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

Running head: Phytoplankton position maintained against 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 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 three to four 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 two days. 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.

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 and Harrington, 1981; Ross, 2004). Some move by swimming and others by changes in buoyancy. Although vertical migration is slow (typically less than 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 e.g. 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 per day (Hill, 1991a; 1991b; Smith & Stoner, 1993).

Tidal channels are shallow, narrow sea straits or creeks connecting two 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 two ends (Pugh, 1987). The water in the channel flows back and forth with the 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 & Levington, 2003). The physical mechanisms which 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 two scenarios. Firstly the migration can happen in the tidal channel. However in a second scenario 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 phytoplankter 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 the first of January. It moves relative to this position for a year, 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 plankter 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 very good swimmers, which spend much more time at their 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:

$$u_s = A\sin(\omega(t-\phi)) \qquad (1)$$

where A is the amplitude of the current, ω is the angular frequency of the main lunar semi diurnal tide (period 12.4 hours), 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 springs neaps cycle, with $A = 1$ 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 and 18:06 – 00:13 on a day of spring tides.

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

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

where z is depth below the surface and h is total water depth. The cell migrates between depth $z = \frac{h}{4}$ during the day (or at noon in the triangle wave forcing) and $z = \frac{3h}{4}$ 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). The phytoplankton also go down 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 $z = \frac{3h}{4}$ at midnight at the start of day 1 (January 1st). With square wave migration, the cell spent all hours of darkness at depth $z = \frac{3h}{4}$ and all daylight hours at $z = \frac{h}{4}$. When day length was greater than 12 hours, between the spring and autumn equinoxes, the cell moved in the negative (ebb) x-direction. When day length was less than 12 hours, 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 months, or of order 1 or 2 km per day. A cell could maintain 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 Figure 2 is for a tidal channel at approximately 48° latitude, with 16 hours 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 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 is less than 12 hours (4 km day^{-1}) and slowing down considerably as the day length increases in summer (to 0.4 km day^{-1}). As in the square wave migration pattern, the motion is temporarily reversed within the springs-neaps cycle, consistent with Smith and Stoner (1993). The motion as modelled by Hill (1991a; 1991b) 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 two-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 greater than 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 two bays: Caernarfon Bay in the south-west and Conwy Bay in the north-east. There is a sand bar (Caernarfon Bar) at the southwest end, which spans more than half the channel width and dries out at low tide. The main channel of the strait varies between 200 – 800 m in width and 6 – 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, 1967; Simpson et al., 1971). The residual flow varies with the springs-neaps cycle (faster at springs) and averages approximately 0.1 m s^{-1} (Simpson, 1971), replacing the water in the strait roughly every 3 days. 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 per tide) 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 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 (c. 83 % of the phytoplankton population in 2002 - 2009; Greenwood et al., 2012), in at least one past year flagellates have dominated (Ewins & Spencer, 1967).

The Menai Strait is home to intensive commercial farming of bivalves, primarily mussels. At 23 – 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 Liverpool Bay. Grazing less than 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 μm s^{-1} (0.072 m hr^{-1}) and movements of colonies (individual aggregated groups) could be on the order of hundreds of μm s^{-1} (or m hr^{-1}).

Mooring deployments, profiling and instrument setup

An instrumented mooring was deployed in the central part of the Menai Strait for nine days, starting on August 16th 2011 (day 228). The mooring was sited at 04°12.71'west, 53°12.14' north in a mean depth of approximately 10 m (Fig. 3). The site is 16 km eastward of the sill separating the strait from Caernarfon Bay to the south west (south sands sill, Fig. 3). Irradiance profiles were taken on August 17th and 23rd, 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 Sequioa LISST-100X for particle size distributions and an upward-looking Workhorse Sentinal 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 using a calibrated Turner 10AU fluorometer. These chlorophyll data were used to calibrate the CTD fluorescence record. LISSTs measure light scattered by particles in suspension (Agrawal & Pottismith, 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 – 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 ends of the first flood tides (and high waters) were at 12:10 and 00:31. 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 (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 chlorophyll a concentration measured by the fluorometer 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 7 – 21 μm where the coefficient of regression, $R^2 > 0.89$ (Fig. 5A). Secondary groups of phytoplankton were in the ranges 21 – 50 μm ($0.60 < R^2 > 0.89$) and 50 – 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 3.6×10^7 L^{-1} at the westward extent of the observations (start of the measurement period, Fig. 5E), hence phytoplankton were in a bloom.

A large peak in chlorophyll a (over 10 mg L^{-1}) occurred at the end of each morning flood tide (Fig. 5D; for flood tide Fig. 4). The chlorophyll a peaked just after noon on the first day and progressively later on subsequent days. There was a second smaller peak in chlorophyll a (3 – 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 chlorophyll a at the mooring at the end of the flood. It is unlikely that the night-time peak is smaller because of fluorescence quenching effects; instead particle size and volume data suggest fewer diatoms and dinoflagellates were present at night time flood slack and chlorophyll a magnitudes were commensurately lower.

The 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 two days the photic zone at the mooring location was the whole water depth (Fig. 6C & D). In those two figures, where the ratio of photic depth : water depth is greater than 1, irradiance is still greater than 1 % of the surface irradiance at the seafloor. The attenuation coefficient, K_d integrated over the visible light spectrum (400 – 700 nm), varied between 0.35 – 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 half the water depth (the top half). At that time a high number of phytoplankton were measured in the bloom (up to 2.9×10^7 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 column. On the other flood tide when irradiance was measured (last period highlighted in blue), the bloom travelled less far past the measurement location and consequently fewer phytoplankton passed the mooring (up to 1.1×10^7 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 was still the whole water column (compare Figs 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).

Chlorophyll a record predicted with vertical migration

The chlorophyll 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

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

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

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

with a representative $\beta = 0.1$ m s^{-1}. With this residual flow and no vertical migration, the bloom moved steadily away from the mooring. The chlorophyll 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 BST (start of the white sections, Fig. 7). They migrated at constant speed, upwards until noon and then downwards until sunset (approx 19:00; start of the black sections). On that course the cells migrated 5 m up and 5 m down at 195 μm s^{-1} (0.7 m hr^{-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 e.g. Ewins and Spencer (1967) and Lucas (1982) prevailed. Kamykowski et al. (1988) show these dinoflagellates could easily have swimming speeds of 100 – 500 μm 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 chlorophyll a pattern (compare Fig. 7A & C) but the scenario of cells swimming successfully in the bay only, represented the chlorophyll 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; Oquist et al., 1982). The night time 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 night time peaks were initially underestimated but the final night time 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 – 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 chlorophyll a record and the vertical migration mechanism of movement in the bay (Fig. 8A). In the first six days the size class 21 – 50 μm had day-night differences in particle volume that were generally less consistent with the chlorophyll a record but in the last two days the structure was more like the chlorophyll a record. This could be due to growth of the individual phytoplankton cells or species succession. In higher size classes (50 – 160 µm) the time series of particle volumes had a tidal advective pattern but no day-night pattern like the chlorophyll a pattern, and in the highest classes sizes measurable by the LISST (160 – 500 µm) the same advective signal was dominated by noise, indicating particles above 50 µm were dominantly non-algal (compare Fig. 4A with Fig. 8C & D). Additionally fluorescence has a linear relationship with chlorophyll a from filtered samples. The alternative mechanism to quenching, explored herein, is that (1) both the difference in daytime and night time chlorophyll 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 that (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.

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, $Pe = \frac{WL}{\kappa}$ is less than one, where W is the vertical velocity scale; L the length scale of migration; κ the eddy diffusivity. Globally, many tidal channels are shallow (order 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 concentration 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 less than 7×10^{-4} m^2 s^{-1} and colonies above 250 μm diameter move effectively with eddy diffusivities less than 10^{-2} m^2 s^{-1} (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 two 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 lots of 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 $\frac{h}{4} - \frac{3h}{4}$ 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 hours before noon and the ebb tide 6.21 hours after noon (Fig. 9). If a cell moves up and down in a symmetrical way before and after noon, it will spend equal times near the surface during flood and ebb tides (Fig. 9). The effects of the tide cancel and there is no net movement 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. The timing of the vertical migration now makes all the difference. If the cell chooses to spend 10 hours near the surface, centred on noon, it will experience six hours of flood and 4 hours of ebb (Fig. 9) when it is near the surface, so an excess of 2 hours of flood tide when near the surface. In the same day, it will also experience an extra 2 hours 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 hours 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 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 chlorophyll 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 two peaks per tide, but there was just one peak per tide. Suspension as high as the mooring location (but not past it) would cause one 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 taken that species known to migrate vertically in the strait at this time of year for more than fifty years 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 infers the possibility of the tidal channel model TC$_\Lambda$ enhancing the bay model B$_\Lambda$ 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, they take advantage of nutrients in tidal channels, which are in short supply offshore. So, 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 fate 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 eight 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 attenuation 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 was 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 eight consecutive days. These patterns are in contrast to the movement of well mixed particles, which pass through the channel used to make observations in two days. 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 chlorophyll a and particle size indicated that phytoplankton were most abundant in the size range 7 – 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.

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Environment Research Council grant NE/H022090/1.

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LIST OF FIGURE CAPTIONS

Figure 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 four stages of the year. The water surface is at $z = 0$, the seafloor at $z = h$ and each day the phytoplankton move between $\frac{h}{4}$ and $\frac{3h}{4}$, 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 on that day.

Figure 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 panel 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 two spring-neap periods where phytoplankton move oppositely to the long term trend, associated with falling and low-amplitude current.

Figure 3. Location and geometry of the tidal channel case study. (A) England and Wales. The Menai Strait (red box) is between the isle of Anglesey and mainland Wales, UK. (B) Map of the tidal channel. The bounding red box corresponds with the red box in (A). The instruments were moored at the position of the orange diamond. (C) Bathymetric section 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. Three red arrows indicate sill-like features at the western end of the strait.

Figure 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 (August 16th – 24th).

Figure 5. Characteristics of the chlorophyll a-bearing species suggest they are diatoms or dinoflagellates. (A) The chlorophyll 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 chlorophyll 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, chlorophyll 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 chlorophyll a). Each daytime chlorophyll peak is higher than both adjacent night time peaks and the mean particle size is smaller too (compare troughs in C with peaks in D).

Figure 6. (A & B) Irradiance attenuation coefficients derived from TriOS Ramses irradiance profiles. (C & D) The ratio of photic depth to the water depth. Where the ratio is greater than one, irradiance at the seafloor is greater than 1 % of the surface irradiance. (E & F) Ratio of

organic suspended sediment to total suspended sediment mass concentrations. These were taken at 1.5 m below the water surface and 1.5 m above the seafloor.

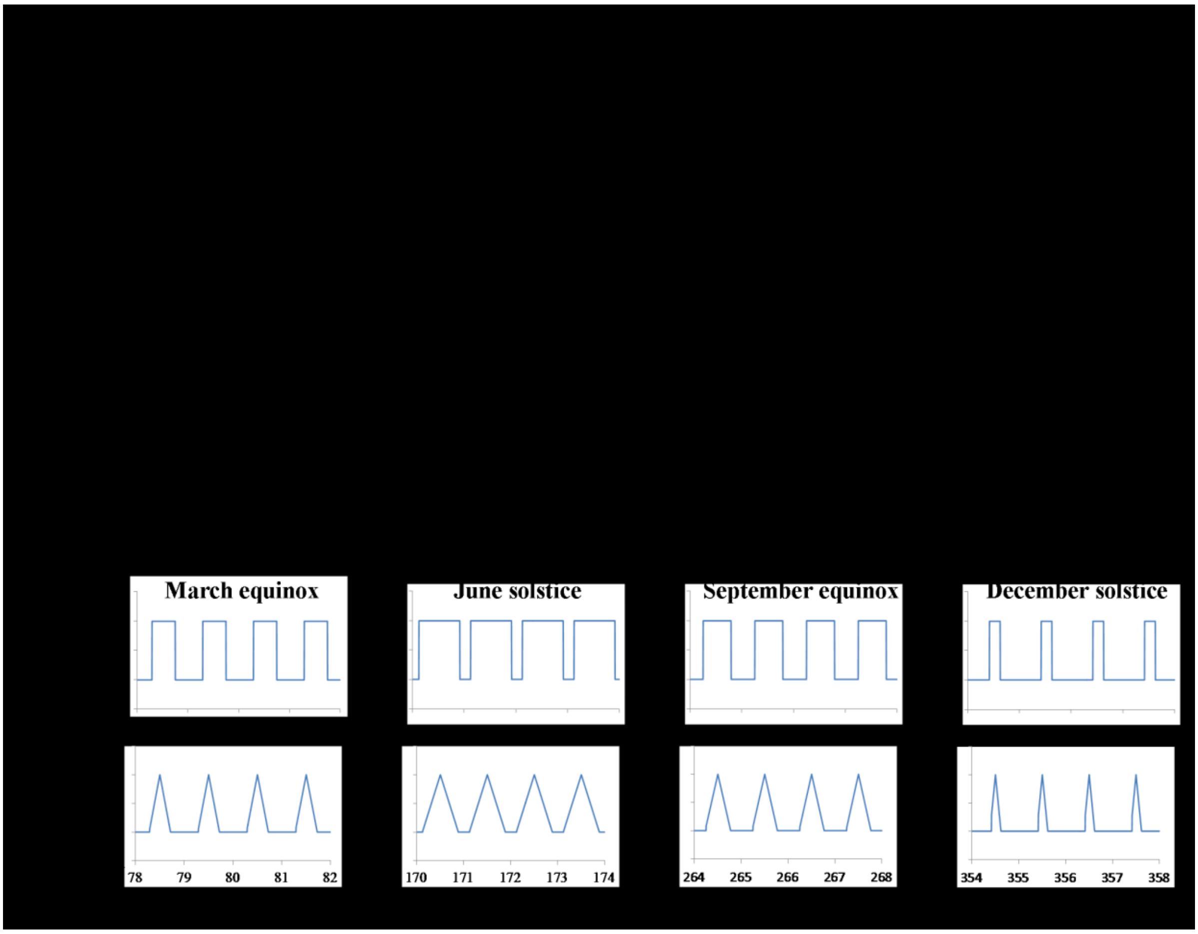
Figure 7. (A) Observed chlorophyll a: five minute average values from a YSI CTD moored in the centre of a 34.5 km long channel between August 16th – 24th 2011. The CTD was 1.5 m above the bed of the strait, in a mean of 10 m water depth and recorded at 60 s intervals. (B – D) Time series of chlorophyll a output from three 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 a day). In model TC_Λ the phytoplankton had a triangular wave diurnal vertical migration in the tidal channel and bay, and in model B_Λ the same migration happened in Caernarfon bay only (cf. Fig. 1B). In both scenarios the phytoplankton bloom resisted the residual flow and the chlorophyll a signal returned to the measurement location on eight consecutive days. White and black tick marks indicate 00:00 and 12:00 BST for that day. Night time 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.

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

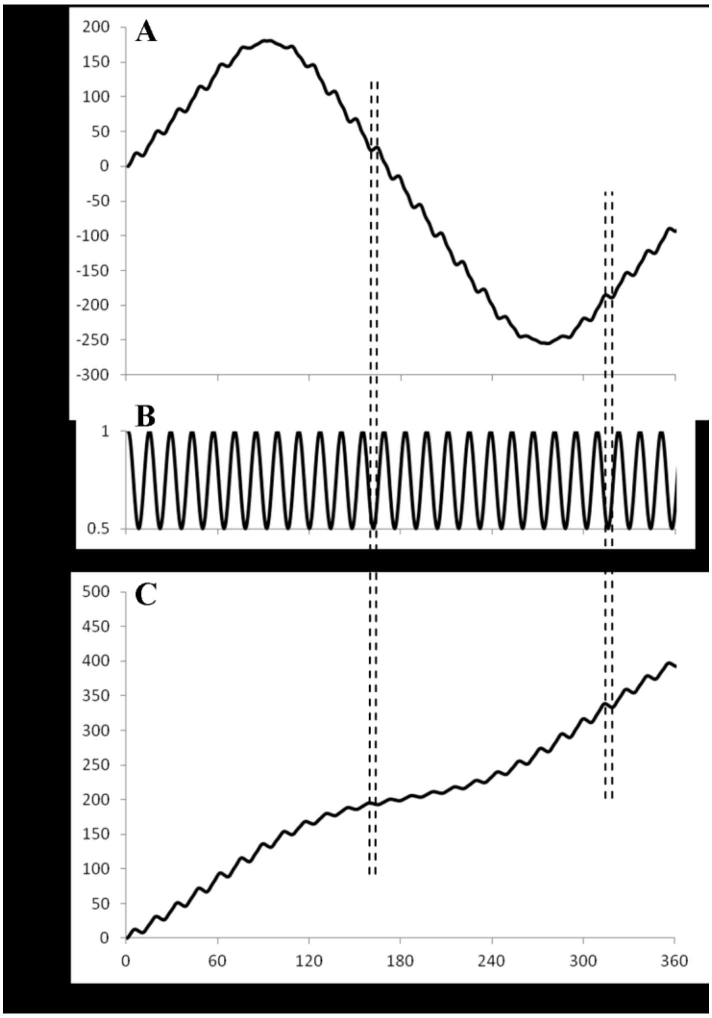
Figure 9. There is net movement of phytoplankton in the flood direction with day length less than twelve hours. (A) For the example of the Menai Strait, spring flood slack water occurs at noon. Any day length covers equal amounts of ebb and flood flow and there is no net movement, however (B) after spring tide there is net movement in the flood direction. More

of the daytime is during flood flow, and whilst more of the night time is during ebb flow, the phytoplankton are lower in the water column where tidal flow is slower. The example in B is three days after spring tides with peak flood around noon.

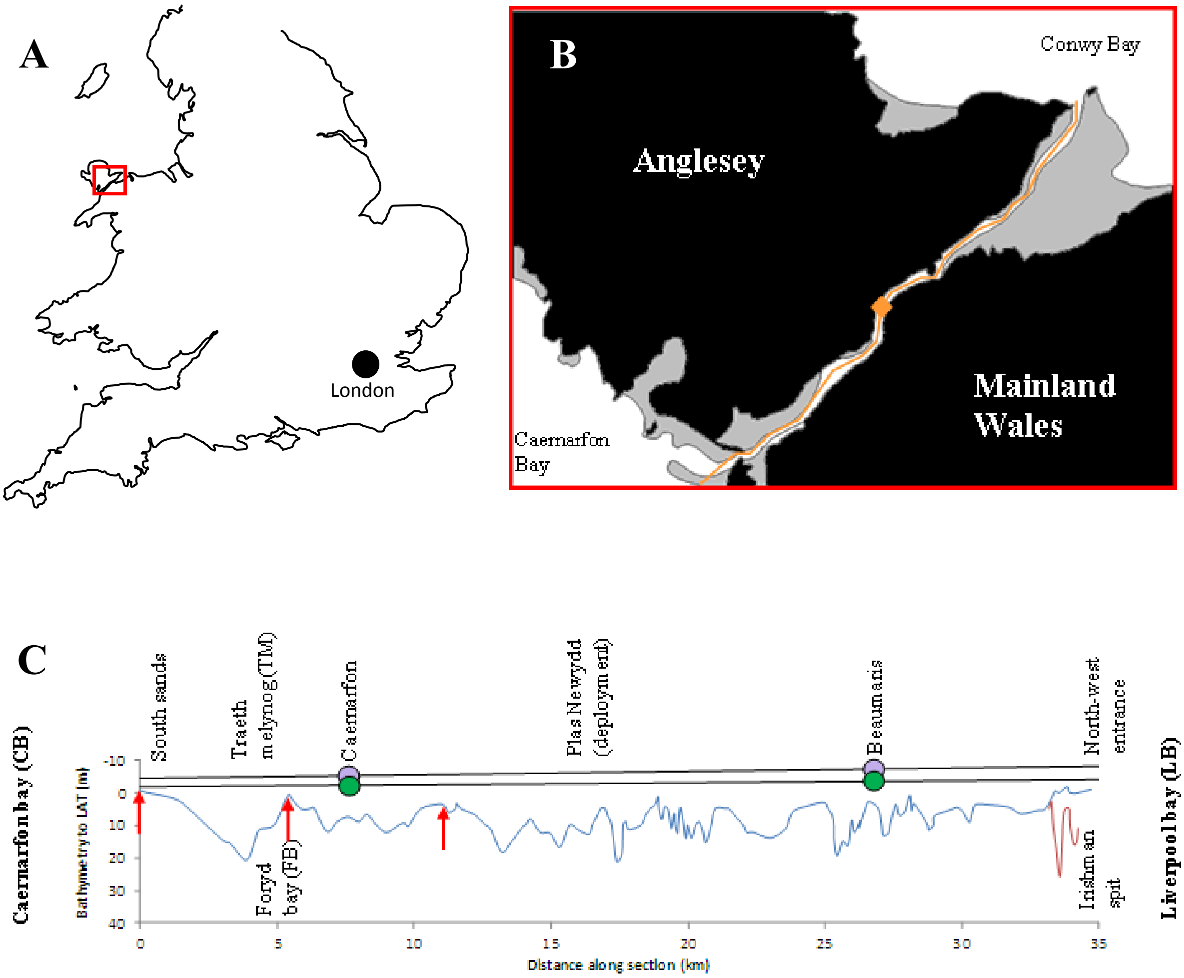
FIGURES



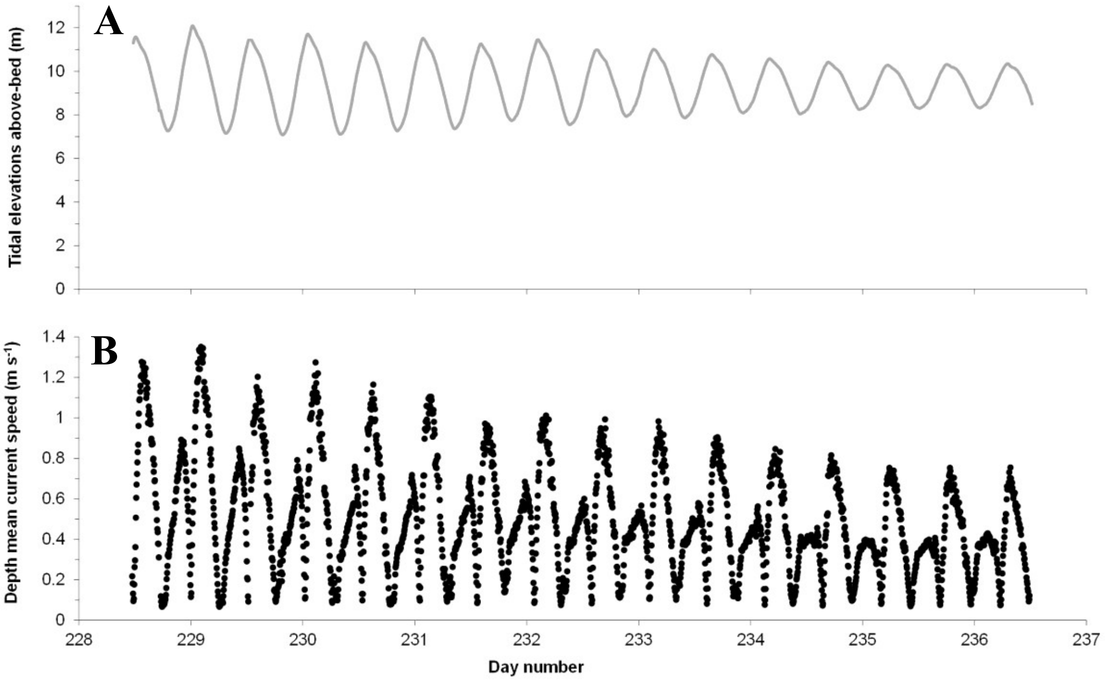
(Figure 1)


A
200
150
100
50
0
-50
-100
-150
-200
-250
-300
B
1
0.5
C
500
450
400
350
300
250
200
150
100
50
0
0
60
120
180
240
300
360

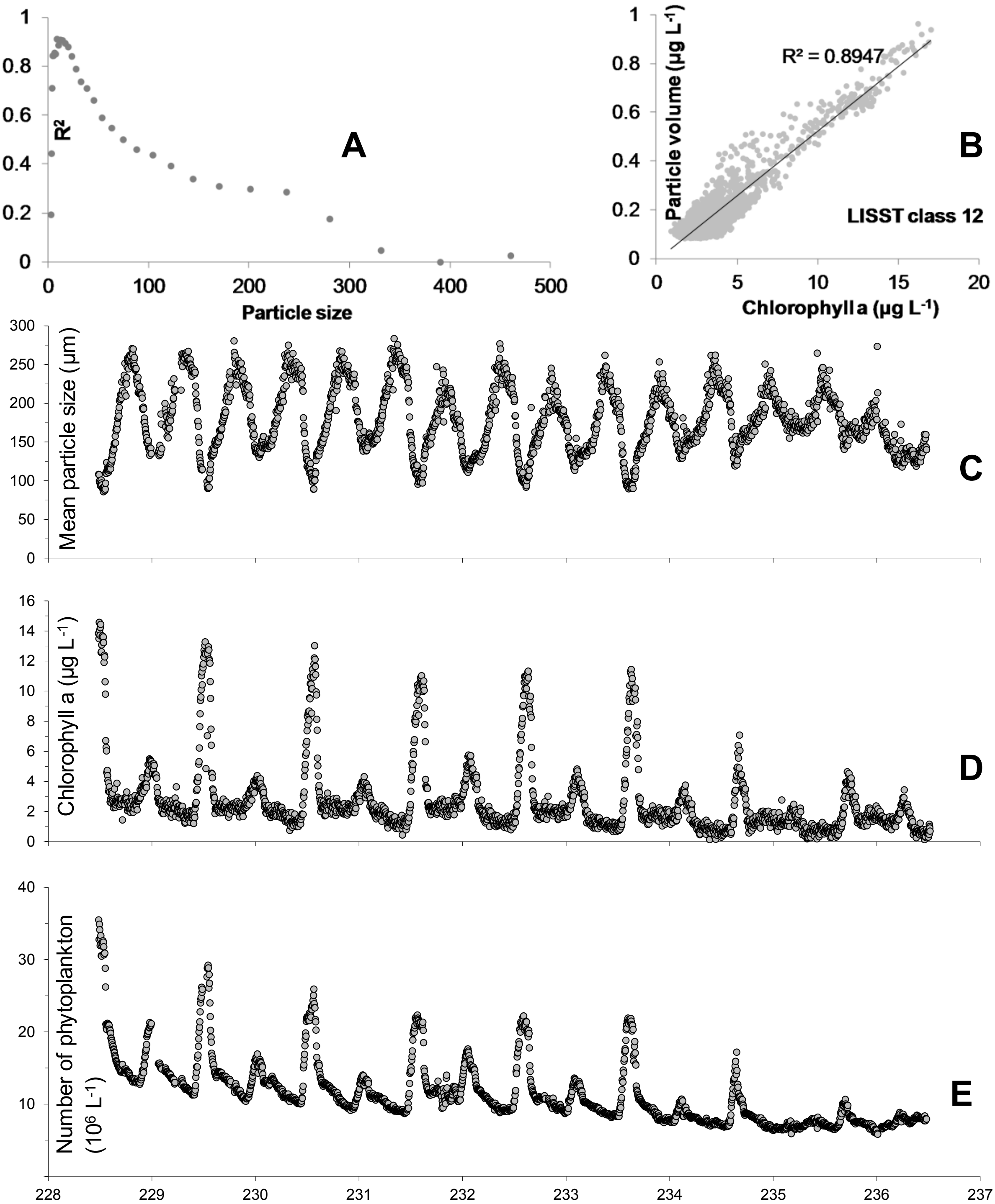
(Figure 2)


A
London
B
Anglesey
Conwy Bay
Mainland Wales
Caernarfon Bay
C
Caernarfon bay (CB)
South sands
Traeth melynog (TM)
Caernarfon
Plas Newydd (deployment)
Beaumaris
North-west entrance
Liverpool bay (LB)
Bathymetry to LAT (m)
-10
0
10
20
30
40
Foryd bay (FB)
Irishman spit
0
5
10
15
20
25
30
35
Distance along section (km)

(Figure 3)

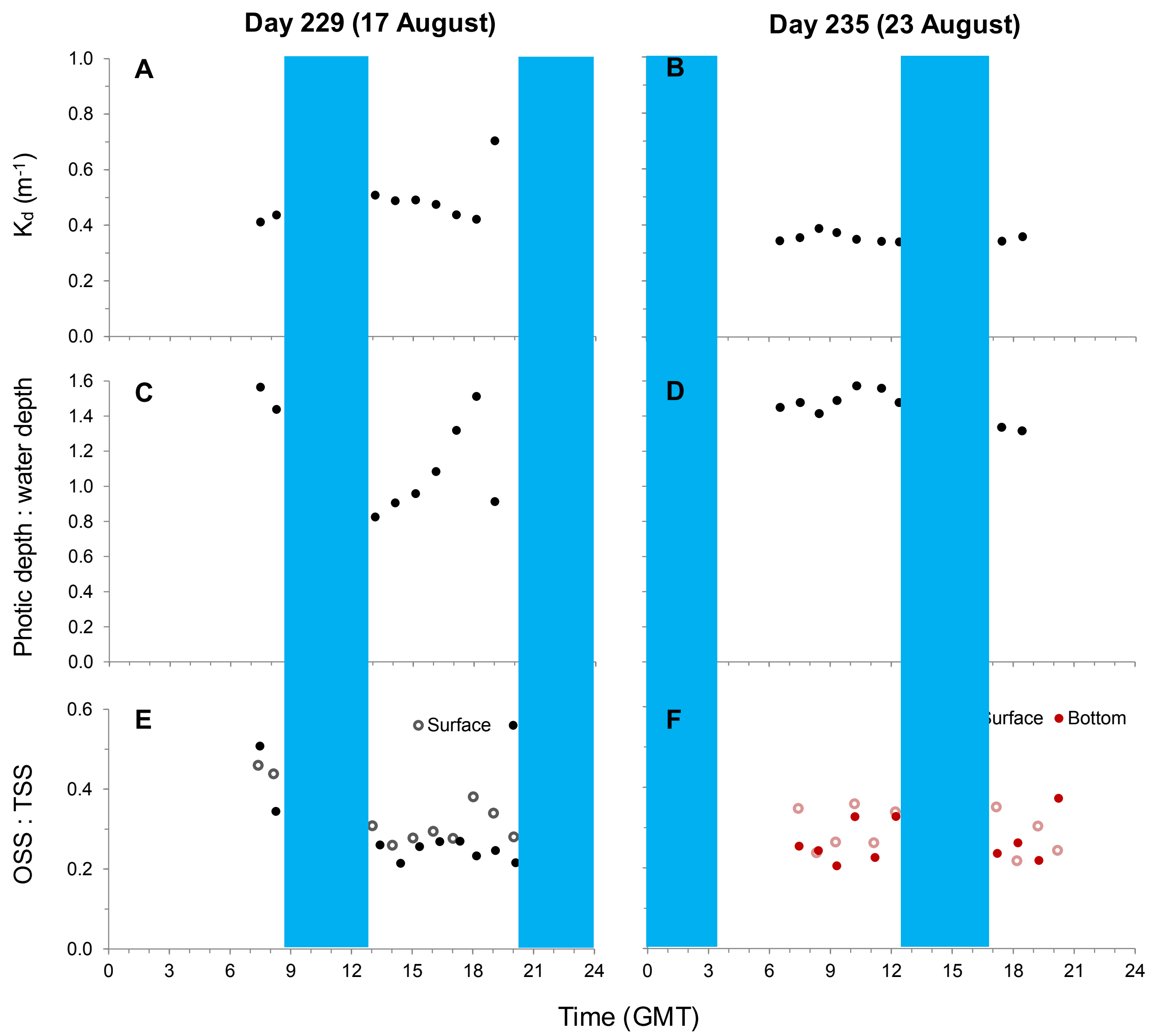

A
Tidal elevations above-bed (m)
0
2
4
6
8
10
12
B
Depth mean current speed (m s^{-1})
0
0.2
0.4
0.6
0.8
1
1.2
1.4
228
229
230
231
232
233
234
235
236
237
Day number

(Figure 4)

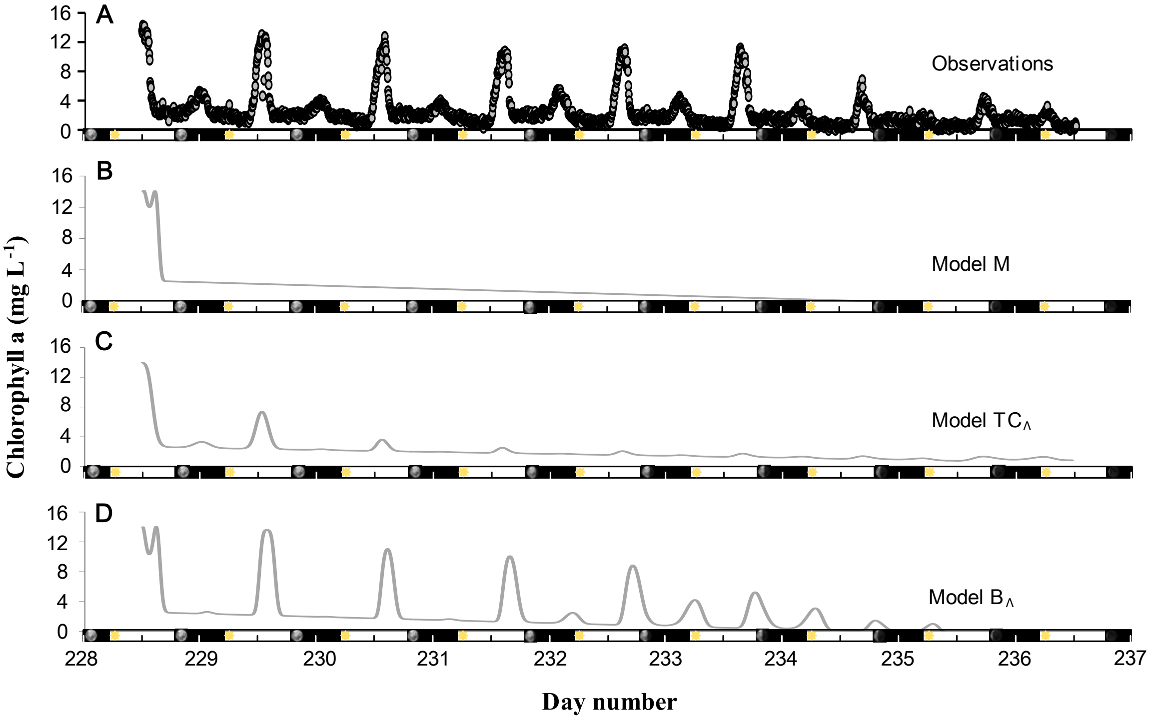


A
R²
1
0.8
0.6
0.4
0.2
0
0
100
200
300
400
500
Particle size
B
Particle volume (µg L⁻¹)
R² = 0.8947
LISST class 12
1
0.8
0.6
0.4
0.2
0
0
5
10
15
20
Chlorophyll a (µg L⁻¹)
C
Mean particle size (µm)
300
250
200
150
100
50
0
D
Chlorophyll a (µg L⁻¹)
16
14
12
10
8
6
4
2
0
E
Number of phytoplankton (10⁶ L⁻¹)
40
30
20
10
228
229
230
231
232
233
234
235
236
237

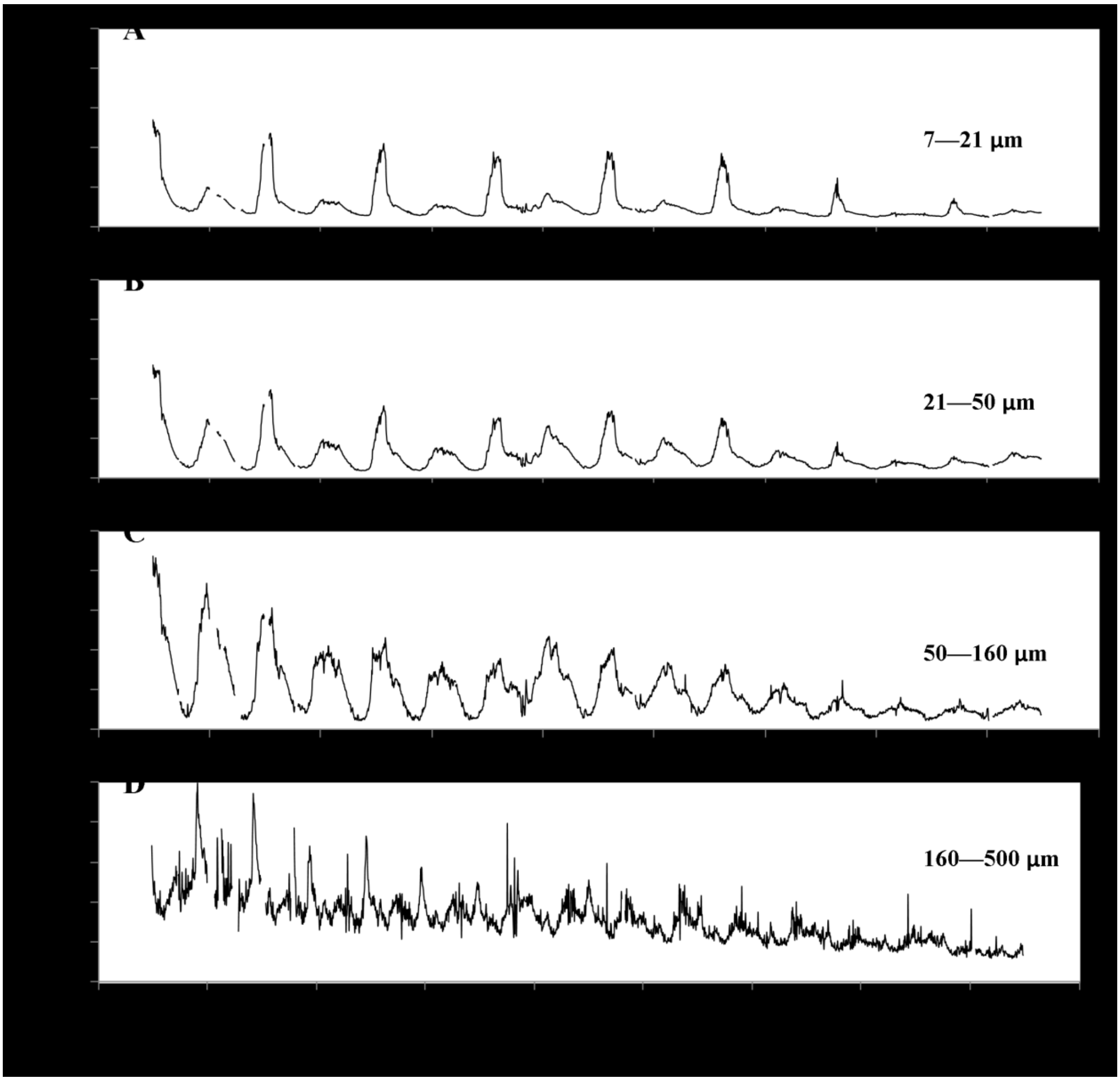
(Figure 5)


Day 229 (17 August)
Day 235 (23 August)
A
B
C
D
E
F
K_d (m^{-1})
Photic depth : water depth
OSS : TSS
Surface
Surface
Bottom
Time (GMT)
1.0
0.8
0.6
0.4
0.2
0.0
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.6
0.4
0.2
0.0
0
3
6
9
12
15
18
21
24

(Figure 6)


A
Observations
B
Model M
C
Model TC$_\Lambda$
D
Model B$_\Lambda$
16
12
8
4
0
Chlorophyll a (mg L^{-1})
228
229
230
231
232
233
234
235
236
237
Day number

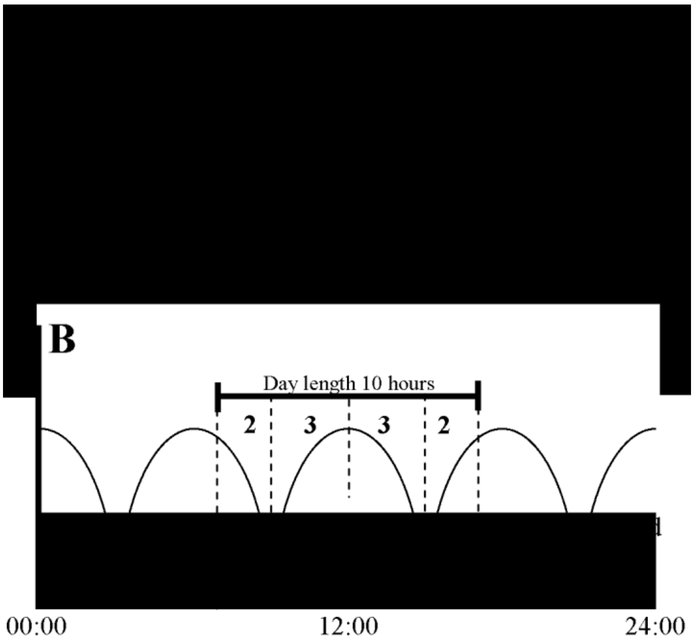
(Figure 7)



(Figure 8)

[redacted]

[redacted]



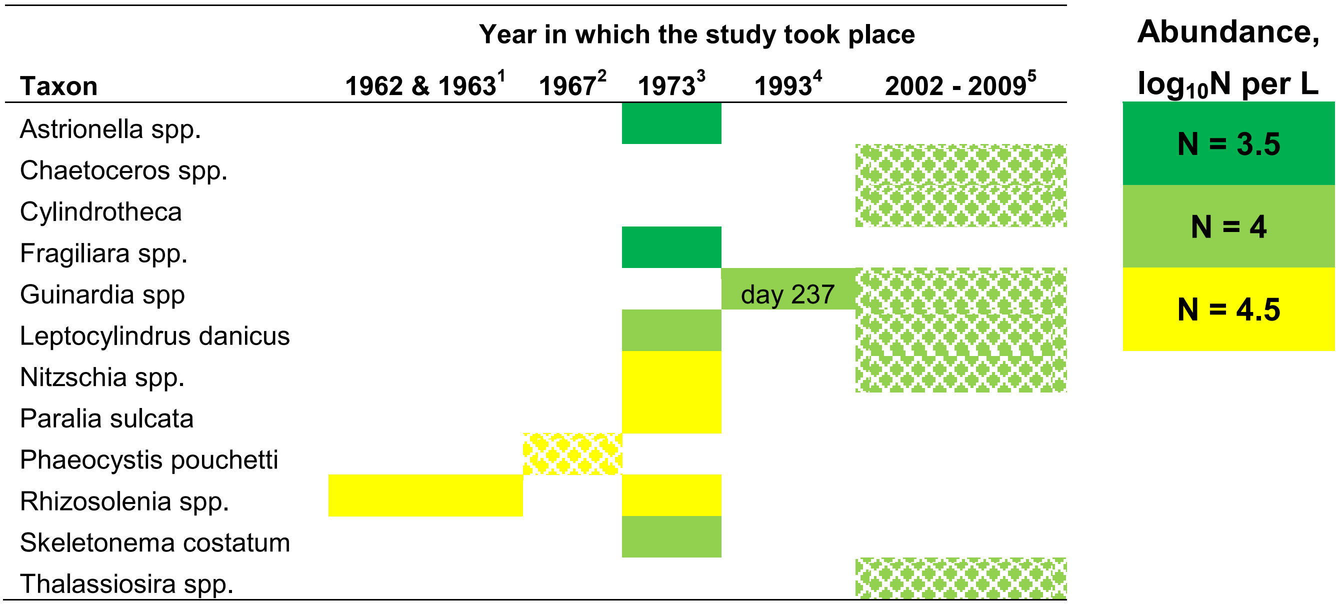
(Figure 9)

LIST OF TABLE CAPTIONS

Table 1. Taxons that dominated phytoplankton populations in August of a given year. Colour code gives their abundance. Data are derived from [1]Jones & Spencer 1970, [2]Kenchington 1970, [3]Al-Hasan et al. (1975), [4]Blight et al. (1995), [5]Greenwood et al. (2012). The data represented by white hatching are calculated from volumetric concentrations by inferring spherical-equivalent diameters.

Table 2. Sizes and achievable speeds of diatoms with buoyant movement. Each of the taxons listed has been recorded to dominate the phytoplankton population in the Menai Strait in August of a given year (Table 1). Data derived from [1]Kenchington (1970), [2]Al-Hasan et al. (1975), [3]Blight et al. (1995), [4]Ross (2004), [5]UBC (2012), [6]Perperzak et al (2003), [7]Moore & Villareal (1996), [8]Skreslet (1988), [9]Smeyda & Boleyn (1965). Size data are from the original works where possible or from the phytoplankton encyclopedia “phyto’pedia” where not (UBC 2012). Recorded sizes and speeds of the same taxons in Southampton Water are given for comparison.

TABLES



Taxon	1962 & 1963[1]	1967[2]	1973[3]	1993[4]	2002 - 2009[5]
	Year in which the study took place				
Astrionella spp.			🟩		
Chaetoceros spp.					▩
Cylindrotheca					▩
Fragiliara spp.			🟩		
Guinardia spp				▤ day 237	▩
Leptocylindrus danicus			▤		▩
Nitzschia spp.			🟨		▩
Paralia sulcata			🟨		
Phaeocystis pouchetti		▨			
Rhizosolenia spp.	🟨		🟨		
Skeletonema costatum			▤		
Thalassiosira spp.					▩

Abundance, $\log_{10}N$ per L
🟩 **N = 3.5**
▤ **N = 4**
🟨 **N = 4.5**

(Table 1)

Taxon	Size (µm) Menai Strait[1,2,3]	Southampton water[4]	Phyto'pedia[5]	W_s[4] (µm s^{-1}) Individual[4,6]	Colonial[7-9]	Number in colony
Astrionella spp.	> 10	30 - 150	7 - 18			
Chaetoceros spp.		10 - 40	2 - 85	0 - 20		
Cylindrotheca			2.5 - 8			
Fragiliara spp.	> 10					
Guinardia spp	25 % <20 75 % 20 - 200		6 - 50	3.8 - 18		
Leptocylindrus danicus	> 10		5 - 16			
Nitzschia spp.	> 10			6.3 - 17		
Paralia sulcata	> 10					
Phaeocystis pouchetti	> 190			0 - 15	> 280	
Rhizosolenia spp.	> 10	4 - 25	4 - 20	0.12 - 12	28 - 2200	75 - 10000
Skeletonema costatum	> 10	5 - 25	2 - 21	0 - 17		
Thalassiosira spp.		12 - 78	2 - 80	0 - 27	< 540	

(Table 2)