Selective retention of two dinoflagellates in a well-mixed estuarine embayment: the importance of diel vertical migration and surface avoidance*

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ABSTRACT: Diel vertical migration patterns of the dinoflagellates *Gonyaulax tamarensis* and *Heterocapsa triquetra* were monitored in an estuarine embayment subject to localized blooms of both species. A concurrent study of tidal flushing using a dye tracer demonstrated an efficient, density-driven mixing process that exchanged water within the embayment at a rate of approximately $0.5 \, d^{-1}$. Loss rates of the whole pond populations of *G. tamarensis* and *H. triquetra* cells were smaller, ranging between 0.02 and $0.13 \, d^{-1}$. The cells were thus able to maintain a non-mixed distribution even under weakly stratified conditions. This selective retention of the 2 species relative to water exchange was due to the differential advection of surface and bottom waters through the inlet channel and the general avoidance of high irradiance surface layers by the dinoflagellates. Both species migrated to irradiances equivalent to 30% of summer sunlight when nutrients were presumably non-limiting, resulting in subsurface aggregations 1 to 2 m deep. Under nutrient-limited conditions, *G. tamarensis* migration was restricted to irradiance at or below 10 to 15% summer sunlight. Planozygotes (a life-cycle stage preceding cyst formation) migrated in a manner indistinguishable from the remainder of the nutrient-limited *G. tamarensis* population. The results help to explain the dominance of dinoflagellates in such embayments, the localization of their blooms, and the distribution of their resting cysts in the region.

INTRODUCTION

Diel vertical migration of marine and freshwater dinoflagellates has been the subject of numerous field and laboratory investigations. Both phototaxis (Forward 1976) and geotaxis (Eppley et al. 1968, Cullen & Horrigan 1981) have been invoked to explain the directionality of swimming behavior, with a variety of physical and chemical factors regulating the extent of vertical movement. These include nutrients (Eppley et al. 1986, Cullen & Horrigan 1981, Heaney & Eppley 1981); light intensity (Harris et al. 1979, Heaney & Talling 1980); temperature or salinity gradients (Seliger et al. 1970, Kamykowski & Zentara 1977, Tyler & Seliger 1978, 1981); and oxygen availability (Heaney 1976, George & Heaney 1978). It is now clear that individual species can respond differently to these parameters (Eppley et al. 1968, Heaney & Eppley 1981) and that the response to one factor can be influenced by others. Heaney & Eppley (1981) provide an example of the complex migration patterns that can arise when dinoflagellates are exposed to simultaneous variations in nutrients, light, and temperature in the laboratory.

There are several important benefits or impacts associated with vertical migration. The most commonly cited advantage is that of access to nutrients located below the depleted surface layers in stratified waters (Holmes et al. 1967, Eppley et al. 1968, Eppley & Harrison 1975, MacIsaac 1978). Another impact is that the vertical accumulation of individual cells may determine the horizontal distribution of the population as a whole. If the cells aggregate at specific depths, possibly due to the suppression of phototaxis at sharp salinity gradients (Seliger et al. 1970, Tyler & Seliger 1981) or to the selection of an optimal light environment (George & Heaney 1978, Heaney & Talling 1980), differential movement of water layers due to wind stress or 2-layer estuarine flow can then selectively transport the populations horizontally (Seliger et al.

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1970, Heaney & Talling 1980, Tyler & Seliger 1981). In all cases, a well-stratified water column has been a prerequisite for the differential horizontal motion.

In this study we describe the role of vertical migration in limiting the horizontal transport and advective losses of 2 dinoflagellates in an estuarine embayment. *Heterocapsa triquetra* is an ecologically successful organism that often dominates the phytoplankton in estuarine and coastal waters; Braarud & Pappas (1951) document the phototactic behavior of this species in culture vessels but there are no quantitative field or laboratory studies to describe the swimming patterns in more detail. *Gonyaulax tamarensis* (= *Protogonyaulax tamarensis*; Taylor 1979), is the toxic dinoflagellate responsible for outbreaks of paralytic shellfish poisoning in many parts of the world; blooms of this species in the coastal zone are often manifest in subsurface accumulations along frontal boundaries separating tidally-mixed and stratified waters (Yentsch 1984). Swimming behavior is clearly important in the formation of these subsurface patches, yet nothing is known of this dinoflagellate's response to the vertical distribution of light and nutrients. *G. tamarensis* also thrives in estuarine environments (Anderson & Morel 1979, Schrey et al. 1984, Yentsch 1984) where the rate of tidal exchange can approximate the dinoflagellate's maximum growth rate (Garcon et al. unpubl.). Recurrent toxic blooms in these locations could only result from the selective retention of the cells relative to the ebbing seawater, but the mechanisms underlying the retention are unknown.

In this paper we describe the vertical migration behavior of these 2 species in Salt Pond, an embayment typical of many within the Cape Cod region that are often dominated by dinoflagellates (Hulburt 1956). In conjunction with a dye experiment to trace water mixing and circulation patterns, the results make it possible to assess the differential advective loss rates of water and cells during tidal exchange and the importance of vertical migration behavior in this process.

METHODS

Study area. Salt Pond (Eastham, Massachusetts) is a circular embayment 82,200 m^2 in area with average and maximum depths of approximately 3.4 and 7 m respectively at slack low tide (Fig. 1). There are no stream or river inputs of freshwater but groundwater does enter the pond via springs. A shallow inlet channel (0.5 km long, 30 m wide, 0.5 m deep at low tide) allows tidal exchange with a large salt marsh system that connects to the ocean at Nauset.

Vertical cell distributions. On May 30 and 31, 1980, June 4 and 5, 1981, and May 25 and 26, 1983, the
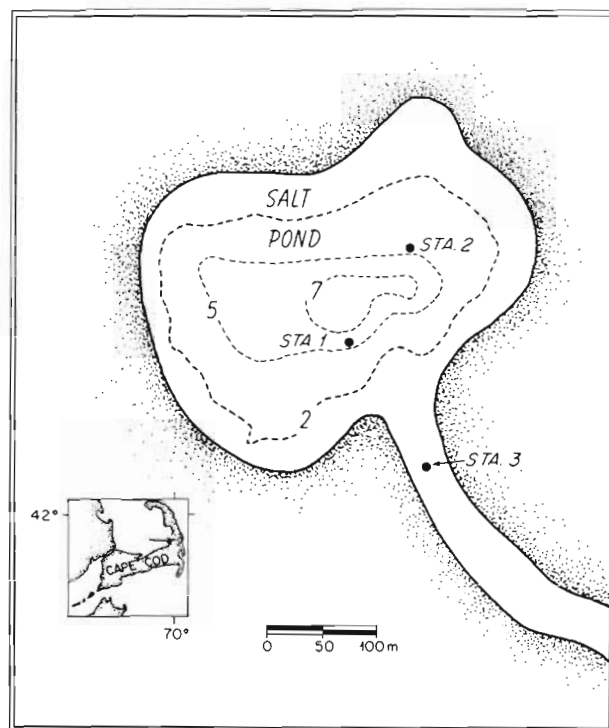

Fig. 1. Map of Salt Pond, Eastham, Massachusetts (USA) with sampling stations. Contours are in m at slack low tide

vertical distribution of *Gonyaulax tamarensis* cells was determined at Station 1 (Fig. 1) along with associated measurements of nutrients (1980, 1981 only), irradiance, salinity, and temperature. *Heterocapsa triquetra* distributions were recorded in 1981 and 1983 only. During 1980 and 1981, vertical sampling was accomplished using 50 ml plastic syringes mounted at 10 cm intervals on a frame (Heaney 1974). The weighted unit was lowered with all syringe plungers fully inserted but under tension from stretched sections of surgical tubing. The tension was released and the syringes filled simultaneously when the rope attached to the locking mechanism was pulled. The unit was taken from the water, the samples dispensed, the syringes reloaded, and the process repeated at lower depths. A maximum of 3 deployments were needed for each profile. Since the syringes were about 10 cm apart and separate syringes were used for cell counts, nutrients, and salinity, the data are reported at different vertical intervals. Profiles of irradiance (PAR, 400 to 700 nm) were made with a Li Cor flat plate (cosine) quantum sensor (LI-192S) at 0.5 m intervals in 1980, and with a Biospherical Instruments spherical (scalar) sensor (QSP-200) in 1981 and 1983. Temperature profiles were obtained with a YSI Model 33 S-C-T meter.

In 1983, the sampling procedure was changed to a pumping system that used lengths of Tygon tubing differing by 0.5 m that were tied together, weighted,

and suspended from a floating rubber tire tube. A DC pump (Fluid Metering, Inc., Model RP) powered with a 12 volt battery was connected to the end of each tube in succession and a sample collected after sufficient time for flushing and rinsing. Samples for cell counts, salinity and dye were collected in this way, and profiles of irradiance and temperature taken as described above. Cell count and irradiance data were collected at 3 h intervals and the other parameters hourly. Similar profiles of salinity, temperature, and dye concentration were collected hourly with the pumping system and temperature probe at a second station (Sta. 2: Fig. 1) to provide additional information on water circulation. A 20 % rhodamine WT dye solution was injected at a rate of 3 ml min^{-1} during the flood tide using a battery-operated peristaltic pump. The injection point was 250

m from the entrance to Salt Pond in the center of the inlet channel.

At hourly intervals, temperature, salinity, dye (1983 only) and *Gonyaulax tamarensis* and *Heterocapsa triquetra* cell concentrations were determined at the inlet (Sta. 3: Fig. 1). Samples were collected by pumping into a bucket while a weighted tube was slowly lowered to the bottom. Other samples for cell counts were collected at the beginning of each migration study at 20 stations spaced uniformly around Salt Pond. Surface-to-bottom integrated samples were collected at each station using the pumping system. Cell concentrations were totalled by taking the average depth of each sector into account, providing estimates of the total *G. tamarensis* and *H. triquetra* populations in the embayment at the start of each study. All cell count
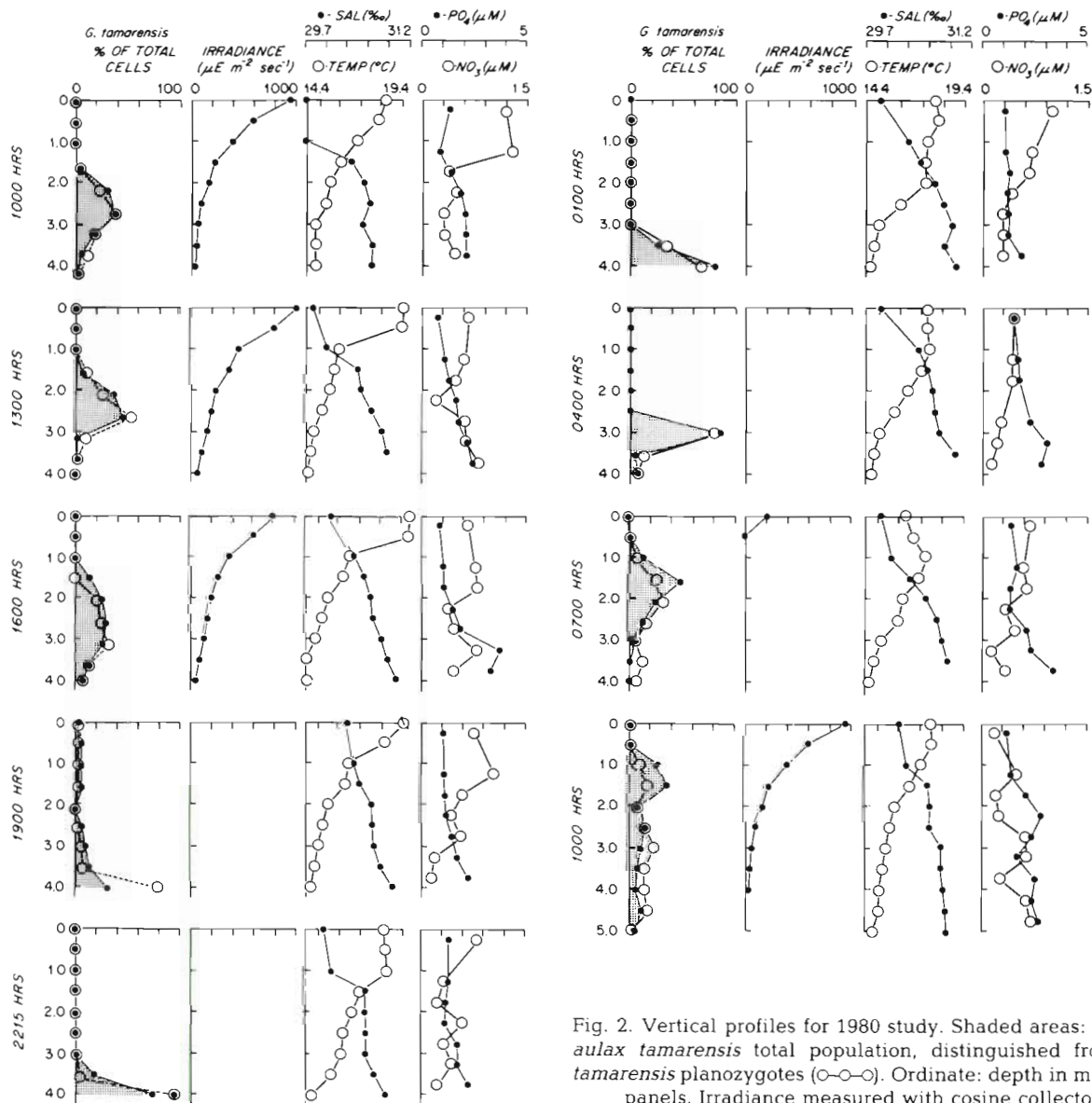

Fig. 2. Vertical profiles for 1980 study. Shaded areas: *Gonyaulax tamarensis* total population, distinguished from *G. tamarensis* planozygotes (o—o—o). Ordinate: depth in m for all panels. Irradiance measured with cosine collector

samples were fixed with Utermöhl's solution, settled in a 50 ml chamber, and enumerated with an inverted microscope. A minimum of 200 cells were counted for each sample. When present, *G. tamarensis* planozygotes were tabulated separately based on the criteria of Anderson et al. (1983). Nutrient samples were filtered as they were dispensed from the syringes through Whatman GFF glass fiber filters, frozen, and analysed at a later date using the methods of Strickland & Parsons (1972). Dye concentrations were measured with a Turner Designs Model 10 fluorometer with a rhodamine filter set. Unreferenced tidal elevations were determined using frequent observations of meter sticks placed in the inlet channel. Tidal volumes were calculated using the average elevation at 15 min intervals and the average pond surface area. These were then totalled over each tidal phase and expressed as a percent of low tide volume.

RESULTS

1980 study

Salt Pond was moderately stratified, with temperature and salinity differences between surface and bottom waters of 3 to 5 C° and 0.2 to 0.5‰ respectively and density varying by 2 σ_t units (Fig. 2). The surface was always warmer and less saline than the waters below. Tidal range was about 1 m, with ebb flow beginning several hours before midnight and noon. The pond filled rapidly on the flood tide (4 h), but took nearly 8 h to drain. Between 18 and 22 % of the low tide volume entered or left the pond with each tidal phase, equivalent to a maximum potential plug flow flushing rate of 0.40 d^{-1} (Table 1). The weather was sunny with scattered clouds and 5 to 10 knot southerly winds. Sunrise was at 0500 and sunset at 1930 h.

A distinct vertical migration pattern was observed for the *Gonyaulax tamarensis* population (Fig. 2). Approximately 30 % of the cells were planozygotes (large, deeply pigmented swimming cells that become cysts) but their migration behavior was the same as that of the population as a whole. During the migration: (a) cells avoided the top 1.5 m of water, even during midday hours; (b) maximum irradiance reached by the population peak was approximately 200 μE m^{-2} s^{-1} (measured with a cosine collector); (c) vertical movement of the population peak through time corresponded to a swimming speed of 0.5 to 0.75 m h^{-1}; (d) cells began their ascent before sunrise, and their descent before sunset; (e) NO_3^- and PO_4^{3-} concentrations

Table 1. Water volume and dinoflagellate cells gained or lost during tidal fluctuations

Year	Tidal stage	Photoperiod	% of low tide volume[*]	% of total population lost or gained[**]	
				G. tamarensis	H. triquetra
1980					
	Ebb	Light	− 18.1	− 8.4	
	Flood	Dark	+ 22.6	+ 0.6	
	Ebb	Dark	− 22.3	− 0.3	
	Flood	Light	+ 19.4	+ 0.3	
			Net 24 h change	− 7.8	
1981					
	Flood	Light	+ 29.0	+ 1.0	+ 0.9
	Ebb	Light	− 29.1	− 7.0	− 0.4
	Flood	Dark	+ 40.2	+ 0.2	+ 1.9
	Ebb	Dark/light	− 40.0	− 6.9	− 0.6
	Flood	Light	+ 29.0	+ 0.1	+ 1.1
			Net 24 h change	− 12.8	+ 2.7
1983					
	Flood	Light	+ 20.7	+ 1.2	+ 4.9
	Ebb	Light	− 19.8	− 1.7	− 3.9
	Flood	Dark	+ 24.2	+ 0.5	+ 4.5
	Ebb	Dark/light	− 21.0	− 1.9	− 4.6
			Net 24 h change	− 1.9	+ 0.9

[*] Change in pond volume as a percent of low tide volume. Plus and minus signs signify gains and losses of water over that tidal stage
[**] Inlet cell counts as a percent of total Salt Pond population at low tide. Plus and minus signs signify gains and losses of cells over that tidal stage

remained at or above 0.5 μM but were highly variable in vertical distribution.

The time course of advective loss of water and dinoflagellates from Salt Pond due to tidal fluctuations is shown in Table 1. During daylight hours, 8.4 % of the whole pond population of *Gonyaulax tamarensis* was removed with the ebb tide. Only 7 % of the advected cells returned when the tide reversed (equivalent to 0.6 % of the total pond population). The ebb tide at night carried fewer cells from the pond (0.3 %). The 24 h advective loss of *G. tamarensis* from Salt Pond was 7.8 %.

1981 study

Weather conditions were similar to the 1980 study, but *Gonyaulax tamarensis* cells migrated differently. With scattered clouds and 7 to 10 knot westerly winds, the water was moderately stratified with nearly 2 σ_t units difference between the surface and bottom (Fig. 3). Spring tide fluctuations were semi-diurnal and large, with a 1.5 m elevation on the first flood and 2.5 m on the second. Ebb tide occurred late in the day near 1500 h and again near 0330 h (Fig. 4). Sunrise and sunset were at 0500 and 1900 h, respectively. Between
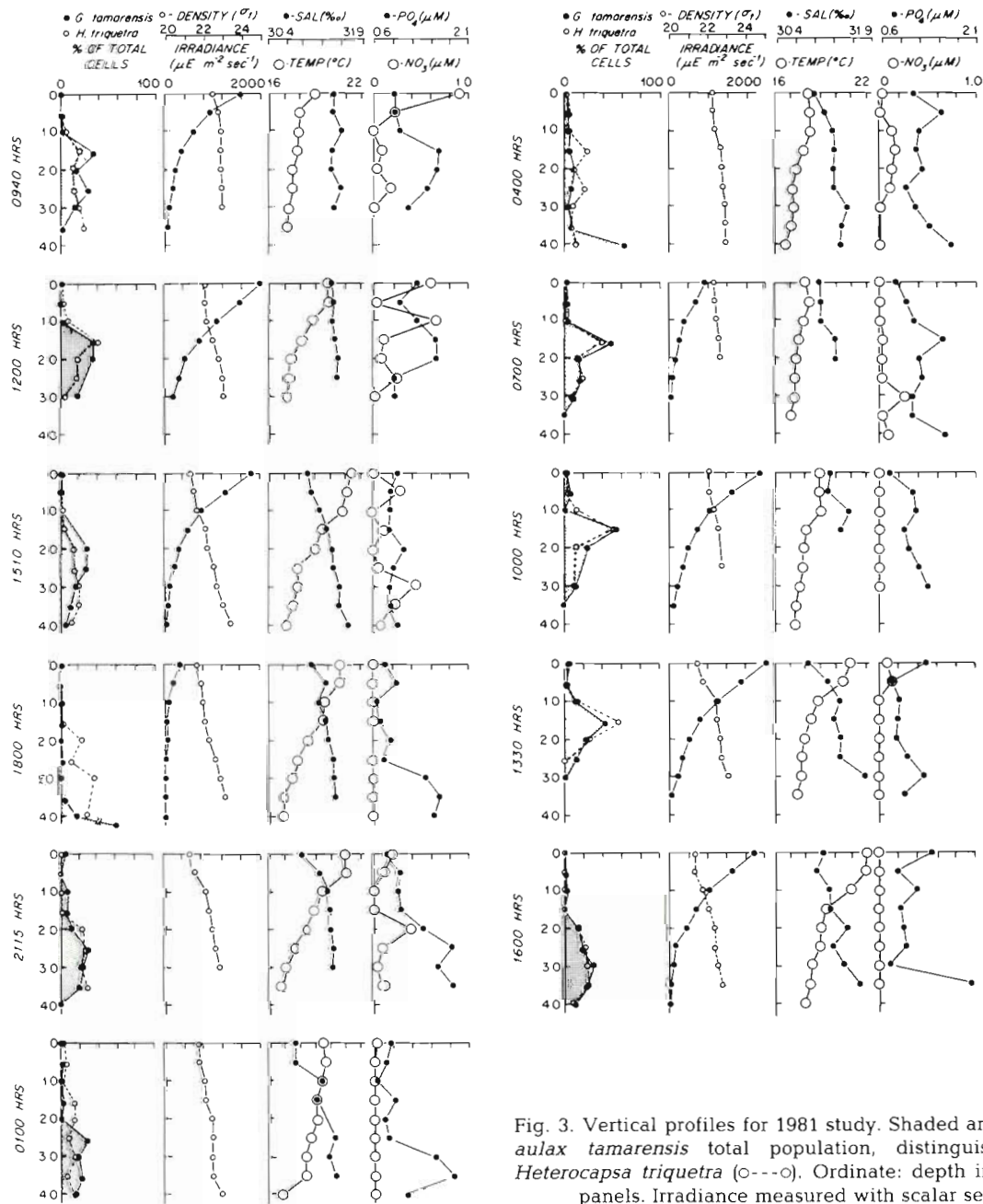

Fig. 3. Vertical profiles for 1981 study. Shaded areas: *Gonyaulax tamarensis* total population, distinguished from *Heterocapsa triquetra* (o---o). Ordinate: depth in m for all panels. Irradiance measured with scalar sensor
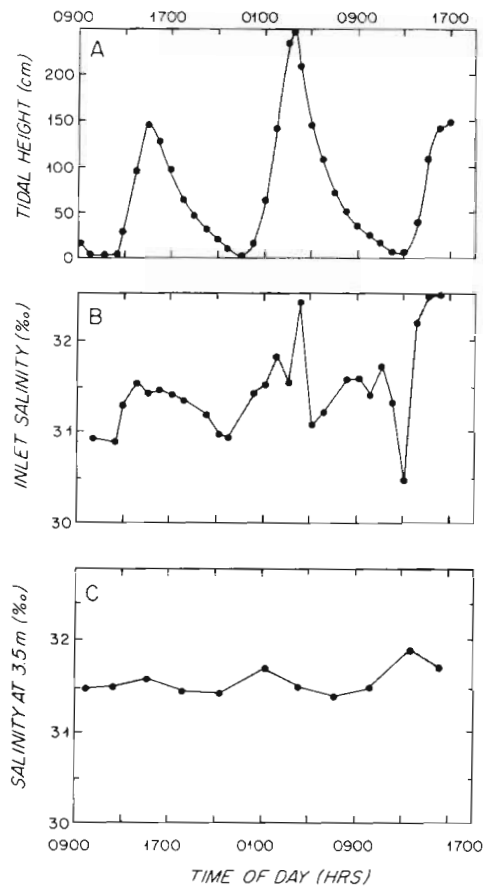
Fig. 4. Tidal elevation and salinity measurements for 1981 study. Shaded area: flood tide interval. (A) Tidal elevation; (B) Inlet salinity, Station 3; (C) Salinity at 3.5 m, Station 1

29 and 40 % of the low tide volume entered or left the pond with each tidal phase, equivalent to a potential flushing rate of nearly 0.70 d^{-1} (Table 1).

Salinity measurements at the inlet demonstrate that water flowing into the pond was typically more saline than that already present (Fig. 4 B). A slight increase in salinity at 3.5 m at Station 1 was observed with each flood tide (Fig. 4 C).

The 1981 Gonyaulax tamarensis population contained no planozygotes, even though NO_3^- concentrations were low. (Ammonium concentrations were not measured.) During the preceding week, NO_3^- concentrations averaged 1.2 μM (Anderson et al. 1983). Details of the migration pattern include: (a) G. tamarensis consistently avoided the top meter of the water column; (b) maximum level of the population peak was 750 to 850 μE m^{-2} s^{-1} (scalar collector); (c) swimming speeds ranged between 0.6 and 0.7 m h^{-1}; (d) cells began their descent before sunset; (e) population losses during ebb tides were near 7 %, with few cells returning with the flood (Table 1). Net daily loss of G. tamarensis from the pond was 12.9 %.

Although more broadly dispersed vertically, the Heterocapsa triquetra population migrated in a manner similar to that of co-occurring Gonyaulax tamarensis (Fig. 3). Maximum irradiance for the population peak was 750 to 850 μE m^{-2} s^{-1} as the cells consistently avoided the surface. Relatively few H. triquetra cells left or entered the pond with tidal flow, ranging between 0.4 and 1.9 % of the total pond population during one tidal stage (Table 1).

1983 study

In addition to the parameters monitored in previous years, the 1983 study used rhodamine dye to track water movement. The water column was weakly stratified, with only fractional differences in σ_t from surface to bottom (Fig. 5). Surface waters were, on average, less dense than bottom waters however. The weather was initially clear with broken clouds and 6 to 10 knot southerly winds, turning to overcast the morning of the second day. Ebb tides began shortly after noon and midnight, starting from a 1.2 to 1.5 m tidal elevation (Fig. 6). Sunrise was at 0515 h and sunset at 1930 h. Tidal flows were 20 to 24 % of low tide volume, equivalent to a potential flushing rate of 0.45 d^{-1} (Table 1). Inlet salinities varied broadly with no apparent trends (Fig. 6).

Dye concentrations measured at the inlet showed an initial pulse from the injection and then a rapid decrease to a relatively constant 0.35 ppb (Fig. 6 C). At Station 1, the dye first appeared at the surface at 1030 h, but when the flood tide ended at 1300 h the highest rhodamine concentrations were at depth (Fig. 5). Vertical dye distribution gradually became more uniform, resembling a well-mixed system by midnight. A similar pattern (not shown) was observed from hourly dye measurements at Station 2 in the pond. Also not shown are hourly dye measurements at Station 1 which are consistent with the general patterns depicted using 3 h intervals in Fig. 5. The volume-weighted vertical average of the dye concentrations at Stations 1 and 2 for each sampling interval gradually decreased through time. A ln-linear regression (dye concentration versus time) gave a slope significantly different from zero (P <.05) and a dye removal rate of 0.46 d^{-1}, both stations combined.

In 1983, both planozygotes and vegetative cells of Gonyaulax tamarensis were present. During the migration: (a) cells consistently avoided the surface, stopping their vertical movement 1 to 2 m deep; (b) maximum irradiance received by the population peak was 300 μE m^{-2} s^{-1} (scalar sensor) ; (c) vertical movement was 0.7 m h^{-1}; (d) cells began their descent before sunset; (e) loss rates of cells during ebb tides were
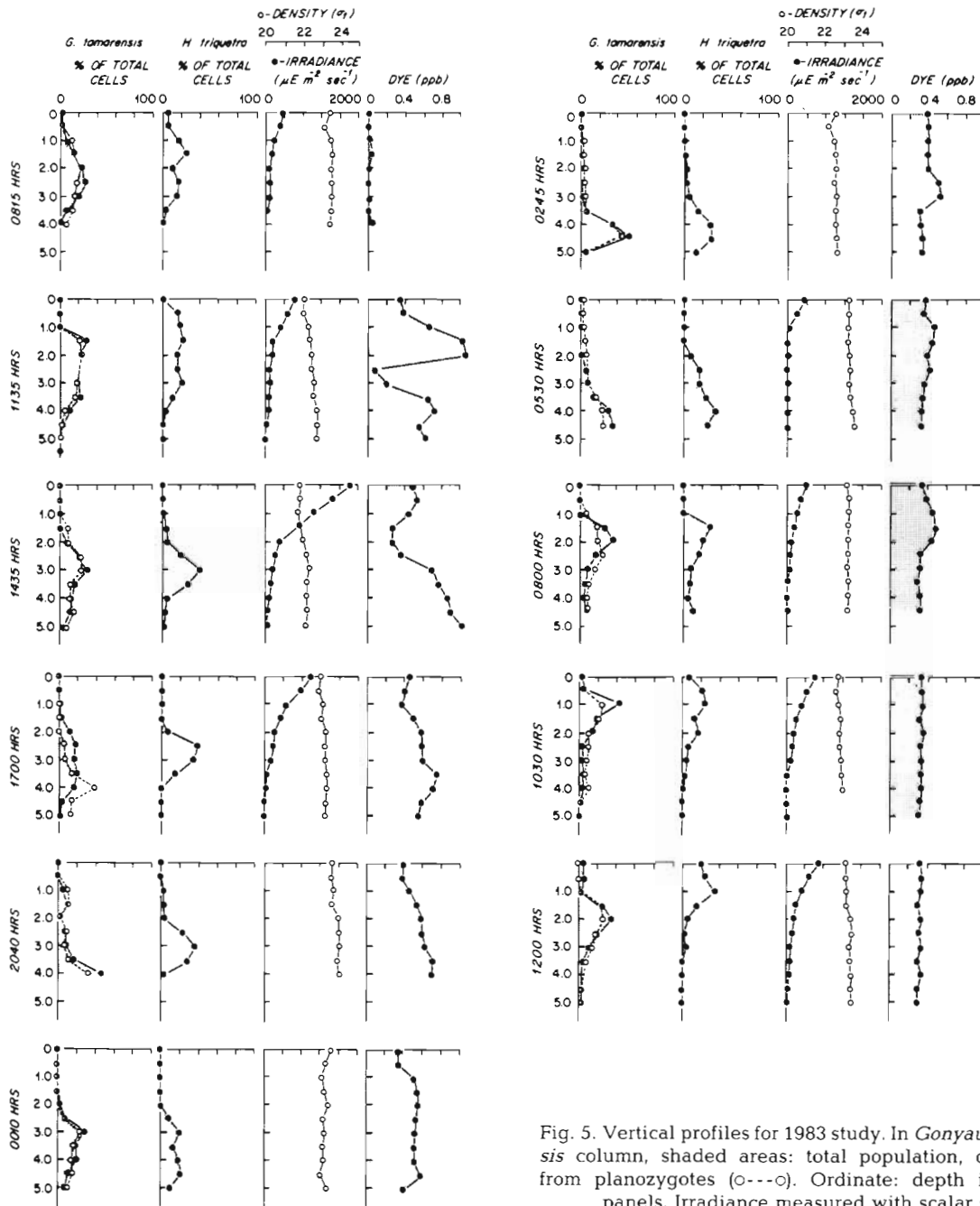
Fig. 5. Vertical profiles for 1983 study. In *Gonyaulax tamarensis* column, shaded areas: total population, distinguished from planozygotes (o---o). Ordinate: depth in m for all panels. Irradiance measured with scalar sensor

small (0.5 and 1.2 %). The daily population loss from the pond was 2 % (Table 1).

Heterocapsa triquetra consistently migrated higher in the water column than *Gonyaulax tamarensis* during 1983, with irradiance levels for the population peak of 700 µE m^{-2} s^{-1}. Timing and rate of migration were otherwise similar for the 2 species. Since the morning of Day 2 was overcast, *H. triquetra* did enter the top meter of the water column in significant numbers. However, timing of the tide and migration were

such that relatively few cells were lost with ebb flow. Population losses and gains were both 4 to 5 % per tidal stage for a net gain of 0.9 % over 24 h.

DISCUSSION

Both *Heterocapsa triquetra* and *Gonyaulax tamarensis* demonstrated diel vertical migration behavior under natural bloom conditions, with the pattern of
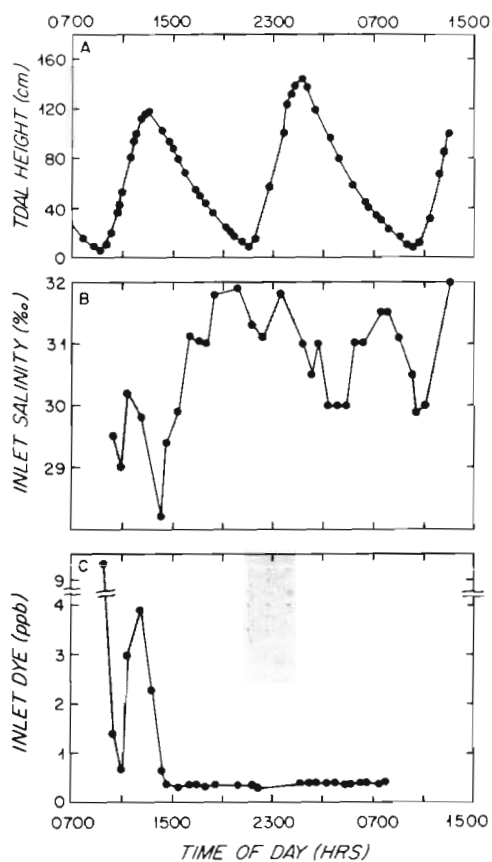
Fig. 6. Tidal elevation, salinity and dye measurements for 1983 study. Shaded area: flood tide interval. (A) Tidal elevation; (B) Inlet salinity; (C) Inlet dye concentration

these migrations differing between species and for the same species through time. The dinoflagellates were selectively retained relative to the water exchanged by the tides despite efficient mixing within the embayment. This retention is consistent with the differential advection of surface and bottom waters and the general avoidance of surface layers by the dinoflagellates. While in general agreement with the laboratory observations of Heaney & Furnass (1980), Cullen & Horrigan (1981) and Heaney & Eppley (1981) for other species, these results document the species-specific response of co-occurring dinoflagellates to a variable environment and emphasize the importance of vertical movement and aggregation in the bloom dynamics of the populations in the study area.

Nutrient status

It is now well established that dinoflagellate migration patterns can be regulated by nutrients (Eppley et al. 1968, Cullen & Horrigan 1981, Heaney & Eppley 1981). The blooms we monitored were not mono-

specific, so intracellular nutrient pools for the species of interest could not be directly measured to determine each species' nutritional status (e.g. Cullen & Horrigan 1981). We thus relied on 2 indirect measures: (a) presence or absence of life cycle stages indicative of nutrient limitation; (b) pattern of population development in Salt Pond during an interval spanning each of our studies.

Gonyaulax tamarensis includes a cyst stage in its life cycle, and recent laboratory studies suggest that encystment of this species occurs only when nutrients become limiting (Anderson et al. 1984, Anderson & Lindquist 1985). Since 30 % or more of the *G. tamarensis* cells in both 1980 and 1983 were the large planozygotes that become cysts, and since the *G. tamarensis* populations decreased rapidly during the interval our studies were conducted (Anderson et al. 1983, unpubl.), nutrient limitation is probable in both years. In contrast, no planozygotes were observed in the 1981 samples nor did the populations suddenly decline, so nutrient-sufficient conditions are assumed.

Heterocapsa triquetra does not form a zygotic cyst to our present knowledge (contrary to the earlier report of Braarud & Pappas 1951), so its nutritional status was inferred from the population dynamics. In 1981 and 1983 the species increased at rates of 0.4 and 0.5 d^{-1} respectively over the 3 wk interval spanning each study, so nutrient limitation was unlikely either year. (These are net rates that include losses due to advection and grazing, so actual growth rates would be higher.) This conclusion conflicts with our contention that *Gonyaulax tamarensis* was nutrient-limited in 1983, but such a difference in the nutritional status of the co-occurring species is supported by a 3 order of magnitude decrease in *G. tamarensis* cell concentrations as *H. triquetra* increased 100-fold in the weeks spanning our study.

Migration patterns

The timing and rates of ascent and descent were similar for *Heterocapsa triquetra* and *Gonyaulax tamarensis* and in the same range as those reported for other dinoflagellates (0.6 to 1 m h^{-1}; Hand et al. 1965, Eppley et al. 1968, Heaney & Eppley 1981). *G. tamarensis* exhibited 2 different migration patterns, with the major difference between the two being the maximum height or irradiance level at which vertical movement ceased. The migration of planozygotes was identical to that of the population as a whole. The nutrient-limited 1983 population aggregated at a depth where irradiance was less than half that where the nutrient-replete cells stopped vertical movement in 1981 (300 *vs* 800 µE m^{-2} s^{-1}). The data for these 2 yr

are directly comparable since they were obtained with the same scalar sensor and light meter. The nutrient-limited cells in 1980 aggregated at or below 200 µE $m^{-2} s^{-1}$, but irradiance was measured with a flat plate or cosine collector. Measurements with a cosine collector can theoretically differ from those made with a scalar instrument by a factor of 4 in totally diffuse light (Booth 1976). However, simultaneous measurements with both instruments in Salt Pond gave scalar values generally twice those of the cosine collector at all depths (Anderson unpubl.). Thus the scalar irradiance where the 1980 *G. tamarensis* population ceased migrating would have been approximately 400 µE $m^{-2} s^{-1}$. This again suggests that nutrient-depleted *G. tamarensis* cells stopped their migration lower in the water column than cells with sufficient nutrients.

The migration patterns for *Gonyaulax tamarensis* are similar in some respects to those reported for other dinoflagellates. *Ceratium furca*, *G. polyedra*, and *Gymnodinium splendens* all aggregated at relatively high irradiance levels when nutrients were plentiful (Cullen & Horrigan 1981, Heaney & Eppley 1981). Unlike these species, however, *G. tamarensis* avoided irradiance above 30 % summer sunlight. When nutrient-limited, *G. tamarensis* aggregated at depths with irradiances 10 to 15 % of surface sunlight, as was reported for *G. polyedra*, *G. splendens* (Cullen & Horrigan 1981, Heaney & Eppley 1981) and *Ceratium hirundinella* (Heaney & Furnass 1980). Maximal growth of a Cape Cod strain of *G. tamarensis* has been reported at or above 150 to 200 µE $m^{-2} s^{-1}$ in laboratory cultures growing on a 14:10 L:D cycle, with no indication of photoinhibition up to 650 µE $m^{-2} s^{-1}$ (Anderson et al. 1984). Thus the nutrient-limited populations that ceased migrating at relatively low irradiances in our study would presumably have had sufficient light for growth.

Heterocapsa triquetra migrations were similar in 1981 and 1983, with cells accumulating at relatively high irradiances (750 to 800 µE $m^{-2} s^{-1}$) at the maximal extent of their movement. This generally kept the cells 1 to 2 m below surface, except on the second day of the 1983 study when 30 % of the population aggregated in the top meter. The day was overcast, however, so the irradiance at that level was also 600 to 800 µE $m^{-2} s^{-1}$. The population development in Salt Pond suggests nutrient-sufficient conditions for *H. triquetra* in both years, so this species can be grouped with those that aggregate high in the water column when nutrients are plentiful. Like *Gonyaulax tamarensis*, *H. triquetra* avoided full summer sunlight at the surface.

The differences between the behavior of *Heterocapsa triquetra* and *Gonyaulax tamarensis* in 1983 are noteworthy since the former was growing rapidly and migrating vigorously while the latter showed signs of nutrient limitation in its population development and migration. These differences could be due to species-specific nutritional requirements, but no data are available for comparison. The differences may also reflect reproductive strategies. Once induced, sexuality and cyst formation are probably not reversible for *G. tamarensis*, whereas *H. triquetra* could resume asexual vegetative growth rapidly if nutrients increased following a brief period of limitation. A third explanation is suggested by Eppley et al. (1968) who reported that a related species, *H. niei* (= *Cachonina niei*; Morril & Loeblich 1981) continued to migrate to the surface of a laboratory tank throughout 5 d of nutrient starvation. Surface irradiance in that study was much lower than the natural levels in Salt Pond, but it is possible that *H. triquetra* does not alter migration behavior with changing nutrient conditions.

Both *Gonyaulax tamarensis* and *Heterocapsa triquetra* migrated to some extent under all conditions. In the shallow salt pond environment stratification does not lead to nutrient-depleted surface waters and higher concentrations at depth (Fig. 2), so migration is probably not linked to nutrient uptake at depth. Others have documented the cessation of dinoflagellate vertical movement at steep salinity or temperature gradients (e.g. Seliger et al. 1970, George & Heaney 1978, Tyler & Seliger 1981), but the gradients we measured were quite small. The simplest explanation is that the cells moved to the depth where they could satisfy photosynthetic requirements without photoinhibition. The upper limit for the 2 species may be near 800 µE $m^{-2} s^{-1}$, typically available 1 to 2 m below the surface.

Population transport

The dominance and localization of dinoflagellates within estuarine embayments like the Cape Cod salt ponds has been attributed to several factors including inefficient tidal flushing that would allow slow-growing species and their encysted stages to accumulate (Anderson & Wall 1978, Anderson & Morel 1979). The combined effects of shallow inlet channels and density stratification was thought to reduce tidal renewal of the deeper layers of the ponds. Our results demonstrate quite the opposite – that tidal mixing is very efficient and that the cells would be flushed from Salt Pond in the absence of a behavior-related retention mechanism. In the 1983 study, dye concentrations within Salt Pond decreased at a rate of 0.46 d^{-1} which is essentially the same as the maximum exchange rate calculated from tidal volumes (Table 1). The principal cause of this mixing efficiency appears to be an estuarine-like circulation in which flood-tide waters sink and vertically displace less dense pond water which is then

removed with the subsequent ebb tide. Springs or groundwater provide the freshwater that keeps the pond more brackish than the incoming tidal flow.

The 1983 dye profiles clearly demonstrate that the flood-tide water crossed the inlet sill and sank below the surface layer. The same pattern was seen in 1981 when the salinity increased at depth with each flood tide (Fig. 4 C). That the shallow sill at the inlet restricted outflow to surface waters is seen in the systematic fluctuation of inlet salinities with flood and ebb tides (Fig. 4 B) and in the small loss of dinoflagellates when ebb tide occurred during the night when the populations were well below the surface (Table 1). Furthermore, in the 1983 study, inlet dye concentrations during the first ebb tide were 0.3 to 0.4 ppb, the same as the surface waters at Station 1 (Fig. 5). Dye concentrations at 2 m and below were double these values throughout ebb tide, so it is clear that outflowing water was from the surface. Selective outflow of surface waters and efficient tidal mixing were also observed in a different Cape Cod salt pond (Garcon et al. unpubl.).

If *Gonyaulax tamarensis* or *Heterocapsa triquetra* behaved like passive, neutrally-buoyant particles, advective population losses would be on the order of 0.5 d^{-1}. Added to grazing mortality, the total loss would preclude bloom formation since the maximum specific growth rates of Cape Cod strains of *G. tamarensis* and *H. triquetra* are 0.4 and 0.7 d^{-1} respectively (Watras et al. 1982, Anderson unpubl.). Blooms of both species do occur, however, occasionally reaching red-tide proportions. The obvious conclusion is that the dinoflagellates' swimming behavior restricts advective losses to manageable levels. The organisms have sufficient motility to maintain a non-well-mixed distribution in the presence of efficient tidal mixing, and their avoidance of surface waters under sunny conditions keeps them below the layer that is removed with each ebb tide. The magnitude of this selective retention is seen in Table 1 which shows population losses of only 0.02 to 0.13 d^{-1} for both species. This is not an artifact of a fortuitous phasing between ebb tides and the maximal vertical height of the migration since population losses were small even when ebb tides occurred near midday (1980, 1983). With advective losses of this magnitude, reasonable population growth rates should allow the dinoflagellates to increase in abundance as non-motile phytoplankton are washed out at a high rate.

Seliger et al. (1970) studied populations of *Pyrodinium bahamense* in Oyster Bay, Jamaica and drew a similar conclusion – that in the absence of an accumulation mechanism, *P. bahamense* should be flushed from the bay. The retention mechanism that was proposed was based on a well-stratified water column that restricted mixing, the subsurface accumulation of *P. bahamense*, and the differential advection of surface waters due to wind stress. Similar patterns have been observed in freshwater lakes (Heaney & Talling 1980) and in large estuaries (Tyler & Seliger 1978, 1981). The scenario for the Cape Cod salt ponds is quite different in comparison, since strong stratification is not necessary for retention. In fact, the stratification of Salt Pond is the principal cause of an efficient tidal mixing process that the cells must counteract through their swimming behavior. The most important factors are the avoidance of high-irradiance surface layers by the dinoflagellates, the physical restriction of ebbing waters by the inlet sill, and the input of freshwater from springs to maintain the salinity difference between the pond and incoming flood tide waters.

One reason these salt ponds have received so much study is that they represent the source for toxic *Gonyaulax tamarensis* populations in the region (Anderson & Wall 1978, Anderson et al. 1982b). Unlike northern New England where coastal blooms of this species are common (Yentsch 1984), blooms on Cape Cod seem to develop within localized embayments and spread slowly to adjacent estuaries (Anderson et al. 1982b). Our data document the 'point-source' nature of *G. tamarensis* blooms at one of these locations and explain the underlying behavioral and hydrographic mechanisms for retention. The results also suggest that advective population losses would be smallest on sunny days with flood tides during midday hours, and largest during periods with overcast skies and low surface irradiance. Since nutrient-sufficient cells aggregate closest to the surface, the largest population losses would generally introduce actively-growing, vigorous cells to nearby waters. In 1981, for example, the daily *G. tamarensis* loss was the highest (12.8 %) and that was the year nutrients appeared to be non-limiting. Conversely, as a bloom matures and nutrients are depleted, advective losses should diminish as the cells limit the height of their vertical movement still further. Planozygote migration does not differ from that of the remainder of the nutrient-limited population, so cysts would be deposited within the embayment and not be widely dispersed. These inferences are consistent with the regional distribution of *G. tamarensis* cysts which are found in high concentrations in the sediments of many salt ponds but are generally scarce in adjacent waters (Anderson et al. 1982a, b).

It is evident from this study and others that the vertical migration of dinoflagellates is a complex phenomenon that can have a number of major impacts on local population dynamics. Our data emphasize the species-specific differences in the migration patterns of co-occurring organisms and emphasize the importance of surface avoidance in limiting advective trans-

port of cells from the study area. The results are most relevant to estuarine blooms of *Gonyaulax tamarensis* and *Heterocapsa triquetra,* but the insight gained should be useful in understanding the dynamics of blooms of these species in coastal waters where monitoring discrete populations is logistically more complex.

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