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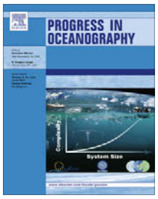

The role of nutrients in regulation and promotion of harmful algal blooms in upwelling systems

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ABSTRACT

The Core Research Project on HABs in upwelling systems, as a component project of the international scientific programme on the Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB), promotes a comparative approach within and across systems to understand and predict the ecology, frequency and occurrence of HABs in eastern boundary current upwelling systems. Unlike other systems, upwelling circulation tends to override nutrient limitation caused by stratification, but is less affected by anthropogenic impacts due to the magnitude of the upwelling nutrient signal. At the same time, upwelling systems are unique in that they undergo seasonal succession as well as short-term spatial and temporal oscillations driven by the time-scale of upwelling wind events. An understanding of nutrient dynamics in upwelling systems is thus critical to any attempt to understand or predict HAB events in these environments. We review the state of knowledge regarding nutrient ecophysiology of a subset of HAB organisms identified in upwelling systems. The upwelling HABs exhibit a number of adaptations previously identified in HAB organisms, such as mixotrophy, osmotrophy and vertical migration. We suggest that, unlike most other HABs, these organisms do not necessarily follow a low nutrient-affinity strategy, and do not fit well with classic allometric scaling relationships. Despite these anomalies, progress has been made in predicting HAB events in upwelling systems, by linking HAB events to the unique environmental conditions associated with these systems. We conclude that this subset of HAB organisms is still poorly described in terms of nutrient ecophysiology, and will benefit from a comparative approach across systems, particularly because the subset of upwelling HABs does not necessarily fit the generic patterns identified for HABs generally.

1. Introduction and background

Harmful algal blooms (HABs) are a global phenomenon that impacts virtually every coastal nation (e.g. Hallegraeff, 1993). Nutrient availability, together with light and temperature, are primary determinants of phytoplankton growth and biomass accumulation. There is growing evidence that the reported increase in HAB events and the increased magnitude of these events is linked to nutrient availability (Anderson et al., 2002; Glibert et al., 2005), and these events are often directly or indirectly linked to anthropogenic eutrophication (Glibert et al., 2005, 2006; GEOHAB, 2006). A common perception is that HABs in coastal upwelling systems such as the California, Iberian, Humboldt and Benguela eastern boundary current systems are relatively less affected by eutrophication (Kudela et al., 2008b) than non-upwelling coastal systems.

The nutrient most often implicated in the limitation of phytoplankton growth in the sea and in particular in coastal upwelling systems is nitrogen (N) (Wilkerson and Dugdale, 2008), though clearly silicate (Si) may shape community dynamics through limitation or co-limitation of diatoms (Kudela, 2008). In a number of instances, changes in the ratio of ambient concentrations of Si to N and N to phosphorus (P) have been implicated in the establishment of dinoflagellate blooms (Hodgkiss and Ho, 1997; Anderson et al., 2002, 2008; Kudela, 2008). Smayda (1990) offers compelling evidence from a number of regions that the global increase in novel phytoplankton blooms may be related to a declining ratio of Si to N as a result of eutrophication, thereby favoring species that do not require Si. Iron (Fe) has received much attention as an important limiting micronutrient, particularly in oceanic high-nutrient, low-chlorophyll (HNLC) regions. Although terrigenous input may offset deficiencies in certain coastal marine environments, recent evidence indicates Fe limitation in parts of the Peruvian and Californian upwelling regions where riverine, aeolian and/or sediment supplies are reduced (Hutchins and Bruland, 1998; Hutchins et al., 1998; Eldridge et al., 2004; Trainer et al., 2009). The stimulation of diatom growth, including *Pseudo-nitzschia* spp., by Fe addition and the relative abundance of dinoflagellates in Fe limited

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waters, suggests Fe availability may play a role in the development of HABs (Hutchins et al., 1998; Rue and Bruland, 2001; Wells et al., 2005; Trick et al., 2010).

Coastal upwelling centers represent an extreme case of natural new nutrient inputs (new production, *sensu* Dugdale and Goering, 1967) and are expected to exhibit equally extreme blooms of both harmful and benign phytoplankton (GEOHAB, 2005; Kudela et al., 2005), driven primarily by the upwelling-relaxation-downwelling cycles and the associated changes in nutrient availability, temperature and stratification. Margalef (1978) formalized this view in what is commonly known as Margalef's Mandala, which depicts the seasonal shift from diatoms in spring to dinoflagellates in summer along a gradient of decreasing turbulence and nutrient availability, with the anomalous "red tide sequence" occurring under a combination of low-turbulence and high-nutrient conditions (Margalef et al., 1979, but see Smayda and Reynolds (2001) for a discussion of the limitations of the Mandala). This classical view of upwelling-dominated species succession fits well with the apparent low affinity (we refer to "affinity" as the ability to sequester nutrients at low [non-saturating for uptake] ambient concentrations) of dinoflagellates for N uptake relative to diatoms when N reserves are limiting growth (Smayda, 1997; Collos et al., 2005). Dinoflagellate blooms off the Iberian Peninsula and in the southern Benguela are generally associated with downwelling conditions following a relaxation in upwelling conditions that allows for the onshore and/or poleward transport of existing populations (Fraga et al., 1988; Pitcher and Boyd, 1996; Moita and da Silva, 2002; Probyn et al., 2000; Sordo et al., 2000). Similarly, toxic events resulting from *Alexandrium catenella* blooms off California occur during relaxation of upwelling and onshore advection (Langlois, 2001), whereas "red tides" have been linked to upwelling relaxation and retentive topographic features (Ryan et al., 2009). In contrast, blooms of *Lingulodinium polyedrum* off California appear to be associated with high levels of nutrient input to near-surface waters via upwelling (Eppley and Harrison, 1975); however, blooms can also occur outside the upwelling season, presumably fueled by high-nutrient freshwater runoff (Hayward et al., 1995; Kudela and Cochlan, 2000; Kudela et al., 2008b). For this reason, *L. polyedrum* has been identified as a good indicator of increased nutrient supply (Lewis and Hallett, 1997), and is often used as a paleo-proxy for human coastal development.

Given the variable association of HABs with different phases of the upwelling cycle and potentially, terrestrial input, it may be expected that different HAB life-forms are characterized by distinct nutrient acquisition strategies. Smayda (1997) attempted to identify the unique ecophysiological properties of HAB dinoflagellates compared to diatoms, chosen as "the norm" due to their dominance in coastal ecosystems and generally benign characteristics. That author identified four unique properties of these HAB organisms relative to diatoms: nutrient retrieval migrations, mixotrophy, secretion of allelochemicals and allelopathy. He further identified major ecophysiological differences such as lower nutrient affinity, greater nutritional diversity, lower growth rates and an aversion to turbulence relative to diatoms.

In the intervening decade, significant advances have been made in our ability to model and/or predict phytoplankton functional group dynamics and the onset of both harmful and benign blooms. In particular, there has been a move towards a "phytoplankton functional group" approach, which allows phytoplankton "types" to compete in an ocean model (Follows et al., 2007). This has obvious benefits for HAB researchers, in that previous models of bulk properties (nutrient, phytoplankton, zooplankton models) have not adequately captured HAB dynamics as the HAB organisms are often a small fraction of the entire plankton community. Despite this advance in numerical modeling, there have been remarkably few studies that address the nutrient utilization characteristics of natural populations of bloom-forming species typical of upwelling regions. Banas et al. (2009) showed that with this information, even simple biological-physical models can capture the dynamics of upwelling systems, whereas more complex models parameterized without appropriate field data fail to adequately represent the biological dynamics of these systems. Therefore, a focus on the basic algal ecophysiology is a necessary pre-requisite for accurate parameterization of models, and more fundamentally will lead towards a better understanding of HAB dynamics in upwelling systems.

The Core Research Project on HABs in upwelling systems, as a component of the scientific programme on the Global Ecology of Harmful Algal Blooms (GEOHAB), espouses a comparative approach to better understand HAB dynamics within and across systems (GEOHAB, 2005; Kudela et al., 2005). Here, we assess the state of knowledge regarding nutrient ecophysiology and HABs in eastern boundary current upwelling regimes, focusing on the California, Iberian, and Benguela systems, with reference to the Humboldt system. Specifically, we pose the question whether the broad patterns identified by Smayda (1997, 2000) for HAB dinoflagellates and HABs in upwelling systems are consistent with our current state of knowledge. We assess whether this knowledge is sufficient to begin parameterizing numerical models with representative HAB functional groups or species. Additionally, we review the current state of knowledge about HAB nutrient sources and acquisition strategies.

2. HAB organisms in upwelling systems

Trainer et al. (this issue) identified 29 groups of phytoplankton (16 genera) that are common to two or more eastern boundary

Table 1
Harmful algal taxa identified in Trainer et al. (this issue) as representative of eastern boundary current upwelling regimes.

HAB organism	Functional group	Chain-forming	Mixotrophic[c]
Akashiwo sanguinea	Dinoflagellate		Yes
Alexandrium catenella	Dinoflagellate	Yes	Yes
Alexandrium minutum	Dinoflagellate		Yes
Ceratium dens	Dinoflagellate		
Ceratium furca	Dinoflagellate		Yes
Ceratium fusus	Dinoflagellate		
Ceratium lineatum	Dinoflagellate		
Cochlodinium fulvescens[a]	Dinoflagellate	Yes	Yes
Dinophysis acuminata	Dinoflagellate		Yes
Dinophysis acuta	Dinoflagellate		Yes
Dinophysis fortii	Dinoflagellate		Yes
Gonyaulax polygramma	Dinoflagellate		Yes
Gymnodinium catenatum	Dinoflagellate	Yes	Yes
Gyrodinium zeta	Dinoflagellate		
Heterosigma akashiwo	Raphidophyte		Yes
Karenia bicuneiformis	Dinoflagellate		
Karenia cristata	Dinoflagellate		
Karenia mikimotoi	Dinoflagellate		
Karlodinium micrum	Dinoflagellate		Yes
Lingulodinium polyedrum	Dinoflagellate		Yes
Noctiluca scintillans	Dinoflagellate		Yes[d]
Prorocentrum balticum	Dinoflagellate		
Prorocentrum micans	Dinoflagellate		Yes
Prorocentrum minimum	Dinoflagellate		Yes
Prorocentrum rostratum	Dinoflagellate		
Prorocentrum triestinum	Dinoflagellate		
Protoceratium reticulatum	Dinoflagellate		Yes
Pseudo-nitzschia[b]	Diatom	Yes	
Scrippsiella trachoidea	Dinoflagellate		Yes

[a] Functionally similar to *C. polykrikoides*.
[b] Multiple species.
[c] As reported in Burkholder et al. (2008), Jeong et al. (2004, 2005a,b), Stoecker et al. (2006).
[d] Heterotrophic, but can harbour photosynthetic symbionts; Sweeney (1976).

current upwelling systems (Table 1). These organisms include the causative agents for paralytic, amnesic and diarrhetic shellfish poisoning, yessotoxin producers, ichthyotoxic organisms, and high-biomass blooms or red tide formers, that are often the cause of anoxia with the bloom's demise. For the purposes of this review, we limit our analyses to just these groups, recognizing that this is a subset of the global list of HAB organisms and impacts. Despite this narrow focus, we note that the list is dominated by dinoflagellates but includes both a diatom genus and raphidophyte, thus roughly mirroring the global composition of HAB organisms.

3. Nutrient ecophysiology

3.1. Nutrient uptake kinetics

As a baseline for comparison of HAB-nutrient interactions, it is appropriate to start with an assessment of nutrient uptake kinetics. HABs are now generally recognized as occurring over a wide range of habitats, from oligotrophic to hypernutrified (GEOHAB, 2005). However, of the 25 HAB organisms targeted in this review, only 10 have reported nitrogen (nitrate, ammonium) uptake kinetics in the literature, six reports include urea, and only three have reported phosphorus (P) kinetics (Table 2; P kinetics not presented). These literature values include both field and laboratory assessment of kinetics. For comparison, Smayda (2000) identified 14 upwelling HAB taxa and reported nitrate kinetics for nine, ammonium and phosphate kinetics for 10 and urea kinetics for zero taxa. However, the broader survey of HABs reported by Smayda (1997) identified 5–15 kinetics values for species representing dinoflagellates, raphidophytes and diatoms, for nitrate, ammonium and phosphate (no urea values were reported). Given the conservative estimate of about 300 HAB species from a total of about 4–6000 phytoplankton, it is apparent that our knowledge of the basic nutrient uptake kinetics for HAB organisms is quite poor.

Despite the lack of full characterization of HAB nutrient kinetics, there is sufficient coverage to assess whether the broad characterization of dinoflagellate HABs as low-affinity organisms compared to diatoms holds true, and to determine whether there are consistent similarities or differences across the HAB upwelling taxa presented here. We focus exclusively on N uptake kinetics, both because nitrogen is considered to be the primary limiting nutrient in upwelling systems and because of the paucity of P kinetics values.

It is generally assumed that dinoflagellates exhibit low affinity for N-substrates relative to diatoms (Smayda, 1997, 2000) and that nutrient uptake kinetics scale as a function of cell size (larger size equals lower affinity; e.g. Irwin et al., 2006; Litchman et al., 2007), although Collos et al. (2005) argue that at high-nutrient concentrations, such as in upwelling systems, multiphasic kinetics may be quite common among a diverse array of phytoplankton species. The nitrate and ammonium half-saturation kinetic parameter (K_s; μM-N) values for representative dinoflagellates, raphidophytes and diatoms, as reported by Smayda (1997, 2000), updated to include *Heterosigma carterae* (Flynn et al., 1999), *Prorocentrum minimum* (Fan et al., 2003), and natural diatom assemblages from the California Current (Kudela and Peterson, 2009), are presented (Fig. 1) and compared to the kinetics values for the upwelling HAB organisms summarized in Table 2. Excluding the upwelling HABs, there is a consistent pattern of lower affinity for nitrate and ammonium in dinoflagellates and raphidophytes compared to diatoms. The upwelling HABs stand out from this pattern, with both a high affinity for nitrate and moderate affinity for ammonium. While admittedly a small data set, it suggests that the upwelling HABs are adapted for both low or pulsed nitrate supplies, and moderate to high ammonium, blending the characteristics of both diatom and dinoflagellate assemblages. This is not simply an artifact of including both a raphidophyte and a diatom in the "upwelling HAB" category, as both *Heterosigma akashiwo* and *Pseudo-nitzschia* exhibited K_s values >1, and the histograms do not change appreciably if those organisms are omitted from the graph in Fig. 1.

Another way to compare relative affinity for nutrients (S) at low concentrations ($S < K_s$) is to compare the initial slope (α) of the Michaelis–Menten plot of specific uptake rate versus nutrient concentration; this is the derivative of the Michaelis–Menten equation with respect to S as S approaches zero (Button, 1978; Healey, 1980). Unfortunately, we cannot make the same direct comparison across algal groups, because many of the publications, including the citations used for Table 1, do not provide the information necessary to estimate α. We thus limit this comparison to the upwelling HAB organisms listed in Table 2. A plot similar to Fig. 1, but for the α parameter, is provided in Fig. 3. Whereas the affinity values for ammonium follow a similar trend as for K_s, the nitrate affinity values demonstrate a relatively even distribution across a large range, including extreme values ~50–100 (*Alexandrium*, *Ceratium*; see Table 2). High initial slopes indicate a correspondingly high ability to sequester nutrients at low concentrations. The upwelling HABs generally show a tendency towards high affinity for both ammonium and nitrate, with nitrate α-values exhibiting a much broader range, and higher maximal affinity, consistent with the low K_s results from Fig. 1.

It is also often assumed that nutrient uptake kinetics scale as a function of cell size (e.g., Eppley et al., 1969; Chisholm, 1991; Irwin et al., 2006; Litchman et al., 2007). This assumption is implicit in foodweb models based on allometric scaling relationships (Moloney and Field, 1989, 1991). Using the nutrient kinetics data (nitrate, ammonium, urea) from Table 2, it is again demonstrated that the upwelling HAB organisms exhibit a poor fit to these expected trends (Fig. 2), with r^2 values for least-squares linear regression of the log-transformed data of 0.02, 0.02, and 0.13 for nitrate, ammonium and urea, respectively. Whereas there is a general tendency for the half-saturation constant to increase with cell size, the variability in the upwelling HAB data increases more dramatically, and suggests that upwelling HAB species, particularly at the larger end of the cell-size spectrum, can exhibit a wide range of nutrient affinities. Similar poor linear fits are obtained when using the maximal uptake velocity (V_m; data not shown). This is also supported by the observation that for a well-studied species such as *L. polyedrum*, nitrate K_s values range from ~0.5 to 15.1 μM NO_3^-, or a factor of 30 (Table 4 in Kudela and Cochlan, 2000). Although allometric scaling laws are well founded on physics and physiology (Aksnes and Egge, 1991; Chisholm, 1991; Irwin et al., 2006; Litchman et al., 2007), the direct application to upwelling HAB organisms is subject to substantial variability.

3.2. Regenerated nitrogen

Several studies have suggested or demonstrated that reduced N forms such as ammonium and urea may be preferentially utilized by flagellates (Glibert et al., 1982; Goldman and Glibert, 1982; Probyn, 1985; Dortch, 1990), but that maximal biomass and bloom formation, particularly in upwelling regions, is effectively controlled by nitrate (Glibert et al., 1982; Goldman and Glibert, 1982; Probyn, 1985; Wilkerson et al., 2000; Wilkerson and Dugdale, 2008; Kudela and Peterson, 2009) because nitrate derived from upwelling is the dominant source of the Liebig-limiting nutrient. Thus there is a tendency to assume that regenerated and/or anthropogenic nutrients are a minor component of upwelling system dynamics, although relatively few studies of upwelling systems have assessed this assumption directly (Anderson et al., 2008; Kudela et al., 2008b). As a corollary, it has been proposed

Table 2

Kinetics values for laboratory and field experiments are provided for upwelling HAB taxa (see Table 1) and for other studies used for the kinetics plots presented in Figs. 1–3. Units are: V_m, $\times 10^{-3}$ h^{-1}; K_s, μM-N; α, V_m/K_s. For references that provide multiple kinetics estimates, the range of reported values is shown.

Organism/region	Lab field	Nitrate			Ammonium			Urea			Reference
		V_m	K_s	α	V_m	K_s	α	V_m	K_s	α	
Akashiwo sanguinea	Field	5.20	1.00	5.20	15.10	2.37	6.37	7.20	0.43	16.74	Kudela et al. (2008b)
Alexandrium catenella	Field	>17.0			14.90	2.52	5.91	3.50	0.65	5. 38	Seeyave et al. (2009)
Alexandrium catenella	Lab	3–47	0.60–28.10	0.11–78.33	26.00	2.00	13.00	25.00	28.40	0.88	Collos et al. (2004)
Alexandrium catenella	Field	24.00	4.60	5.22	64.00	8.40	7.62	61.00	43.90	1.39	Collos et al. (2004)
Alexandrium catenella	Lab				13–23	0.31–6.49	3.54–80.64	0.5–2.0	0.53–3.31	0.60–2.26	Jauzein et al. (2008a)[a]
Alexandrium catenella	Lab				2–4	0.40–4.10	0.7–3.9	0.4	2.3	0.17	Jauzein et al. (2008b)[b]
Alexandrium minutum	Lab	10.0	1.18	8.47							Ignatiades et al. (2007)[c]
Alexandrium minutum	Lab	29.1–69.0	0.29–0.70	98.6–100.5	62.0–154.7	0.65–1.49	95.5–103.8				Maguer et al. (2007)
Ceratium furca	Lab	30.33	0.44	68.92							Qasim et al. (1973)
Ceratium furca	Lab	22.50	0.49	45.92							Baek et al. (2008)[c]
Ceratium fusus	Lab	18.75	0.32	58.59							Baek et al. (2008)[c]
Cochlodinium fulvescens	Field	0.93	1.01	0.92	>4.00		0.31	1.94–2.23	1.57–6.56	0.35–1.24	Kudela et al. (2008c)
Dinophysis acuminata	Field	3.50	0.79	4.43	13.90	0.67	20.75	6.20	0.53	11.69	Seeyave et al. (2009)
Gymnodinium catenatum	Lab	207.08	7.59	27.28	107.50	33.60	3.20				Yamamoto et al. (2004)[d]
Heterosigma akashiwo	Lab	17.1–18.1	1.35–1.68	10.2–13.4	27.2–30.6	1.17–2.23	12.2–26.1	2.89	0.42	6.88	Herndon and Cochlan (2007)
Karenia mikimotoi	Field	10–27	37.0–50.2	0.19–0.72	46–59	0.12–12.67	4.65–383.3	12–31	0.42–2.09	8.13–28.57	Li et al. (submitted for publication)
Lingulodinium polyedrum	Field	3.85	0.47	8.19	8.09	0.59	13.71	10.6	0.99	10.71	Kudela and Cochlan (2000)[e]
Prorocentrum minimum	Field	6.57–14.18	1.36–7.12	1.99–5.49	83.56–228.98	2.38–9.83	16.37–67.01	1.36–7.12	6.64–17.89	1.38–7.71	Fan et al. (2003)[f]
Pseudo-nitzschia spp.	Field	15.00	1.21	12.40	18.00	1.34	13.43	4.90			Seeyave et al. (2009)
P. australis	Lab	105.3	2.82	37.3	70.96	5.37	13.2	30.4		2.8	Cochlan et al. (2008)[g]
P. delicatissima	Lab				30–58	0.38–2.2	21–34	1.7–2.1	0.28–0.54	2.0	Loureiro et al. (2009a)[h]
Other studies											
Heterosigma carterae	Lab		1.00			0.40					Flynn et al. (1999)
Washington (USA) coast, Diatom assemblage	Field	44.8	3.57	12.55	61.5	3.14	19.58				Kudela and Peterson (2009)
Washington (USA) coast	Field	5.8	0.05	116	6.8	0.71	9.58	4.6	0.78	5.89	Dortch and Postel (1989)
Oregon (USA) coast	Field	11.89	1.26	9.44							Dickson and Wheeler (1995)[i]
California Current & coastal Alaska (eutrophic)	Field	16.3–36.1	0.98–4.21	3.87–36.84	36.2	1.30	27.85				MacIsaac and Dugdale (1969)
Northwest Africa	Field	36–41	0.80–1.81	19.89–45.0							Harrison and Davis (1977)
California Current & coastal Alaska (oligotrophic)	Field	1.0–7.4	0.01–0.21	65–190	5.7–8.8	0.10–0.62	10.36–58.0				MacIsaac and Dugdale (1969)
Benguela Current (oceanic stations)	Field	9.8	0.10	98.0	4.1	0.17	24.1	8.2	0.93	8.8	Probyn (1985)
Western New Zealand (>70% picoplankton)	Field	13.8	1.1	12.6	20.7	0.5	41.4	11–13	0.4–0.6	18.3–32.5	Chang et al. (1995)
Northern Pacific (primarily open ocean)	Field	0.64–2.76	0.02–4.47	0.46–60.0	2.67–14.07	0.05–0.41	12.38–182.9	0.63–8.69	0.01–0.13	6.07–591.7	Kanda et al. (1985)[j]

[a] Range of values from Jauzein et al. (2008b) Tables 2 and 3.

[b] Values from T_0 time point; only strain ACT03 (from their Table 3) reported for urea kinetics.

[c] Values for V_m estimated from reported μ_{max} values, assuming $V_m = \mu_m$ under steady state culture conditions.

[d] Reported as nitrate $V_m = 210$ by Nishikawa et al. (2009), Yamamoto and Hatta (2004) also reported nitrate $K_s = 7.60$.

[e] As reported in Kudela et al., 2008a.

[f] Values from field data presented in Table 2 of Fan et al. (2003) (Choptank stations); V_m was converted from the reported values using PN data provided by C. Fan (pers. comm.).

[g] V_m and α for urea estimated respectively from the uptake achieved at 40 μM-N and the initial slope (<2.4 μM-N) of the linear uptake plot of specific uptake vs. urea concentration.

[h] Reported α values from Loureiro et al. (2009a) (not calculated as V_m/K_s).

[i] Reported V_m values were normalized to chlorophyll; this was converted to PN (V_m, h^{-1}) units using the Chl:PN relationship from Table 3, Dickson and Wheeler (1995).

[j] K_s values reported as $K_s + S$; V_m values calculated from reported data.

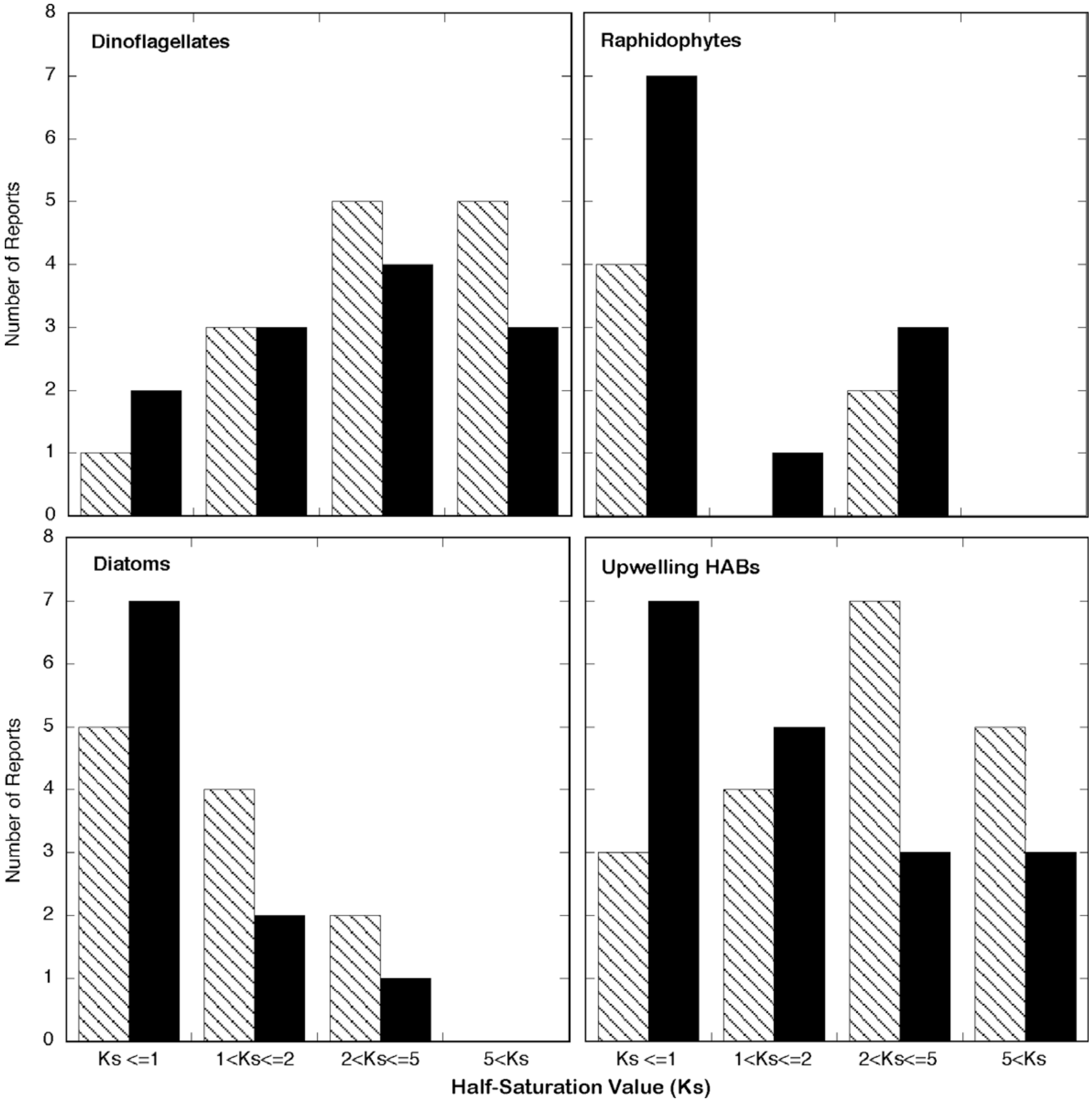

Fig. 1. Kinetics values for nitrate (solid bars) and ammonium (hashed bars) were binned based on the half-saturation (K_s) value using the same categories as Smayda (2000) for Dinoflagellates, Raphidophytes, Diatoms, and Upwelling HABs. Data were obtained from Smayda (1997, 2000), Kudela and Cochlan (2000) and Table 2. Smayda (2000) reported a general trend of low K_s values for diatoms and high K_s values for dinoflagellates, as is seen here. Note that for the Upwelling HAB group, nitrate K_s values more closely approximate the Diatom grouping, while for ammonium the pattern is similar to the Dinoflagellate grouping.

that elevated levels of ammonium may in fact inhibit the growth of diatom assemblages (Dugdale et al., 2006, 2007), and there is evidence for the molecular basis of this inhibition in a model diatom (Parker and Armbrust, 2005). Given that the vast majority of HAB organisms are flagellates, there are clear implications for the promotion of HAB events in upwelling systems. There are several examples of flagellate HAB events in the Iberian (Ríos et al., 1995), Benguela (Seeyave et al., 2009), Humboldt (Smith, 1978) and California (Kudela and Cochlan, 2000) upwelling systems that are driven predominantly by regenerated nutrients, as well as reports of *Pseudo-nitzschia* blooms being sustained by ammonium (Trainer et al., 2007; Seeyave et al., 2009), suggesting that regenerated N is an important nutritional component of some upwelling HAB organisms.

To evaluate the relative importance of different N sources, we compare the nutrient kinetics for the upwelling HABs (Table 2) using α, the initial slope of the Michaelis–Menten curve, indicative of nutrient affinity at low ambient concentrations (Healey, 1980); and the maximal uptake rate (V_{max}), indicative of uptake capacity at elevated ambient nutrients. Uptake kinetics can vary considerably as a function of strain variability, preconditioning of the cells (Fan et al., 2003), and enhanced short-term or surge uptake in response to elevated nutrient concentrations when starved of N (Conway et al., 1976; Goldman and Glibert, 1982). We thus refer the reader to the source publications for a discussion of the background conditions related to the values reported herein, but present these data assuming these values are generally indicative of these upwelling HAB organisms.

The upwelling HAB kinetics data plotted as the ratio of nitrate:ammonium and nitrate:urea for α, and the same ratios plotted for V_{max} are shown in Fig. 4. A ratio $\gg$1 indicates a greater utilization potential for nitrate versus ammonium or urea at low α and high V_{max} nutrient concentrations, whereas a ratio $\ll$1 indicates a greater potential to utilize regenerated N farms. At low nutrient concentrations, regenerated N farms are favored at ratios <1 for all species except *Pseudo-nitzschia australis*, *Ceratium fulves-*

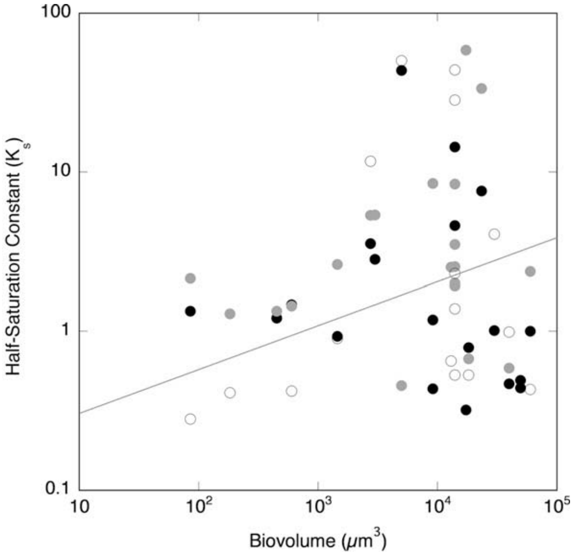

Fig. 2. Half-saturation constants (K_s) for nitrate (black symbols), ammonium (grey symbols) and urea (open symbols) from Table 2 are plotted versus biovolume. The solid line represents the allometric relationship proposed by Litchman et al. (2007). Kinetics values are from Table 2; biovolume was taken from the references in Table 2 when provided, from Seeyave et al. (2009) and from idealized geometric shape to volume relationships using typical cell dimensions from the literature.

cens and *Gymnodinium catenatum*, which exhibit a strong bias for nitrate relative to ammonium, whereas natural assemblages of *Pseudo-nitzschia* spp. (Seeyave et al., 2009) show similar utilization of both substrates. At high-nutrient concentrations, there is a strong bias towards nitrate compared to urea for *H. akashiwo* and *Pseudo-nitzschia*, while only *G. catenatum* exhibits a strong bias for nitrate relative to ammonium (note that urea data were not available). Contrary to expectations, *Pseudo-nitzschia* does not show a strong bias toward nitrate at high concentrations, nor do any of the other organisms (which are all associated with upwelling ecosystems) with the exception of *G. catenatum*. We note that the *G. catenatum* results are based on laboratory kinetics studies. Field results (Ríos et al., 1995) directly contradict this pattern in that *G. catenatum* is associated with mixed assemblages in regenerated-N dominated environmental conditions, highlighting again the potential bias of the small number of kinetics data available for upwelling HAB organisms. As has been pointed out by others (Howard et al., 2007; Cochlan et al., 2008; Kudela et al., 2008b), the general assumption that upwelling HAB taxa are predisposed to utilize nitrate, and/or that upwelling taxa are poorly adapted to utilize regenerated or anthropogenic sources of nutrients, is not well supported by the limited laboratory and field data. With the exception of *G. catenatum* (which may be an anomaly from laboratory kinetics experiments), the upwelling HAB taxa generally exhibit an equal or greater potential to utilize ammonium at low or high concentrations compared to nitrate. This includes *Pseudo-nitzschia* species, which grow equally well or better on reduced N substrates (Howard et al., 2007; Cochlan et al., 2008; Radan, 2008; Auro and Cochlan, submitted for publication) and *P. australis* which shows evidence of simultaneous uptake in the field of both nitrate and ammonium (Howard et al., 2007), rather than inhibition of nitrate uptake by the presence of ammonium. Within the upwelling HAB taxa, *Karenia*, *Prorocentrum* and *Dinophysis* are most closely associated with regenerative conditions, whereas the chain-forming species of *Pseudo-nitzschia*, *Cochlodinium*, *Alexandrium* and *Gymnodinium* are, from a kinetics perspective, best equipped to deal with upwelling conditions and high ambient concentrations of nitrate.

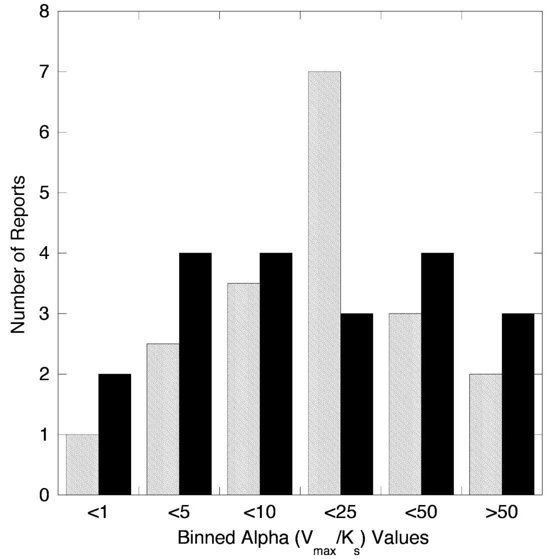

Fig. 3. Kinetics values for nitrate (solid bars) and ammonium (hashed bars) were binned based on the initial slope of the Michaelis–Menten plot (α value) for the Upwelling HABs reported in Table 2. The patterns are generally similar to the trend for K_s as seen in Fig. 1.

Uptake kinetics determined for a natural bloom of *A. catenella* indicates a preference for ammonium over a broad range of concentrations (Collos et al., 2004, 2007) Studies in the southern Benguela (Probyn, unpublished data) show that a dense bloom of *Gyrodinium zeta* was maintained almost exclusively by ammonium and urea, with nitrate contributing <5% of the N requirements. Ríos et al. (1995) similarly inferred that regenerated ammonium provided 91% of the total N taken up by a phytoplankton community in which *Dinophysis acuta*, *G. catenatum*, *Ceratium fusus* and *C. furca* comprised 85% of the autotrophic biomass. During a dense *L. polyedrum* bloom from California, Kudela and Cochlan (2000) showed that the bloom could meet its entire nutritional N requirement from ambient urea and ammonium concentrations. Kudela et al. (2008b) demonstrated that urea, a proxy for terrestrial nutrient sources, could be a significant source of N for coastal California, while both urea and ammonium were utilized at substantially higher rates than nitrate by *C. fulvescens* blooms in the field (Kudela et al., 2008c). Kudela and Chavez (2004) linked riverine input to large (ca. 300 km) phytoplankton blooms during El Niño conditions in California. Kahru et al. (2004) inferred that a red tide off Peru that had devastating consequences for the local fisheries economy was directly linked to regenerated nutrients derived from fish processing facilities. Switzer (2008) linked urea from storm runoff to the proliferation of dinoflagellate blooms in otherwise pristine South African estuaries. We therefore conclude that urea and ammonium can be as important as nitrate in these upwelling systems for maintaining or stimulating HAB organisms.

4. Nutrient acquisition strategies

4.1. Mixotrophy

Whereas uptake kinetics can provide some basis for a comparison of physiological capacity to acquire nutrients, at least two other nutritional factors are associated with HABs and upwelling organisms, namely mixotrophy and vertical migration. For a more detailed discussion of the role of mixotrophy and autotrophy in HAB organisms, we refer the reader to the reviews of Burkholder et al. (2008) and Stoecker et al. (2006). Mixotrophy refers to the ability of an organism to acquire nutrients phototrophically in

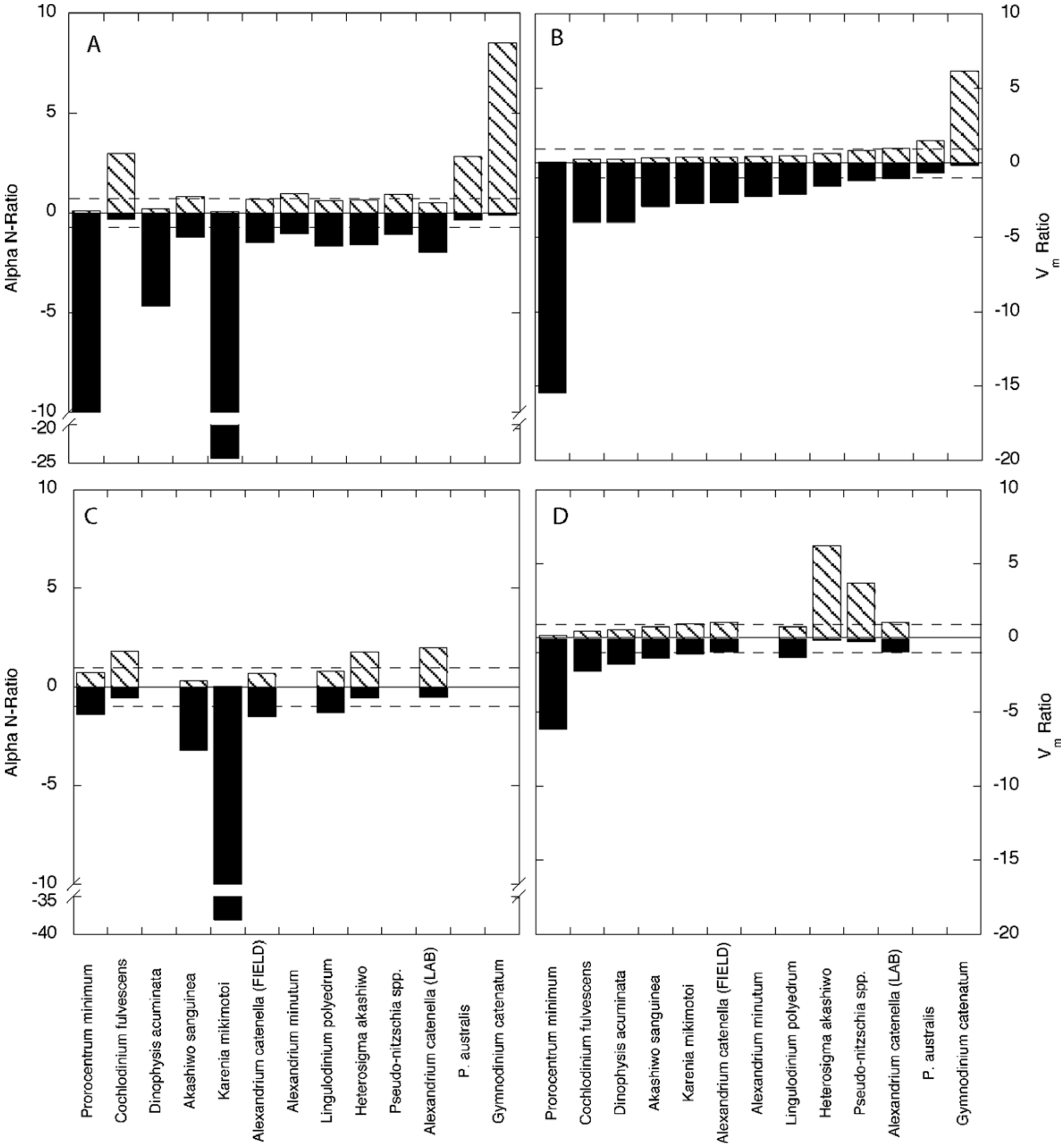

Fig. 4. Kinetics data from Table 2 were used to calculate the ratio of the initial slope of the kinetics curve (α) and the ratio of $V_{\max}$ for nitrate:ammonium (panel A, C; hashed bars) and nitrate:urea (panel B, D; hashed bars). Black (negative) bars represent the inverse of the ratio (i.e. ammonium:nitrate, urea:nitrate). In each panel, values near 1 indicate no strong bias for uptake of nitrate versus ammonium or urea, whereas positive values $\gg 1$ (hashed bars) or negative values $\ll 1$ (black bars) indicate greater (lesser) uptake of nitrate compared to ammonium (panels A, C) or urea (panels B, D). Species with strong negative biases for both α and $V_{\max}$ (e.g. *Dinophysis*) are associated with higher affinity and higher capacity for a reduced substrate, while strong positive biases (e.g. *G. catenatum*) show higher affinity and capacity for elevated nitrate uptake. Species with equal positive/negative bars show no strong bias towards nitrate versus ammonium or urea. Note the difference in *y*-axes for panels A and C, which include an axis break for *K. mikimotoi*.

combination with heterotrophic or phagotrophic acquisition. Stoecker (1998) divided this broad grouping into three physiological "types", comprising ideal mixotrophs, equally adept at both nutritional modes, predominantly phototrophic algae, which includes the upwelling HAB organisms, and predominantly heterotrophic algae. Mixotrophy is sometimes extended to include osmotrophy – the use of dissolved organic compounds such as urea or organic phosphorous compounds.

Induction of feeding appears to be a response to the relative availability of ambient nutrients and cellular nutrient ratios rather than absolute concentrations. For instance, feeding in field populations of *Gyrodinium galatheanum* was negatively correlated with dissolved inorganic N:P ratios (Li et al., 2000). Phagotrophy by *C. furca* in culture was regulated by internal C:P and N:P ratios and increased markedly as these ratios deviated from optimal growth conditions (Smalley et al., 2003). In *Prorocentrum minimum*, mixotrophy could be halted by the addition of P and N to the media (Stoecker et al., 1997). Jeong et al. (2005a) demonstrated that all of 17 cultured red tide dinoflagellates tested fed mixotrophically on *Synechococcus*, strongly suggesting that mixotrophy is a common nutritional mode in these HAB organisms. Although the feeding response to nutrients is complex, it is clear that phagotrophy provides a potentially important alternative mechanism by which certain, and perhaps most, HAB-forming dinoflagellates could supplement their nutrient demands during periods of deprivation (Stoecker et al., 1997, 2006; Burkholder et al., 2008).

4.2. Osmotrophy

Of the 29 upwelling HAB organisms considered (Table 1), 18 are known mixotrophs, with several more likely candidates based on mixotrophy in related species. If this is expanded to include osmotrophy, the eight reported organisms for which we present urea kinetics are confirmed osmotrophs. Of particular relevance to upwelling HABs is that urea utilization has been shown to stimulate domoic acid production in *P. australis* in both field and laboratory studies (Howard et al., 2007), whereas Loureiro et al. (2009a) showed comparable growth and photosynthetic rates for *Pseudo-nitzschia delicatissima* grown on dissolved organic nitrogen compared to ammonium-enriched cultures. Even less is known about other forms of organic N, although recent laboratory studies demonstrate that *P. australis* can utilize glutamine, another anthropogenically derived N source (Cochlan et al., 2008), as well as other reduced N substrates (ammonium and urea). Field observations also suggest that DON is a significant source of nitrogen for *Pseudo-nitzschia* spp. within the Iberian system, and presumably elsewhere (Loureiro et al., 2009b). There is also evidence for direct acquisition of N from high molecular weight humic material in both *A. catenella* (Carlsson and Granéli, 1998) and *G. catenatum* (Doblin et al., 1999, 2006).

Despite the lack of information about the uptake kinetics for inorganic phosphorus in upwelling HAB species, appreciably more is known about the osmotrophic utilization of organic P. Oh et al. (2002) report that *G. catenatum* grows well on organic P compounds, and suggest that conditions of depleted dissolved inorganic phosphorus may favor blooms of this organism. *Ceratium furca* and *C. fusus* were similarly reported to do well at elevated N:P ratios in both the laboratory and field (Baek et al., 2008), which the authors attributed to a combination of physiological acclimation and mixotrophy. *Prorocentrum minimum* blooms and laboratory cultures have also exhibited alkaline phosphatase activity, the enzyme diagnostic of DOP utilization, and blooms of this organism have been linked to a competitive advantage for *P. minimum* in eutrophied systems (Heil et al., 2005). Although DOP acquisition could be construed as a competitive advantage for HAB organisms, there is also evidence that dinoflagellates in general are less competitive for DIP, as reported by Nicholson et al. (2006) for the Monterey Bay region. These authors reported that dinoflagellates accounted for >78% of the cells exhibiting alkaline phosphatase activity from eight cruises over 17 months, despite contributing only 14% to the diatom-dominated assemblage. Intriguingly, several HAB organisms, including *P. minimum*, *Gymnodinium* and *Ceratium lineatum* showed less alkaline phosphatase activity than the bulk dinoflagellate community. This is consistent with our reported trends for N-kinetics, and again suggests that upwelling HABs are not necessarily low-nutrient affinity adapted, as is normally assumed.

4.3. Vertical migration

As noted in the discussion of the kinetics data, the organisms with a more pronounced bias towards nitrate acquisition are also the chain-forming species. The two strong vertical migrators, *Akashiwo sanguinea* and *C. fulvescens*, which do not form chains, but for which there are kinetics data, perhaps coincidentally exhibit a stronger bias for ammonium uptake (Table 2; Fig. 4). A vertical migration strategy is most advantageous in the presence of a nutrient-depleted surface layer bounded by a shallow, steep thermocline (Eppley and Harrison, 1975). Strong swimmers such as *G. catenatum* can retrieve nutrients from depth to supplement the depleted surface layer (Fraga et al., 1989; Figueiras and Fraga, 1990; Doblin et al., 2006). Such behaviors involve geotaxis, phototaxis and/or diel rhythms, and imply an ability to take up nutrients at low levels of irradiance and in the dark (Cullen and Horrigan, 1981; Heaney and Eppley, 1981; Dortch and Maske, 1982; Kudela and Cochlan, 2000; Doblin et al., 2006). More recent studies have demonstrated vertical migration coupled with nutrient uptake in *Cochlodinium* (c.f. Kudela et al., 2008c) and *A. sanguinea* (Ryan et al., 2009). Species with a poor capacity for nitrate uptake, a poor dark-uptake capacity, or lack of motility may still exploit vertical positioning through association with zones of elevated ammonium or iron (Ryan et al., 2005a; McManus et al., 2008), or by maximizing encounters with preferred prey for mixotrophic growth (e.g., *Dinophysis*; Velo-Suárez et al., 2008).

It is well known that chain-forming dinoflagellates also have an adaptive advantage in terms of swimming speed and ability to withstand vertical velocities (Fraga et al., 1989; Smayda, 2000; Anderson et al., 2005a,b). Sullivan et al. (2003) showed that *A. catenella* increases chain length in response to increasing turbulence, although this was also associated with reduced growth rates. Blackburn et al. (1989) showed a direct correlation between chain length and growth for *G. catenatum*, with short chains and single cells associated with poor growth conditions. *Cochlodinium* also exhibits decreasing chain length with suboptimal growth conditions (Whyte et al., 2001) and increasing chain length during periods of active vertical migration (Park et al., 2001). Further details relating HABs to vertical migratory behavior, mixing and thin-layer formation can be found in Smayda (2000), Gentien et al. (2005), and the GEOHAB Core Research Programme report on HABs in stratified systems (GEOHAB 2008).

5. Physics-nutrient interactions

In any discussion of upwelling systems, it is impossible to separate nutrient availability and supply from physical dynamics, because the primary source of nutrients results from upwelling-favorable wind stress forcing the supply of cold, nutrient-rich water (Kudela et al., 2005, 2008a). The physiological adaptations and responses to this physical forcing by individual organisms, as well as the importance of renewal times, advective loss and retention are beyond the scope of this review and are covered in greater detail elsewhere (Berdalet and Estrada, 1993; Estrada and Berdalet, 1997; Smayda, 2000, 2002; Pitcher et al., this issue).

Several studies have demonstrated that phytoplankton diversity increases with increasing frequency of disturbance, such as nutrient pulsing (Gaedeke and Sommer, 1996; Ghosh et al., 1999; Huisman and Weissing, 1999), so long as the disturbances do not exceed one generation time (“washout” in continuous culture experiments). Over long time periods, relative to cell division rates, or over different biogeographic regimes, identifiable phytoplankton groupings are also apparent, such as the categorization of dinoflagellates into nine functional groups responding to nutrients and turbulence (Smayda and Reynolds, 2001). A unique feature of upwelling systems is the pulsed nature of the physical forcing. In addition to seasonal succession (Margalef, 1978), upwelling systems have the ability to “reset” over the time scales of upwelling-relaxation-downwelling events (days to weeks), thus providing additional “ecological windows” for HAB and benign species to proliferate (Kudela et al., 2005; Bernard et al., 2006). The exact subset of species that proliferates for any given event is often stochastic (Smayda and Reynolds, 2001; Estrada et al., 2003), but is typically set by the selection for some particular functional type of organism (e.g., turbulence and high-nutrient adapted, stratified and low-light adapted, etc.).

The “behavior” of different algae can be used to infer or predict the general conditions under which that species will succeed. For example, Yamamoto and Hatta (2004) used a model to identify the conditions favoring a diatom (*Skeletonema costatum*), dinoflagellate (*G. catenatum*) and raphidophyte (*Chattonella antiqua*) in Hong Kong Harbour. As with previous authors, results confirmed that pulsed nutrient supplies at intermediate frequency resulted in the most stable multispecies assemblage. Continuous nutrients with low dilution favored *G. catenatum*, which utilizes a ''storage strategy'', compared to *S. costatum*, which has higher nutrient affinity and higher growth rates, and is considered to be an ''affinity'' or ''growth'' strategist (Sommer, 1984; Collos, 1986; Yamamoto and Hatta, 2004). A similar investigation was conducted in a laboratory-based competition experiment between *Heterocapsa triquetra* and *A. minutum*, under different degrees of P limitation (Labry et al., 2008). In these experiments, *A. minutum* was identified as a ''storage strategist'', and was more competitive under P-depleted conditions interrupted by a pulsed nutrient supply, whereas *H. triquetra* exhibited a ''growth'' strategy, favoring excess nutrient conditions.

Extending these nutrient ''behaviors''' to field data from upwelling systems can be difficult, because there are numerous factors other than nutrients involved in species succession and dominance. However, there is ample evidence that the general pattern holds true for diatom dominance in strong upwelling-relaxation conditions and dinoflagellate dominance in pulsed, low nutrient environments. For example, Fawcett et al. (2007) reported an alternation of diatom (*Pseudo-nitzschia*) and dinoflagellate (*P. reticulatum*, *Dinophysis*) HAB events in the southern Benguela predictably driven by changes in upwelling intensity and stratification. Seeyave et al. (2009) reported for the same region that *Pseudo-nitzschia* and *A. catenella* exhibited ''growth'' or ''velocity'' nutrient strategies, in association with pulsed upwelling, while *Dinophysis* was associated with regenerated nutrients and was characterized as an ''affinity'' strategist.

In the California Current system, *Pseudo-nitzschia* has been associated with the beginning or end of strong upwelling periods, when nutrients are elevated but declining (Kudela et al., 2004), as well as during periods of onshore advection (Trainer, 2002). Trainer et al. (2007) also reported that *Pseudo-nitzschia pseudodelicatissima* grew especially well following elevated ammonium concentrations, with cell density as high as 23 million cells l^{-1}, suggesting that at least some toxigenic *Pseudo-nitzschia* are in some ways more ''dinoflagellate-like'' than other diatoms, adapted to both upwelling and post-upwelling conditions. This is supported by field evidence from the Pacific Northwest (USA), where Olson et al. (2008) reported that *Pseudo-nitzschia* spp. exhibited a growth and/or mortality rate substantially different from other phytoplankton in the same waters, and concluded that *Pseudo-nitzschia* are ''physiologically dissimilar from other diatoms''.

Since 2004, there have been numerous and increasing dinoflagellate red tides in central California caused by *A. sanguinea*, *C. fulvescens* and *Ceratium* spp., as well as increasing numbers of *Dinophysis* spp. and *A. catenella* (Kudela et al., 2005, 2008c; Curtiss et al., 2008; Ryan et al., 2005b, 2008, 2009; Jester et al., 2009). These blooms have been associated with warm, nutrient-depleted retentive features, vertical migration, presumably to acquire nutrients, and a multi-year increase in surface temperatures and stratification, coupled with reduced upwelling-favorable wind stress (Kudela et al., 2008c; Ryan et al., 2008, 2009; Kudela, unpublished data). The Iberian system exhibits similar predictable succession in phytoplankton composition, with seasonal and spatial segregation of diatom and flagellate blooms strongly associated with upwelling-downwelling and retentive circulation (Figueiras and Rios, 1993; Tilstone et al., 1994; Crespo et al., 2008), and a similar increase in HAB problems associated with a long-term decrease in upwelling intensity (Alvarez-Salgado et al., 2008).

6. Trace metals

Iron (Fe), and perhaps copper (Cu), are the most widely recognized trace metals contributing to upwelling HAB dynamics, because of their association with domoic acid production by *Pseudo-nitzschia* (c.f. reviews by Bates and Trainer (2006) and Sunda (2006)). Domoic acid binds to both trace metals (Rue and Bruland, 2001), and Fe deficiency as well as Cu toxicity have been associated with domoic acid production in the laboratory (Maldonado et al., 2002; Ladizinsky, 2003) and in field studies (Wells et al., 2005; Trainer et al., 2009). While there is a clear link between Cu, Fe and domoic acid production (Wells et al., 2005; Trick et al., 2010), frequent Fe limitation is likely to be an issue only in the California and Humboldt upwelling systems. It is therefore unlikely that domoic acid production is an adaptive response in the multiple *Pseudo-nitzschia* species capable of its production, which exhibit cosmopolitan distribution (Hasle, 2002).

Other trace elements linked to upwelling HAB species include lithium (Li), selenium (Se) and nickel (Ni). Both Li and Se are associated with terrestrial runoff. Subba Rao et al. (1998) reported that Li stimulates domoic acid production in *P. multiseries*, while Doblin et al. (1999, 2000) linked Se to the growth of *G. catenatum*, particularly in the presence of organic matter. Mitrovic et al. (2004) identified high requirements for both Fe and Se in *P. reticulatum* and linked these trace elements to yessotoxin production. Two enzymatic pathways are used by microalgae to process urea; one of these, urea amidohydrolase, requires a Ni cofactor (Antia et al., 1991). In at least one upwelling species, *A. catenella*, growth in the presence of urea and Ni is equal to growth on nitrate or ammonium, and Ni is an obligate requirement (Dyhrman and Anderson, 2003). It is likely that other upwelling HAB organisms also utilize the urea amidohydrolase pathway and therefore require Ni, but, as with trace metals generally, this has not been extensively addressed in either HABs or upwelling systems.

7. Nutrients and toxins

Both macronutrients and micronutrients have been shown to have a profound influence on the expression of harmful effects through control of cellular toxin content (c.f. Granéli and Flynn, 2006). These influences occur in response to absolute concentration and nutrient ratios, as well as nutrient speciation. For instance, deficiencies in inorganic P and increased availability of inorganic N have been shown to enhance PSP toxin content in *Alexandrium* species (Boyer et al., 1985, 1987; Matsuda et al., 1996; Bechemin et al., 1999; Guisande et al., 2002; Anderson et al., 2009). In the diatom *Pseudo-nitzschia*, P and Si depletion are the best-characterized triggers for increased domoic acid production in culture studies (Bates, 1988; Pan et al., 1996a,b), although Fe and Cu stress have also been implicated in both the laboratory and field (Rue and Bruland, 2001; Maldonado et al., 2002; Ladizinsky, 2003; Wells et al., 2005; Trick et al., 2010). Nutrient speciation effects are of particular interest with regard to the availability of oxidized and reduced N. It has been demonstrated, for example, that ammonium utilization leads to a greater enhancement of toxin content than nitrate utilization in both *Alexandrium* (Levasseur et al., 1995; John and Flynn, 2000; Hamasaki et al., 2001) and *G. catenatum* (Flynn et al., 1996). In *Alexandrium tamarense*, urea stimulates PSP toxin production relative to growth on nitrate, but with lower cell quotas than for cells grown on ammonium (Leong et al., 2004). Growth on urea also enhances domoic acid production (resulting in greater cellular domoic acid concentrations) compared to growth on nitrate or ammonium under comparable conditions for the larger cell-sized toxigenic diatoms *P. australis* (Howard et al., 2007) and *P. multiseries* (Radan, 2008). For the smaller cell-sized *P. cuspidata* there is no difference in toxin content for nitrate, ammonium, or urea-grown cells during the exponential phase of growth at saturating light levels (Auro and Cochlan, submitted for publication). Thessen et al. (2009) suggest that the impact of N substrates on domoic acid production is likely a byproduct of a more direct effect of N substrate on growth rate, with considerable variability of growth and toxin production at the strain level making broad (species-level) generalizations difficult. Further studies are needed to clarify the interactions between species, strain, cell size and N substrate.

As pointed out by Granéli and Flynn (2006), “it seems more the rule that limitation by either N or P increases toxin content” in ichthyotoxic harmful algae. This is a common enough feature across multiple algal groups (diatoms, dinoflagellates, raphidophytes, cyanobacteria) for several authors to have suggested this as an adaptive strategy by HAB organisms. Mitra and Flynn (2006) develop this hypothesis using a modeling framework, and suggest that algae with a lower intrinsic competitive ability for nutrients (i.e. low-affinity algae, classically assumed to be dinoflagellates; Smayda, 1997) in the presence of grazers will produce more grazing-deterrent chemicals, including toxins, so long as they remain nutrient stressed, which can occur at moderately elevated nutrient concentrations compared to high-affinity algae. Grazers will thus selectively predate the benign algae, reducing competition for HAB organisms. Based on empirical data from the Norwegian coast, Johannessen et al. (2006) reached a similar conclusion; that HAB events are caused by selective zooplankton grazing on palatable species, leaving unpalatable HAB organisms to bloom. Estrada et al. (2006) reported that N:P ratios in assemblages containing *A. catenella* affected food quality, with P-sufficient conditions promoting non-selective grazing by the copepod *Acartia granii*. However, these authors concluded that the grazing response was independent of the presence of *A. catenella* at low abundances (comparable to values reported for the Catalan coast), and that there was no apparent role for toxins in grazer control. Flynn (2008) similarly cautioned against assuming that what humans identify as toxins actually play that role in the foodweb, and suggested that toxin-induced predator mortality may be a poor strategy for HAB organisms. Thus, while nutrient limitation and nutrient ratios play an important role in both toxin production and palatability, it is not yet clear that this is an adaptive strategy developed by HAB organisms to overcome low-nutrient affinity and low growth rates, as is often assumed (Smayda, 1997).

Nutrient loading can also have indirect ecosystem effects. Irigoien et al. (2005) and Stoecker et al. (2008) have advocated for the concept of ‘‘loopholes’’ or ‘‘windows’’ in predator–prey coupling, which can result in high-biomass bloom events, including HAB events. While these authors acknowledge that direct effects such as toxicity and palatability are undoubtedly important, they suggest that enhancing nutrients has an indirect positive feedback on bloom-forming algae. Irigoien et al. (2005) point out that the size-nutrient relationship, of increasing cell size with increasing nutrients, may have less to do with nutrient kinetics per se (i.e. increasing storage capacity, changing surface/volume ratios) and more to do with a cell size and intrinsic growth rate relationship, which allows larger cells to outgrow their competitors. Stoecker et al. (2008) also discuss grazing pressure, but from the perspective of trophic cascades. Based on multi-year field experiments, they suggest that eutrophication results in increasing top-down pressure from copepods on microzooplankton, resulting in bloom formation by organisms normally controlled by microzooplankton grazing. Thus, the nutrient-bloom relationship will not necessarily manifest in direct physiological parameters such as toxin production or nutrient kinetics, but as an ecosystem response to opening and closing of these ‘‘loopholes’’ or ‘‘windows’’ in predator–prey coupling.

8. Predicting HABs in upwelling systems

Despite the ability to “predict” functional groups seasonally and spatially in upwelling systems, there remains a great deal of variability at both the event-scale and the seasonal scale. Pitcher et al. (1991) reported classic phytoplankton succession from diatoms to flagellates in the southern Benguela during a 27-day period. They attributed this to the intrusion of a high-nutrient water mass that gradually warmed, stratified and became nutrient-depleted. There was no predictability, however, at the species-level, making HAB-specific predictions challenging. Similarly, the increase in red tides in California is consistent with environmental forcing, but the particular species that becomes dominant appears to be random, in accordance with the conclusions of Smayda and Reynolds (2001). Indeed, Estrada et al. (2003) concluded that community composition as a whole should be monitored, rather than tracking any specific organism or HAB species, and that higher predictive capability would evolve from modeling the assemblage, assuming that if HAB organisms are present they will be problematic at some point within that assemblage.

Despite these difficulties in predicting HAB species dynamics, progress in predicting HABs from upwelling systems has been made in some specific cases. Alvarez-Salgado et al. (2008) report a long-term (decades) decrease in upwelling intensity off the Iberian Peninsula, which they linked to an increase in the renewal time of the Rias Baixas, a highly productive region for raft cultivation of the mussel *Mytilus galloprovincialis*. These authors were able to link these changes to a corresponding increase in closures from Diarrhetic Shellfish Poisoning (DSP), caused by *Dinophysis*, and can explain 80% of the variability in closure-days using only upwelling intensity. They speculate that this ecosystem shift favors *Dinophysis*, a stratification- and low-nutrient adapted organism (Fig. 4).

In the California Current, attempts have also been made to link environmental conditions to domoic acid concentrations (Anderson et al., 2007, 2009) or to blooms of toxigenic *Pseudo-nitzschia* spp. (Lane et al., 2009). Anderson et al. (2009) identified the Si:N ratio as a significant factor related to toxin production in the Santa Barbara region, while Lane et al. (2009) identified Si, N and river-flow as predictors for toxigenic blooms in Monterey Bay. Lane et al. (2009) concluded that nutrients from either upwelling or cultural eutrophication were directly linked to *Pseudo-nitzschia* blooms, and suggested that a reduced set of environmental variables, similar to the Iberian modeling effort, could be applied to similar upwelling systems.

9. Summary

A main focus of this review is to update the excellent summaries of Smayda (1997, 2000) with regards to HABs in upwelling systems. In the intervening years, a handful of ecophysiological studies have been added to the relatively short list of upwelling HAB species that have been characterized. In contrast to these previous reviews, we suggest that upwelling HABs are not necessarily low-affinity adapted, but rather exhibit moderate to high affinity for nitrate, with a capacity to utilize many forms of N (nitrate, ammonium, urea). There is intriguing evidence suggesting that at least some upwelling dinoflagellates may be less P-limited at low DIP concentrations than dinoflagellates as a group. The list of mixotrophic species continues to grow, with 18 of 29 organisms (Table 1) reported as mixotrophic. While these upwelling HABs generally follow allometric scaling relationships identified from global analyses of phytoplankton and from first principles, there is considerable variability in these patterns. We conclude that the upwelling HABs as a group span a wide range of nutrient acquisition strategies and cannot easily be characterized using simple relationships. This is perhaps not surprising, given the numerous ecological niches, and spatial and temporal opening and closing of "ecological windows" (Irigoien et al., 2005; Bernard et al., 2006; Stoecker et al., 2008) that are inherent to the dynamic environments of eastern boundary current upwelling systems. Within the context of the GEOHAB Core Research Project on HABs in upwelling systems, we encourage additional comparative studies of nutrient ecophysiology within and between systems. Even within the small number of studies conducted to date, there is a great deal of diversity of reported nutrient parameters for the same species (e.g. *L. polyedrum*; c.f. Kudela and Cochlan, 2000; *A. catenella*; Collos et al., 2004, 2007; Seeyave et al., 2009). While this has not been extensively examined, the results from Collos et al. (2005) and Jauzein et al. (2008a) provide some information on the potential physiological mechanisms driving this response. This variability is likely the norm rather than the exception, but will not become apparent until more comparative studies are commenced. The ultimate goal of many HAB research programmes is to predict, and possibly mitigate, harmful algal events. Statistical or numerical modeling is clearly required to address the complexity of these coupled physical-biological interactions (GEOHAB, 2001, 2003, 2005). Although progress is being made in upwelling systems, we conclude that there is much work to be done before we can adequately represent HAB species or even functional groups in these models. Some recommendations emerge from our synthesis. First, we clearly need more detailed ecophysiological studies of the HAB organisms identified in Table 1. Our focus, by necessity, on nitrogen highlights the lack of information about phosphorus, trace metals, DOM, etc., as well as the paucity of studies using a true matrix approach (i.e. temperature, salinity, light, nutrients). Second, an ecosystem-level approach that encompasses mixotrophy and predator–prey interactions is likely necessary to understand and ultimately predict, HAB events in upwelling systems. Third, we advocate for the comparative approach espoused by GEOHAB, with particular emphasis on less well-documented regions such as the Humboldt Current.

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