

A sulfur hexafluoride-based Lagrangian study on initiation and accumulation of the red tide *Cochlodinium polykrikoides* in southern coastal waters of Korea

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Abstract

We report continuous in situ measurements of a population of the harmful algal bloom species *Cochlodinium polykrikoides* in a fixed volume of inshore waters near the island of Naro-do (34.47°N and 127.55°W), off the southern coast of Korea and where the earliest bloom of *C. polykrikoides* occurs regularly. This Lagrangian experiment was carried out by injecting the inert chemical tracer sulfur hexafluoride (SF₆) into a patch of seawater carrying *C. polykrikoides* and tracking the SF₆-labeled water mass for 4 d. Our results suggest that in situ growth of *C. polykrikoides* within the SF₆-labeled water accounts for only a fraction of the total cell increase. A probable mechanism we invoke here is that bloom initiation and much of the cell accumulation in inshore waters near Naro-do are due to the input of *C. polykrikoides* cells via lateral mixing of inshore waters with the alongshore current containing high *C. polykrikoides* cell density.

During the last two decades, massive accumulations of autotrophic algae and some heterotrophic protists, collectively referred to as harmful algal blooms (HABs), have increased considerably in frequency, size, and cell density across the globe (Anderson 1989; Pelley 1998; Sellner et al. 2003). Several lines of evidence suggest that this trend is due to increasing coastal eutrophication; however, strong evidence for this relation is not yet available, largely because of the ephemeral and complex nature of HABs (Smayda

1990; Kudela et al. 2002; Parsons et al. 2002). There is also considerable evidence indicating that natural processes are equally important for HAB formation, including rain-induced river discharge (Smith et al. 1990; Trainer et al. 1998), wind-induced coastal upwelling (Scholin et al. 1997; Adams et al. 2000; Trainer et al. 2000), basin-scale circulation (Anderson 1997; Tester and Steidinger 1997; Trainer et al. 2002), physically controlled layer formation and its maintenance (Rines et al. 2002), and various types of frontal formation (Franks 1992, 1997).

Nontoxic *Cochlodinium polykrikoides* is one of many algae species that cause red tides in Korean marine waters (Kim et al. 1993). *C. polykrikoides* blooms generally occur in warmer and saltier waters in the south of the Korean peninsula that are not directly affected by nutrient loading from rivers (Kim et al. 1999). Blooms of *C. polykrikoides* have increased in size, frequency, and cell density throughout the southern coastal waters of Korea since their first reported appearance in 1982 (Kim et al. 2001a). The duration of *C. polykrikoides* blooms has lengthened considerably from less than a week before 1990 to longer than a month in recent years (Fig. 1). However, the reason for the longer duration of the recent blooms has not been identified. *C. polykrikoides* blooms have inflicted massive fish kills every year since 1990, with total annual losses to Korean fish farmers from

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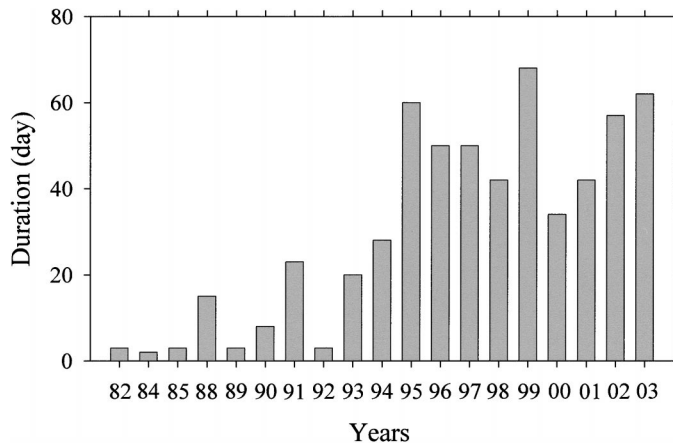


Fig. 1. Duration of *C. polykrikoides* blooms along the southern coast of Korea between 1982 and 2003. Data were collected from the routine observations made by the National Fisheries Research Development Institute.

as low as US \$2–3 million to as high as US \$60 million per year (Kim 1998). There is growing interest in *C. polykrikoides* blooms in Korean waters because of these losses to the aquaculture industry and because of the increasing cost required to control these blooms.

The recurring outbreaks of *C. polykrikoides* blooms have received high-level attention from the Korean government and have generated much public interest. In response to this growing concern, the National Fisheries Research and Development Institute (NFRDI) of Korea has conducted comprehensive surveys of physical, chemical, and biological parameters in bloom-infected inshore waters south of the Korean peninsula between 1997 and 2001 with the aim of forecasting bloom events. In the present study, NFRDI-led survey data were used to determine the patterns of *C. polykrikoides* blooms along the southern coast of Korea. More importantly, we performed continuous in situ measurements of a *C. polykrikoides* population in a fixed volume of the southern coastal waters of Korea (near Naro-do, 34.47°N and 127.55°W) where the earliest blooms of *C. polykrikoides* occur. Results obtained from this Lagrangian experiment were used to identify factors that may affect the initiation and accumulation of *C. polykrikoides* cells in waters near Naro-do.

Methods

NFRDI-led time-series observations between 1997 and 2001—Between 1997 and 2001, routine field surveys were conducted in five habitats (labeled A to E; Fig. 2) nearly every day between mid-July and late August, when *C. polykrikoides* persists in the southern coastal waters of Korea. Discrete water samples taken from the five habitats were analyzed in the field by microscope to identify dominant phytoplankton species and to determine concentrations of *C. polykrikoides*. Additional parameters were measured only in inshore waters near Naro-do (site B) where the earliest bloom has occurred. The temperature and salinity were measured in situ from the surface to the bottom of the water

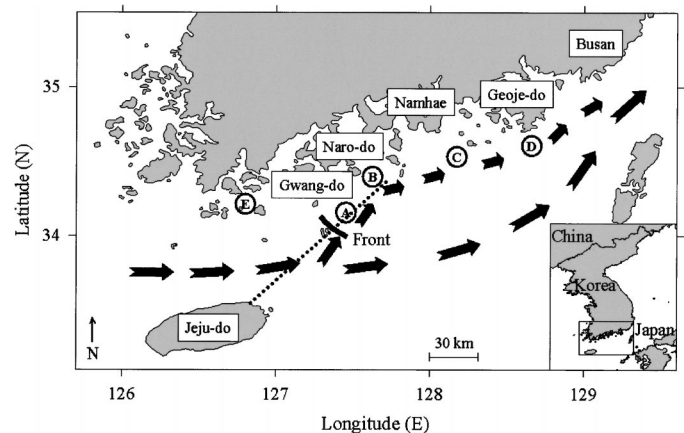


Fig. 2. The five coastal habitats tested labeled A through E. Arrows represent the flow directions of the Tsushima warm current. The solid line immediately on the offshore side of site A represents a potential site for the upwelled front. The dashed line shows the cross-frontal transect of observations.

column near site B using a SeaBird model SBE 19 conductivity–temperature–density (CTD) profiler. Discrete water samples for *C. polykrikoides* analysis were collected at targeted depths using a 10-liter Van-Dorn-type bottle. Aliquots of these same water samples were also collected and frozen at -20°C for shore-based analysis of nutrients using an autoanalyzer.

A SF₆-based Lagrangian experiment in the bloom-infected water—Inshore waters near the island of Naro-do were selected as a study site for the present SF₆-based Lagrangian experiment. A total of 2.7 mol of SF₆ was released at a depth of 5 m over a 2 km × 1 km area by bubbling it into the water column through a 0.5-mm porous tube (1 m in length and 2 cm in diameter). The injection was performed using even track spacing (~100 m apart between tracks) immediately aft of the ship's propellers as the ship moved over a 2-km² rectangular deployment grid. The SF₆-labeled seawater already contained *C. polykrikoides* prior to the SF₆ infusion. A global positioning system (GPS) buoy was simultaneously deployed to follow the movement of the SF₆ patch. Patch surveys were performed only during the day (~10 h per day) because the research vessel used was not equipped for overnight operation.

An automated SF₆ detection system tracked the evolution of the SF₆ patch over a 4-d period. This system included a gas chromatograph with an electron-capture detector, a SF₆-extraction device, a GPS, and data acquisition via Visual Basic software. The extraction device was made up of an assemblage of parallel microporous hollow polypropylene fibers bound into an array set around a distribution tube. This device is efficient at extracting SF₆ because it transfers SF₆ from the liquid to the gas phase without dispersion. Seawater is continuously pumped from the ship's seawater intake to the outside surface of the aggregated hollow fibers at approximately 4 to 5 liters min⁻¹, whereas pure N₂ gas (>99%) simultaneously flows in the opposite direction to the seawater stream through the inside of the fibers. The simultaneous but opposite flows of seawater and the carrier N₂ gas

cause, in their enforced proximity, a change in the partial pressure equilibrium between the liquid and gas phase, creating a driving force to transfer the SF₆ from the seawater into the gas phase. This is similar to the system described by Ho et al. (2002). The current system allows rapid and accurate analysis of multiple samples (1.5 min per sample), a lower detection limit (~10 femtomol L⁻¹), and computer-based automatic data collection and display. This analysis system requires minimal daily maintenance and provides reliable data on the concentration of SF₆ injected into a marine surface mixed layer.

The SF₆ patch was mapped so that water samples would have temporal coherence. Much of the experiment was spent locating the patch center for the CTD water sampling. Each daily survey started with the location of the GPS buoy, which was usually found near the SF₆ patch. Once the patch was located, the concentrations of SF₆ were continuously measured and the corresponding sampling locations were obtained with the GPS. The results were then plotted on the screen in near real time, and an evolving map of the tracer patch was developed and used to direct the ship's navigation as sampling continued.

To obtain a daily mean profile of cell density within the tracer patch, three hydrographic stations were sampled between 1000 h and 1600 h each day. One of three stations was sampled at the center of the patch where the daily maximum SF₆ concentration was found. For each station, discrete water samples were collected at three depths for the determination of *C. polykrikoides* cell concentrations. Aliquots of these same samples were also collected for onboard analysis of nitrate, nitrite, and phosphate using an autoanalyzer.

Results and discussion

Hydrographic features—The physical characteristics of the southern coastal waters of Korea in spring and summer are largely determined by interactions of inshore waters with the nutrient-depleted Tsushima warm current (Jung et al. 1999) (Fig. 2). The Tsushima warm current flows through the Korean strait between the southern Korean peninsula and Jeju-do and first contacts inshore waters near the island of Naro-do (34.47°N, 127.55°W). This current then flows in a northeasterly direction and eventually enters the East Sea.

Because the offshore waters between Naro-do and Gwang-do are adjacent to a continental shelf break, as the Tsushima warm current approaches Naro-do via Gwang-do (~20 km south of Naro-do), the bottom depth becomes abruptly shallower from ~100 m near Jeju-do to 20–30 m near Naro-do and Gwang-do. Thus, bottom topography-induced upwelling likely occurs when the intensity of the Tsushima warm current is strong enough to cause turbulence at the shelf break. In particular, in summer of 1995, when the intensity of the Tsushima warm current was stronger than other years, an upwelled front was formed in the offshore waters immediately outside of Gwang-do; its existence is evident in the 1995 temperature and chlorophyll *a* (Chl *a*) concentration sections running from Naro-do to Jeju-do (Fig. 3). We are not sure whether the same upwelled front was

formed in offshore waters near Gwang-do in 2003 because we did not make the same measurements during our tracer study. However, the possible existence of this upwelled front is supported by the section of Chl *a* concentration representing the 3-yr mean. Specifically, Chl *a* maximum centered at a depth of 20 m occurred widely in the waters between Naro-do and Gwang-do. If this mean condition prevailed in this region from July to August in 2003, an upwelled front, albeit weaker than the front formed in 1995, would probably be formed.

In the present study, the northeasterly current on the shore side of the upwelled front is arbitrarily referred to as the “alongshore current.” It is also important to note that waters on the inshore and offshore side of the alongshore current are arbitrarily defined here as “inshore” and “offshore” waters, respectively. On the shore side of the front, the alongshore current flows in a northeasterly direction, contacts inshore waters near Naro-do, and then continues to flow in a northeasterly direction. This alongshore current has physical and chemical properties similar to those of the Tsushima warm current and runs parallel to the coast from site B to D. A more detailed description of the circulation pattern in the southern coastal waters of Korea is not possible because adequate measurements are not yet available and because circulation pattern significantly varies regionally and temporally.

For each of the past 5 yr from 1997 to 2001, the earliest bloom of *C. polykrikoides* occurred in the region around Naro-do. Therefore, field surveys were concentrated in the inshore waters near Naro-do and on the shore side of the Tsushima current. The temporal coverage of the surveys was from mid-July to late August, encompassing the period for bloom initiation and termination.

Distribution of C. polykrikoides cells along the south coast of Korea—From mid-July to late August each year between 1997 and 2001, nontoxic red tide *C. polykrikoides* cells were abundant and broadly dispersed in the waters between Naro-do (site B in Fig. 2) and Geoje-do (site D), which span the central part of the coastal waters south of the Korean peninsula. However, the distribution of *C. polykrikoides* was far from uniform across this large area. In fact, we found three habitats (B–D in Fig. 2) where *C. polykrikoides* blooms occurred. Two additional habitats (A and E in Fig. 2) were identified in which *C. polykrikoides* cells appeared but did not reach bloom level. The three habitats (B–D) where blooms occur are to the east of Naro-do and are located on the shore side of the alongshore current. Habitat E is west of Naro-do, where the influence of the alongshore current is minimal.

C. polykrikoides cells first appeared in Gwang-do (34.27°N, 127.53°W; site A in Fig. 2), which is approximately 20 km south of Naro-do (near site B in Fig. 2). However, the earliest bloom occurs at site B approximately 1 week after the initial appearance of *C. polykrikoides* cells in offshore waters near Gwang-do (site A), and this is followed by outbreaks approximately 2 weeks later at site C and 3 weeks later at site D (Fig. 4). In contrast, cell densities measured at site E remained low during each bloom season (Fig. 4).

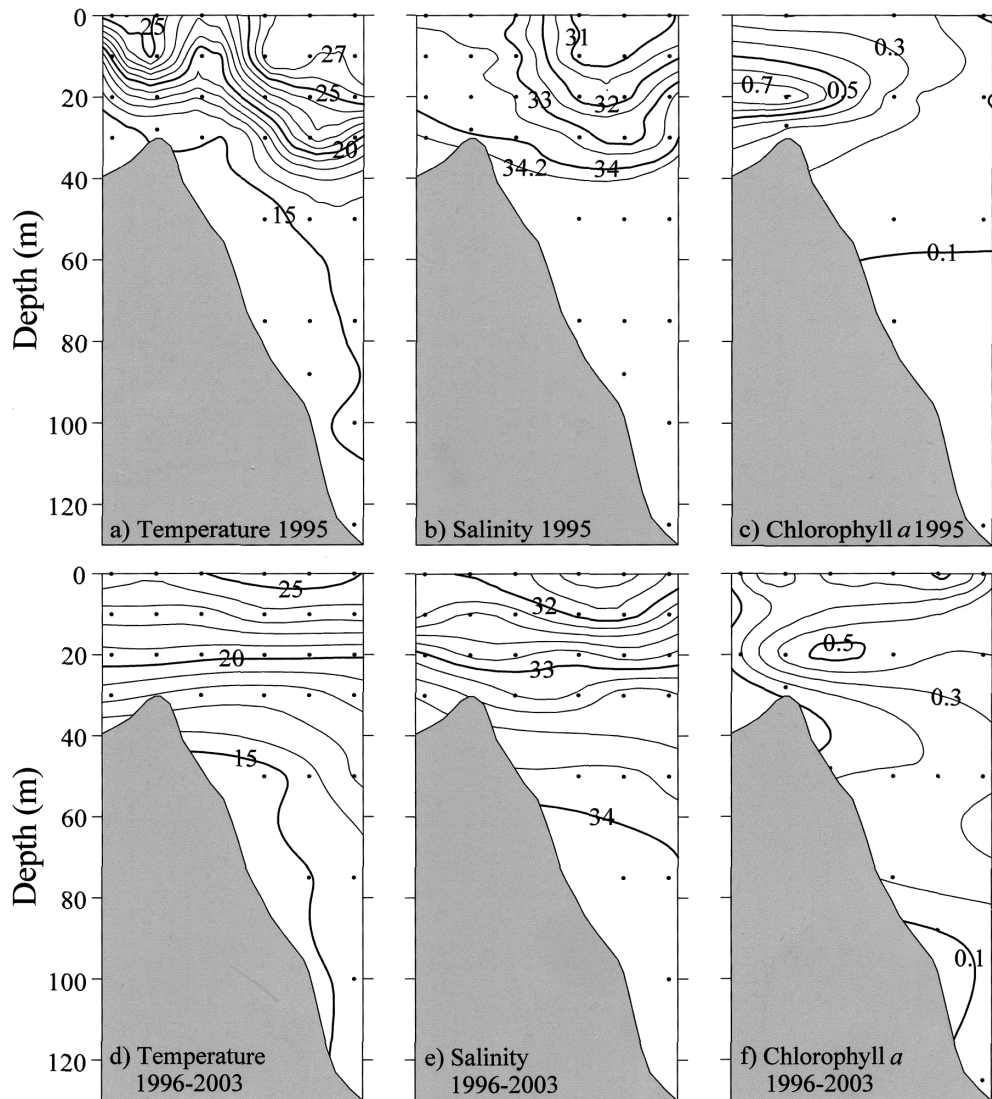


Fig. 3. Sections of temperature, salinity, and chlorophyll *a* concentration from Naro-do to Jeju-do (a, b, c) in August 1995, (d, e) in August 1996–2003, and (f) in August 1996–1998. Points on the plot indicate locations of data.

The rapid increase in cell density along the pathway of the alongshore current suggests that, along with in situ growth, established *C. polykrikoides* cells at site B are transported parallel to the coast by the alongshore current and then delivered to inshore waters at sites C and D via lateral mixing across the alongshore current borders. However, the relative contributions of physical and biological processes to the increase in cell density have not been quantified. The possible physical mechanism invoked here will be more thoroughly presented later in the paper. Site E did not appear to be clearly linked to the other sites within the pathway of the alongshore current because there is little hydrographic linkage between site E and the other sites during the bloom seasons. The southwestward transport of *C. polykrikoides* cells is restricted, mostly because of the presence of coastal waters that were typically 1 to 3°C cooler than the alongshore current. Cooler coastal waters on the west side of site

B were not favorable for the growth of vegetative *C. polykrikoides* cells.

The persistent northeasterly flow of the alongshore current during the bloom season still raises an important question: If *C. polykrikoides* cells are transported to the northeast each year with no return flow, how does the bloom at site B restart each subsequent year? Without the replenishment of cells to site B, the occurrence of the red tide within the pathway of the alongshore current to the northeast would gradually weaken and eventually disappear. As described in the preceding paragraph, the shoreward movement of the warm current containing vegetative *C. polykrikoides* cells flows in a northeasterly direction, first supplying vegetative cells to site B early in the bloom season each year and subsequently to the other sites within the pathway of the alongshore current to the northeast (Fig. 2).

Our analysis of the 5-yr time-series data suggests that the

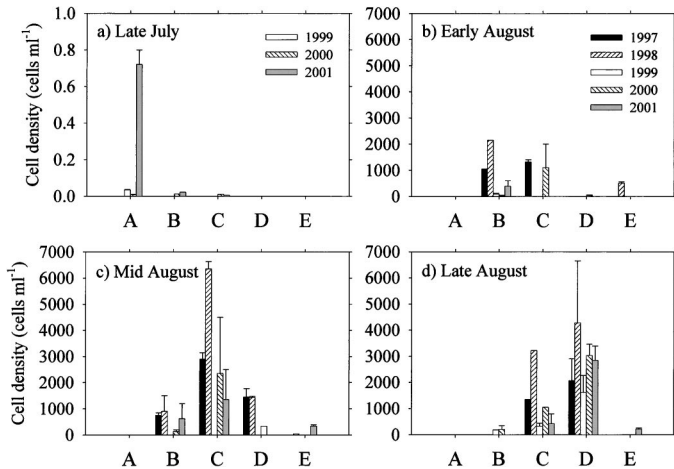


Fig. 4. Cell density of *C. polykrikoides* in five coastal habitats from 1997 to 2001. Data were obtained from NFRDI-led routine field surveys that were conducted nearly every day between mid-July and late August. Error bars represent the standard deviations from the 5-yr mean values. The scale showing cell density in (a) is three orders of magnitude smaller than those in (b, c, d).

alongshore current plays an important role in transporting *C. polykrikoides* along the south coast of Korea and, thus, the timing of *C. polykrikoides* blooms in each habitat. However, because a firm link between the Tsushima warm current and *C. polykrikoides* blooms has not been established, our hypothesis with respect to the patterns of *C. polykrikoides* blooms in the study area needs further validation and more research must be conducted to elucidate how the distribution of blooms is controlled.

A SF₆-based Lagrangian experiment on bloom initiation and accumulation—The patch of SF₆-labeled surface water mass near site B was sampled for 4 d in August 2003. Daily mapping of the patch indicates that it moved less than 8 km from the injection point over the observation period (Fig. 5a). This shows that the waters near site B were coherent.

For each day, three profiles of cell density were averaged and a resulting daily mean profile was then vertically integrated. The vertically integrated cell density of *C. polykrikoides* increased from less than 5 cells ml⁻¹ on day one (SF₆ release) to 172 cells ml⁻¹ on day four (Fig. 6), which is an order of magnitude greater than the value predicted from population growth using the following equation:

$$N_1 = N_0 \times \exp [k_G (t_1 - t_0)/1.443] \quad (1)$$

where k_G is the optimal growth rate of *C. polykrikoides* determined in the laboratory (0.43 divisions per day), and N_1 and N_0 are cell densities at time t_1 and t_0 , respectively (Stein 1973; Kim et al. 2001b). Based on this formula, approximately 12 d would be required to reach a cell density of 172 cells ml⁻¹. If it is assumed that each cell contains an average of 1.75 pmol of phosphorus (Kim et al. 2001b) and that the phosphorus decrease is exclusively due to in situ growth of *C. polykrikoides*, a surface-to-bottom mean decrease in phosphate concentration of $\sim 0.06 \mu\text{mol kg}^{-1}$ within the patch between days three and four corresponds to a population increase of $\sim 40 \text{ cells ml}^{-1}$ on day four (Fig. 7). This esti-

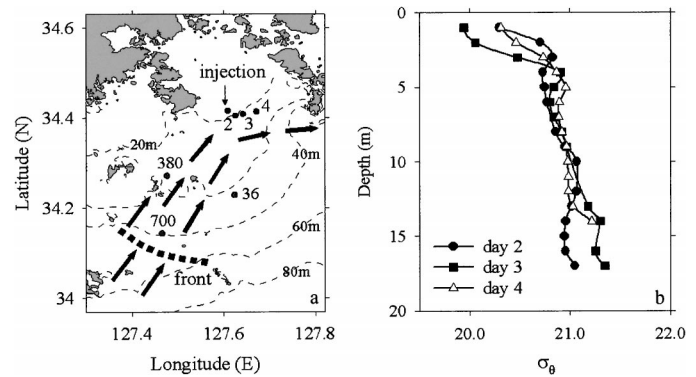


Fig. 5. (a) The temporal evolution of location of the SF₆-labeled water mass containing *C. polykrikoides*. Offshore waters between Naro-do and Gwang-do were sampled during our tracer experiment and are labeled with *C. polykrikoides* cell population 36, 380, 700 cells ml⁻¹. (b) The evolution of density profile (σ_θ) within the patch over a period of 3 d.

mated increase in the population of *C. polykrikoides* is probably too high because there were also other dinoflagellates present in the SF₆-labeled water mass that can consume phosphorus. Therefore, although the concentrations of phosphate and nitrate decreased, the reduction in nutrients was not large enough to account for this increase in cell concentration. Furthermore, the cell concentrations 1 and 2 weeks prior to the SF₆ release at site B near the injection point were largely homogeneous throughout the study site. This SF₆-based experiment suggests that, during this tracer experiment, a significant part of the total *C. polykrikoides* population could be supplied by the input of cells via lateral mixing between the SF₆-labeled inshore water and the alongshore current containing more than 300 cells ml⁻¹. Therefore, only a fraction of the total population was accounted for by in situ growth.

Validity of the SF₆-based Lagrangian study—A key assumption in our SF₆-based study is that, during this tracer experiment, the SF₆-labeled mixed layer water did not sep-

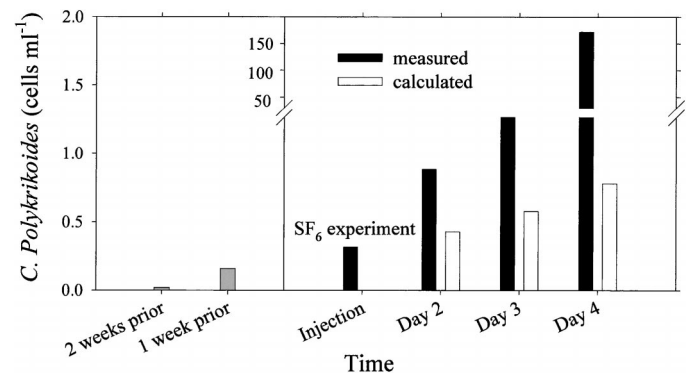


Fig. 6. Comparison of measured *C. polykrikoides* cell density inside the SF₆-labeled patch of seawater with those calculated assuming an optimal growth rate. The cell concentrations 1 and 2 weeks prior to the SF₆ release at the injection point at site B are also shown as baseline values. Note the scale break in the cell number for the right-hand portion of the figure.

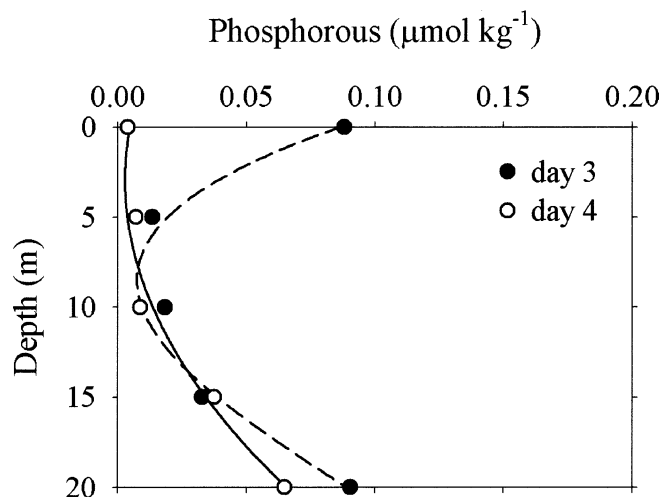


Fig. 7. Profiles of phosphorous concentration ($\mu\text{mol kg}^{-1}$) for days three and four.

arate from subsurface-to-bottom (~ 20 m depth) waters lying immediately below it. The validity of this assumption is essential in the mass balance calculation of cell numbers and nutrients because *C. polykrikoides* undergo vertical diel migration. Separation of the SF_6 -labeled surface patch from the subsurface waters can occur when current shear exists. Such vertical current shear could be generated by surface wind or vertical density gradients in the water column. During the present tracer experiment, vertical current velocity was not directly measured. Therefore, it is not clear whether there was a vertical gradient in the current velocity at the study site large enough to cause a separation of the surface SF_6 patch from the underlying subsurface water. However, given an average wind speed over the 4-d period of 3.6 m s^{-1} , separation of the surface SF_6 patch from the underlying water probably did not occur.

An independent SF_6 -based Lagrangian experiment in the North Sea by Burkill et al. (2002) also supports the idea that a separation between the surface mixed layer and the underlying subsurface water is unlikely. Burkill et al. deployed two buoys drogued at depths of 10 and 65 m within the SF_6 -labeled water to trace the movement of the SF_6 -labeled water. Good coherence was observed between the surface SF_6 patch and buoys drogued at different depths when there were low winds (2 to 7 m s^{-1}) at the study site (Burkill et al. 2002). However, the two buoys drifted away from the SF_6 patch when the wind speed reached 16 m s^{-1} .

Additional evidence that the surface SF_6 patch was not separated from the underlying subsurface water comes from measurements of the evolution of the density profile within the SF_6 patch. Specifically, our results suggest that the vertical density structure remained approximately the same during the tracer experiment, and there was no clear sign of an intrusion from either offshore or inshore water masses (Fig. 5b).

Taken together, these findings suggest that current shear over the vertical distance of migrating *C. polykrikoides* cells is small and, thus, unlikely to result in the separation of the SF_6 patch from the subsurface water during the present tracer

experiment. These findings further suggest that the mass balance calculation of cell numbers and nutrients within the patch center is valid.

SF₆ mass balance for the surface mixed layer at the patch center—The evolution of SF_6 concentrations at the center of the patch provides important data for identifying mechanisms that may control bloom initiation and accumulation at site B. During the 4-d tracer experiment, mixed layer SF_6 concentrations at the patch center decreased by gas exchange with the atmosphere ($L_{\text{air-sea}}$), horizontal diffusion (L_{diff}), and deepening of the mixed layer (L_{entrain}):

$$d[\text{SF}_6]_{\text{ml}}/dt = L_{\text{air-sea}} + L_{\text{diff}} + L_{\text{entrain}} \quad (2)$$

The deepening of the mixed layer induces mixing with the underlying subsurface waters, leading to the decrease in the mixed layer SF_6 concentration. However, an approximately constant mixed layer depth over the 4-d experiment suggests that the subsurface water was not introduced into the mixed layer and, thus, did not discernibly contribute to the decrease of the mixed layer SF_6 concentration ($L_{\text{entrain}} \sim 0$). Thus, the temporal evolution of the SF_6 concentration in the surface mixed layer was largely determined by air-sea gas exchange and horizontal diffusion.

Horizontal diffusion-induced changes in the mixed layer SF_6 concentration, L_{diff} , have important implications for the transfer of phytoplankton cells and nutrients between the patch and the surrounding water at the outside edge of the patch. L_{diff} was estimated from measured decreases in the mixed layer SF_6 concentrations at the patch center ($d[\text{SF}_6]_{\text{ml}}/dt$) corrected for air-sea SF_6 flux. The loss of SF_6 to the atmosphere was calculated from the measured differences in SF_6 concentrations between seawater ($\text{SF}_{6\text{sw}}$) and air ($\text{SF}_{6\text{air}}$) and an empirical gas exchange relationship (k): $L_{\text{air-sea}} = k(\text{SF}_{6\text{sw}} - \text{SF}_{6\text{air}})$. Because seawater SF_6 concentrations are several orders of magnitude greater than those in air, $\text{SF}_{6\text{sw}} - \text{SF}_{6\text{air}}$ can be estimated to be nearly equal to $\text{SF}_{6\text{sw}}$. The relationship proposed by Wanninkhof (1992) uses a quadratic fit of the bomb ^{14}C inventory: $k = 0.39WS_{10}^2(Sc/660)^{-1/2}$, where Sc is the Schmidt number for SF_6 and WS_{10} is the wind speed in m s^{-1} at a height of 10 m. The resulting gas transfer rate is 4.5 cm h^{-1} at an average wind of 3.6 m s^{-1} . This empirical relationship yielded that the loss of SF_6 to the atmosphere accounted for 57% of the daily decrease in SF_6 concentration at the patch center over a 4-d period (Fig. 8). The remaining 43% decrease occurred over the same period due to lateral diffusion. The lateral diffusion-induced decrease of 43% in SF_6 concentrations suggests that a corresponding fraction of the SF_6 -labeled water mass was exchanged with adjacent inshore and alongshore current waters.

Our SF_6 -based Lagrangian study provides three lines of evidence suggesting that cell accumulation in inshore waters at site B was largely via delivery of cells from the alongshore current. First, the loss of SF_6 , injected as a conservative tracer and corrected for outgassing, suggests a substantial amount of dilution by lateral mixing. Second, the alongshore current flows with a velocity of $\sim 22 \text{ cm s}^{-1}$, whereas water mass at site B flows with a velocity of $\sim 3 \text{ cm s}^{-1}$. This slower water mass movement at site B was

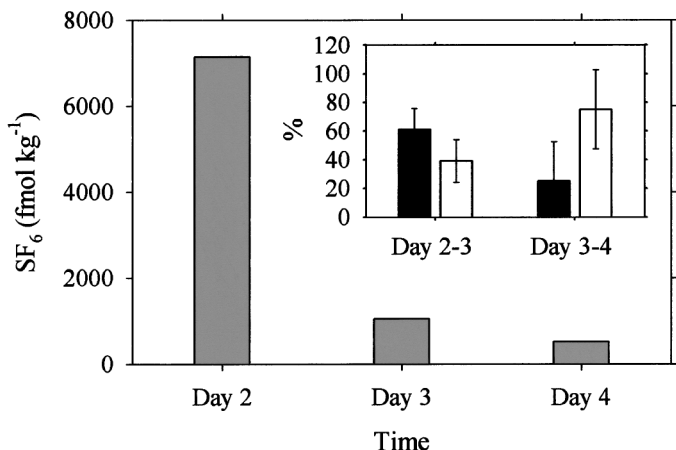


Fig. 8. Measured maximum SF₆ concentrations. The inset shows the percentage loss of SF₆ at the patch center due to lateral diffusion (filled bars) and gas exchange (open bars).

confirmed by tracing a SF₆-labeled patch over a 4-d period. Such horizontal current shear may lead to a situation where a significant fraction of the SF₆-labeled water mixes with the adjacent alongshore current. Third, cell concentrations of *C. polykrikoides* in the alongshore current are of an order (~300 cells ml⁻¹) that could explain the observed change. Taken together, three findings suggest that a significant fraction of the total increase in cell density within the patch could be attributed to the input of cells from alongshore waters. It is also interesting to note that the increase in cell concentration between days three and four is particularly sharp relative to the increases from days one to three. This sharp increase further suggests that lateral mixing may be an episodic event or cell concentrations in the incoming alongshore current likely vary on a daily time scale.

The accuracy of our conclusion is subject to error due to several uncertainties. First, there was considerable geographic variation in the cell concentration of *C. polykrikoides*. Therefore, the measured cell concentrations inside the patch and in the alongshore current are subject to substantial inaccuracy. A second source of error is uncertainty in the fraction of water exchanged with the alongshore current versus the fraction exchanged with adjacent inshore water. A third source of error is inaccuracies in the daily maximum SF₆ concentrations. In our analysis, the patch center was defined as the location of the daily maximum SF₆ concentration. This assumes that the patch center was found during each daily survey. Although this is a reasonable assumption, it is not precise. The fourth major source of error is uncertainty in the accuracy of the gas exchange coefficient k . Wanninkhof (1992) estimated a $\pm 25\%$ uncertainty of k , which was derived from the approximate error estimate of ¹⁴C invasion rates. The use of $\pm 25\%$ uncertainty in k yielded a 25–76% range in the fraction of the SF₆-labeled water mass exchanged with adjacent inshore and alongshore current waters between days 3 and 4. Of the four major sources of error, only the fourth one is quantifiable. The error in the lateral diffusion-induced dilution of SF₆-labeled water between days 3 and 4 was estimated as 25% assuming that it is dominated by the error in k . However, the true magnitude of error

is significantly greater than this value because the errors in the measured cell concentrations and daily maximum SF₆ concentrations are likely even greater than the error in k .

Proposed mechanisms for bloom initiation and accumulation at site B—It is not possible to propose robust mechanisms leading to observed cell accumulation at site B because current patterns and water mass structures in inshore and offshore waters near site B were not simultaneously measured during the tracer experiment. However, the limited physical data collected from other independent surveys performed in the past provide circumstantial evidence for cell accumulation at site B. Offshore waters near Gwang-do (~20 km south of site B) are adjacent to a continental shelf break that intersects with the permanent seasonal thermocline (Fig. 2). Consequently, bottom topography-induced upwelling could occur intermittently in waters near Gwang-do in August. Such an upwelling-induced front was clearly observed in the 1995 survey but was less clear in the surveys of other years (Fig. 3). Regardless of the year of observations, Chl *a* concentration in waters near Gwang-do was generally elevated relative to measurements at similar depth in adjacent regions and was distributed as a horizontal band crossing this upwelling-induced divergent front. This pattern is consistent to that predicted by a two-dimensional model of steady cross-frontal circulations developed by Franks (1992), which predicts that phytoplankton cells at a divergent front are largely concentrated in horizontal layers with cells scattered away from the center of the front. Such a distribution pattern contrasts with that observed at a convergent front in that cells traverse isopycnal surfaces.

During our tracer experiment, waters near Gwang-do contained *C. polykrikoides* cell concentrations of ~300 cells ml⁻¹, which was probably accumulated by the physical mechanism described by Franks (1992). The alongshore current on the shore side of the front then carried *C. polykrikoides* cells in a northeasterly direction, first supplying cells to waters near site B. At this point, the SF₆-labeled patch of water slowly mixed by lateral diffusion with the alongshore current, which contained *C. polykrikoides* at a concentration of over 300 cells ml⁻¹. Although the *C. polykrikoides* cell concentration is patchy, it is generally higher in waters between Naro-do and Gwang-do than in inshore waters near Naro-do. Site B is also physically favorable for the accumulation of cells. As described in the preceding section, there was a large contrast in velocity between the alongshore current and inshore water mass movement at site B. As suggested by Franks (1992), this shoreward decrease in current velocity could result in an accumulation of cells at site B without invoking a biological factor. However, concurrent measurements of spatially resolved maps of SF₆ concentration and hydrographic features in inshore and offshore waters near site B are needed to prove this more conclusively.

The initiation and accumulation of *C. polykrikoides* at site B could potentially be driven by mechanisms other than the supply of vegetative cells from offshore waters. One possibility is the germination of cysts from local sediment beds near Naro-do. Cysts are generally produced and sink to the bottom during the senescent periods of less optimal growth conditions. After a dormancy period, the cysts release veg-

etative cells that can swim to the surface (Aguilera et al. 1995; Adams et al. 2000; Sellner et al. 2003). This resting stage, therefore, could provide HAB species with a competitive advantage over other plankton species that cannot persist under poor conditions. However, limited surveys of sediments near Naro-do and within the pathway of the alongshore current between 1999 and 2002 by C.-K. Lee and H.-G. Kim of NFRDI found no evidence of cysts, and the presence of cysts in sediments at these sites has not been reported to date. A more comprehensive survey is needed to check the validity of cyst germination as a possible mechanism for bloom initiation and accumulation at site B.

Blooms of *C. polykrikoides* species are neritic phenomena that are not directly influenced by anthropogenic nutrient loading. Our SF₆-based Lagrangian experiment suggests that a shoreward expansion of the Tsushima warm current through the alongshore current contributes to the initiation and accumulation of *C. polykrikoides* cells at site B, where the earliest bloom has occurred for each of the past 5 yr. Much of the cell increase in the SF₆-labeled patch of water at site B could be caused by delivery of cells via lateral mixing between the SF₆-labeled inshore water and the alongshore current containing high *C. polykrikoides* cell concentration. Conclusions drawn from our study can be strengthened if spatially resolved SF₆ distributions and concurrent measurements of hydrographic features are available. Therefore, in the future, the use of the tracer SF₆ in studying the dynamics of HABs should be coupled with concurrent measurements of physical, biological, and chemical parameters in bloom-infected and surrounding waters. Such collective measurements will offer a great potential for quantifying the relative contributions of the biological and physical mechanisms to the cycle of *C. polykrikoides* blooms.

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