

Vertical migration maintains phytoplankton position in a tidal channel with residual flow

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ABSTRACT: A tidal channel can retain phytoplankton, despite a residual flow, if the phytoplankton migrate vertically with a daily rhythm. Tidal currents are slowed down by bed friction and so plankton experience faster flow when higher in the water column. The lateral movement of the plankton depends on the nature of the vertical migration, particularly the time spent near the surface and the phase of the tide. A model of this process accorded with observations of chlorophyll derived from *in situ* fluorescence at a mooring in a tidal channel. Peaks in chlorophyll at the end of the flood tide indicated the presence of a phytoplankton bloom downstream of the mooring. Peaks in chlorophyll at the ends of the morning flood tides were 3 to 4 times larger than at the ends of the evening floods, over several days. In contrast, well-mixed particulates were removed from the channel by the residual flow in just 2 d. Both the day–night asymmetry and the sustained presence of chlorophyll were explained by allowing for vertical migration of the phytoplankton and constraining the period during which they were near the surface. Tidal channels retaining phytoplankton that migrate vertically can be ecologically more diverse and yield higher commercial output of farmed bivalves. The natural timings of some phytoplankton blooms in tidal channels are controlled by the nature of the migration. Although a by-product of vertical migration, longer residence in the tidal channel affords the phytoplankton more nutrients than phytoplankton that advect offshore.

KEY WORDS: Chlorophyll *a* · Diel vertical migration · Tidal channel · Phytoplankton particle size · Menai Strait

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INTRODUCTION

Vertical migration with a daily rhythm is a characteristic of many plankton. Phytoplankton travel upwards with daylight (light ascent) and downwards as daylight is lost, whilst zooplankton have the opposite sense of migration (dark ascent) (Eppley et al. 1968, Cullen & Horrigan 1981, Ross 2004). Some move by swimming and others by changes in buoyancy. Although vertical migration is slow (typically <1 mm s⁻¹) compared to flow speeds (typically 100s to 1000s mm s⁻¹), the combination of vertical migration and a vertical shear in horizontal current speed can lead to

significant horizontal transport of organisms. For example, if a plankter is high in the water column during the day with a tidal current flowing eastward, and sinks at night into weaker currents flowing westward, there is a net movement towards the east over a tidal cycle. That movement can be up to several km d⁻¹ (Hill 1991a,b, Smith & Stoner 1993).

Tidal channels are shallow, narrow sea straits or creeks connecting 2 larger bodies of water. For a relatively short channel compared to the tidal wavelength, the tidal flow is driven by the difference in water level between its 2 ends (Pugh 1987). The water in the channel flows back and forth with the

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period of the tide at the ends of the channel; maximum flow occurs when the level difference is greatest, and slack tide when the levels are the same. Because the gradient in the water surface can be large, fast turbulent flows are characteristic of many tidal channels. Differences in friction on the flood and ebb tides in the channel can lead to a residual current.

Phytoplankton are the major food source for commercial bivalve species such as cockles, mussels and oysters living in tidal channels (Cohen et al. 1984, Wildish & Kristmanson 1984, Simpson et al. 2007, Malham et al. 2009). Commercial bivalves can feed selectively on light-ascending species (Shumway et al. 1985, Baker & Levinton 2003). The physical mechanisms that can retain phytoplankton blooms in tidal channels (against a residual flow) would tend to improve commercial yields. The retention of phytoplankton (as primary producers) also potentially improves biodiversity at higher trophic levels. Such retention can occur with vertical migration in a daily rhythm in 2 scenarios. Firstly, the migration can happen in the tidal channel. In a second scenario, however, high turbulence in tidal channels prevents weakly-swimming phytoplankton from making meaningful vertical migrations. Instead, the phytoplankton are vertically mixed in the channel and vertical migration happens in a quiescent bay at one end. In the theory section next, annual movement patterns are presented for a phytoplankton migrating vertically in a tidal current which diminishes in amplitude towards the sea bed. In a case study that follows the theory, short periods of the movement patterns are considered alongside coincident observations of chlorophyll in the Menai Strait.

THEORY

The following theory determines the motion of a single phytoplankton cell along a tidal channel, taking a diurnal vertical migration in an advective flow. The phytoplankton cell has an initial position, set as 0 km along-channel, on 1 January. It moves relative to this position for 1 yr, effectively in an infinite channel (i.e. it doesn't move into a water body where other processes dominate). The theory can be applied to movements starting on any day of the year by resetting a new initial position. The limits of the theory in any case study are the length of the channel over which this linear advection dominates and the lifetime of the plankton or plankton community.

Consider a single phytoplankton cell migrating vertically in a tidal channel, close to the surface during the day and towards the bed at night (Fig. 1A,B). In the simplest model, this movement is represented by a square wave with a shape modified by the day length, so that the cell spends longer at the surface in summer, when days are longer, than it does in winter (Fig. 1C). The square wave represents a very good swimmer, which spends much more time at its intended locations than swimming between them. In a variation of this model, the vertical motion is governed by a triangle wave, such that the cell spends time near the bed during darkness and starts moving towards the surface at sunrise, reaching closest to the surface at noon. In the afternoon, the cell swims back towards the sea bed, reaching maximum depth at sunset.

The tidal current at the surface, u_s , varies with a semi-diurnal period:

$$u_s = A \sin[\omega(t - \phi)] \quad (1)$$

where A is the amplitude of the current, ω is the angular frequency of the main lunar semi-diurnal tide (period 12.4 h), t is time and ϕ is tidal phase. For convenience, periods in which u_s has a positive sign are defined as the flood tide, and periods of negative u_s as the ebb tide. High water occurs at the end of the flood tide. The current amplitude was varied with the spring–neap cycle, with $A = 1 \text{ m s}^{-1}$ at spring tides and 0.5 m s^{-1} at neap tides. The tidal phase was set with high water spring tides at noon. The direction of flood tide is therefore the direction of the flow between 05:54–12:00 h and 18:06–00:13 h on a day of spring tides.

Tidal current speed decreased linearly with depth, such that the current at depth, z , is given by

$$u(z) = u_s \left(1 - \frac{z}{h}\right) \quad (2)$$

where z is depth below the surface and h is total water depth. The cell migrates between depth $z = h/4$ during the day (or at noon in the triangle wave forcing) and $z = 3h/4$ at night (Fig. 1C). The daytime value of z was chosen to match a case study presented later. In the model, the phase of the phytoplankton movements is set to be the same as the phase of daylight. This infers the need of phytoplankton to move upwards in the water column as soon as daylight arrives. This is most pertinent for channels that are sufficiently deep or concentrated with particles so that the photic zone is less than the whole water depth. It is also pertinent for phytoplankton with the most energy needs (from photosynthesis).

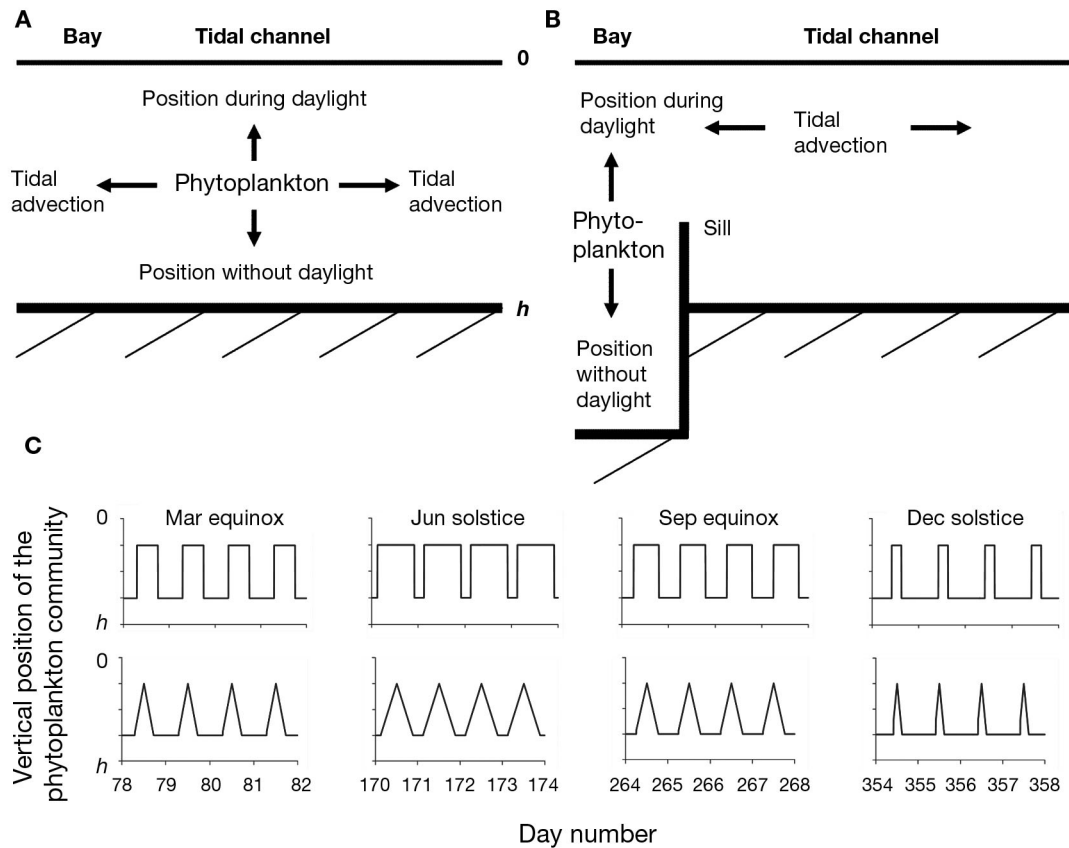


Fig. 1. Phytoplankton migrating vertically in an advective tidal channel. (A) Conceptual model with vertical swim in the tidal channel. (B) Conceptual model with vertical swim in a quiescent bay at one end of the tidal channel. Phytoplankton can move into the channel when they are higher than the sill. The phytoplankton are well-mixed in the tidal channel and can move back into the bay at any time, with the tide. (C) The vertical migratory pattern of the phytoplankton at 4 stages of the year. The water surface is at $z = 0$; the seafloor at $z = h$, and each day the phytoplankton move between $h/4$ and $3h/4$, starting at sunrise and finishing at sunset. The timing of sunrise and sunset sets the width of the pattern. The square waves represent good swimmers that spend much more time at their intended locations than travelling between them. The triangle waves represent moderate swimmers that spend more time reaching the location. The label of day number represents 00:00 h on that day

The phytoplankton descend on the disappearance of daylight, and this fact assumes no environmental pressures such as dissolved chemicals, nutrient availability or adverse temperature or salinity.

The horizontal motion of the cell in an infinitely long tidal channel at a temperate latitude varied by hundreds of kilometres per year depending on the vertical migratory pattern and the tidal phase (Fig. 2). The cell was released at position $x = 0$ and depth $z = 3h/4$ at midnight at the start of Day 1 (1 Jan). With square wave migration, the cell spent all hours of darkness at depth $z = 3h/4$ and all daylight hours at $z = h/4$. When day length was >12 h (between the spring and autumn equinoxes), the cell moved in the negative (ebb) x -direction. When day length was <12 h, the general direction of movement was in the positive (flood) x -direction. The extent of the horizontal motion was considerable: over 200 km in 6 mo, or of order 1 or 2 km d^{-1} . A cell could main-

tain its position, or make headway against moderate residual flows by riding the tide in this way. The general seasonal pattern of movement had small oscillations associated with the springs-neaps tidal cycle. Despite being small compared to the annual oscillations, these oscillations were large enough to reverse the direction of motion for short periods (Fig. 2).

The particular solution in Fig. 2 is for a tidal channel at approximately 48° latitude, with 16 h daylight on Midsummer Day. Solutions for other temperate latitudes for these tidal conditions had similar patterns, with lower amplitude at lower latitudes. At higher latitudes, the amplitude was lower in the first half of the year and higher in the second half of the year.

The horizontal motion of a cell undergoing triangle-wave vertical migration could be considered appropriate for slower swimmers which spend more time closer to the sea floor than the sea surface. For a

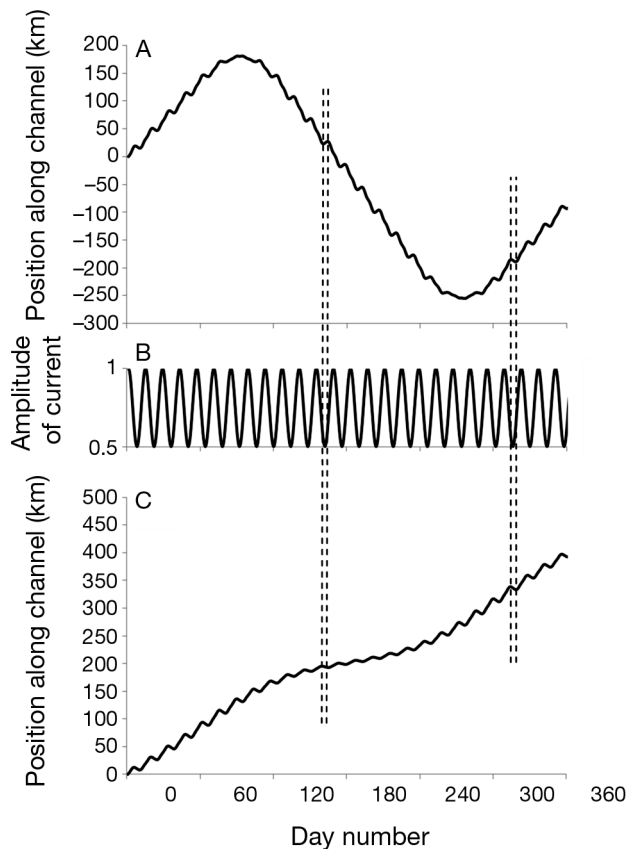


Fig. 2. Variation of position along a tidal channel by an organism making a diurnal vertical migration between three-quarters of the flow depth above the bed during daylight hours, and one-quarter above the bed in hours of darkness. Positive values are oriented with the flood tide and negative values with the ebb tide. Solid lines represent the daily mean values. Panel (A) Represents square wave migration and (C) represents triangular wave migration (cf. Fig. 1C). Panel (B) represents the tidal current amplitude; in spring tide conditions amplitude is 1 and in neap tide conditions amplitude is 0.5. The vertical dashed lines highlight portions of 2 spring–neap periods where phytoplankton move oppositely to the long-term trend, associated with falling and low-amplitude current

tidal channel in temperate latitudes for which high water springs occurs at midday, the motion of the cell was generally in the flood direction throughout the year, being faster when day length was <12 h (4 km d^{-1}) and slowing down considerably as the day length increased in summer (to 0.4 km d^{-1}). As in the square wave migration pattern, the motion is temporarily reversed within the springs–neaps cycle, consistent with Smith & Stoner (1993). The motion as modelled by Hill (1991a,b) did not have a spring–neap pattern and was associated with different velocity in the water column (one a power law velocity profile, the other a linear 2-layer problem for deeper water).

To allow for unsuccessful swimming in a turbulent channel, a second model represented a channel that opens into a more quiescent bay at one end (Fig. 1B). In the bay, turbulence is low, the Péclet number of a plankter is >1 , and phytoplankton are able to migrate vertically. To match conditions in the case study presented in the next section, a sill separates the bay from the channel. The concentration of cells above the level of the sill increases in the day and decreases at night because of vertical migration in the bay and that concentration is carried in and out of the channel with the tide. Results from this alternative model are compared to observations later in the paper.

CASE STUDY METHODS: CHLOROPHYLL TIME SERIES IN THE MENAI STRAIT, UK

The study site

The Menai Strait lies between the isle of Anglesey and the north coast of Wales, UK (Fig. 3). It is 34.5 km long and stretches between 2 bays: Caernarfon Bay in the south-west and Conwy Bay in the north-east. There is a sand bar (Caernarfon Bar) at the south-west end, which spans more than half the channel width and dries out at low tide. The main channel of the strait varies between 200 and 800 m in width, and between 6 and 33 m in depth, with mean depth 15.7 m below mean high water. Tides are semi-diurnal; mean spring tidal range varies between 5.2 m at the southwest end (Caernarfon) and 7.4 m at the northeast end (Beaumaris). Tidal streams exceed 1 m s^{-1} at several places, especially in the narrow central part of the strait where maximum speeds reach 4 m s^{-1} at spring tides. Flow depth is greater during the ebb tide than during flood tide, causing higher bottom friction on the flood and resulting in a residual flow towards the south-west (Harvey 1968, Simpson et al. 1971). The residual flow varies with the spring–neap cycle (faster at springs) and averages approximately 0.1 m s^{-1} (Simpson et al. 1971), replacing the water in the strait roughly every 3 d. Turbulence associated with the fast tidal streams produces well-mixed conditions throughout the strait. There is no stratification of turbulence despite the complex bottom topography. Dissolved and particulate material advects along the strait with the tide (excursion of order 10 km tide^{-1}) and leaves via the south-western end with the residual flow.

A number of vertically migrating species of diatoms have been recorded in the strait in summer. The buoyancy of each of these varies between positive

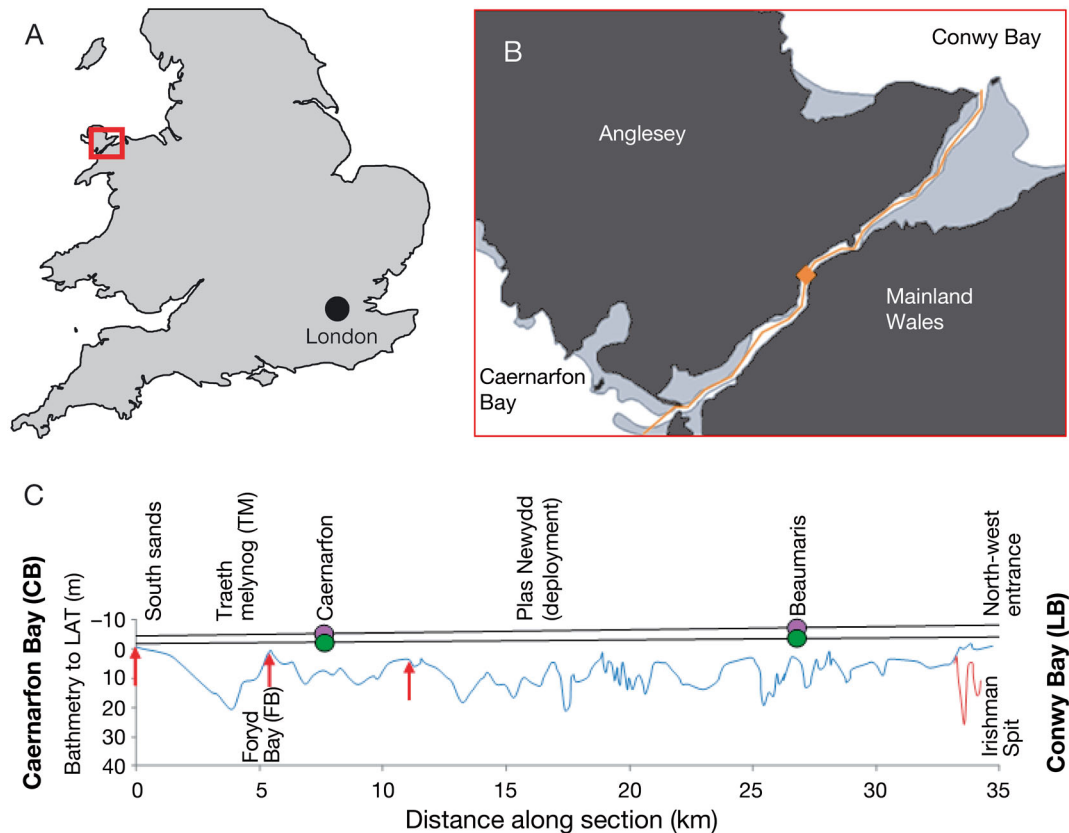


Fig. 3. Location and geometry of the tidal channel case study. (A) England and Wales, showing the location of the Menai Strait (red box), between the Isle of Anglesey and mainland Wales, UK. (B) Map of the tidal channel (inset from A). The instruments were moored at the position of the orange diamond. (C) Bathymetric section (blue line) of the strait highlighted by orange line in (B). Mean high water slack (MHWS) = 0 m depth. The purple and green dots indicate spring and neap tidal ranges respectively, at Caernarfon and Beaumaris, which are 19 km apart. The black lines interpolate and extrapolate the tidal ranges from these towns. The 3 red arrows indicate sill-like features at the western end of the strait, and the red line shows the bathymetry of a secondary channel terminating at Irishman Spit

and negative due to (1) the production and consumption of carbohydrates, (2) regulation of gas in vesicles during photosynthesis, (3) ballasting by adsorbed polysaccharides and particles that may stick to them and (4) colonial behavior. In August of any year, a set of the following have dominated: *Astrionella* spp., *Chaetoceros* spp., *Cylindrotheca*, *Fragiliara* spp., *Guinardia* spp., *Leptocylindrus danicus*, *Nitzschia* spp., *Paralia sulcata*, *Phaeocystis pouchetti*, *Rhizosolenia* spp., *Skeletonema costatum* and *Thalassiosira* spp. (Table 1). All the quantitative data found and tabulated are from diatoms. Although diatoms normally dominate the Menai Strait in August (ca. 83% of the phytoplankton population between 2002 and 2009; Greenwood et al. 2012), in at least 1 yr flagellates have dominated (Ewins & Spencer 1967).

The Menai Strait is home to intensive commercial farming of bivalves, primarily mussels. At 23 to 30 km into the strait in the direction of the flood tide, they are beyond the excursion of algal blooms sited in

Caernarfon Bay, but would graze on background levels of algae and any algal blooms passing through the channel from Conwy Bay. Grazing <1% of algae in the bottom metre of water only (Simpson et al. 2007), they do not affect the particular case study given here. The buoyant speeds of diatoms in the Menai Strait are likely to be up to $20 \mu\text{m s}^{-1}$ (0.072 m h^{-1}) and movements of colonies (individual aggregated groups) could be on the order of hundreds of $\mu\text{m s}^{-1}$ (or m h^{-1}).

Mooring deployments, profiling and instrument setup

An instrumented mooring was deployed in the central part of the Menai Strait for 9 d, starting on 16 August 2011 (Day 228). The mooring was sited at $53^{\circ} 12.14' \text{ N}$, $04^{\circ} 12.71' \text{ W}$ in a mean depth of approximately 10 m (Fig. 3). The site is 16 km eastward of

Table 1. Abundance of taxa (\log_{10} abundance l^{-1}) that dominated phytoplankton populations in the Menai Strait in August of the given years. Data sources are provided in the footnotes. Data in *italics* were calculated from volumetric concentrations by inferring spherical-equivalent diameters

Taxon	Year of study				
	1962 & 1963 ^a	1967 ^b	1973 ^c	1993 ^d	2002–2009 ^e
<i>Astrionella</i> spp.			3.5		
<i>Chaetoceros</i> spp.					4
<i>Cylindrotheca</i> spp.					4
<i>Fragiliara</i> spp.			3.5		
<i>Guinardia</i> spp.				4 ^f	4
<i>Leptocylindrus danicus</i>			4		4
<i>Nitzschia</i> spp.			4.5		4
<i>Paralia sulcata</i>			4.5		
<i>Phaeocystis pouchetti</i>		4.5			
<i>Rhizosolenia</i> spp.	4.5		4.5		
<i>Skeletonema costatum</i>					
<i>Thalassiosira</i> spp.					4

^aJones & Spencer (1970); ^bKenchington (1970); ^cAl-Hasan et al. (1975); ^dBlight et al. (1995); ^eGreenwood et al. (2012); ^fDay 237

the sill separating the strait from Caernarfon Bay to the south-west (south sands sill, Fig. 3). Irradiance profiles were taken on 17 and 23 August, approximately hourly from just after dawn to just before dusk. This profiling was done from an 8 m long boat that started at the mooring location and drifted with the tide to follow the water.

The moored instruments were in a frame on the seabed and included a YSI CTD to measure depth, temperature, salinity and chlorophyll fluorescence, a Sequoia LISST-100X for particle size distributions and an upward-looking Workhorse Sentinel ADCP for flow velocities. The fluorescence and particle size measurements were 1.5 m above-bed. The velocity measurements were in 90 bins between 1.5 m above-bed and the water surface. Velocity and particle size distributions were recorded at 1.5 s intervals, and fluorescence at 60 s intervals. Water samples were collected using an opaque 4.2 l Wildco Beta Water Sampler (van Dorn type) approximately hourly from just after dawn to just before dusk. They were analysed for chlorophyll *a* (chl *a*) using a calibrated Turner 10AU fluorometer. These chlorophyll data were used to calibrate the CTD fluorescence record. LISSTs measure light scattered by particles in sus-

pension (Agrawal & Pottsmith 2000). By assuming that the particles are spherical, Mie theory is used to estimate the size distribution of the particles. The LISST-100X type C used returned the volume of particles in 32 size classes ranging from 2.5 to 500 μm . A TriOS Ramses irradiance meter was used to measure downwards irradiance at a series of depths through the water column, with multiple measurements averaged at each depth and integration time allowed to vary to optimise signal to noise.

CASE STUDY RESULTS

Tides

Spring tides occurred at the start of the record. The first flood tides ended at 12:10 and 00:31 h. At spring tides, the current speeds exceeded 1 m s^{-1} . The flood current, which occurs before high water and flows north-east, is slower than the ebb current flowing south-west (Fig. 4). The residual flow averaged over a tide varied from 0.15 m s^{-1} at springs to 0.08 m s^{-1} at neaps. The residual depended on the square of the tidal range, consistent with Simpson et al. (1971).

Characteristics of the algal bloom

To estimate the size of the phytoplankton in the Menai Strait in August 2011, the volumes of particles in each of the 32 LISST-C size classes were regressed against the chl *a* concentration measured by the fluo-

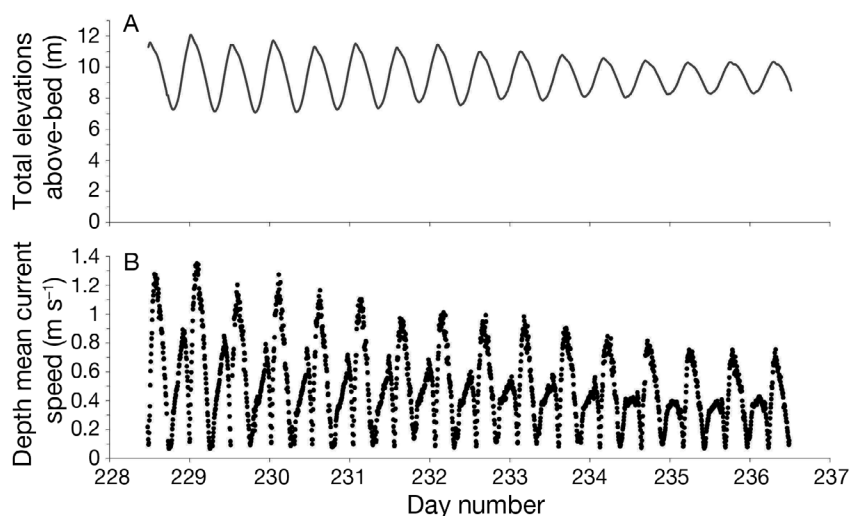


Fig. 4. Time series of (A) tidal elevation and (B) depth mean current speed at the mooring location (orange diamond, Fig. 3B) during the observational period (16 to 24 August; Day 228 to 236)

rometer on the CTD for the whole mooring period to determine likely numbers of chlorophyll-bearing particles (example correlation Fig. 5B). High correlation coefficients indicate that a change in particle volume of that particular size class was associated with a change in chlorophyll, and therefore that particles of that size were phytoplankton. The phytoplankton were most likely most abundant in the range of 7 to 21 μm , where the coefficient of regression, R^2 , was >0.89 (Fig. 5A). Secondary groups of phytoplankton were in the ranges 21 to 50 μm ($0.60 <$

$R^2 > 0.89$) and 50 to 115 μm ($0.40 < R^2 > 0.60$). Above 115 μm , $R^2 < 0.40$ and so fewer of these particles are likely to have been phytoplankton. To estimate the number concentration of particles present, the particle volume concentrations of the LISST-C size classes were converted to particle number concentrations by assuming spherical particles of median diameter for each class. To estimate how many of the particles were phytoplankton, the particle number concentrations were multiplied by the R^2 value for each class. Phytoplankton concentrations were up to $3.6 \times 10^7 \text{ l}^{-1}$

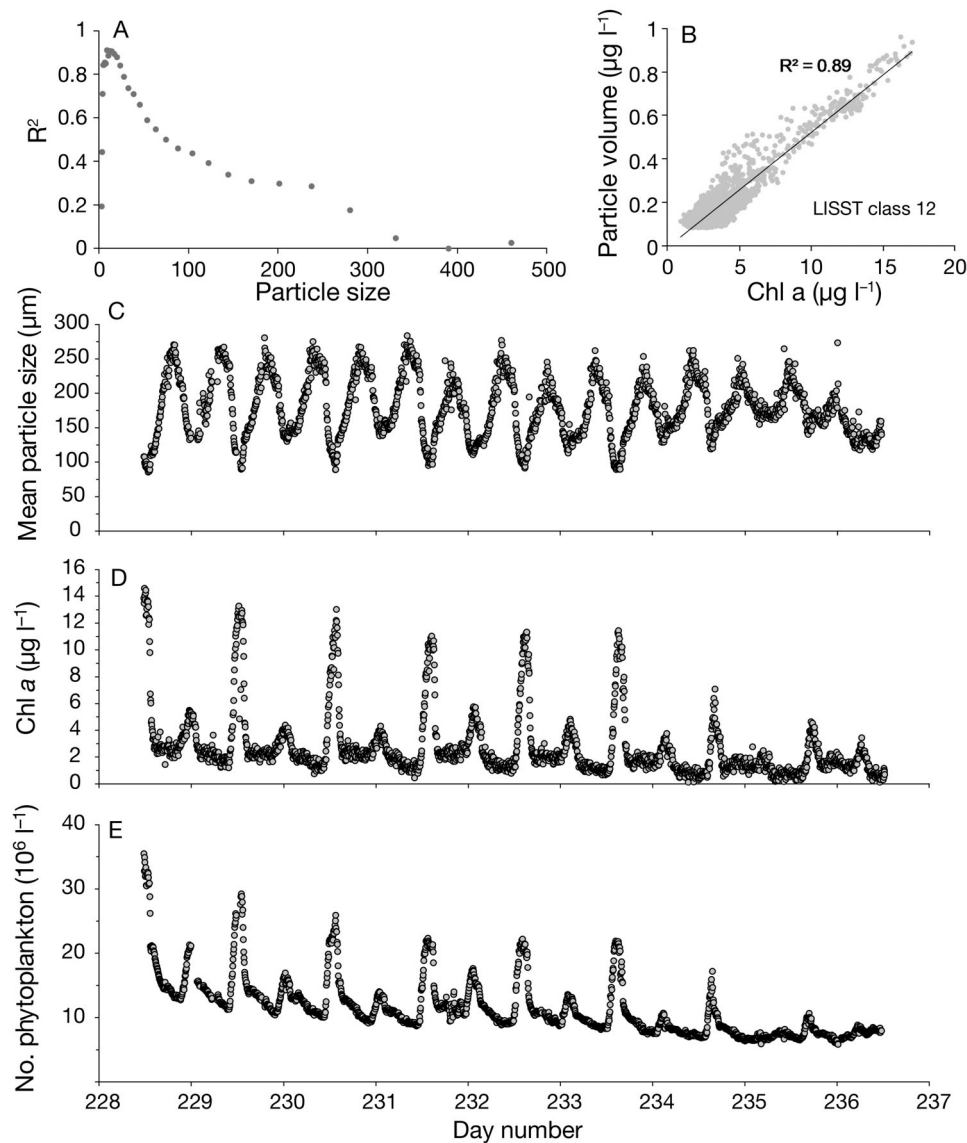


Fig. 5. The characteristics of the chl *a*-bearing species suggest they are diatoms or dinoflagellates. (A) The chl *a* concentration was correlated with total particle volume for each LISST-100X class for the whole mooring period. High correlation coefficients (R^2) indicate that most of the particulate material in the particular size class is phytoplankton. (B) Example correlation between chl *a* and total particle volume, which is for LISST-100C class 8 (class range 8–9.5 μm) and had $R^2 = 0.89$. (C–E) Time series of mean particle size, chl *a* and number of phytoplankton. Mean particle size varies with tidal advection, and lowest mean particle sizes are associated with the phytoplankton bloom (with high chl *a*). Each daytime chlorophyll peak is higher than both adjacent nighttime peaks, and the mean particle size is smaller (compare troughs in C with peaks in D)

at the westward extent of the observations (start of the measurement period, Fig. 5E); hence, phytoplankton were in a bloom.

A large peak in chl *a* (over 10 mg l^{-1}) occurred at the end of each morning flood tide (Fig. 5D; for flood tide Fig. 4). The chl *a* peaked just after noon on the first day and progressively later on subsequent days. There was a second, smaller peak in chl *a* (3 to 4 mg l^{-1}) at the end of the evening flood tide. Both these peaks were consistent with a bloom to the south-west being advected with the tide, producing maximum chl *a* at the mooring at the end of the flood. It is unlikely that the nighttime peak is smaller because of fluorescence quenching effects; instead, particle size and volume data suggest fewer diatoms and dinoflagellates were present at nighttime flood slack, and chl *a* magnitudes were commensurately lower.

Photic zone and the phytoplankton bloom

Irradiance profiles were taken on the day after spring tides (Day 229) and the day of neap tides (Day 235). For most of those 2 d, the photic zone at the mooring location was the whole water depth (Fig. 6C,D); where the ratio of photic depth: water depth was >1 , irradiance was still $>1\%$ of the surface irradiance at the seafloor. The attenuation coefficient, K_d , integrated over the visible light spectrum (400 to 700 nm), varied between 0.35 and 0.5 during most of that measurement period (Fig. 6A,B). The exception was on Day 229, when the algal bloom traveled past the mooring on a spring flood tide (first period highlighted in blue). With the algal bloom present, K_d approximately doubled to 0.75–0.95 (Fig. 6A) and the photic zone decreased to the top half of the water depth. At that time, a high number of phytoplankton were measured in the bloom (up to $2.9 \times 10^7 \text{ l}^{-1}$; Fig. 5E). There was also a greater proportion of organic material (possibly phytoplankton) closer to the surface than the bed (Fig. 6E). This suggests that the numbers of phytoplankton nearer the surface were attenuating light sufficiently to constrain the photic zone to the top half of the water col-

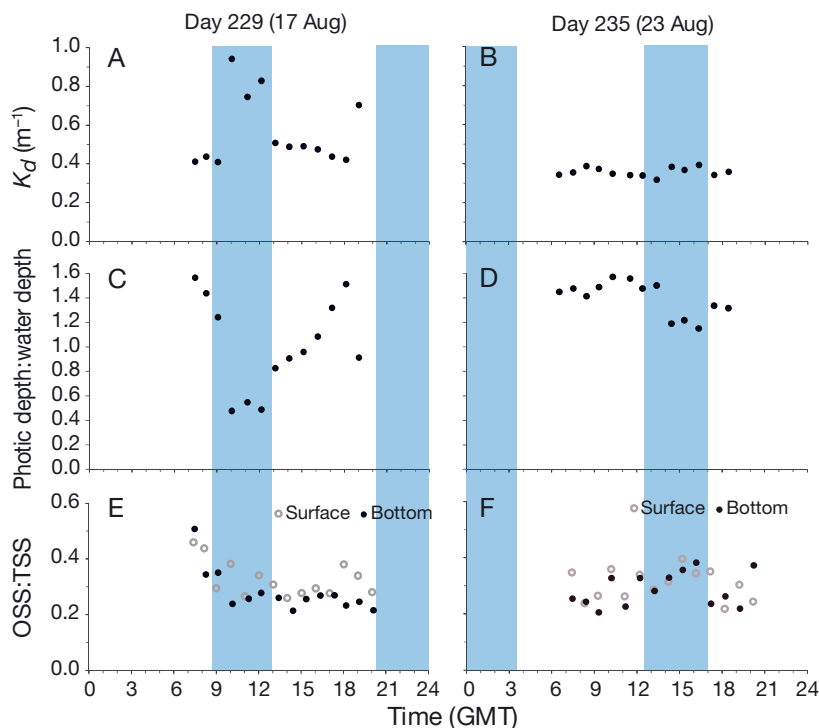


Fig. 6. (A,B) Irradiance attenuation coefficients (K_d) derived from TriOS Ram-ses irradiance profiles. (C,D) Ratio of photic depth to water depth. Where the ratio is >1 , irradiance at the seafloor is $>1\%$ of the surface irradiance. (E,F) Ratio of organic suspended sediment (OSS) to total suspended sediment (TSS) mass concentrations. These were taken at 1.5 m below the water surface and 1.5 m above the seafloor. Algal blooms were present in the periods highlighted in blue

umn. On the other flood tide when irradiance was measured (last period highlighted in blue), the bloom did not travel as far past the measurement location, and consequently fewer phytoplankton passed the mooring (up to $1.1 \times 10^7 \text{ l}^{-1}$; Fig. 5E). This smaller concentration of phytoplankton had less effect on K_d than the first flood tide measured; K_d increased to just 0.49 and the photic zone still encompassed the whole water column (compare Fig. 6B & D). The proportion of the organic fraction of suspended material increased when the bloom was present at the mooring location, but there was little difference in proportion between the surface and bottom waters (blue section, Fig. 6F).

Chl *a* record predicted with vertical migration

The chl *a* concentration south-west of the mooring is represented by a Gaussian curve, though the exact shape is not critical to the solution. If the position of the centre of the bloom in the channel is x_C and the

position of the mooring is x_M , then the chlorophyll concentration measured at the mooring is given by:

$$c = c_0 \exp[-a(x_M - x_C)^2] \quad (3)$$

where c_0 is the concentration of chlorophyll in the centre of the bloom and a sets the size of the bloom. The position of the centre of the bloom, x_C moves with the tide and the residual flow, which varied with the tidal current amplitude A as:

$$u_R = \beta A^2 \quad (4)$$

with a representative $\beta = 0.1 \text{ m s}^{-1}$. With this residual flow and no vertical migration, the bloom moved steadily away from the mooring. The chl a at the mooring rapidly decreased and did not return on subsequent tides, but passed away with the ebb (Fig. 7B). Vertical migration was then imposed. Cells began migrating on cue of sunrise at approximately

05:00 h BST (start of the white sections, Fig. 7). They migrated at constant speed, upwards until noon and then downwards until sunset (ca. 19:00 h; start of the black sections). On that course, the cells migrated 5 m up and 5 m down at $195 \mu\text{m s}^{-1}$ (0.7 m h^{-1}). This would be high for individual diatoms moving buoyantly in the Menai Strait (Table 2), but achievable if they were aggregated into colonies or if the dinoflagellate blooms noted by Ewins & Spencer (1967) and Lucas (1982) prevailed. Kamykowski et al. (1988) show these dinoflagellates could easily have swimming speeds of 100 to 500 $\mu\text{m s}^{-1}$. The cells had a net motion in the flood direction, almost compensating the residual flow (Fig. 7C,D). This matched the annual observations (Fig. 2C). After the first day, the scenario of cells achieving successful swims in the strait underestimated the chl a pattern (compare Fig. 7A & C), but the scenario of cells swimming successfully in

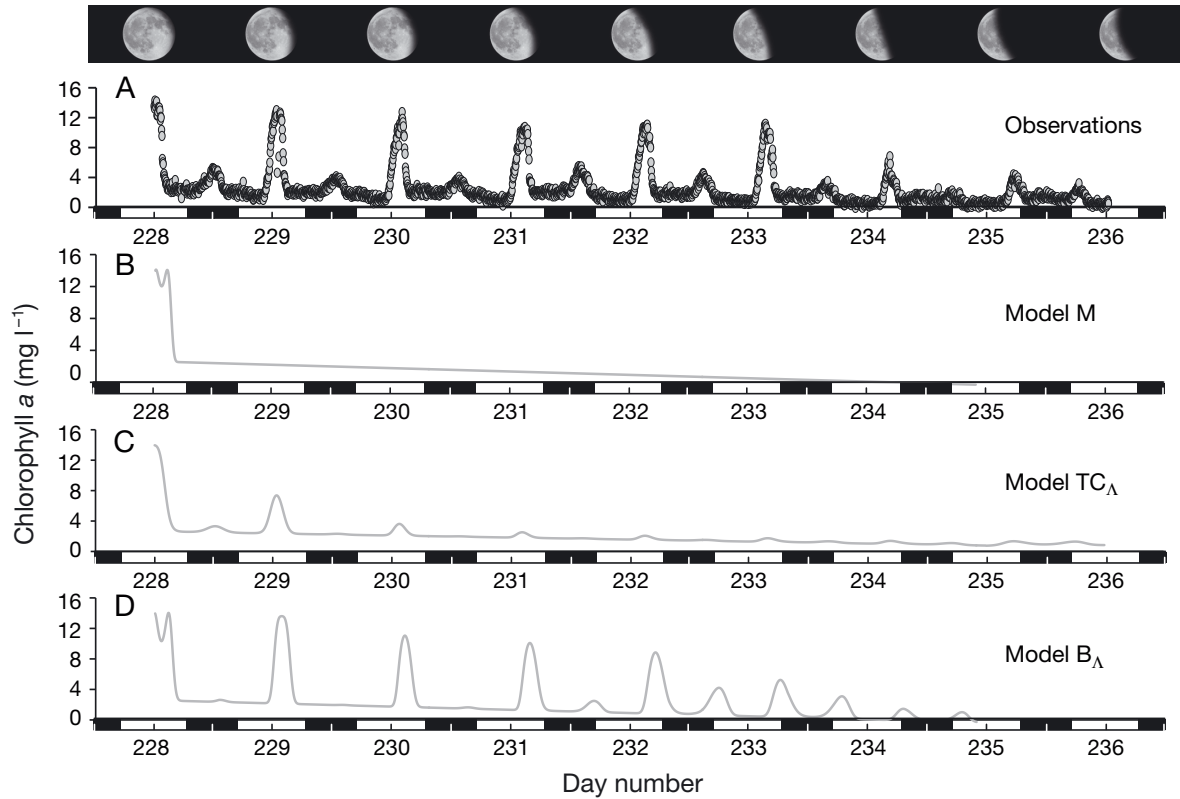


Fig. 7. (A) Observed chl a : 5 min average values from a YSI CTD moored in the centre of a 34.5 km long channel between 16 and 24 August 2011. The CTD was 1.5 m above the bed of the strait, in a mean of 10 m water depth and recorded at 60 s intervals. (B–D) Time series of chl a output from 3 models of a phytoplankton bloom advecting in a tidal channel. In model M, the phytoplankton were always vertically mixed. They left the mooring site with the residual flow on the first tide (leaving the Menai Strait in about 1 d). In model TC_A , the phytoplankton had a triangular wave diurnal vertical migration in the tidal channel and bay, and in model B_A the same migration happened in Caernarfon Bay only (cf. Fig. 1B). In both scenarios, the phytoplankton bloom resisted the residual flow and the chl a signal returned to the measurement location on 8 consecutive days. White and black tick marks indicate 00:00 and 12:00 h BST for that day. Nighttime periods (from sunset to sunrise) are highlighted in black on the x-axes and daytime in white. The phase of the moon is shown as tides varied from springs to neaps

Table 2. Sizes and achievable speeds (settling velocity, W_s) of diatoms with buoyant movement. Each taxon listed has been recorded to dominate the phytoplankton population in the Menai Strait in August of a given year (Table 1). Data derived from size data are from the original works where possible (see footnotes) or from the phytoplankton encyclopedia 'Phyto'pedia' (UBC 2012) where not. Recorded sizes and speeds of the same taxa in Southampton Water (south coast of UK) are given for comparison

Taxon	Size (μm)		W_s ($\mu\text{m s}^{-1}$) ^d		No. in colony
	Menai Strait ^{a,b,c}	Southampton Water ^d	Individual ^{d,f}	Colonial ^{f-i}	
<i>Astrionella</i> spp.	>10	30–150	7–18		
<i>Chaetoceros</i> spp.		10–40	2–85	0–20	
<i>Cylindrotheca</i>			2.5–8		
<i>Fragilaria</i> spp.	>10				
<i>Guinardia</i> spp.	25% <20 75% 20–200		6–50	3.8–18	
<i>Leptocylindrus danicus</i>	>10		5–16		
<i>Nitzschia</i> spp.	>10		6.3–17		
<i>Paralia sulcata</i>	>10				
<i>Phaeocystis pouchetti</i>	>190		0–15	>280	
<i>Rhizosolenia</i> spp.	>10	4–25	4–20	0.12–12	75–10000
<i>Skeletonema costatum</i>	>10	5–25	2–21	0–17	
<i>Thalassiosira</i> spp.		12–78	2–80	0–27	<540

^aKenchington (1970); ^bAl-Hasan et al. (1975); ^cBlight et al. (1995); ^dRoss (2004); ^eUBC (2012); ^fPeperzak et al. (2003); ^gMoore & Villareal (1996); ^hSkreslet (1988); ⁱSmayda & Boleyn (1965)

the bay only represented the chl *a* pattern well (compare Fig. 7A & D).

Minor effect of fluorescence quenching

Chlorophyll fluorescence is a mechanism for releasing excess light energy not needed for photosynthesis. In the daytime, solar light energy is more likely to be in excess of requirements for photosynthesis than at night. In consequence, fluorescence is quenched in the day when the plankton are flooded by light from the sun (Amesz & Fork 1967, Öquist et al. 1982). The nighttime chlorophyll peaks in the bay model infer that quenching was not a major contributory factor in the recorded chlorophyll time series. In that model output, the nighttime peaks were initially underestimated, but the final nighttime peaks were overestimated compared to the observations (Fig. 7D). Quenching would have caused all peaks to be underestimated.

Further evidence of the minor effect of quenching is in the LISST data. The time series of the volume of 7 to 21 μm particles at the mooring, in which phytoplankton were most likely to have been most abundant, show day–night differences in peak concentration consistent with the chl *a* record and the vertical migration mechanism of movement in the bay (Fig. 8A). In the first 6 d, the size class 21 to 50 μm had day–night differences in particle volume that

were generally less consistent with the chl *a* record, whereas in the last 2 d, the structure was more like the chl *a* record. This could be due to growth of the individual phytoplankton cells or species succession. In higher size classes (50 to 160 μm), the time series of particle volumes had a tidal advective pattern but no day–night pattern like the chl *a* pattern, and in the highest classes sizes measurable by the LISST (160 to 500 μm), the same advective signal was dominated by noise, indicating particles above 50 μm were predominantly non-algal (compare Fig. 4A with Fig. 8C & D). Additionally, fluorescence has a linear relationship with chl *a* from filtered samples. The alternative mechanism to quenching, explored herein, is that (1) both the difference in daytime and nighttime chl *a* peaks and (2) the retention of the bloom in the strait against the residual flow are consequences of diel vertical migration.

DISCUSSION

The essentials of the modelled mechanism are: (1) bottom friction creates a vertical shear in the tidal flow, with the fastest flow near the surface. A plankter will therefore experience a greater tidal velocity when it is near the sea surface than when it is deeper in the water. (2) The net horizontal movement over a day will then depend on the phase of the tide and the nature and timing of the cell's movements up and down.

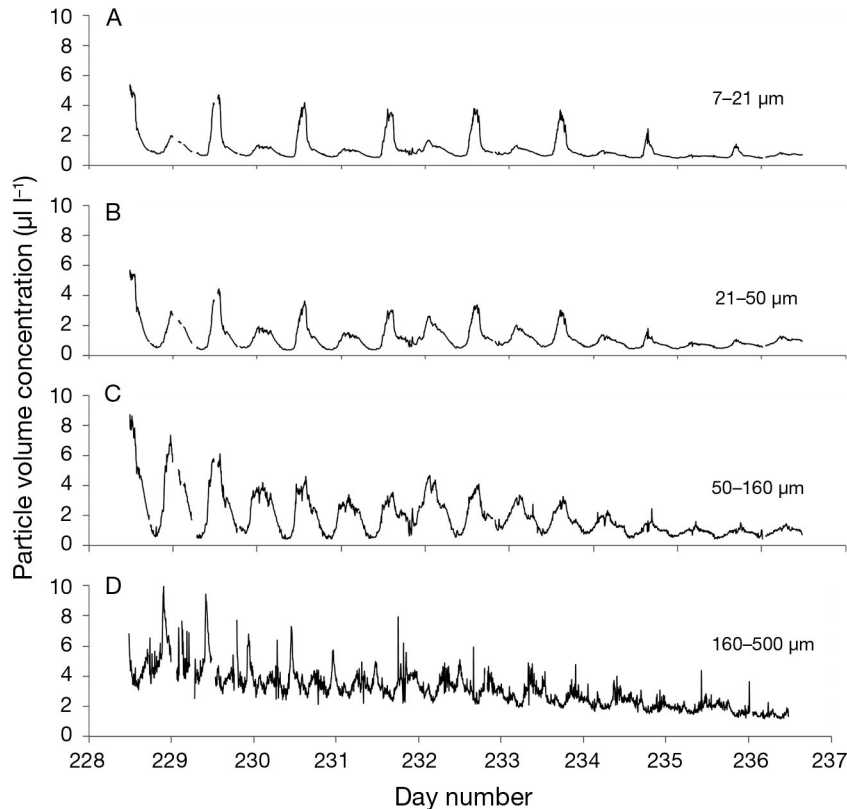


Fig. 8. Time series of total particle volume for 4 particle size classes. There was a large daytime peak and small nighttime peak in total particle volume between 7 and 21 μm corresponding to the end of the flood tide, in the same pattern as the chl *a* time series (compare Fig. 4A). Short breaks in the data occurred around the start of Day 229

Phytoplankton physiological effects on the theoretical results

Annual movements of phytoplankton communities were presented, and these movements hold for the case that the plankter can move up and down despite turbulent mixing (Fig. 2). To achieve this, the swimming timescale should be shorter than the mixing timescale, i.e. the ratio of timescales: the Péclet number, $Pe = WL/\kappa < 1$, where W is the vertical velocity scale, L the length scale of migration and κ the eddy diffusivity. Globally, many tidal channels are shallow (on the order of 10 m deep) and the full depth of water is mixed on the order of minutes to hours, associated with vertical velocities of a few percent of the tidal current speed (Rippeth et al. 2002). Typical migration speeds of diatoms (buoyant movers) and dinoflagellates (swimmers) cannot overcome the mixing. Commensurately, $Pe > 1$. However, blooms of dinoflagellates, normally mixed vertically by turbulence, can exhibit gradients in number concentra-

tion if aggregated into colonies. Bigger colonies (individual aggregates) move more effectively against turbulence than smaller ones. For instance, small colonies above 50 μm diameter move effectively with eddy diffusivities $< 7 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$ and colonies above 250 μm diameter move effectively with eddy diffusivities $< 10^{-2} \text{ m}^2 \text{ s}^{-1}$ (see section 5.5.2 of Ross 2004). Both of these eddy diffusivities lie in the range common to tidal channels (Lu et al. 2000). In consequence, if blooms contain colonies, the centre of gravity of the bloom can move up and down with a daily rhythm. The theoretical result is not limited to suitably strong swimmers.

The 2 ubiquitous limitations on using the annual theoretical migration patterns were natural channel lengths and phytoplankton community lifetimes. In site-specific or taxon-specific contexts, light availability and environmental pressures would provide further limiting factors. It is not the purpose of this paper to present model runs for specific scenarios; instead, previously published literature is referred to here for guidance. For the given latitude, the annual results (Fig. 2) hold if the community

moves between $h/4$ and $3h/4$ daily. That pattern is modified for weaker swimmers or deeper channels. The amplitude of the excursion (Fig. 2) decreases with smaller daily excursions. Diatoms moving buoyantly with the proposed model would not resist the residual flow. However, dinoflagellates clearly can when they are abundant in the Menai Strait (around April, occasionally in the summer).

Correspondence between observations and model output in the case study

At the observation site, high water spring tides occurred at the end of the flood tide, around noon. At springs, the flood tide lasted for 6.21 h before noon, and the ebb tide for 6.21 h after noon (Fig. 9). If a cell moves up and down in a symmetrical way before and after noon, it will spend an equal amount of time near the surface during flood and ebb tides (Fig. 9). The effects of the tide cancel, and there is no net move-

ment at spring tides. If there is a residual flow, the cell will move in the direction of this residual. Now consider a time shortly after spring tides, when the end of the flood occurs in the afternoon. For illustration, let the end of the flood occur at 15:00 h. The timing of the vertical migration now makes all the difference. If the cell chooses to spend 10 h near the surface, centred on noon, it will experience 6 h of flood and 4 h of ebb (Fig. 9) when it is near the surface—so an excess of 2 h of flood tide when near the surface. In the same day, it will also experience an extra 2 h of ebb tide when at depth, but because the surface currents are faster there will be a net movement, over the day, in the flood direction. This motion will therefore enable a cell in a tidal channel with residual flow towards the ebb direction to make headway against (or at least resist) the residual flow in the days after spring tides. It is proposed that this happened in the case study of the Menai Strait, and could happen for other tidal channels with similar properties (chiefly a quiescent bay at the ebb end, a velocity profile with constant gradient and spring tide slack water approximately at noon). It can be shown in the same way that if the cell spends more than 12 h near the surface there will be a net movement in the ebb tide direction. This explains why the triangular wave motion (which limits the time spent

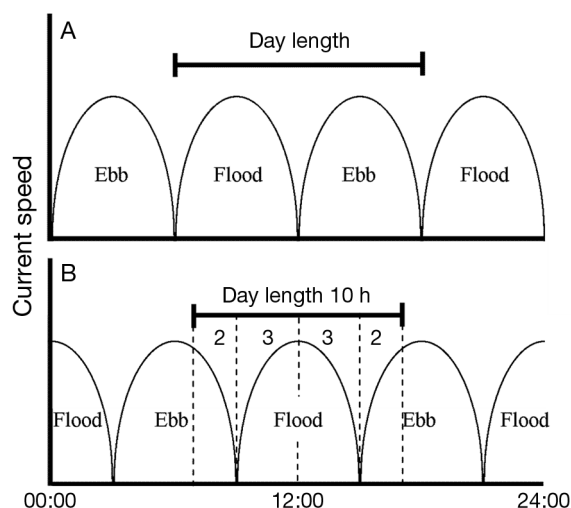


Fig. 9. There is net movement of phytoplankton in the flood direction with day length < 12 h. (A) For the example of the Menai Strait, spring flood slack water occurs at noon. Any day length covers equal amounts of ebb and flood flow and there is no net movement, however (B) after spring tide there is net movement in the flood direction. More of the daytime is during ebb flow, and whilst more of the nighttime is during flood flow, the phytoplankton are lower in the water column where tidal flow is slower. The example in (B) is 3 d after spring tides with peak flood around noon

near the surface) is a better mode of motion than the square wave for producing net movement in the flood direction. For buoyant movers, the more rapid the change from positive to negative buoyancy, the more effective the resistance to the residual flow. Since for colonial diatoms this change in sense of buoyancy requires the colony to break up (which can be achieved quickly; Ross 2004), the triangular-like movement patterns are likely, so long as buoyant movement overcomes turbulence. Note again that the bay model is preferred for the particular case study because the key there is migration above and below a sill, not migration dependent on an excursion of the phytoplankton up and down.

The vertical migration model presented in this paper represents a plausible mechanism for explaining the observed chlorophyll record. Unfortunately, there are no measurements of chlorophyll in Caernarfon Bay to confirm the presence of a bloom there. Instead, it is inferred from observations that the chlorophyll concentration at the mooring increased at the end of the flood tides. The existence of the bloom, however, is the only reasonable inference from this evidence. The values of 14 mg l^{-1} chlorophyll recorded at the start of the observation period are high for blooms in that particular strait (Al-Hasan et al. 1975, Blight et al. 1995). Other motile chl *a*-bearing species (chiefly seaweed and zooplankton) are not abundant in the water column of the strait. Suspension of microphytobenthos is also not the cause. Suspension above the mooring height followed by subsequent settling would result in 2 peaks per tide, whereas just 1 peak per tide occurred. Suspension as high as the mooring location (but not past it) would cause 1 peak that was in phase with maximum shear, but each peak was in phase with flood tide slack water.

Unfortunately, there were no observations that phytoplankton migrated vertically; the model study was undertaken opportunistically because of the puzzle presented by the chlorophyll observations. It is not possible to confirm vertical migration from a record of chlorophyll taken near the sea bed; the assumption is that species known to migrate vertically in the strait at this time of year for more than 50 yr were again present (Table 1). However, near the start of the observation period there had been a greater proportion of organic mass closer to the water surface than the seafloor at the end of the flood tides, and that was not true near the end of the observation period (compare Fig. 6E & F). This suggests the possibility of the tidal channel model TC_A enhancing the bay model B_A at the start of the observation period.

The ecological diversity and commercial opportunities within tidal channels can be dramatically enhanced by the supposed mechanism of diel vertical migration countering a residual flow. Furthermore, many tidal channels are likely to have a residual flow causing throughput of water and non-motile particulates in days or even hours. Whilst non-migrating phytoplankton will not establish themselves in the channel, those with optimum vertical migrations do. By chance virtue of doing so, they take advantage of nutrients in tidal channels, which are in short supply offshore. Therefore, natural retention of high phytoplankton abundances promotes high commercial yields in tidal channels. This is especially true of near-sedentary species such as cockles, mussels and oysters, which cannot follow phytoplankton to adjacent water bodies. Since the ability to overcome a residual flow depends critically on the nature and timing of vertical migration, the mechanism contributes to the succession of phytoplankton species and their predators in tidal channels. Non-migratory species that necessarily move out of tidal channels with advection (often in just a few days) would normally find their fate in the water body they move into, be that of growth, death or dispersal. However, migratory species that remain in tidal channels or even re-enter them twice daily, probably find their fate in the tidal channel. Tidal channels with vertically-migrating phytoplankton are likely to be abundant in zooplankton, bivalves and other predators, in turn enriching those particular tidal channel ecosystems. In contrast, non-migrating phytoplankton more likely enrich water bodies downstream of tidal channels, promoting ecological diversity there.

CONCLUSIONS

(1) In a tidal channel, phytoplankton can maintain their position or move against a residual flow if they migrate vertically with a daily rhythm. How the phytoplankton move along the channel depends on the vertical migration, especially the phase of the tide and time spent near the water surface.

(2) A simple model of phytoplankton migration in a tidal channel accorded with observations of chlorophyll for 8 consecutive days. A phytoplankton bloom above 10^7 plankton per litre occurred downstream of a mooring, from which observations were made. The bloom advected into and back out of the mooring location on each flood tide, and at the time of each flood tide, peaks in chlorophyll were observed.

(3) The phytoplankton number concentration near the centre of the bloom caused significant attenua-

tion of light, with maximum phytoplankton numbers (and chlorophyll levels) being associated with a doubling of the attenuation coefficient. Where phytoplankton were most abundant, and attenuation highest, the photic zone covered the top half of the 10 m deep channel. In this fact, there is an associated need for diel vertical migration, on top of common optimisation strategies for light and against predation. Away from the bloom, the photic zone encompassed the whole water depth.

(4) Chlorophyll peaks at night were one-quarter to one-third the magnitude of chlorophyll peaks during the day. Chlorophyll peaks recurred for 8 consecutive days. These patterns are in contrast to the movement of well-mixed particles, which pass through the channel used to make observations in 2 d. Both the day–night asymmetry and the sustained presence of chlorophyll were explained by allowing for vertical migration of the phytoplankton and constraining the period during which they were near the surface.

(5) Regressions between chl *a* and particle size indicated that phytoplankton were most abundant in the size range 7 to 21 μm . Judging by historical occurrences of phytoplankton in the tidal channel used for observations, they were almost certainly diatoms existing as individuals or small colonies.

(6) Tidal channels that retain phytoplankton against a residual flow can be more diverse ecologically than channels without this retention mechanism. Channels that retain phytoplankton can be prime sites for commercial farming of bivalves.

(7) The natural timings of some phytoplankton blooms in tidal channels are controlled by the nature of the migration. Although a by-product of vertical migration, longer residence in the tidal channel affords the phytoplankton more nutrients than phytoplankton that advect offshore.

(8) Annually, phytoplankton can migrate or effectively resist a residual flow by up to hundreds of kilometres, effectively limited by the natural length of a tidal channel or the duration of existence of a phytoplankton bloom.

Acknowledgements. Special thanks to Gwyn Parry Jones and Peter Hughes of Bangor University and the captain and crew of the Caernarfon Harbour Trust vessel MV 'Seiont IV' for help with fieldwork. The Conwy Centre kindly allowed the filtering in their boat house. Peter Hughes set up the instruments and downloaded the raw data. Catherine Mitchell and Roseanne Clement kindly undertook a portion of data processing. Oliver Ross and Stephanie Wilson gave helpful advice on dinoflagellate swimming and predation, and the comments of 3 anonymous reviewers have helped the manuscript. The work was funded by the UK Natural Environment Research Council grant NE/H022090/1.

LITERATURE CITED

- Agrawal Y, Pottsmith H (2000) Instruments for particle size and settling velocity observations in sediment transport. *Mar Geol* 168:89–114
- Al-Hasan RH, Coughlan SJ, Pant A, Fogg GE (1975) Seasonal variations in phytoplankton and glycolate concentrations in the Menai Straits, Anglesey. *J Mar Biol Assoc UK* 55:557–565
- Amesz J, Fork DC (1967) Quenching of chlorophyll fluorescence by quinines in algae and chloroplasts. *Biochim Biophys Acta* 143:97–107
- Baker SM, Levinton JS (2003) Selective feeding by three native North American freshwater mussels implies food competition with zebra mussels. *Hydrobiologia* 505: 97–105
- Blight SP, Bently TL, Lefevre D, Robinson C, Rodrigues R, Rowlands J, Williams PJLeB (1995) Phasing of autotrophic and heterotrophic plankton metabolism in a temperate coastal ecosystem. *Mar Ecol Prog Ser* 128:61–75
- Cohen RRH, Dresler PV, Phillips EJP, Cory RL (1984) The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. *Limnol Oceanogr* 29:170–180
- Cullen JJ, Horrigan SG (1981) Effects of nitrate on the diurnal vertical migration, carbon to nitrogen ratio, and the photosynthetic capacity of the dinoflagellate *Gymnodinium splendens*. *Mar Biol* 62:81–89
- Eppeley RW, Holm-Hansen O, Strickland JDH (1968) Some observations on the vertical migration of dinoflagellates. *J Phycol* 4:333–340
- Ewins PA, Spencer CP (1967) The annual cycle of nutrients in the Menai Straits. *J Mar Biol Assoc UK* 47:533–542
- Greenwood N, Forster RM, Créach V, Painting SJ and others (2012) Seasonal and interannual variation of the phytoplankton and copepod dynamics in Liverpool Bay. *Ocean Dyn* 62:307–320
- Harvey J (1968) The flow of water through the Menai Straits. *Geophys J R Astron Soc* 15:517–528
- Hill AE (1991a) A mechanism for horizontal zooplankton transport by vertical migration in tidal currents. *Mar Biol* 111:485–492
- Hill AE (1991b) Vertical migration in tidal currents. *Mar Ecol Prog Ser* 75:39–54
- Jones M, Spencer CP (1970) The phytoplankton of the Menai Straits. *J Cons Int Explor Mer* 33:169–180
- Kamykowski D, McCollum SA, Kirkpatrick GJ (1988) Observations and a model concerning the translational velocity of a photosynthetic marine dinoflagellate under variable environmental conditions. *Limnol Oceanogr* 33:66–78
- Kenchington RA (1970) An investigation of the detritus in Menai Straits plankton samples. *J Mar Biol Assoc UK* 50: 489–498
- Lu Y, Lueck RG, Huang D (2000) Turbulence characteristics in a tidal channel. *J Phys Oceanogr* 30:855–867
- Lucas IAN (1982) Observations on *Noctiluca scintillans* Macartney (Ehrenb.) (Dinophyceae) with notes on an intracellular bacterium. *J Plankton Res* 4:401–409
- Malham SK, Cotter E, O'Keeffe S, Lynch S and others (2009) Summer mortality of the Pacific oyster, *Crassostrea gigas*, in the Irish Sea: the influence of temperature and nutrients on health and survival. *Aquaculture* 287: 128–138
- Moore JK, Villareal TA (1996) Size-ascent rate relationships in positively buoyant marine diatoms. *Limnol Oceanogr* 41:1514–1520
- Öquist G, Hagström A, Alm P, Samuelson G, Richardson K (1982) Fluorescence as an alternative method for establishing primary production. *Mar Biol* 68:71–75
- Peperzak L, Colijn F, Koeman R, Gieskes WWC, Joordens JCA (2003) Phytoplankton sinking rates in the Rhine region of freshwater influence. *J Plankton Res* 25: 365–383
- Pugh DT (1987) Tides, surges and mean sea-level. John Wiley & Sons, Chichester
- Rippeth TP, Williams E, Simpson JH (2002) Reynolds stress and turbulent energy production in a tidal channel. *J Phys Oceanogr* 32:1242–1251
- Ross ON (2004) Algal motility in variable turbulence. PhD thesis, University of Southampton
- Shumway SE, Cucci TL, Newell RC, Yentsch CM (1985) Particle selection, ingestion, and absorption in filter-feeding bivalves. *J Exp Mar Biol Ecol* 91:77–92
- Simpson JH, Forbes AMG, Gould WJ (1971) Electromagnetic observations of water flow in the Menai Strait. *Geophys J R Astron Soc* 24:245–253
- Simpson JH, Berx B, Gascoigne J, Saurel C (2007) The interaction of tidal advection, diffusion and mussel filtration in a tidal channel. *J Mar Syst* 68:556–568
- Skreslet S (1988) Buoyancy in *Phaeocystis pouchetii* (Hariot) Lagerheim. *J Exp Mar Biol Ecol* 119:157–166
- Smayda TJ, Boleyn BJ (1965) Experimental observations on the flotation of marine diatoms. I. *Thalassiosira* cf. *nana*, *Thalassiosira rotula* and *Nitzschia seriata*. *Limnol Oceanogr* 10:499–509
- Smith NP, Stoner AW (1993) Computer simulation of larval transport through tidal channels: role of vertical migration. *Estuar Coast Shelf Sci* 37:43–58
- UBC (2012) Phyto'pedia—the phytoplankton encyclopaedia project. University of British Columbia, Vancouver, BC, www.eos.ubc.ca/research/phytoplankton/
- Wildish DJ, Kristmanson DD (1984) Importance to mussels of the benthic boundary layer. *Can J Fish Aquat Sci* 41: 1618–1625

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Submitted: July 8, 2013; Accepted: May 17, 2014
Proofs received from author(s): August 6, 2014