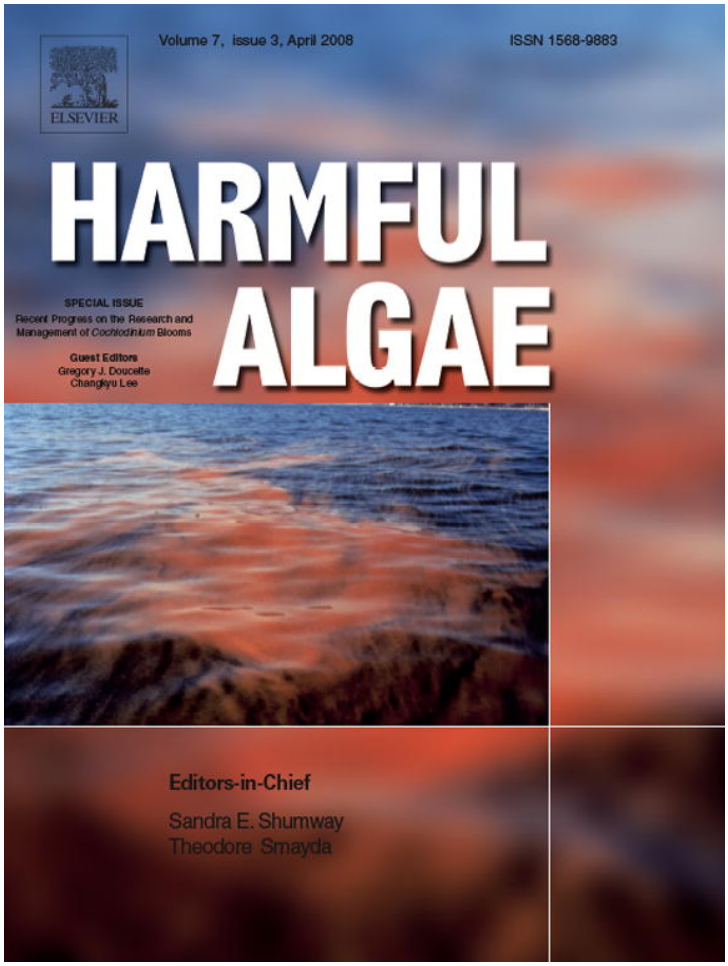

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Linking the physiology and ecology of *Cochlodinium* to better understand harmful algal bloom events: A comparative approach

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Abstract

The red tide forming dinoflagellate genus *Cochlodinium* appears to be expanding globally, as well as blooming and/or causing more economic losses within its previously reported geographic distribution. Despite the widespread occurrence of this organism in the Pacific, Atlantic, and Indian oceans, relatively few studies of its ecophysiology have been conducted. Here we summarize the ecophysiological characteristics through both a literature review and by assessing recent bloom events in Monterey Bay, CA, USA. Using this comparative approach, we identify the basic characteristics of this organism: *Cochlodinium* is found in both warm and cool (11–30 °C) waters in the western and eastern Pacific, respectively, at moderate salinities (30–34). The production of pelagic vegetative seed banks or benthic seed beds by this organism and ability to survive ballast water transport likely facilitate its ability to colonize and establish itself in new habitats. It is a strong vertical migrator capable of utilizing both inorganic and organic nitrogen sources as well as mixotrophy and may be associated with moderate nutrient loading. These characteristics provide *Cochlodinium* with an adaptive capability conducive to rapid colonization of newly opened ecological niches, which may partially explain the apparent global expansion of its geographic range and bloom frequency.

Keywords: Ammonium; *Cochlodinium*; Dinoflagellate; Nitrate; Nitrogen uptake kinetics; Urea

1. Introduction

The athecate, red tide producing dinoflagellate *Cochlodinium* cf. *polykrikoides* Margalef is one of a growing number of harmful algal bloom (HAB) species exhibiting an apparent increase in deleterious impacts worldwide, particularly in the coastal waters of Japan (Yuki and Yoshimatsu, 1989), China (Qi et al., 1993), and especially Korea (e.g., Kim, 1998; Cho and Costas, 2004). Although dominant in Korean waters, *Cochlodinium* has also been found elsewhere in tropical, subtropical, and temperate waters after first being identified in the coastal waters of Puerto Rico (Margalef, 1961). Bloom events have been reported since the late 1990s, particularly in the Pacific Ocean, in both the eastern and western margins. In 2000 and 2001, large blooms were reported in Mexico in the eastern Pacific (Morales-Blake et al., 2001; Gárate-Lizárraga et al., 2004). Blooms were also reported along the Pacific coast of Costa Rica between 2002 and 2004, reaching densities of 1.7×10^5 cells L^{-1} (Vargas-Montero et al., 2004, 2006). Further north, *Cochlodinium* has recently been observed in southern California (Mazzillo, Carter, Busse, and McGowan, personal communication), central California (Curtiss et al., 2008), and British Columbia, Canada (Whyte et al., 2001), while cysts have been identified in eastern Russian waters (Orlova et al., 2004). Although widespread in the Pacific, *Cochlodinium* has also been reported from the Adriatic Sea, the Black Sea, and the Indian and Atlantic oceans: Saracino and Rubino (2006) reported *C. polykrikoides* from field samples in 2000–2001 off the Croatian coast in the Adriatic, while Terenko (2005) reported both cysts and cells from Black Sea ports, presumably introduced via ballast water. In the Indian Ocean, Bhat and Matondkar (2004) documented an event in coastal Goa in 2001, which they also attributed to ballast water transport. In 2002 and again in 2004 *C. polykrikoides* reached densities of 2×10^6 cells L^{-1} in the Peconic Estuary (Long Island, NY, USA), after previously being identified in other

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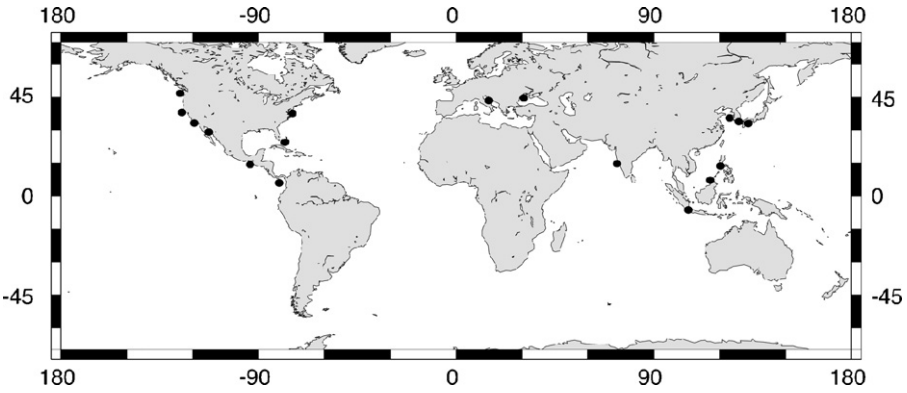

Fig. 1. A partial listing of the geographic locations for *Cochlodinium* sp. events from the past 10 years, showing the global nature of this red tide forming organism.

bays and estuaries along the US east coast including Barnegat Bay, NJ (Nuzzi, 2004; Silva, 1967) and the York River, VA (Ho and Zubkoff, 1979; Zubkoff et al., 1979).

Cochlodinium is globally widespread and occurs in the Pacific, Atlantic, and Indian oceans (Fig. 1). As such, the study of this organism's ecophysiology lends itself to a *comparative approach*, as recommended by the Global Ecology and Oceanography of HABs program (GEOHAB, 2001; Anderson et al., 2005). Using this approach, causal mechanisms of HAB initiation, bloom formation, and demise are inferred by comparing similarities and differences in the conditions and phenomena associated with blooms during multiple, well-described natural events. This method of comparison represents a powerful alternative to experimental manipulation in the characterization of highly varying, synoptic events such as phytoplankton blooms, which are often ephemeral in nature. Recent bloom events in Monterey Bay, CA (USA) are characterized in relation to other reported bloom events of this organism. We provide an overview of the similarities (and differences) between *Cochlodinium* events worldwide, focusing on the common subset of ecophysiological conditions conducive to bloom formation, and we conclude by suggesting critical areas where further research is warranted.

We focus primarily on the species *C. polykrikoides* (synonymous with *C. heterolobatum*; Silva, 1967), which is superficially similar in size and shape to *C. helix* and *C. helicoides* (Silva, 1967). Another organism, *C. catenatum* (Okamura, 1916; Kofoid and Swezy, 1921) has also been described, with similar morphology and geographic distribution (e.g., Gárate-Lizárraga et al., 2004). However, it has recently been suggested (Matsuoka et al., 2006, 2008) that *C. polykrikoides* and *C. catenatum* are the same species, with the latter possibly being the senior synonym based on its earlier description by Okamura (1916). In addition, Iwataki et al. (2007, 2008) recently described a new species, *C. fulvescens*, also with overlapping geographical range and similar morphology and behavior. For the purposes of this manuscript, we will refer to *Cochlodinium* sp., and will not differentiate between these three taxa, which are athecate, photosynthetic, chain-forming dinoflagellates that have been implicated in fish and shellfish mortalities, with similar (or possibly identical) geographic ranges and ecology.

2. Materials and methods

Data from *Cochlodinium* spp. bloom events occurring in 2004 and 2006 are presented from Monterey Bay, CA. Three observational data sets were used: (1) moored and wharf (discrete water) sampling for environmental parameters; (2) autonomous underwater vehicle (AUV) surveys; (3) laboratory kinetics experiments using field assemblages collected during 2006.

2.1. Moored and wharf sampling

Data from the Center for Integrated Marine Technology mooring M0 (operated by Monterey Bay Aquarium Research Institute (MBARI); 36°50′N, 121°54′W) were used to provide continuous monitoring of environmental conditions and surface chlorophyll fluorescence during *Cochlodinium* bloom studies in 2004. For this contribution, data from surface and subsurface CTD packages, surface fluorometer, and surface meteorological packages were used. The moorings and quality control procedures are similar to those described by Chavez et al. (1997).

For the laboratory experiments, near-surface (0–2 m integrated water depth) field assemblages were collected from the Santa Cruz Wharf (36°57.48′N, 122°1.02′W) as part of the California Program for Regional Enhanced Monitoring of PhycoToxins (Cal-PReEMPT). Ancillary measurements for temperature, salinity, and total (GF/F) chlorophyll, were taken using standard methods. Samples were preserved for species identification using 0.8% (final concentration) paraformaldehyde in whole water.

2.2. AUV operation, sensors, and data processing

The MBARI AUV *Dorado* was deployed daily during a 1-week intensive study period in late August 2004. Each survey extended from the inner northern shelf to the mouth of the bay, crossing the region from which the dinoflagellate bloom spread. The AUV was equipped with a multidisciplinary sensor suite for measuring physical, chemical and optical properties. In this paper we present observations from three of the sensors essential to description of the bloom: a SeaBird CTD that

measured temperature, conductivity and pressure, a HOBI Labs HS-2 sensor that measured optical chlorophyll fluorescence, and a Sequoia Scientific LISST-100 particle size sensor. The LISST-100 provides particle size spectra in the range 1–250 μm. It has been tested in lab and field studies and is highly effective for phytoplankton ecology research (Rienecker et al., in press).

2.3. Laboratory determination of kinetics parameters

Chlorophyll *a* (chl *a*) samples were collected on Whatman GF/F filters, extracted for 24 h in 7 mL of 90% acetone (−20 °C) and analyzed using a Turner Designs 10-AU fluorometer calibrated with pure chl *a* (*Anacystis nidulans*; Sigma) using the non-acidification technique (Welschmeyer, 1994). For September 2006, an additional chl *a* sample was collected using 5 μm polycarbonate filters (Poretics) to match the ^{15}N data, also collected on 5 μm filters. Samples for nutrients were filtered through Whatman GF/F filters into polyethylene bottles and frozen pending analysis. Nitrate plus nitrite (hereafter referred to as nitrate), phosphate, and silicic acid were analyzed using a LaChat Instruments automated ion analyzer (8000 series) using standard methods (Parsons et al., 1984). Samples for ammonium and urea analysis were collected using 60 mL low-density polyethylene tubes and stored frozen before analysis using the fluorometric ammonium (Holmes et al., 1999) or the diacetyl monoxime thiosemicarbizide technique (Goeyens et al., 1998) for ammonium and urea, respectively. Whole water samples were preserved with 0.8% paraformaldehyde and subsequently counted on a Zeiss Axiovert 200 microscope using a Palmer-Maloney counting chamber. Net tow material was also examined to qualitatively determine the dominant flora and relative proportions of *Cochlodinium* sp.

Three nitrogen substrates (nitrate, ammonium, urea) were used to determine the uptake response kinetics of the surface samples collected from the Santa Cruz Wharf. In the laboratory, water was dispensed into pre-cleaned, 70 mL polycarbonate flasks at the same time that nutrient, cell abundance, and pigment samples were collected. ^{15}N-ammonium chloride (99 at%; Cambridge Isotopes) ^{15}N-sodium nitrate (99 at%) or ^{15}N-urea (98.2 at%) at a range of initial substrate concentrations was added to the flasks. The flasks were then transferred to an environmental chamber where ambient seawater temperatures were maintained (15–16 °C), and incubated under 240 μmol(photons) m^{-2} s^{-1} irradiance using standard (GE "soft white") fluorescence illumination. Incubations were terminated after 30 min by filtration at <100 mm Hg onto either precombusted GF/F (August) or 5.0 μm Osmonics silver membrane filters (September). Filters were immediately dried at 50 °C and subsequently analyzed for total particulate nitrogen and isotopic enrichment on a Finnigan Delta XP mass spectrometer.

Nitrogen-specific uptake rates (V, h^{-1}) were estimated from the accumulation of ^{15}N in the particulate material and calculated as described by Dugdale and Wilkerson (1986). Rates were not corrected for the effects of isotopic dilution (Glibert et al., 1982) due to the short (30 min) incubation. Curve fitting was carried out using an iterative non-linear least squares technique (Kaleidagraph; Abelbeck Software), which utilizes the Levenberg–Marquardt algorithm (Press et al., 1992), to determine the half-saturation (K_s, μg(at) L^{-1}) and maximum uptake (V_{max}, h^{-1}) parameters of a Michaelis–Menten curve for nitrogen kinetics. The substrate affinity constant at low concentrations (i.e., ambient nutrients < K_s) was determined from the initial slope (α) of the Michaelis–Menten plot and was calculated as $\alpha = V_{max}/K_s$, for nitrate and urea; the ammonium kinetics curve did not exhibit a Michaelis–Menten fit, so the α value was determined by linear regression. Substrate affinity (α) is a metric of nutrient uptake at sub-saturating nutrient concentrations and is functionally equivalent to the initial slope of carbon uptake for a P versus E curve. Although less commonly reported than V_{max} and K_s, it has the advantage of utilizing both factors and provides a better estimate of nutrient affinity at sub-saturating concentrations (<K_s) when inter-species competition is likely to occur (e.g., Healey, 1980; Harrision et al., 1989; Cochlan and Harrison, 1991).

For September 2006, additional measurements were conducted using a WATER-PAM (Walz, Effeltrich, Germany) pulsed amplitude modulation fluorometer to determine relative electron transport rate (rETR) curves. This technique can be used to describe the photosynthesis-irradiance response for a given assemblage (e.g., Kromkamp and Forster, 2003) and is used here for comparison to previous reports of the irradiance response functions for *Cochlodinium*. Samples were analyzed after brief (20 min) dark adaptation with 0.2 μm filtered seawater blank correction, using the rapid ETR protocol in the WinControl (Walz) software. Irradiance values were calibrated using a micro quantum scalar irradiance sensor (Walz). We also assessed the short-term (5 min to 24 h) response in rETR curves to the addition of phosphate and ammonium, by adding 10 μM phosphate or ammonium to the sample and successively measuring the rETR response. As described by Beardall et al. (2001), addition of limiting nutrients to phytoplankton results in fluorescence transients that persist until the external nutrient is depleted. We thus used this method to assess potential phosphorus and nitrogen limitation in the September 2006 field sample. We did not test for interactive effects. Results from the rETR measurements were used to estimate the maximum rETR (unitless), E_k (μmol(photons) m^{-2} s^{-1}) and α (initial slope of rETR versus irradiance) using a hyperbolic tangent function (Jassby and Platt, 1976).

3. Results

3.1. Oceanographic conditions

Similar to Korea (Kim, 1998), *Cochlodinium* has been observed, albeit infrequently, for many years at low to moderate concentrations (e.g., Holmes et al., 1967) in coastal waters of California. During 2004, *Cochlodinium* became the dominant organism during a large red tide event in Monterey Bay, reaching concentrations of at least 6×10^4 cells L^{-1}

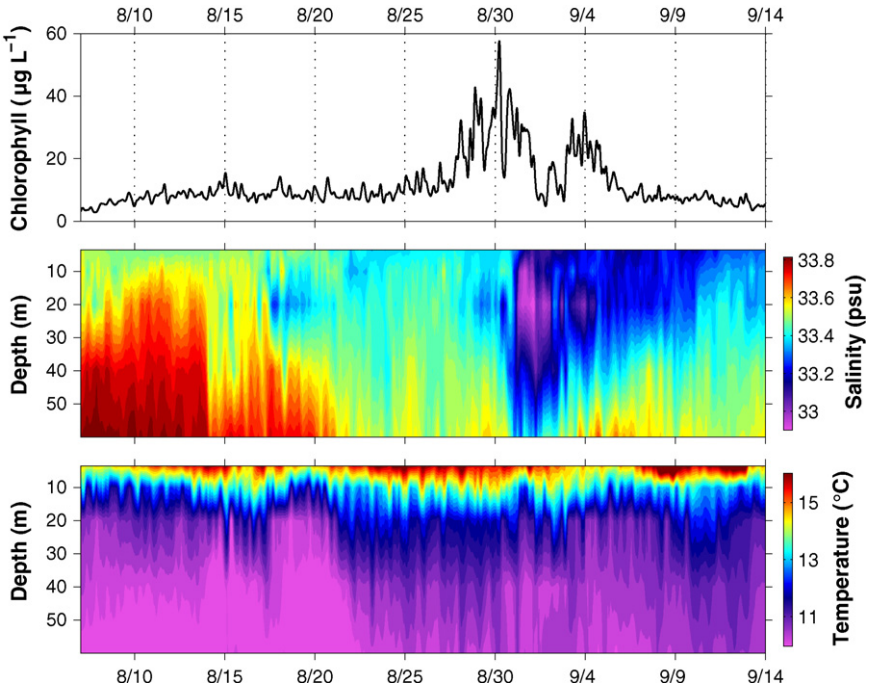

Fig. 2. Data from the CIMT/MBARI M0 mooring from 7 August to 14 September 2004 are plotted. Panels represent near-surface chlorophyll fluorescence (top), salinity (middle), and temperature (bottom). The large bloom event from ca. 25 August to 7 September was dominated by *Cochlodinium* sp., and was associated with the intrusion of lower salinity, cool waters at depth with strong surface stratification.

(Curtiss et al., 2008). In 2006, *Cochlodinium* was also reported in elevated numbers (5.6×10^4 L^{-1}) in southern California (Mazzillo, Carter, Busse, and McGowan, personal communication). In August–September 2004, we observed warm waters (16–20 °C) from the NE bay mixing with cool (14 °C) upwelled waters and fresh (33) but warm (17–18 °C) offshore waters at the M0 mooring (cf. Ryan et al., in preparation); this was associated with the onset of a large red tide event (peak chlorophyll values > 30 mg/m^3) during which *Cochlodinium* and another dinoflagellate, *Akashiwo sanguinea*, dominated. As with another red tide (Ryan et al., 2005a,b), the bloom spread from a localized region in NE Monterey Bay and the development and fate of these blooms was strongly influenced by water mass circulation and intrusions of offshore water. Approximately 2 months later, a second large red tide event, also observed from the M0 mooring, was dominated by *A. sanguinea*, which has similar ecophysiological characteristics (e.g., Smayda, 2002a).

In California, *Cochlodinium* has persisted at elevated background concentrations since we observed the first large bloom event in 2004 (Curtiss et al., 2008); prior to 2004, *Cochlodinium* was not routinely observed in Monterey Bay, although this organism was present and occasionally bloomed in both Monterey Bay and coastal California (Curtiss et al., 2008). In summer and autumn (August–September) 2006, *Cochlodinium* was again a dominant bloom-forming organism (together with *A. sanguinea*), reaching concentrations of 1.2–2.0 $\times$ 10^5 cells L^{-1}. Physical conditions during the two bloom events in northern Monterey Bay were similar. The 2004 event was associated with transport from the NE bay and mixing with both offshore and freshly upwelled waters (Fig. 2), while the persistent dominance of *Cochlodinium* sp. in 2006 was associated with water temperatures ranging from 14 to 18 °C with salinity of 32.8–33.6 as measured at Santa Cruz Wharf; note that this is the same region where the 2004 event initiated. During the 2004 event, the bloom was subsequently disrupted (on approximately 31 August; Fig. 2) by a "flushing" event (Ryan et al., 2005a,b) caused by a brief wind reversal that brought lower salinity (<33.2) waters into Monterey Bay from the south (Ryan et al., in preparation).

3.2. Photosynthesis-irradiance response

We tested short-term irradiance response using the WATER-PAM. As in previous studies, there was little to no sign of photoinhibition, extending to 1600 µmol(photons) m^{-2} s^{-1}

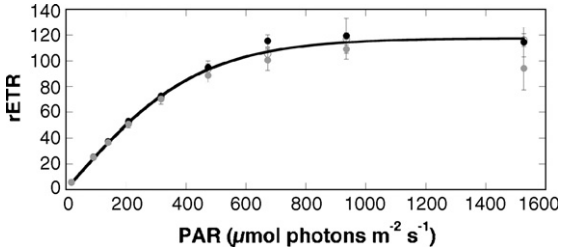

Fig. 3. Relative electron transport rate (rETR, unitless) for whole water collected in September 2006, dominated by *Cochlodinium* sp. Open symbols are unamended; solid symbols are with 10 µM phosphorous added; grey symbols are with 10 µM ammonium added. The symbols for each represent the mean ± 1S.D. for three replicate samples. The solid line represents a hyperbolic tangent fit to the unamended data, with maximum rETR = 117.65 (1.19), E_k = 0.0267 (0.005) and α = 440 µmol(photons) m^{-2} s^{-1} (values in parentheses are 1S.D.).

Table 1
Environmental and kinetics parameters for whole water samples collected from Monterey Bay, CA

	21 August 2006	28 September 2006
Temperature (°C)	14.98	15.7
Salinity	33.30	33.51
Chlorophyll (μg L^{-1})	26.08	22.58
Nitrate (μg(at N) L^{-1})	0.71	n.d.
Ammonium (μg(at N) L^{-1})	0.36	0.26
Urea (μg(at N) L^{-1})	0.64	0.42
Phosphate (μM)	0.11	0.32
Nitrate, V_{max} ($\times 10^3$ h^{-1})	0.93 (1.30×10^{-2})	
Ammonium, V_{max} ($\times 10^3$ h^{-1})	–	
Urea, V_{max} ($\times 10^3$ h^{-1})	1.94 (0.10)	2.23 (0.29)
Nitrate, K_s (μg(at N) L^{-1})	1.01 (0.36)	
Ammonium, K_s (μg(at N) L^{-1})	–	
Urea, K_s (μg(at N) L^{-1})	1.57 (0.24)	6.56 (2.04)
Nitrate, α (μg(at N) L^{-1} h^{-1})	0.921	
Ammonium, α (μg(at N) L^{-1} h^{-1})	0.310	
Urea, α (μg(at N) L^{-1} h^{-1})	1.240	0.347

The kinetics parameters were fit as described in the text. Values in parentheses indicate 1S.D. The r^2 values for each curve were 0.85, 0.94, 0.96, and 0.94 for nitrate, ammonium, urea (August), and urea (September), respectively.

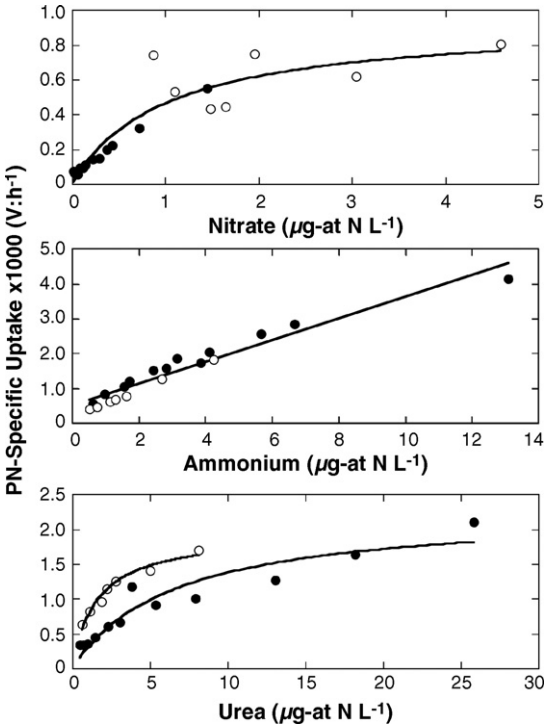

Fig. 4. PN-specific uptake rates (h^{-1}) for nitrate (top), ammonium (middle), and urea (bottom) for natural assemblages dominated by *Cochlodinium* sp. collected from Santa Cruz Wharf, CA, plotted vs. substrate concentrations (μg(at N) L^{-1}). Open symbols are for August 2006, closed symbols are for September 2006; for nitrate and ammonium, the two sampling periods were combined prior to curve fitting using either a Michaelis–Menten (nitrate) or linear (ammonium) relationship. Urea kinetics was separately fit to Michaelis–Menten curves for August (open symbols) and September (closed symbols).

(Fig. 3). We recorded an E_k value about 10× higher than previous reports (400 μmol(photons) m^{-2} s^{-1}), although it is important to note that we assessed this using a short-term fluorescence technique, while previous authors were assessing long-term growth versus irradiance responses in laboratory cultures. Results are consistent with field observations showing that *C. polykrikoides* is positively phototactic and is typically found in the near surface at midday (Park et al., 2001; Fig. 5), which would imply that *Cochlodinium* sp. is capable of utilizing elevated near-surface irradiances.

3.3. Nutrient kinetics

To assess the nutrient utilization of the California *Cochlodinium* sp., we conducted nutrient kinetics experiments during August and September 2006 using natural assemblages in which *Cochlodinium* was the dominant organism. At the time of collection, nitrogenous nutrients were moderately low (Table 1). Phosphorus concentrations were similarly low but detectable, as is typically the case for the Santa Cruz Wharf region. Biomass was reasonably elevated (26.08 and 22.58 μg(chl *a*) L^{-1} for August and September), with 1.2×10^5 and 2.0×10^5 *Cochlodinium* cells L^{-1}. Cell enumeration showed *Cochlodinium* to be >90% dominant by biomass in August 2006 and >75% in September 2006 (with *A. sanguinea* comprising about 23% by biomass). At these concentrations, the waters were noticeably discolored but not forming a red tide, although visible red tides (predominantly *A. sanguinea* and less commonly *Cochlodinium* sp.) were persistent throughout this time period in Monterey Bay. For the purposes of determining the field assemblage kinetics parameters, we combined the uptake rate measurements for the two time periods for nitrate and ammonium, but we plotted the urea kinetics separately, since distinctly different uptake parameters were obtained from the two sampling periods (Fig. 4). Because we assessed uptake kinetics on natural field assemblages, we cannot attribute our kinetics rates to *Cochlodinium* specifically; however, since it was dominant (numerically and in terms of biomass) in the samples, we assume that the reported values are indicative of *Cochlodinium*.

While nitrate and urea exhibited a Michaelis–Menten response, ammonium uptake was distinctly linear, precluding the estimation of K_s and V_{max}. At low N concentrations (e.g., <5 μg(at N) L^{-1}), nitrate, ammonium, and urea uptake kinetics were similar, within a factor of 2, consistent with the similarity in K_s values for nitrate and urea (1.01 and 1.57 μg(at N) L^{-1}, respectively). At elevated nutrient concentrations (>K_s), the differences between N substrates became more apparent: ammonium and urea uptake rates exceeded that of nitrate by twofold. This was largely due to the linear uptake kinetics exhibited for ammonium and the suggestion of linearity at higher urea concentrations (Fig. 4; it is important to note that nitrate uptake was not assessed at concentrations >5 μg(at N) L^{-1}). Using the kinetic parameters from August and September 2006 for Monterey Bay, we obtained affinity values of 0.921, 0.310, and 0.347–1.24 $\times 10^3$ μg(at N) L^{-1} h^{-1} (note that urea values would be doubled if reported as μM N) for nitrate, ammonium, and urea, respectively.

3.4. Chain length and motility

In the laboratory, California strains of *Cochlodinium* are positively phototactic and highly motile. During the 2004 Monterey Bay event, there was also strong evidence for diel vertical migration by dinoflagellates, as evidenced from AUV transects obtained during the peak of the red tide event in August (Fig. 5). In Monterey Bay, pairs of cells were the dominant chain morphology observed from the two sampling events (Table 1) and from the time series, with increasing length (four and eight cells) more common during warm periods and with single cells occasionally observed both in the time series and in the discrete samples analyzed in the laboratory experiments.

4. Discussion

4.1. Bloom initiation

Although red tides have an inherently stochastic component (Smayda, 1997), by comparing the ecological conditions conducive to bloom formation in the various geographic regions, it should be possible to identify a common set of conditions associated with these events. The occurrence and increasing frequency of *Cochlodinium* blooms exemplify the observed global increase in HAB events (Glibert et al., 2005), and in particular dinoflagellate HAB events. Smayda (2002a,b) has suggested that this increase in dinoflagellate blooms can be categorized as responses to either a changing environment (including the effects of aquaculture, cultural eutrophication, and variable climate dynamics) or dispersal by transport (via ballast water and/or transplanted shellfish). Under this paradigm, regardless of whether *Cochlodinium* was always present but not common (Smayda defines this as a ''hidden niche'' species) or a newly invasive species, the emergence of an organism such as *Cochlodinium* from the background to become a red tide HAB requires an ''open niche'' in ecological conditions that is conducive to bloom formation by this particular organism (Smayda and Villareal, 1989; Smayda, 2002a); in other words, there should be a common set of ecological characteristics globally that support bloom events of *Cochlodinium*.

Historically, red tide forming dinoflagellates have been clustered into a single ecological niche of high irradiance, low turbulence, and moderate to elevated nutrients (Margalef et al., 1979). Smayda (2002a) has refined this by classifying dinoflagellate taxa into nine functional groups, based on ecophysiological preferences organized by an onshore–offshore gradient in decreasing nutrients, reduced mixing, and increasing photic depth. Smayda (2002a), for example, classifies the larger group of Gymnodinoids as a functional group characteristic of moderately eutrophic, coastal waters that are generally positively phototactic, aggregating (i.e., forms red tides), fish killing, and forms perennial blooms. According to this scheme, *Cochlodinium* falls within Smayda's Type IV to VI (frontal zone, upwelling-relaxation, and coastal current entrained taxa), all of which are characterized by a ''mixing-drift'' lifestyle, chain formation, and strong swimming capability. These organisms can withstand both the vertical mixing associated with weak (i.e., not vigorous spring upwelling conditions) upwelling-relaxation cycles and the increased horizontal velocities and shear associated with frontal zones (hence the ''mixing-drift'' nomenclature).

When a niche opens, any number of ecologically similar organisms have the opportunity to fill the niche; in Monterey Bay, this is exhibited by the frequent co-occurrence or sequential blooming of *Cochlodinium* sp., *A. sanguinea*, and *Ceratium* sp., all of which belong to Type IV–VI of Smayda's functional group categorization. For these mixing-drift organisms, Smayda (2002b) has also suggested that the seed populations may come from pelagic rather than benthic habitats. These pelagic sources may result from advective transport of an actively growing population, or it may consist of a small seed population of vegetative cells associated with offshore fronts (the so-called pelagic seed bank hypothesis). When the fronts move onshore, the vegetative cells are poised to take advantage of an ''open niche'' and thus act as seed populations for nearshore blooms. This is distinct from the

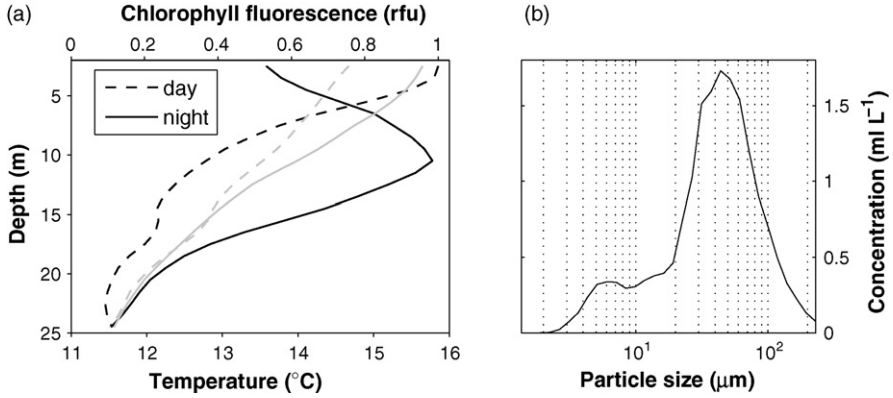

Fig. 5. Observations made by AUV during the *Cochlodinium* bloom period. (a) Average profiles of chlorophyll fluorescence and temperature along a 12 km transect. The surveys were done during the day on 26 August 2004, and during the following night. Warming of surface waters was due to transport, from the NE bay, of warm waters containing the bloom. Movement of the chlorophyll fluorescence maximum to deeper depths at night is consistent with vertical migration of the *Cochlodinium* bloom. (b) Particle size spectrum from the bloom source region in the NE bay on 23 August. The peak near 40 μm is consistent with the size of *Cochlodinium* sampled in Monterey Bay (Curtiss et al., 2008).

onshore propagation of an existing (offshore) bloom event, such as described by Donaghay and Osborn (1997), in that a pelagic seed bank implies that a small seed population is advected into an (onshore) ecologically favorable environment conducive to bloom development. Although there is some evidence for physical transport and an ''open niche'' resulting in red tide bloom dynamics in Monterey Bay (Ryan et al., 2005a,b), this ultimately remains an open hypothesis, since to date there has been no definitive analyses of vegetative or cyst populations in sediments versus coastal and pelagic fronts in this region.

The life history of *C. polykrikoides* is not well known. It is known to produce cysts (e.g., Rosales-Loessener et al., 1996; Matsuoka and Fukuyo, 2002; Kim et al., 2002, 2007) and the recurrence of annual blooms following the initial colonization of an area by *Cochlodinium* strongly implicates seed populations (e.g., cyst beds) in the establishment of this organism in new habitats. Although initially described as an athecate organism, Kim et al. (2007) identified multiple types of *C. polykrikoides* in the laboratory, including the well-described athecate vegetative cells, armored vegetative cells (identified before and after blooms), resting cells, and cysts. The widespread geographic distribution of *Cochlodinium* in the eastern Pacific (central and southern California, Mexico, Gulf of California, Costa Rica) suggests that this is a widespread organism that is present at background levels throughout the region, either as a single species or as functionally similar species. This is corroborated by Curtiss et al. (2008), who have documented *Cochlodinium* in coastal California at low concentrations since 1992, while others (e.g., Holmes et al., 1967) identified a San Diego red tide as *Cochlodinium* in 1964. Similarly, in coastal waters of Korea where *C. polykrikoides* is most dominant, there is strong evidence that this species has gone from a minor background component of the phytoplankton assemblage prior to 1980, to a persistent bloom former today (e.g., Ahn et al., 2006).

Previous authors have typically described *Cochlodinium* in general terms as a pelagic organism that can be transported shoreward and appear as a red tide. For example, Park et al. (2005) demonstrated that a *Cochlodinium* bloom event in Korean coastal waters was unlikely to have resulted from *in situ* growth alone. Instead, they implicated lateral transport and mixing of coastal and offshore waters in a manner similar to that described by Franks (2002), whereby physical concentration of cells resulted in abundances sufficient to constitute a bloom.

In Costa Rica, the recurrence of *Cochlodinium* blooms was linked to wind stress (Vargas-Montero et al., 2006), which the authors suggested promoted cyst germination similar to the model described for *Alexandrium* in the Gulf of Maine (McGillicuddy et al., 2003). Lee (2006) proposed that annual *C. polykrikoides* bloom events between 1995 and 2000 near Naro-Do, Korea were directly correlated with alongshore wind events that resulted in either cyst germination stimulated by intrusion of warm waters, or of onshore transport of vegetative cells (i.e., a pelagic seed bank) into coastal waters conducive to growth. Kim et al. (2007) have proposed that the multiple life stages of *C. polykrikoides*, including the armored stages that are presumably more tolerant of advective transport and shear, would be adaptive to the alternating pattern of offshore to onshore transport followed by bloom formation. Similar to Korea, *Cochlodinium* has been observed, albeit infrequently, for many years (e.g., Holmes et al., 1967) in coastal waters of California. *Cochlodinium* has persisted at elevated background concentrations since the bloom event documented in 2004 (Curtiss et al., 2008). In summer and autumn (August–September) 2006, *Cochlodinium* was again a dominant bloom-forming organism (together with *A. sanguinea*), reaching concentrations of $1.2–2.0 \times 10^5$ L^{-1}. The recurrence of this organism in waters of central California is reminiscent of the evolution from background level to multi-year bloom events as exemplified in coastal waters of Korea. Similar behavior has been observed in other ''new'' locations for *Cochlodinium* blooms as well: Gárate-Lizárraga et al. (2004) reported successive, annual blooms of *Cochlodinium* in the Gulf of California; Morales-Blake et al. (2001) reported the persistence and repetitive blooming of *Cochlodinium* in central Mexico; and Vargas-Montero et al. (2004) reported that *Cochlodinium* has steadily increased spatially and temporally from 2000 to 2004 in coastal waters of Costa Rica. We suggest that the initial introduction of the organism to a region may be the result of onshore transport; maintenance of that organism in the newly established region is then consistent with the formation of either a seed bed or pelagic seed bank, which allows *Cochlodinium* to reappear seasonally and to persist for months at a time (Kim, 1998; Morales-Blake et al., 2001; Gárate-Lizárraga et al., 2004; Vargas-Montero et al., 2004).

4.2. Ecophysiological characteristics of Cochlodinium

4.2.1. Temperature and salinity

Despite the large number of recorded blooms, there is a scarcity of data on the physiological response of *Cochlodinium* to such basic factors as temperature, salinity, and light. Kim et al. (2001b) and Lee et al. (2001) examined the growth response to temperature, salinity, and nutrients (nitrate, ammonium, phosphate). Both studies reported similar results: maximal growth rates were 0.30–0.55 d^{-1} and the organism had wide tolerances for both salinity (15–50, with an optimum from 25 to 40) and growth temperature (ca. 10–30 °C, with optimal growth at 25 °C). These results were corroborated by data from Kim et al. (2004), who examined the temperature and salinity tolerance for a Japanese strain of *C. polykrikoides* in culture. Optimal conditions were again identified as 25 °C and a salinity of 34, which resulted in maximal growth (0.41 d^{-1}).

Field observations indicate the presence of *Cochlodinium* at a range of temperatures (18–30 °C) and salinities (30–35.8) during bloom events in the western Pacific (Table 2), suggesting that this taxon is eurythermal and euryhaline, and well-adapted to warm (25 °C), offshore waters. However, blooms off the west coast of North America have tended be associated with the intrusion of cool water masses. For example, in Mexico, blooms were associated with anomalously cool (decrease from 25.5 to 21.2 °C) waters relative to conditions prior to the bloom event (Morales-Blake et al., 2001), while the 2004 event in Monterey

Table 2
Temperature and salinity ranges for naturally occurring *Cochlodinium* bloom events

Location (year)	Temperature (°C)	Salinity	Source
Phosphorescent Bay, Puerto Rico (1958)	29.8–30.1	35.3–35.8	Margalef (1961)[a]
Yatsushiro Sea, Japan (1978)	23.0–29.9	31.7–34.2	Honda et al. (1980)[a]
Quanshou Bay, China (1990)	22.4–26.7	31.3–33.8	Du et al. (1993)[a]
South Coast, Korea (1995–1998)	22.5–27.0	30.0–33.4	NFRDI (1998); Suh et al. (2000)[a]
Namhae Island, Korea (1996)	24.0–25.2	28.94–31.78	Park et al. (2001)
Vancouver Island, Canada (1999)	11.4–13.5	29.6–31.4	Whyte et al. (2001)
South Sea, Korea (1999)	22.8–26.5		Lee et al. (2001)
Manzanillo Bay, Mexico (1999–2000)	25.5	34.5–34.7	Morales-Blake et al. (2001)[a]
Yatsushiro Sea, Japan (2000)	24.5–26.6	32.0–33.0	Kim et al. (unpublished)[a]
Gulf of California, Mexico (2000)	29.0–31.0		Gárate-Lizárraga et al. (2000)[a]
Inokushi Bay, Japan (2002)	18.9–20.3	32.6–34.6	K. Miyamura, pers. comm. to Kim et al. (2004)[a]
Yeoja Bay, Korea (2003)	24.0–26.0	27.8–30.3	Kim et al. (2006)
South Sea, Korea (2004)	18.10–19.99	32.81–33.66	Lee and Lee (2006)
Monterey Bay, CA (2004, 2006)	14.0–18.0	32.8–33.6	This study

[a] As reported in Kim et al. (2004).

Bay was similarly associated with mixing of cool (14–16 °C) and also fresher water to the interior of the bay (Fig. 2). The persistent dominance of *Cochlodinium* sp. in 2006 was associated with water temperatures ranging from 14 to 18 °C. Kim et al. (2004) suggested that vegetative cells in Korean waters could overwinter at temperatures >14–15 °C and reported that morphological changes (including shortening of chain length) were a stress response to low temperature and salinity. Whyte et al. (2001) reported *Cochlodinium* at ambient temperatures of 11.4–13.5 °C in the coastal waters of British Columbia; however, those authors also suggested, based on chain morphology, that *Cochlodinium* was temperature stressed in those waters. In Monterey Bay, chains were also short but longer than observed in British Columbia; increasing chain length was associated with warmer waters and eight-cell chains were occasionally observed.

Based on these observations from the laboratory and field, it appears that *Cochlodinium* has a reasonably high temperature and salinity optimum (25 °C, 33–38). Although *Cochlodinium* exhibits a wide tolerance for both temperature and salinity in lab studies, natural assemblages reaching bloom concentrations generally occur in a much narrower temperature and salinity range (Table 2). Particularly in the eastern Pacific, *Cochlodinium* is capable of surviving and initiating new bloom events at much lower temperatures, albeit with some evidence of stress (e.g., shorter chain length). Some of this variability is presumably due to strain, or even species, differences between geographical regions. While generally described as eurythermal and euryhaline in west Pacific waters, *Cochlodinium* bloom events are more often associated with the intrusion of cool (<25 °C) waters in the eastern Pacific.

4.2.2. Irradiance response

Previous authors have examined the irradiance-growth response in *C. polykrikoides* cultures, but did not extend these measurements past 200 μmol(photons) m^{-2} s^{-1} irradiance (Kim et al., 2001b, 2004; Lee et al., 2001). Those authors reported that *C. polykrikoides* exhibited no signs of photoinhibition and recorded a half-saturation value (E_k) of 45 μmol(photons) m^{-2} s^{-1} (Kim et al., 2004). As in previous studies, our results also demonstrated no sign of photoinhibition extending to 1600 μmol(photons) m^{-2} s^{-1} (Fig. 3). Park et al. (2001) also correlated chain length with cell division (longer chain length equals greater cell division rates), which corresponded to vertical migration from depth. They suggested that shorter chains, with higher area:volume ratios (per cell), could be an adaptive strategy to maximize photosynthesis in surface waters. Chain length might then be indicative of the proportion of migrating versus photosynthesizing cells, or a combination of population stress and ecophysiological status (e.g., photosynthesizing versus vertical migration). We have insufficient data to comment on the relationship between chain length and photosynthetic capacity; however, there is good evidence for vertical migration (Fig. 5), with maximum densities near surface during the day. Based on the reported photosynthetic response from Korean and California waters, *Cochlodinium* is well-adapted to a high-light environment and does not exhibit photoinhibition at typical near-surface irradiances.

4.2.3. Nutrient kinetics

Nutrient uptake kinetics parameters can be used to assess the relative preference and affinity of various substrates for low and high nutrient environments, and also provide a convenient metric for comparison of *Cochlodinium* to other organisms (Table 3). Some caution must be taken when assessing these values, however, since uptake kinetics can vary considerably as a function of strain variability, preconditioning of the cells (i.e., what N substrates or environmental conditions they were previously exposed to; Fan et al., 2003), and enhanced short-term (surge) uptake in response to elevated nutrient concentrations (Conway et al., 1976; Goldman and Glibert, 1982). As with temperature and salinity, the nutrient acquisition characteristics of *Cochlodinium* have been most extensively examined in Korea. Kim et al. (2001b) reported half-saturation constant (K_s) values for growth of 2.10, 1.03, and 0.57 μM for nitrate, ammonium, and phosphate, respectively, with a preference for ammonium versus nitrate. Lee et al. (2001)

Table 3
Summary of literature values for nitrogen kinetics of representative algal cultures and natural assemblages, emphasizing those studies where urea kinetics were included

Species	Nitrate			Ammonium			Urea			Reference
	V_{max}	K_s	α	V_{max}	K_s	α	V_{max}	K_s	α	
Cultures										
Cochlodinium polykrikoides		2.10			1.03					Kim et al. (2001b)
Heterosigma akashiwo	18.0	1.47	12.2	28.0	1.44	19.4	2.89	0.42	6.88	Herndon and Cochlan (2006)
Gymnodinium catenatum	207.1	7.59	27.28	107.5	33.6	3.19				Yamamoto et al. (2004)[a]
Alexandrium catenella	3–47	0.6–28.1	0.1–78.3	26.0	2.0	13.0	25.0	28.4	0.88	Collos et al. (2004)
Alexandrium tamarense		1.5–2.8			2.00					MacIsaac et al. (1979)
Micromonas pusilla	48.6	0.47	103	129	0.40	322	53.8	0.38	141	Cochlan and Harrison (1991)
Lingulodinium polyedrum[b]		8.6-10.3			5.3–5.7					Eppley et al. (1969)
Natural assemblages										
Monterey Bay (*Cochlodinium bloom*)	0.9	1.01	0.89	>4.0		0.3	0.19–0.22	1.57–6.56	0.35–1.24	This study
Oceanic										
Central North Pacific Gyre	3.0	0.03	100	16.0	0.03	533	16.0	0.02	800	Sahlsten (1987)
Benguela Upwelling region	8.2	0.93	8.81	9.8	0.10	98.0	4.1	0.17	24.1	Kristiansen (1983)
Polar										
Eastern Canadian Arctic	1.85	0.87	2.13	1.91	0.17	11.23	2.84	0.30	9.47	Smith and Harrison (1991)
Ross Sea, Antarctica	1.096–14.001			0.977–4.826	0.040–0.333	12.1–36.8	0.889	0.120	7.41	Cochlan and Bronk (2001)
Coastal										
Washington Coast, USA	5.8	0.05	116	6.8	0.710	9.58	4.6	0.78	5.89	Dortch and Postel (1989)
Western New Zealand	13.8	1.1	12.5	20.7	0.5	41.4	12	0.5	24.0	Chang et al. (1995)
Southern France (*A. catenella*)	24.0	4.6	5.21	64.0	2.8	22.8	61.0	43.9	1.39	Collos et al. (2004)
Neuse Estuary, NC, USA	3.98	0.54	7.37	52.9	2.38	22.2	5.77	0.37	15.6	Fan et al. (2003)[c]
Choptank Estuary, NC, USA (*Prorocentrum minimum*)	53.77	7.12	7.55	868.6	5.09	170.6	492.6	16.84	29.2	Fan et al. (2003)[c]
Southern California, USA (*L. polyedrum*)	0.480	0.467	1.03	1.01	0.586	1.72	1.321	0.989	1.34	Kudela and Cochlan (2000)[d]

Rates are reported as V_{max} (10^3 h^{-1}), K_s (μg(at N) L^{-1}), and α for (10^3 μg(at N) L^{-1} h^{-1}).
[a] V_{max} reported in units of d^{-1}; converted to 10^3 h^{-1}.
[b] Reported as *Gonyaulax polyedra*.
[c] V_{max} reported as fg(at N) $cell^{-1}$ h^{-1}, α reported as V_{max}/K_s.
[d] V_{max} reported as pg(at N) $cell^{-1}$ h^{-1}, α reported as V_{max}/K_s.

obtained similar growth responses for the same set of nutrients, with no obvious difference in maximal growth rates. Kim et al. (2001b) concluded that, while *Cochlodinium* responds positively to nutrients, the relatively low K_s values suggest that it is adapted to neritic waters, but is not a true "eutrophic" dinoflagellate.

Results from Monterey corroborate these studies, demonstrating that *Cochlodinium* is capable of acquiring all forms of nitrogen tested (nitrate, ammonium, urea). At low N concentrations (less than K_s), nitrate, ammonium, and urea uptake kinetics were similar, within about a factor of 2. At elevated nutrient concentrations ($>K_s$), ammonium and urea uptake rates exceeded that of nitrate by about twofold. Substrate preference is often assessed by comparing maximum uptake rates (V_{max}) for one nitrogen source in the absence of other N substrates (e.g., Dortch, 1990). Based on these single substrate experiments, the N preference of *Cochlodinium* follows the order: ammonium > urea ≫ nitrate during high ambient N conditions, but based on the half-saturation constants, which are generally thought to be indicative of substrate utilization under nutrient-limited conditions, nitrate and urea are essentially equivalent (ammonium could not be calculated). *Cochlodinium* nutrient uptake kinetics thus align more with oceanic conditions (low and equivalent K_s values for all N substrates) than with blooms and organisms previously described as eutrophic or responding to eutrophic conditions (e.g., *Lingulodinium polyedrum*, *Prorocentrum minimum*, and *Alexandrium catenella*, as cited in Table 3).

These findings are consistent with the purported pelagic origins of *Cochlodinium*, where ambient nutrients would likely be low. Using the derived kinetics parameters and the ambient nutrient concentrations from the time of collection, we estimate that in August, 37% of the N uptake was from nitrate, 8% from ammonium, and 55% from urea; for September (when no nitrate was detected), the percentages were 38% from ammonium and 62% from urea. These results are consistent with previously reported percentages for other organisms when all three substrates have been measured (Kudela and Cochlan, 2000). We conclude that for these natural assemblages, there is good evidence for utilization of multiple N sources. These half-saturation constants are similar to previous reports for *C. polykrikoides* (Kim et al., 2001b) and in the same range as other neritic flagellates (Table 3).

4.3. Nutrient affinities and eutrophication

No strong evidence implicates coastal eutrophication in the development of *Cochlodinium* blooms, although they are found in coastal waters, often under mesotrophic conditions. Blooms of this taxon have been observed both in non-eutrophic waters and in eutrophic waters. For example, Yoon et al. (2004) documented *Cochlodinium* blooms in cool, oceanic waters low in suspended solids and nutrients and Park et al. (2005) identified blooms as being predominantly neritic and not directly influenced by anthropogenic nutrients. In contrast, blooms have been observed in eutrophic waters subject to significant coastal runoff and high in phosphate (Gárate-Lizárraga et al., 2004) and an increasing frequency of bloom events has been attributed to eutrophication of Korean coastal waters (Ahn et al., 2006). These results suggest a wide tolerance for nutrient conditions in addition to temperature and salinity.

To assess the likelihood of a response by *Cochlodinium* to eutrophication, Kim et al. (2001a) directly examined the nutrient response of a natural population (before, during, and after a red tide event) to nitrate, ammonium, phosphate, trace metals, and vitamins. Those authors reported a positive growth response when both N and P were added prior to or subsequent to a *Cochlodinium* bloom event, although they reported no response when a single nutrient (N or P) was added, or when trace metals or vitamins were provided. During the bloom event, the addition of nutrients (alone or in combination) did not elicit an increase in growth rates. Those authors speculated that at the time of sampling the bloom was not nutrient limited (ambient nutrient concentrations were 0.58, 24.33, and 1.61 μM for nitrate, ammonium, and phosphate, respectively), but that bloom events could potentially be initiated by the addition of both N and P.

We attempted to assess potential N and P (but not the interactive effects) limitation from the September 2006 sampling event by monitoring rETR responses to added nutrients. As with Kim et al. (2001a), we observed no short-term (several minutes; Fig. 3) or long-term (16–24 h; not shown) response in rETR to either nutrient. Nicholson et al. (2006) suggested that despite measurable P year-round in Monterey Bay, dinoflagellates may nonetheless be P-limited, as evidenced by elevated alkaline phosphatase activities. Within this context, our limited results are not conclusive and the question of whether *Cochlodinium* (and other dinoflagellates) responds to P remains open.

Regardless of the response to phosphorus, we can compare the uptake kinetics for nitrate, ammonium, and urea to assess this organism's potential response to low levels of limiting N, as would be encountered in a pelagic or eutrophied environment. Since at least one N substrate (ammonium) demonstrated distinctly linear kinetics, it may be more relevant to compare the affinity (initial slope of the kinetics curve) for nitrate, ammonium, and urea to assess this organism's potential response to low levels of limiting N, as would be encountered in a pelagic environment or in neritic conditions during a bloom event subsequent to nutrient drawdown. A high affinity (large value for α) for at least one nitrogen species is an adaptive strategy that would enable growth in more oligotrophic conditions; similarly, a higher affinity for ammonium versus nitrate is generally characteristic of oligotrophic organisms. Using the kinetic parameters from August and September 2006 for Monterey Bay, we obtained affinity values of 0.921, 0.310, and 0.347–1.240 $\times 10^3$ μg(at N) L^{-1} h^{-1} (note that urea values would be doubled if reported as μM N) for nitrate, ammonium, and urea, respectively. Statistically, these affinity values are identical, indicative of similar affinities for all N substrates at low ($\ll K_s$) concentrations. These results are consistent with the purported pelagic origins of *Cochlodinium*, where ambient nutrients would likely be low.

Collos et al. (2005) provide a recent review supporting the hypothesis that phytoplankton can exhibit multi-phasic kinetics for nitrogen (nitrate in the review), which may be viewed as an adaptive strategy optimizing nutrient transport (and presumably growth) across a wide range of ambient nutrient concentrations. Collos et al. (2004) similarly reported the possibility of biphasic kinetics for ammonium and urea in the HAB dinoflagellate *A. catenella* (resulting in widely varying kinetics parameters; Table 3), which was accompanied by unbalanced C:N assimilation. Those authors concluded that N-uptake at elevated concentrations could provide enough N in 2 h to meet the growth requirements for 24 h and suggested that *A. catenella* may be adapted to a nutrient pulsing frequency that is longer than the corresponding division rates. Our results for ammonium are consistent with the hypothesis that many phytoplankton are capable of linear uptake kinetics, which would clearly serve as an adaptive advantage for a dinoflagellate capable of both neritic and pelagic life histories. *Cochlodinium* thus appears to exhibit characteristics of both a pelagic organism (low and similar K_s values for multiple N substrates) and of more neritic, mesotrophic to eutrophic organisms (linear or biphasic kinetics for some substrates). Its ability to utilize multiple organic and inorganic N sources (as well as heterotrophy: see below) may confer a competitive advantage to this organism in a wide variety of habitats. Even though *Cochlodinium* has much lower nutrient response kinetics than classically "eutrophic" organisms such as *P. minimum* (Fan et al., 2003), the large percentage of urea-N supporting these bloom events in California is consistent with an increased role for cultural eutrophication in the promotion of red tide organisms in California (Kudela and Cochlan, 2000) and globally (Glibert et al., 2006).

4.4. Other behavioral adaptations

Recent evidence also demonstrates that *C. polykrikoides* can grow mixotrophically (Jeong et al., 2004), effectively feeding on prey organisms less than about 11 μm equivalent spherical diameter. Jeong et al. (2004) reported that mixotrophic growth rates were substantially higher than photoautotrophic growth rates (0.324 d^{-1} versus 0.166 d^{-1}), suggesting that mixotrophy is one mechanism supporting the formation of red tides of this organism. Although mixotrophy was not assessed from the California bloom events, the relatively low N-specific uptake rates and utilization of dissolved organic N (Table 3) are also consistent with mixotrophic behavior.

C. polykrikoides is also a strong vertical migrator (e.g., Park et al., 2001). In the laboratory, California strains of *Cochlodinium* are positively phototactic and highly motile. During the 2004 Monterey Bay event, there was also strong evidence for diel vertical migration by dinoflagellates, as evidenced from AUV transects obtained during the peak of the red tide event in August (Fig. 5). As discussed above, this vertical migratory behavior may provide some photosynthetic advantage, as well as providing access to the deep nutricline at night (e.g., Eppley et al., 1969; Cullen and Horrigan, 1981; Smayda, 1997). 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; Anderson et al., 2005), while 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. Similarly, Blackburn et al. (1989) showed a direct correlation between chain length and growth for the dinoflagellate *Gymnodinium catenatum*, with short chains and single cells associated with poor growth conditions. Based on reported field observations, *Cochlodinium* exhibits similar strategies to that of *A. catenella* and *G. catenatum*, decreasing chain length with sub-optimal growth conditions (e.g., Whyte et al., 2001) and increasing chain length during periods of active vertical migration (Park et al., 2001). Observations from California suggest increasing chain length with increasing surface temperatures, consistent with both better growth conditions (closer to the temperature optima) and increased vertical migration due to decreasing availability of nitrate in surface waters. *Cochlodinium* thus exhibits a range of behavioral responses to the environment to maximize growth and exhibits consistent behavior in both Korea and California.

5. Summary

5.1. Ecophysiological characteristics of Cochlodinium

Based on existing field and laboratory studies, a picture of the physiological ecology of *C. polykrikoides* is beginning to emerge. *Cochlodinium* is associated with warm (18–30 °C), euryhaline (30–34) conditions in the western Pacific, but exhibits a wider (cooler) range of temperatures (11–31 °C) in the eastern Pacific, with similar salinities (29.6–35.8); field observations exhibit a much narrower salinity range for bloom formation than would be expected based solely on culture experiments (15–50). It is a strong vertical migrator capable of mixotrophy and is flexible in its strategies for acquiring nutrients. It may be associated with moderate, indirect nutrient loading, although evidence for association with nutrient loading is not conclusive. For the assemblages in California, nutrient affinity responses suggest that *Cochlodinium* is both adapted to low-nutrient environments (high affinity) and capable of responding to eutrophication (moderately high K_s for both ammonium and urea; linear kinetics for ammonium uptake). There is little evidence for photoinhibition, which in combination with the strong phototactic response and persistence in near-surface waters at midday, suggests that *Cochlodinium* is capable of utilizing (and potentially prefers) high ambient light levels, as would be found in the near surface.

Smayda and Reynolds (2001) suggest that phytoplankton life history and habitat preferences can be categorized into one of three groups: small, fast-growing high surface to volume colonizers (C), acquisitive, large, slow-growing, nutrient stress tolerant species (S), and ruderal (e.g., positive response to anthropogenic loading), light-harvesting, disturbance-tolerant (R) species, which together make up a three-dimensional ecological successional pattern referred to as Reynold's Intaglio. Smayda has further categorized the dinoflagellates

into nine subcategories within the C–S–R successional framework (e.g., Smayda, 2002a,b; Smayda and Reynolds, 2001) with *Cochlodinium* and related species falling into categories IV–VI, or frontal zone, upwelling-relaxation, and coastal current entrained taxa. We suggest that *Cochlodinium* has ecophysiological characteristics of all three categories, consistent with Smayda's observation that the ecophysiological adaptations of any individual species within these categories are overlapping. Based primarily on field observations from a variety of geographical locations, *Cochlodinium* bloom events can be associated with a consistent set of environmental parameters, including intrusion of nutrient-depleted offshore waters. Compared to organisms such as *A. sanguinea*, with which it is frequently co-occurs, at least in California, *Cochlodinium* is substantially smaller, but has the potential to change its effective surface:volume ratio by changing cell length (Park et al., 2001). It is relatively slow growing (ca. 0.3–0.4 d^{-1} maximal growth; Jeong et al., 2004; Kim et al., 2004) and can augment its nutrient requirements through either osmotrophy (urea assimilation) or heterotrophy (Jeong et al., 2004). It is also high-light tolerant, with the capacity to utilize elevated nutrient concentrations. Evidence is mixed for the role of inorganic nutrient supply, with some authors proposing a more or less direct connection with runoff and eutrophication, while many other studies show no direct link to nutrients. *Cochlodinium* may exhibit multiple, possibly sequential, nutrient acquisition strategies. Its ecophysiology is consistent with both a pelagic and neritic life history, and it may form both pelagic seed banks and shallow seed beds; there is also good evidence for ballast water transport of this organism (Whyte et al., 2001; Bhat and Matondkar, 2004; Smayda, 2004; Terenko, 2005).

5.2. Recommendations for further research

To better understand (and ultimately predict or control) the occurrence of *Cochlodinium* red tide events, we suggest that the following ecophysiological characteristics of *Cochlodinium* should be elucidated: (1) evaluation of the growth response and uptake kinetics for both organic and inorganic nutrients, emphasizing phosphorus; (2) identification of trophic strategies for *Cochlodinium* blooms in the field (i.e., mixotrophy versus phototrophy) in relation to nutrient concentrations; (3) identification of the relative importance of either benthic cysts or pelagic vegetative seed banks in annual bloom formation. *Cochlodinium* appears to be undergoing a global expansion. Based on its ecophysiological characteristics, we suggest that this is consistent with Smayda's conclusions that ''there is seemingly a very high degree of habitat specialization accompanied by multiple adaptive strategies'' (Smayda, 2002a), which provide dinoflagellates generally, and *Cochlodinium* specifically, the ability to occupy new ecological niches, allowing formerly rare HAB organisms to proliferate in response to changes in our coastal environment. *Cochlodinium* is well poised to take advantage of widely varying range of ecological conditions, and the global expansion of this red tide organism is probably due to both changing environmental conditions conducive to bloom development and introduction to new regions via transport.

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