (months) and anoxic pre-conditioning for excystment (Lewis and Hallett, 1997; Figueroa and Bravo, 2005), requirements that demand a benthic seedbed. In contrast, *G. catenatum* requires neither a dormancy period – or it is very short – nor environmental pre-conditioning, although its germination rate is influenced by temperature and enhanced by irradiance (Bravo and Anderson, 1994). This life-cycle behaviour favours the accumulation of its vegetative cells in pelagic seed banks.

The shared feature of *G. catenatum* and *L. polyedrum* is their bloom irregularity; i.e. multidecadal gaps in their Iberian blooms; the co-occurrence of their resting cysts in the Benguela system, but absence of blooms. Somewhere along the latitudinal gradient from the Benguela to the Iberian upwelling systems, passing through the Northwest African and Moroccan upwelling systems, both species appear to encounter conditions that favour their blooms, notwithstanding their irregularity. To the north of this ecotone – in the Iberian and Moroccan systems – both species bloom; to the south of this ecotone their blooms are inhibited. This transition appears to begin at, or just north of, the robust Northwest African system (see Trainer et al., this issue). In the eastern boundary current region in the Pacific along the gradient from the Chilean upwelling system to the California Current system, *L. polyedrum* is favoured in the Peruvian and California Current upwelling systems. Aperiodic blooms of *G. catenatum* develop along the Mexican sector of this gradient (Cortés Altamirano et al., 1996; Mee et al., 1986).

9. Ecological dormancy, ecological release and dinoflagellate bloom irregularity

The cause(s) of the enigmatic bloom irregularity of meroplanktonic *G. catenatum* and *L. polyedrum*, of dinoflagellates generally, and the factors that select for bloom species are unresolved. Bloom irregularity is a trait that transcends whether a resting cyst is present or absent in the life cycle of the dinoflagellate. For example, holoplanktonic upwelling species such as *Akashiwo sanguinea* also bloom irregularly. The dominant bloom species in the regional upwelling systems differ despite a common species pool (Trainer et al., this issue), but it is unresolved whether these differences primarily have a biotic (life cycle) or an environmental (synecological) basis. Equally enigmatic is the opening and closure of bloom windows operative on decadal scales and symptomatic of a habitat-bloom species relationship influenced by a puzzling combination of ecological dormancy and ecological release. It is uncertain whether oscillatory bloom behaviour is a species-specific trait or whether the observed ecological dormancy and release cycles are selectively imposed by habitat conditions on the available species pool.

The distributional patterns and bloom behaviour of *L. polyedrum* and *G. catenatum*, and evidence that cryptic dinoflagellate blooms are common, collectively point to unrecognized upwelling system behaviour within the physical–chemical–biological domain as being more important in the selection of the dominant bloom species than their specific survival-seeding strategies and ecophysiological adaptations for growth in the physically robust upwelling systems. The expectation that the species selected from among the common upwelling flora for bloom dominance would be the same in all eastern boundary upwelling systems is not realized (Trainer et al., this issue). For example, *Akashiwo sanguinea* is a signature bloom species in the Peruvian system, but not elsewhere; *A. catenella* is a signature bloom species in the Benguelan system, but

not elsewhere; and *L. polyedrum* and *G. catenatum* are signature bloom species in the Iberian system, but not in the Benguela system. Rigorous comparison of the physical, chemical and biological oceanographic properties of the eastern boundary current systems would help to identify and quantify the factors that regulate the observed bloom lags, mismatches between cyst presence and blooms, and interspecific differences in bloom behaviour within and among upwelling systems.

10. Summary

Dinoflagellates selected to bloom in upwelling systems must contend with significant spatial–temporal differences in habitat conditions associated with the vagaries of wind-driven oscillations in the upwelling intrusion and upwelling-relaxation periods that serially make up the individual upwelling cycles embedded within the overall upwelling cycle. Diatom mini-blooms are intercalated with bloom-disruptive retractions of the nutrient-rich upwelled waters that dampen water column mixing, halt the bloom and disperse the diatom community. The floristic and environmental changes during these relaxation periods provide dinoflagellates with bloom opportunities. The accompanying dispersal of the diatoms reduces functional group competition, and the physically less robust habitat conditions favour dinoflagellate blooms, should they be seeded in sufficient numbers during the relaxation period. For a dinoflagellate to bloom during the short-lived and temporary interruption of the diatom bloom, the time available prior to the next upwelling intrusion is fundamental. This bloom window is defined by the ratio of the duration of the upwelling to relaxation periods in the upwelling cycle. The ratio varies significantly within and among systems, and probably accounts for some of the variability found in upwelling dinoflagellate blooms.

The duration of the relaxation period determines the time available for sufficient seed stock to arrive and to propagate the bloom. Three types of propagules are associated with life-cycle behaviour: vegetative cells, resting cells and resting cysts. Resting-cell behaviour is poorly known. Most upwelling diatoms have all three types of propagules; upwelling dinoflagellates do not. A major divide separates upwelling dinoflagellates, based on their capacity to produce a resting cyst. Most upwelling dinoflagellates are holoplanktonic – they lack a resting cyst. Such species, which include those in the genera *Ceratium*, *Prorocentrum*, *Karenia* and *Akashiwo*, rely on vegetative cells dispersed from pelagic seed banks (Smayda, 2002) that develop at offshore sites during upwelling (Pitcher and Boyd, 1996) to survive inhospitable growth conditions and to seed blooms, including meroplanktonic species (see also Crespo et al., 2007; Figueiras et al., 2006; Pitcher and Nelson, 2006). A minority of the upwelling dinoflagellates form resting cysts, including red tide (*Heterocapsa*, *Scrippsiella*) and HAB species (*A. catenella*, *G. catenatum*, *L. polyedrum*), which commonly bloom in upwelling systems. Dinoflagellate upwelling and general bloom behaviour does not confirm the hypothesis that meroplanktonic dinoflagellates are better adapted than holoplanktonic species for growth in upwelling systems, nor can bloom behaviour be inferred from the capacity of a species to produce resting cysts, from cyst abundance or their presence in sedimentary deposits.

The enigma of HAB behaviour is the cause(s) of the exceptional short- and long-term variability in blooms and the gaps in blooms, which can be decadal in length, that characterize meroplanktonic and holoplanktonic dinoflagellates. There is no current explanation for this trait. Whatever factor or combination of factors are determinative, the seeding potential of the propagules resultant from the species life history appears to be either of secondary importance, or subsumed within the overall strategy in combination with other unknown and modifying cellular or habitat factors.

The enigmatic bloom-seeding and resting cyst-bloom relationships suggest that a combination of biotic and abiotic (habitat) factors regulates the observed duet of ecological dormancy and ecological release, which together influence the bloom locations, times and abundance of dinoflagellates in both upwelling and non-upwelling regions, and among species. Just as wind-driven changes in upwelling current systems disperse propagules spatially, extended ecological dormancy with intermittent germination may supply propagules through time (see also Wyatt and Jenkinson, 1997). That is, seeding strategies may have both spatial and temporal components. For dinoflagellates that bloom at non-upwelling coastal sites, the temporal component may be more important; for dinoflagellates adapted to upwelling systems, the spatial aspect may be more important. Notwithstanding the impressive advances in knowledge of the life histories of the microalgal species causing harmful blooms (see Garcés et al., 2002), the role of life-history stages in bloom seeding remains obscure.

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