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

3

4 Running head: Phytoplankton position maintained against residual flow

5

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14 **KEY WORDS**

15 Chlorophyll a, diel vertical migration, tidal channel, phytoplankton particle size, Menai Strait

16

17 **ABSTRACT**

18

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

36

37 **INTRODUCTION**

38

39 Vertical migration with a daily rhythm is a characteristic of many plankton.
40 Phytoplankton travel upwards with daylight (light ascent) and downwards as daylight is lost,
41 whilst zooplankton have the opposite sense of migration (dark ascent) (Eppley et al., 1968;

42 Cullen and Harrington, 1981; Ross, 2004). Some move by swimming and others by changes
43 in buoyancy. Although vertical migration is slow (typically less than 1 mm s^{-1}) compared to
44 flow speeds (typically 100s to 1000s mm s^{-1}), the combination of vertical migration and a
45 vertical shear in horizontal current speed can lead to significant horizontal transport of
46 organisms. For example, if a plankter is high in the water column during the day with a tidal
47 current flowing e.g. eastward, and sinks at night into weaker currents flowing westward, there
48 is a net movement towards the east over a tidal cycle. That movement can be up to several
49 km per day (Hill, 1991a; 1991b; Smith & Stoner, 1993).

50 Tidal channels are shallow, narrow sea straits or creeks connecting two larger bodies
51 of water. For a relatively short channel compared to the tidal wavelength, the tidal flow is
52 driven by the difference in water level between its two ends (Pugh, 1987). The water in the
53 channel flows back and forth with the period of the tide at the ends of the channel; maximum
54 flow occurs when the level difference is greatest and slack tide when the levels are the same.
55 Because the gradient in the water surface can be large, fast turbulent flows are characteristic
56 of many tidal channels. Differences in friction on the flood and ebb tides in the channel can
57 lead to a residual current.

58 Phytoplankton are the major food source for commercial bivalve species such as
59 cockles, mussels and oysters living in tidal channels (Cohen et al., 1984; Wildish &
60 Kristmanson, 1984; Simpson et al., 2007; Malham et al., 2009). Commercial bivalves can
61 feed selectively on light-ascending species (Shumway et al., 1985; Baker & Levington,
62 2003). The physical mechanisms which can retain phytoplankton blooms in tidal channels
63 (against a residual flow) would tend to improve commercial yields. The retention of
64 phytoplankton (as primary producers) also potentially improves biodiversity at higher trophic
65 levels. Such retention can occur with vertical migration in a daily rhythm, in two scenarios.
66 Firstly the migration can happen in the tidal channel. However in a second scenario high

67 turbulence in tidal channels prevents weakly-swimming phytoplankton from making
68 meaningful vertical migrations. Instead the phytoplankton are vertically mixed in the channel
69 and vertical migration happens in a quiescent bay at one end. In the theory section next,
70 annual movement patterns are presented for a phytoplankter migrating vertically in a tidal
71 current which diminishes in amplitude towards the sea bed. In a case study that follows the
72 theory, short periods of the movement patterns are considered alongside coincident
73 observations of chlorophyll in the Menai Strait.

74

75 **THEORY**

76

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

85 Consider a single phytoplankton cell migrating vertically in a tidal channel, close to
86 the surface during the day and towards the bed at night (Fig. 1A & B). In the simplest model,
87 this movement is represented by a square wave with a shape modified by the day length, so
88 that the cell spends longer at the surface in summer, when days are longer, than it does in
89 winter (Fig. 1C). The square wave represents very good swimmers, which spend much more
90 time at their intended locations than swimming between them. In a variation of this model,
91 the vertical motion is governed by a triangle wave, such that the cell spends time near the bed

92 during darkness and starts moving towards the surface at sunrise, reaching closest to the
93 surface at noon. In the afternoon, the cell swims back towards the sea bed, reaching
94 maximum depth at sunset.

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

96

$$97 \quad u_s = A \sin(\omega(t - \phi)) \quad (1)$$

98

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

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

108

$$109 \quad u(z) = u_s \left(1 - \frac{z}{h}\right) \quad (2)$$

110

111 where z is depth below the surface and h is total water depth. The cell migrates
112 between depth $z = \frac{h}{4}$ during the day (or at noon in the triangle wave forcing) and $z = \frac{3h}{4}$ at
113 night (Fig. 1C). The daytime value of z was chosen to match a case study presented later. In
114 the model the phase of the phytoplankton movements is set to be the same as the phase of
115 daylight. This infers the need of phytoplankton to move upwards in the water column as soon

116 as daylight arrives. This is most pertinent for channels that are sufficiently deep or
117 concentrated with particles so that the photic zone is less than the whole water depth. It is
118 also pertinent for phytoplankton with the most energy needs (from photosynthesis). The
119 phytoplankton also go down on the disappearance of daylight and this fact assumes no
120 environmental pressures such as dissolved chemicals, nutrient availability or adverse
121 temperature or salinity.

122 The horizontal motion of the cell in an infinitely long tidal channel at a temperate
123 latitude varied by hundreds of kilometres per year depending on the vertical migratory pattern
124 and the tidal phase (Fig. 2). The cell was released at position $x = 0$ and depth $z = \frac{3h}{4}$ at
125 midnight at the start of day 1 (January 1st). With square wave migration, the cell spent all
126 hours of darkness at depth $z = \frac{3h}{4}$ and all daylight hours at $z = \frac{h}{4}$. When day length was
127 greater than 12 hours, between the spring and autumn equinoxes, the cell moved in the
128 negative (ebb) x -direction. When day length was less than 12 hours, the general direction of
129 movement was in the positive (flood) x -direction. The extent of the horizontal motion was
130 considerable: over 200 km in 6 months, or of order 1 or 2 km per day. A cell could maintain
131 its position, or make headway against moderate residual flows by riding the tide in this way.
132 The general seasonal pattern of movement had small oscillations associated with the springs-
133 neaps tidal cycle. Despite being small compared to the annual oscillations, these oscillations
134 were large enough to reverse the direction of motion for short periods (Fig. 2).

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

140 |The horizontal motion of a cell undergoing triangle-wave vertical migration could be
141 considered appropriate for slower swimmers which spend more time closer to the sea floor
142 than the sea surface. For a tidal channel in temperate latitudes for which high water springs
143 occurs at midday, the motion of the cell was generally in the flood direction throughout the
144 year, being faster when day length is less than 12 hours (4 km day^{-1}) and slowing down
145 considerably as the day length increases in summer (to 0.4 km day^{-1}). As in the square wave
146 migration pattern, the motion is temporarily reversed within the springs-neaps cycle,
147 consistent with Smith and Stoner (1993). The motion as modelled by Hill (1991a; 1991b) did
148 not have a spring-neap pattern and was associated with different velocity in the water column
149 (one a power law velocity profile, the other a linear two-layer problem for deeper water).

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

158

159 **CASE STUDY METHODS: CHLOROPHYLL TIME SERIES IN THE MENAI**

160 **STRAIT, UK**

161

162 *The Study Site*

163

164 The Menai Strait lies between the isle of Anglesey and the north coast of Wales, UK
165 (Fig. 3). It is 34.5 km long and stretches between two bays: Caernarfon Bay in the south-west
166 and Conwy Bay in the north-east. There is a sand bar (Caernarfon Bar) at the southwest end,
167 which spans more than half the channel width and dries out at low tide. The main channel of
168 the strait varies between 200 – 800 m in width and 6 – 33 m in depth, with mean depth 15.7
169 m below mean high water. Tides are semi-diurnal; mean spring tidal range varies between 5.2
170 m at the southwest end (Caernarfon) and 7.4 m at the northeast end (Beaumaris). Tidal
171 streams exceed 1 m s^{-1} at several places, especially in the narrow central part of the strait
172 where maximum speeds reach 4 m s^{-1} at spring tides. Flow depth is greater during the ebb
173 tide than during flood tide, causing higher bottom friction on the flood and resulting in a
174 residual flow towards the south-west (Harvey, 1967; Simpson et al., 1971). The residual flow
175 varies with the springs-neaps cycle (faster at springs) and averages approximately 0.1 m s^{-1}
176 (Simpson, 1971), replacing the water in the strait roughly every 3 days. Turbulence
177 associated with the fast tidal streams produces well-mixed conditions throughout the strait.
178 There is no stratification of turbulence despite the complex bottom topography. Dissolved
179 and particulate material advects along the strait with the tide (excursion of order 10 km per
180 tide) and leaves via the south-western end with the residual flow.

181 A number of vertically migrating species of diatoms have been recorded in the strait
182 in summer. The buoyancy of each of these varies between positive and negative due to (1) the
183 production and consumption of carbohydrates, (2) regulation of gas in vesicles during
184 photosynthesis, (3) ballasting by adsorbed polysaccharides and particles that may stick to
185 them and (4) colonial behavior. In August of any year a set of the following have dominated:
186 *Astrionella spp.*, *Chaetoceros spp.*, *Cylindrotheca*, *Fragiliara spp.*, *Guinardia spp.*,
187 *Leptocylindrus danicus*, *Nitzschia spp.*, *Paralia sulcata*, *Phaeocystis pouchetti*, *Rhizosolenia*
188 *spp.*, *Skeletonema costatum* and *Thalassiosira spp.* (Table 1). All the quantitative data found

189 and tabulated are from diatoms. Although diatoms normally dominate the Menai Strait in
190 August (c. 83 % of the phytoplankton population in 2002 - 2009; Greenwood et al., 2012), in
191 at least one past year flagellates have dominated (Ewins & Spencer, 1967).

192 The Menai Strait is home to intensive commercial farming of bivalves, primarily
193 mussels. At 23 – 30 km into the strait in the direction of the flood tide, they are beyond the
194 excursion of algal blooms sited in Caernarfon Bay, but would graze on background levels of
195 algae and any algal blooms passing through the channel from Liverpool Bay. Grazing less
196 than 1 % of algae in the bottom metre of water only (Simpson et al., 2007) they do not affect
197 the particular case study given here. The buoyant speeds of diatoms in the Menai Strait are
198 likely to be up to $20 \mu\text{m s}^{-1}$ (0.072 m hr^{-1}) and movements of colonies (individual aggregated
199 groups) could be on the order of hundreds of $\mu\text{m s}^{-1}$ (or m hr^{-1}).

200

201 *Mooring deployments, profiling and instrument setup*

202

203 An instrumented mooring was deployed in the central part of the Menai Strait for nine
204 days, starting on August 16th 2011 (day 228). The mooring was sited at $04^{\circ}12.71'$ west,
205 $53^{\circ}12.14'$ north in a mean depth of approximately 10 m (Fig. 3). The site is 16 km eastward
206 of the sill separating the strait from Caernarfon Bay to the south west (south sands sill, Fig.
207 3). Irradiance profiles were taken on August 17th and 23rd, approximately hourly from just
208 after dawn to just before dusk. This profiling was done from an 8 m-long boat that started at
209 the mooring location and drifted with the tide to follow the water.

210 The moored instruments were in a frame on the seabed and included a YSI CTD to
211 measure depth, temperature, salinity and chlorophyll fluorescence; a Sequoia LISST-100X
212 for particle size distributions and an upward-looking Workhorse Sentinel ADCP for flow
213 velocities. The fluorescence and particle size measurements were 1.5 m above-bed. The

214 velocity measurements were in 90 bins between 1.5 m above-bed and the water surface.
215 Velocity and particle size distributions were recorded at 1.5 s intervals and fluorescence at 60
216 s intervals. Water samples were collected using an opaque 4.2 L Wildco Beta Water Sampler
217 (van Dorn type) approximately hourly from just after dawn to just before dusk. They were
218 analysed for chlorophyll a using a calibrated Turner 10AU fluorometer. These chlorophyll
219 data were used to calibrate the CTD fluorescence record. LISSTs measure light scattered by
220 particles in suspension (Agrawal & Pottsmith, 2000). By assuming that the particles are
221 spherical, Mie theory is used to estimate the size distribution of the particles. The LISST-
222 100X type C used returned the volume of particles in 32 size classes ranging from 2.5 – 500
223 μm . A TriOS Ramses irradiance meter was used to measure downwards irradiance at a series
224 of depths through the water column, with multiple measurements averaged at each depth and
225 integration time allowed to vary to optimise signal to noise.

226

227 **CASE STUDY RESULTS**

228

229 *Tides*

230

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

237

238 *Characteristics of the algal bloom*

239

240 To estimate the size of the phytoplankton in the Menai Strait in August 2011, the
241 volumes of particles in each of the 32 LISST-C size classes were regressed against the
242 chlorophyll a concentration measured by the fluorometer on the CTD for the whole mooring
243 period to determine likely numbers of chlorophyll-bearing particles (example correlation Fig.
244 5B). High correlation coefficients indicate that a change in particle volume of that particular
245 size class was associated with a change in chlorophyll and therefore that particles of that size
246 were phytoplankton. The phytoplankton were most likely most abundant in the range 7 – 21
247 μm where the coefficient of regression, $R^2 > 0.89$ (Fig. 5A). Secondary groups of
248 phytoplankton were in the ranges 21 – 50 μm ($0.60 < R^2 < 0.89$) and 50 – 115 μm ($0.40 < R^2$
249 > 0.60). Above 115 μm , $R^2 < 0.40$ and so fewer of these particles are likely to have been
250 phytoplankton. To estimate the number concentration of particles present, the particle volume
251 concentrations of the LISST-C size classes were converted to particle number concentrations
252 by assuming spherical particles of median diameter for each class. To estimate how many of
253 the particles were phytoplankton the particle number concentrations were multiplied by the
254 R^2 value for each class. Phytoplankton concentrations were up to $3.6 \times 10^7 \text{ L}^{-1}$ at the
255 westward extent of the observations (start of the measurement period, Fig. 5E), hence
256 phytoplankton were in a bloom.

257 A large peak in chlorophyll a (over 10 mg L^{-1}) occurred at the end of each morning
258 flood tide (Fig. 5D; for flood tide Fig. 4). The chlorophyll a peaked just after noon on the first
259 day and progressively later on subsequent days. There was a second smaller peak in
260 chlorophyll a ($3 - 4 \text{ mg L}^{-1}$) at the end of the evening flood tide. Both these peaks were
261 consistent with a bloom to the south-west being advected with the tide, producing maximum
262 chlorophyll a at the mooring at the end of the flood. It is unlikely that the night-time peak is
263 smaller because of fluorescence quenching effects; instead particle size and volume data

264 suggest fewer diatoms and dinoflagellates were present at night time flood slack and
265 chlorophyll a magnitudes were commensurately lower.

266

267 *The photic zone and the phytoplankton bloom*

268

269 Irradiance profiles were taken on the day after spring tides (day 229) and the day of
270 neap tides (day 235). For most of those two days the photic zone at the mooring location was
271 the whole water depth (Fig. 6C & D). In those two figures, where the ratio of photic depth :
272 water depth is greater than 1, irradiance is still greater than 1 % of the surface irradiance at
273 the seafloor. The attenuation coefficient, K_d integrated over the visible light spectrum (400 –
274 700 nm), varied between 0.35 – 0.5 during most of that measurement period (Fig. 6A & B).
275 The exception was on day 229 when the algal bloom traveled past the mooring on a spring
276 flood tide (first period highlighted in blue). With the algal bloom present, K_d approximately
277 doubled to 0.75 – 0.95 (Fig. 6A) and the photic zone decreased to half the water depth (the
278 top half). At that time a high number of phytoplankton were measured in the bloom (up to 2.9
279 $\times 10^7 \text{ L}^{-1}$, Fig. 5E). There was also a greater proportion of organic material (possibly
280 phytoplankton) closer to the surface than the bed (Fig. 6E). This suggests that the numbers of
281 phytoplankton nearer the surface were attenuating light sufficiently to constrain the photic
282 zone to the top half of the water column. On the other flood tide when irradiance was
283 measured (last period highlighted in blue), the bloom travelled less far past the measurement
284 location and consequently fewer phytoplankton passed the mooring (up to $1.1 \times 10^7 \text{ L}^{-1}$, Fig.
285 5E). This smaller concentration of phytoplankton had less effect on K_d than the first flood tide
286 measured; K_d increased to just 0.49 and the photic zone was still the whole water column
287 (compare Figs 6B & D). The proportion of the organic fraction of suspended material
288 increased when the bloom was present at the mooring location but there was little difference

289 in proportion between the surface and bottom waters (blue section, Fig. 6F).

290

291 *Chlorophyll a record predicted with vertical migration*

292

293 The chlorophyll a concentration south-west of the mooring is represented by a
294 Gaussian curve; though the exact shape is not critical to the solution. If the position of the
295 centre of the bloom in the channel is x_C and the position of the mooring is x_M , then the
296 chlorophyll concentration measured at the mooring is given by

297

$$298 \quad c = c_0 \exp[-a(x_M - x_C)^2] \quad (3)$$

299

300 where C_0 is the concentration of chlorophyll in the centre of the bloom and a sets the size of
301 the bloom. The position of the centre of the bloom, x_C moves with the tide and the residual
302 flow, which varied with the tidal current amplitude A as

303

$$304 \quad u_R = \beta A^2 \quad (4)$$

305

306 with a representative $\beta = 0.1 \text{ m s}^{-1}$. With this residual flow and no vertical migration, the
307 bloom moved steadily away from the mooring. The chlorophyll a at the mooring rapidly
308 decreased and did not return on subsequent tides, but passed away with the ebb (Fig. 7B).

309 Vertical migration was then imposed. Cells began migrating on cue of sunrise at

310 approximately 05:00 BST (start of the white sections, Fig. 7). They migrated at constant

311 speed, upwards until noon and then downwards until sunset (approx 19:00; start of the black
312 sections). On that course the cells migrated 5 m up and 5 m down at $195 \mu\text{m s}^{-1}$ (0.7 m hr^{-1}).

313 This would be high for individual diatoms moving buoyantly in the Menai Strait (Table 2)

314 but achievable if they were aggregated into colonies or if the dinoflagellate blooms noted by
315 e.g. Ewins and Spencer (1967) and Lucas (1982) prevailed. Kamykowski et al. (1988) show
316 these dinoflagellates could easily have swimming speeds of $100 - 500 \mu\text{m s}^{-1}$. The cells had a
317 net motion in the flood direction, almost compensating the residual flow (Fig. 7C & D). This
318 matched the annual observations (Fig. 2C). After the first day, the scenario of cells achieving
319 successful swims in the strait underestimated the chlorophyll a pattern (compare Fig. 7A &
320 C) but the scenario of cells swimming successfully in the bay only, represented the
321 chlorophyll a pattern well (compare Fig. 7A & D).

322

323 *Minor effect of fluorescence quenching*

324

325 Chlorophyll fluorescence is a mechanism for releasing excess light energy not needed
326 for photosynthesis. In the daytime, solar light energy is more likely to be in excess of
327 requirements for photosynthesis than at night. In consequence fluorescence is quenched in the
328 day when the plankton are flooded by light from the sun (Amesz & Fork, 1967; Oquist et al.,
329 1982). The night time chlorophyll peaks in the bay model infer that quenching was not a
330 major contributory factor in the recorded chlorophyll time series. In that model output the
331 night time peaks were initially underestimated but the final night time peaks were
332 overestimated compared to the observations (Fig. 7D). Quenching would have caused all
333 peaks to be underestimated.

334 Further evidence of the minor effect of quenching is in the LISST data. The time
335 series of the volume of $7 - 21 \mu\text{m}$ particles at the mooring, in which phytoplankton were most
336 likely to have been most abundant, show day-night differences in peak concentration
337 consistent with the chlorophyll a record and the vertical migration mechanism of movement
338 in the bay (Fig. 8A). In the first six days the size class $21 - 50 \mu\text{m}$ had day-night differences

339 in particle volume that were generally less consistent with the chlorophyll a record but in the
340 last two days the structure was more like the chlorophyll a record. This could be due to
341 growth of the individual phytoplankton cells or species succession. In higher size classes (50
342 – 160 μm) the time series of particle volumes had a tidal advective pattern but no day-night
343 pattern like the chlorophyll a pattern, and in the highest classes sizes measurable by the
344 LISST (160 – 500 μm) the same advective signal was dominated by noise, indicating
345 particles above 50 μm were dominantly non-algal (compare Fig. 4A with Fig. 8C & D).
346 Additionally fluorescence has a linear relationship with chlorophyll a from filtered samples.
347 The alternative mechanism to quenching, explored herein, is that (1) both the difference in
348 daytime and night time chlorophyll a peaks and (2) the retention of the bloom in the strait
349 against the residual flow, are consequences of diel vertical migration.

350

351 **DISCUSSION**

352

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

358

359 ***Phytoplankton physiological effects on the theoretical results***

360

361 Annual movements of phytoplankton communities were presented and these
362 movements hold for the case that the plankter can move up and down despite turbulent
363 mixing (Fig. 2). To achieve this, the swimming timescale should be shorter than the mixing

364 timescale, i.e. the ratio of timescales: the Péclet number, $Pe = \frac{WL}{\kappa}$ is less than one, where W
365 is the vertical velocity scale; L the length scale of migration; κ the eddy diffusivity. Globally,
366 many tidal channels are shallow (order 10 m deep) and the full depth of water is mixed on the
367 order of minutes to hours, associated with vertical velocities of a few percent of the tidal
368 current speed (Rippeth et al., 2002). Typical migration speeds of diatoms (buoyant movers)
369 and dinoflagellates (swimmers) cannot overcome the mixing. Commensurately $Pe > 1$.
370 However blooms of dinoflagellates, normally mixed vertically by turbulence, can exhibit
371 gradients in number concentration if aggregated into colonies. Bigger colonies (individual
372 aggregates) move more effectively against turbulence than smaller ones. For instance small
373 colonies above 50 μm diameter move effectively with eddy diffusivities less than $7 \times 10^{-4} \text{ m}^2$
374 s^{-1} and colonies above 250 μm diameter move effectively with eddy diffusivities less than 10^{-2}
375 $\text{m}^2 \text{ s}^{-1}$ (section 5.5.2 of Ross, 2004). Both of these eddy diffusivities lie in the range
376 common to tidal channels (Lu et al., 2000). In consequence, if blooms contain colonies, the
377 centre of gravity of the bloom can move up and down with a daily rhythm. The theoretical
378 result is not limited to suitably strong swimmers.

379 The two ubiquitous limitations on using the annual theoretical migration patterns were
380 natural channel lengths and phytoplankton community lifetimes. In site-specific or taxon-
381 specific contexts, light availability and environmental pressures would provide further
382 limiting factors. It is not the purpose of this paper to present lots of model runs for specific
383 scenarios; instead previously published literature is referred to here for guidance. For the
384 given latitude, the annual results (Fig. 2) hold if the community moves between $\frac{h}{4} - \frac{3h}{4}$ daily.
385 That pattern is modified for weaker swimmers or deeper channels. The amplitude of the
386 excursion (Fig. 2) decreases with smaller daily excursions. Diatoms moving buoyantly with

387 the proposed model would not resist the residual flow. However dinoflagellates clearly can
388 when they are abundant in the Menai Strait (around April, occasionally in the summer).

389

390 *Correspondence between observations and model output in the case study*

391

392 At the observation site, high water spring tides occurred at the end of the flood tide,
393 around noon. At springs, the flood tide lasted for 6.21 hours before noon and the ebb tide
394 6.21 hours after noon (Fig. 9). If a cell moves up and down in a symmetrical way before and
395 after noon, it will spend equal times near the surface during flood and ebb tides (Fig. 9). The
396 effects of the tide cancel and there is no net movement at spring tides. If there is a residual
397 flow, the cell will move in the direction of this residual. Now consider a time shortly after
398 spring tides, when the end of the flood occurs in the afternoon. For illustration, let the end of
399 the flood occur at 15:00. The timing of the vertical migration now makes all the difference. If
400 the cell chooses to spend 10 hours near the surface, centred on noon, it will experience six
401 hours of flood and 4 hours of ebb (Fig. 9) when it is near the surface, so an excess of 2 hours
402 of flood tide when near the surface. In the same day, it will also experience an extra 2 hours
403 of ebb tide when at depth, but because the surface currents are faster there will be a net
404 movement, over the day, in the flood direction. This motion will therefore enable a cell in a
405 tidal channel with residual flow towards the ebb direction to make headway against (or at
406 least resist) the residual flow in the days after spring tides. It is proposed that this happened in
407 the case study of the Menai Strait and could happen for other tidal channels with similar
408 properties (chiefly a quiescent bay at the ebb end, a velocity profile with constant gradient
409 and spring tide slack water approximately at noon). It can be shown in the same way that, if
410 the cell spends more than 12 hours near the surface there will be a net movement in the ebb
411 tide direction. This explains why the triangular wave motion (which limits the time spent near

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

420 The vertical migration model presented in this paper represents a plausible
421 mechanism for explaining the observed chlorophyll record. Unfortunately there are no
422 measurements of chlorophyll in Caernarfon Bay to confirm the presence of a bloom there.
423 Instead it is inferred from observations that the chlorophyll concentration at the mooring
424 increased at the end of the flood tides. The existence of the bloom, however, is the only
425 reasonable inference from this evidence. The values of 14 mg L^{-1} chlorophyll recorded at the
426 start of the observation period are high for blooms in that particular strait (Al-Hasan et al.,
427 1975; Blight et al., 1995). Other motile chlorophyll a-bearing species (chiefly seaweed and
428 zooplankton) are not abundant in the water column of the strait. Suspension of
429 microphytobenthos is also not the cause. Suspension above the mooring height followed by
430 subsequent settling would result in two peaks per tide, but there was just one peak per tide.
431 Suspension as high as the mooring location (but not past it) would cause one peak that was in
432 phase with maximum shear, but each peak was in phase with flood tide slack water.

433 Unfortunately there were no observations that phytoplankton migrated vertically; the
434 model study was undertaken opportunistically because of the puzzle presented by the
435 chlorophyll observations. It is not possible to confirm vertical migration from a record of
436 chlorophyll taken near the sea bed; the assumption is taken that species known to migrate

437 vertically in the strait at this time of year for more than fifty years were again present (Table
438 1). However, near the start of the observation period there had been a greater proportion of
439 organic mass closer to the water surface than the seafloor at the end of the flood tides and that
440 was not true near the end of the observation period (compare Fig. 6E & F). This infers the
441 possibility of the tidal channel model TC_{Λ} enhancing the bay model B_{Λ} at the start of the
442 observation period.

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

462 promoting ecological diversity there.

463

464 CONCLUSIONS

465

- 466 1. In a tidal channel phytoplankton can maintain their position or move against a
467 residual flow if they migrate vertically with a daily rhythm. How the phytoplankton
468 move along the channel depends on the vertical migration, especially the phase of the
469 tide and time spent near the water surface.
- 470 2. A simple model of phytoplankton migration in a tidal channel accorded with
471 observations of chlorophyll for eight consecutive days. A phytoplankton bloom above
472 10^7 plankton per litre occurred downstream of a mooring, from which observations
473 were made. The bloom advected into and back out of the mooring location on each
474 flood tide and at the time of each flood tide, peaks in chlorophyll were observed.
- 475 3. The phytoplankton number concentration near the centre of the bloom caused
476 significant attenuation of light, with maximum phytoplankton numbers (and
477 chlorophyll levels) being associated with a doubling of the attenuation coefficient.
478 Where phytoplankton were most abundant, and attenuation highest, the photic zone
479 covered the top half of the 10 m deep channel. In this fact there is an associated need
480 for diel vertical migration, on top of common optimisation strategies for light and
481 against predation. Away from the bloom the photic zone was the whole water depth.
- 482 4. Chlorophyll peaks at night were one quarter to one third the magnitude of chlorophyll
483 peaks during the day. Chlorophyll peaks recurred for eight consecutive days. These
484 patterns are in contrast to the movement of well mixed particles, which pass through
485 the channel used to make observations in two days. Both the day-night asymmetry
486 and the sustained presence of chlorophyll were explained by allowing for vertical

- 487 migration of the phytoplankton and constraining the period during which they were
488 near the surface.
- 489 5. Regressions between chlorophyll a and particle size indicated that phytoplankton were
490 most abundant in the size range 7 – 21 μm . Judging by historical occurrences of
491 phytoplankton in the tidal channel used for observations, they were almost certainly
492 diatoms existing as individuals or small colonies.
- 493 6. Tidal channels that retain phytoplankton against a residual flow can be more diverse
494 ecologically than channels without this retention mechanism. Channels that retain
495 phytoplankton can be prime sites for commercial farming of bivalves.
- 496 7. The natural timings of some phytoplankton blooms in tidal channels are controlled by
497 the nature of the migration. Although a by-product of vertical migration, longer
498 residence in the tidal channel affords the phytoplankton more nutrients than
499 phytoplankton that advect offshore.
- 500 8. Annually phytoplankton can migrate or effectively resist a residual flow by up to
501 hundreds of kilometres, effectively limited by the natural length of a tidal channel or
502 the duration of existence of a phytoplankton bloom.

503

504

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509 Clement kindly undertook a portion of data processing. Oliver Ross and Stephanie Wilson
510 gave helpful advice on dinoflagellate swimming and predation and the comments of three
511 anonymous reviewers have helped the manuscript. The work was funded by the UK Natural

512 Environment Research Council grant NE/H022090/1.

513

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595 **LIST OF FIGURE CAPTIONS**

596

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

608

609 Figure 2. Variation of position along a tidal channel by an organism making a diurnal vertical
610 migration between three quarters of the flow depth above the bed during daylight hours and
611 one quarter above the bed in hours of darkness. Positive values are oriented with the flood
612 tide and negative values with the ebb tide. Solid lines represent the daily mean values. Panel
613 A represents square wave migration and panel C represents triangular wave migration (cf.
614 Fig. 1C). Panel B represents the tidal current amplitude; in spring tide conditions amplitude is
615 1 and in neap tide conditions amplitude is 0.5. The vertical dashed lines highlight portions of
616 two spring-neap periods where phytoplankton move oppositely to the long term trend,
617 associated with falling and low-amplitude current.

618

619 Figure 3. Location and geometry of the tidal channel case study. (A) England and Wales. The
620 Menai Strait (red box) is between the isle of Anglesey and mainland Wales, UK. (B) Map of
621 the tidal channel. The bounding red box corresponds with the red box in (A). The instruments
622 were moored at the position of the orange diamond. (C) Bathymetric section of the strait
623 highlighted by orange line in (B). Mean high water slack (MHWS) = 0 m depth. The purple
624 and green dots indicate spring and neap tidal ranges respectively, at Caernarfon and
625 Beaumaris, which are 19 km apart. The black lines interpolate and extrapolate the tidal ranges
626 from these towns. Three red arrows indicate sill-like features at the western end of the strait.

627 Figure 4. Time series of (A) tidal elevation and (B) depth mean current speed at the mooring
628 location (orange diamond, Fig. 3B) during the observational period (August 16th – 24th).

629

630 Figure 5. Characteristics of the chlorophyll a-bearing species suggest they are diatoms or
631 dinoflagellates. (A) The chlorophyll a concentration was correlated with total particle volume
632 for each LISST-100X class for the whole mooring period. High correlation coefficients (R^2)
633 indicate that most of the particulate material in the particular size class is phytoplankton. (B)
634 Example correlation between chlorophyll a and total particle volume, which is for LISST-
635 100C class 8 (class range 8 – 9.5 μm) and had $R^2 = 0.89$. (C – E) Time series of mean particle
636 size, chlorophyll a and number of phytoplankton. Mean particle size varies with tidal
637 advection and lowest mean particle sizes are associated with the phytoplankton bloom (with
638 high chlorophyll a). Each daytime chlorophyll peak is higher than both adjacent night time
639 peaks and the mean particle size is smaller too (compare troughs in C with peaks in D).

640

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

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

646 Figure 7. (A) Observed chlorophyll a: five minute average values from a YSI CTD moored in
647 the centre of a 34.5 km long channel between August 16th – 24th 2011. The CTD was 1.5 m
648 above the bed of the strait, in a mean of 10 m water depth and recorded at 60 s intervals. (B –
649 D) Time series of chlorophyll a output from three models of a phytoplankton bloom
650 advecting in a tidal channel. In model M the phytoplankton were always vertically mixed.
651 They left the mooring site with the residual flow on the first tide (leaving the Menai Strait in
652 about a day). In model TC_Λ the phytoplankton had a triangular wave diurnal vertical
653 migration in the tidal channel and bay, and in model B_Λ the same migration happened in
654 Caernarfon bay only (cf. Fig. 1B). In both scenarios the phytoplankton bloom resisted the
655 residual flow and the chlorophyll a signal returned to the measurement location on eight
656 consecutive days. White and black tick marks indicate 00:00 and 12:00 BST for that day.
657 Night time periods (from sunset to sunrise) are highlighted in black on the *x*-axes and
658 daytime in white. The phase of the moon is shown as tides varied from springs to neaps.

659

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

664

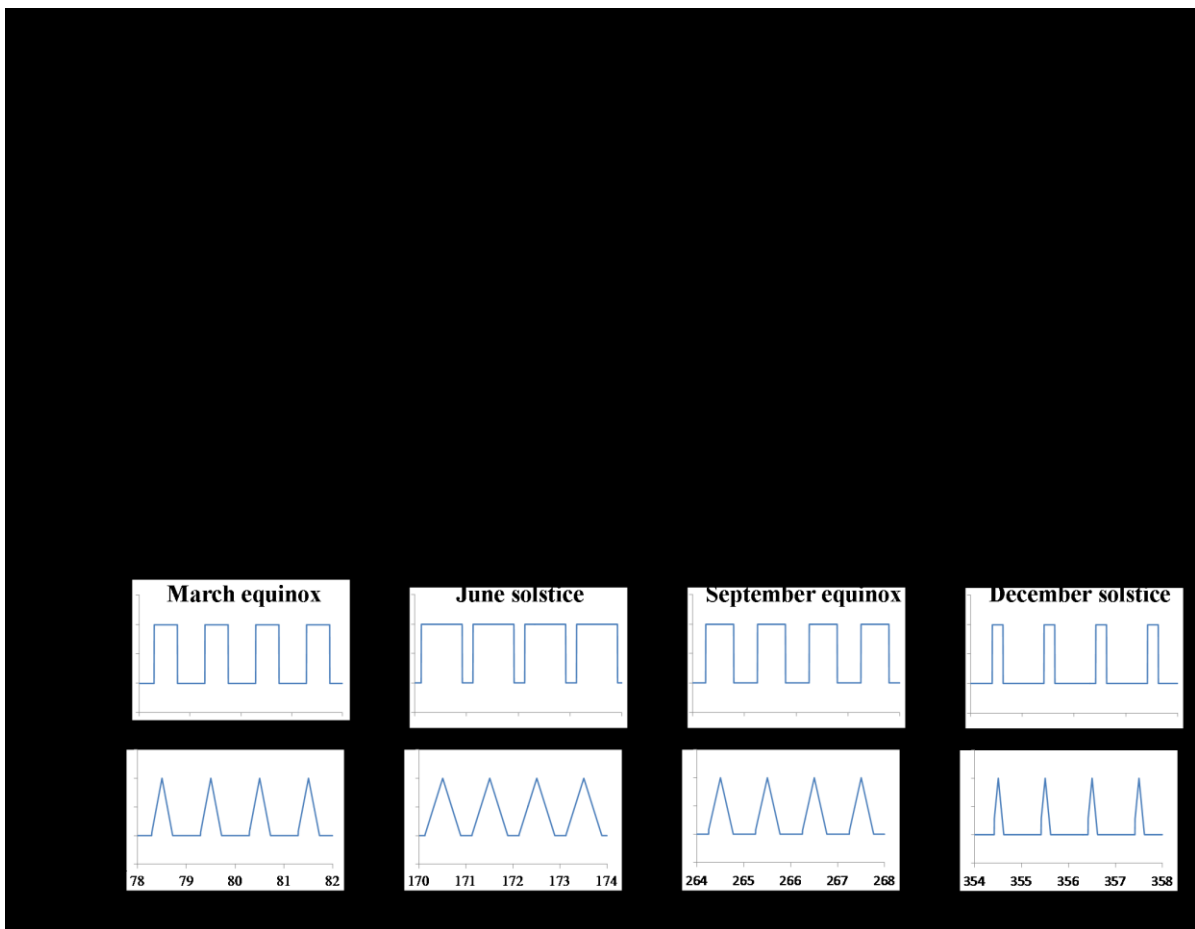
665 Figure 9. There is net movement of phytoplankton in the flood direction with day length less
666 than twelve hours. (A) For the example of the Menai Strait, spring flood slack water occurs at
667 noon. Any day length covers equal amounts of ebb and flood flow and there is no net
668 movement, however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

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

672

673 **FIGURES**

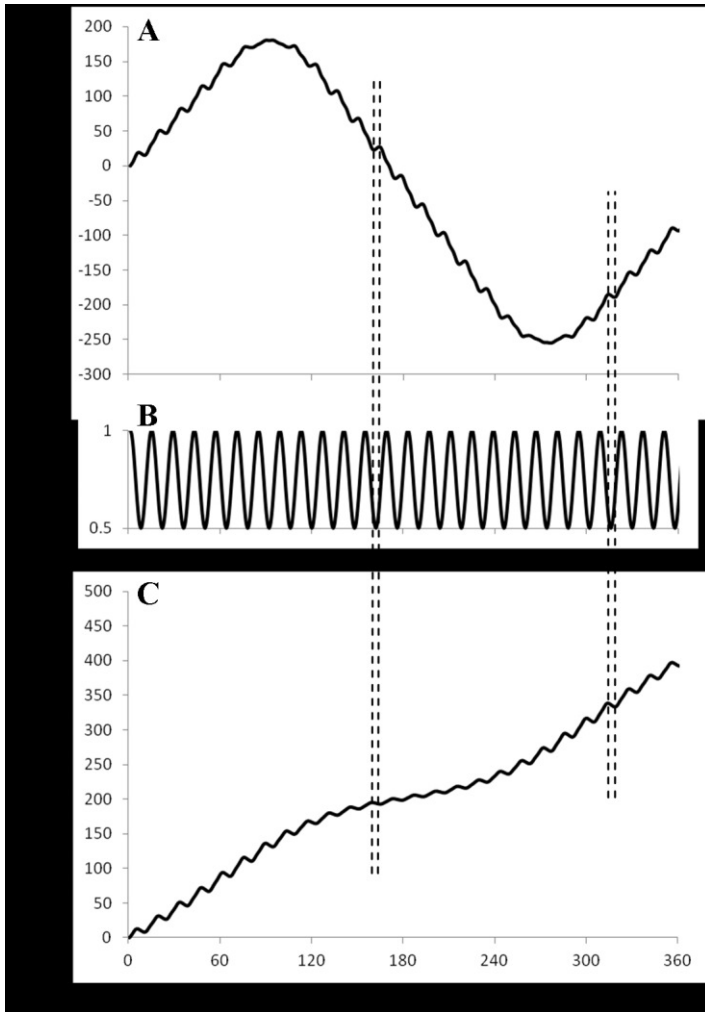
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676 (Figure 1)

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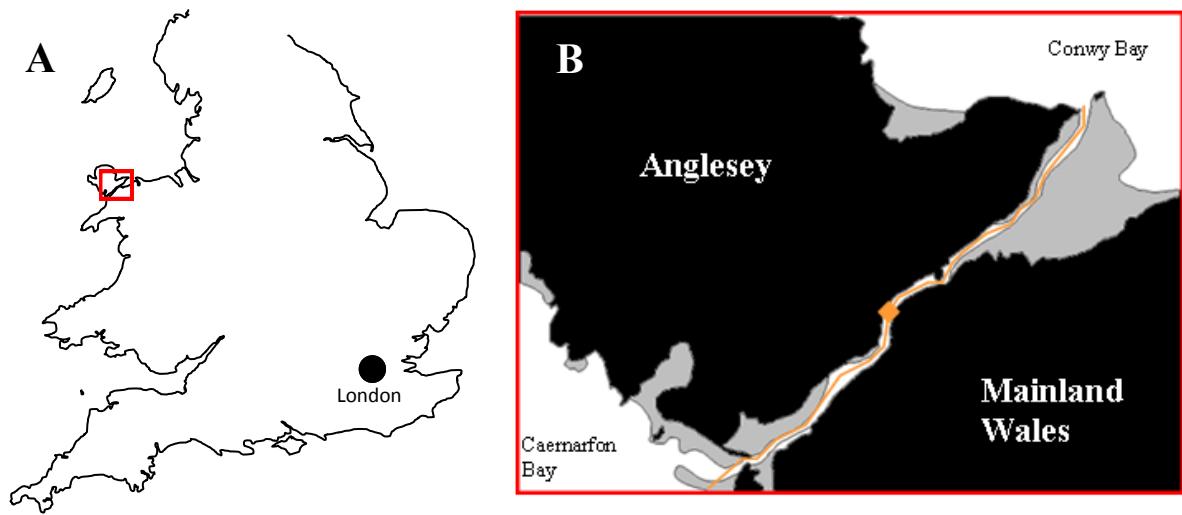


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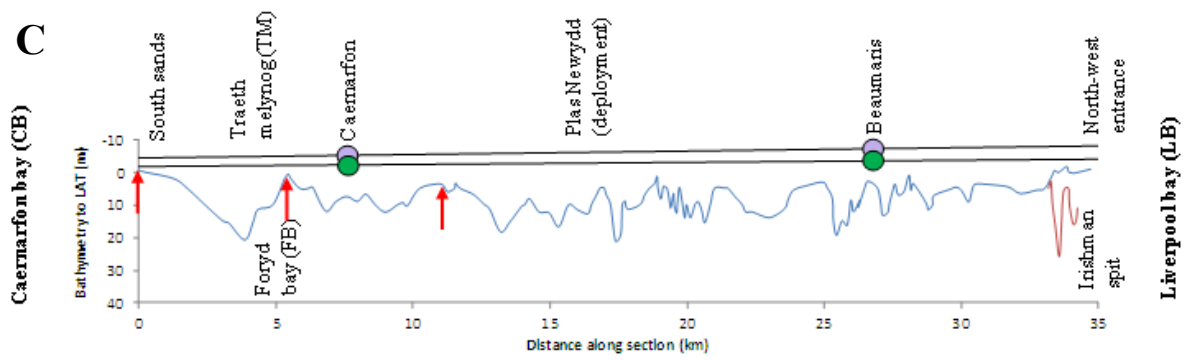
679 (Figure 2)

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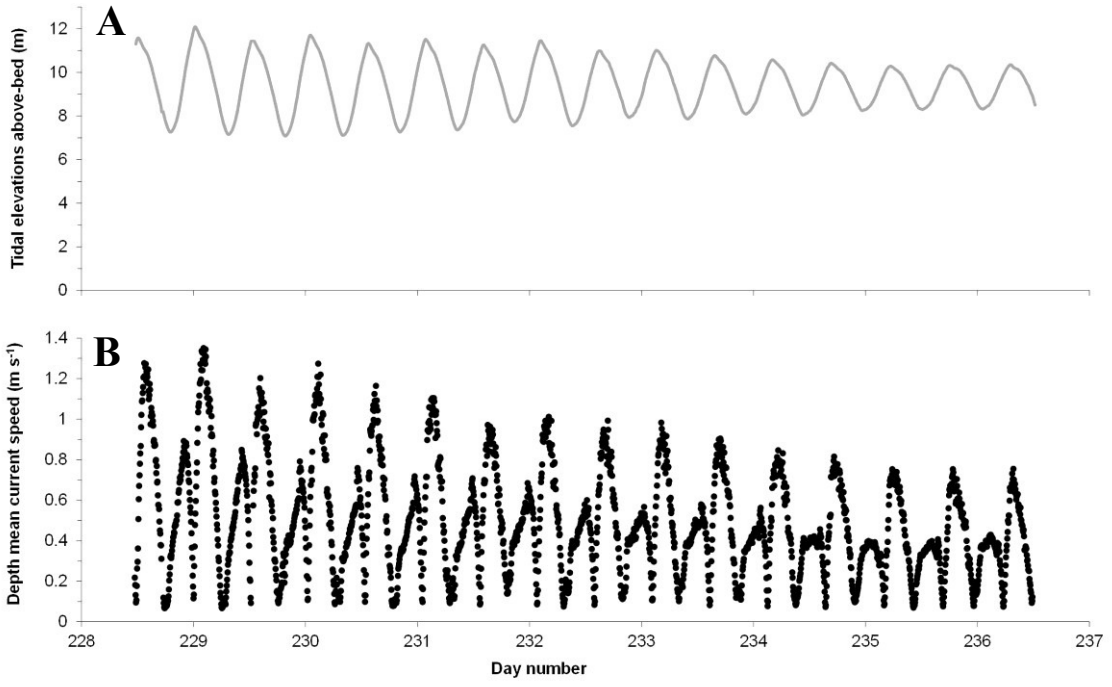
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684 (Figure 3)

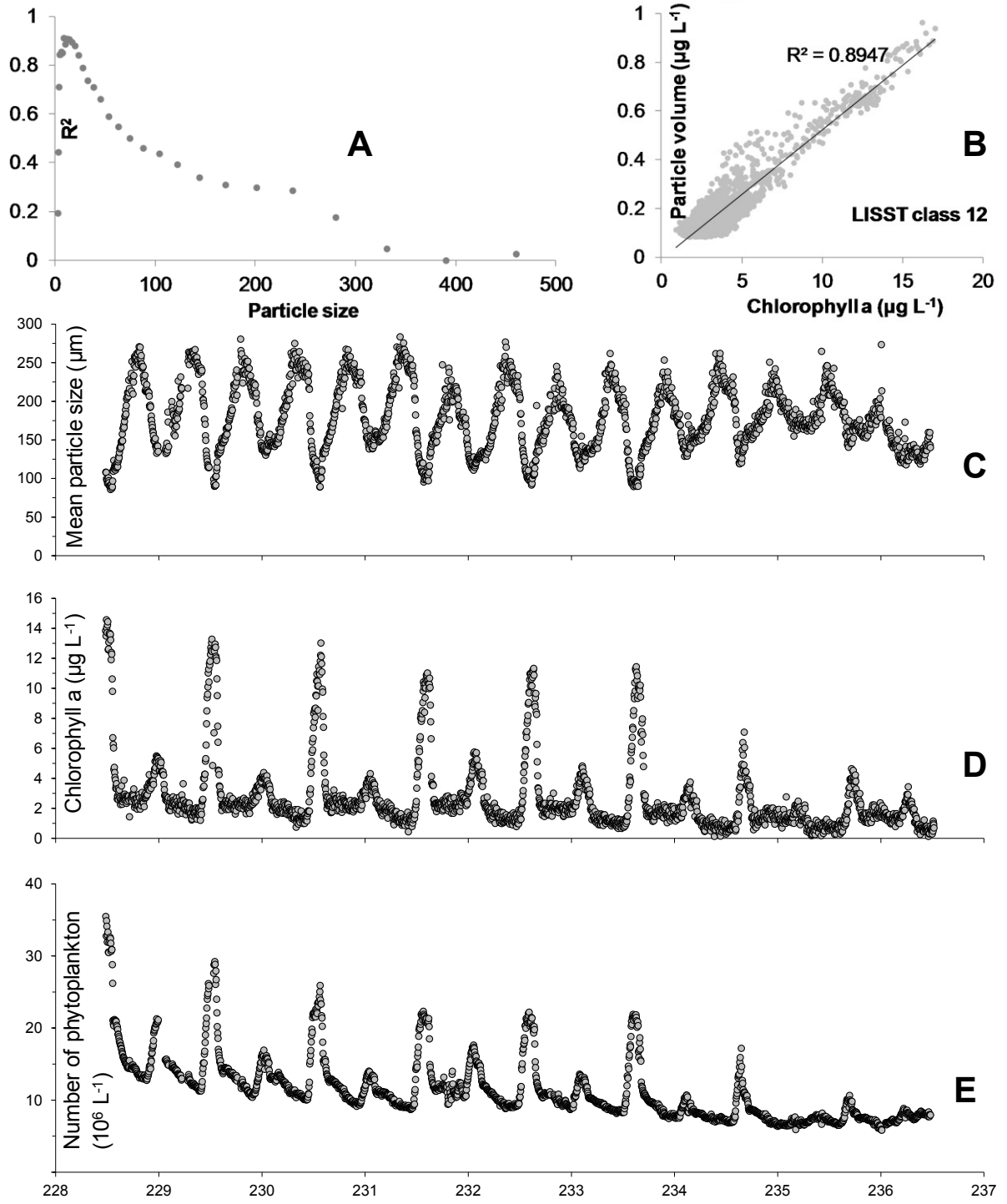
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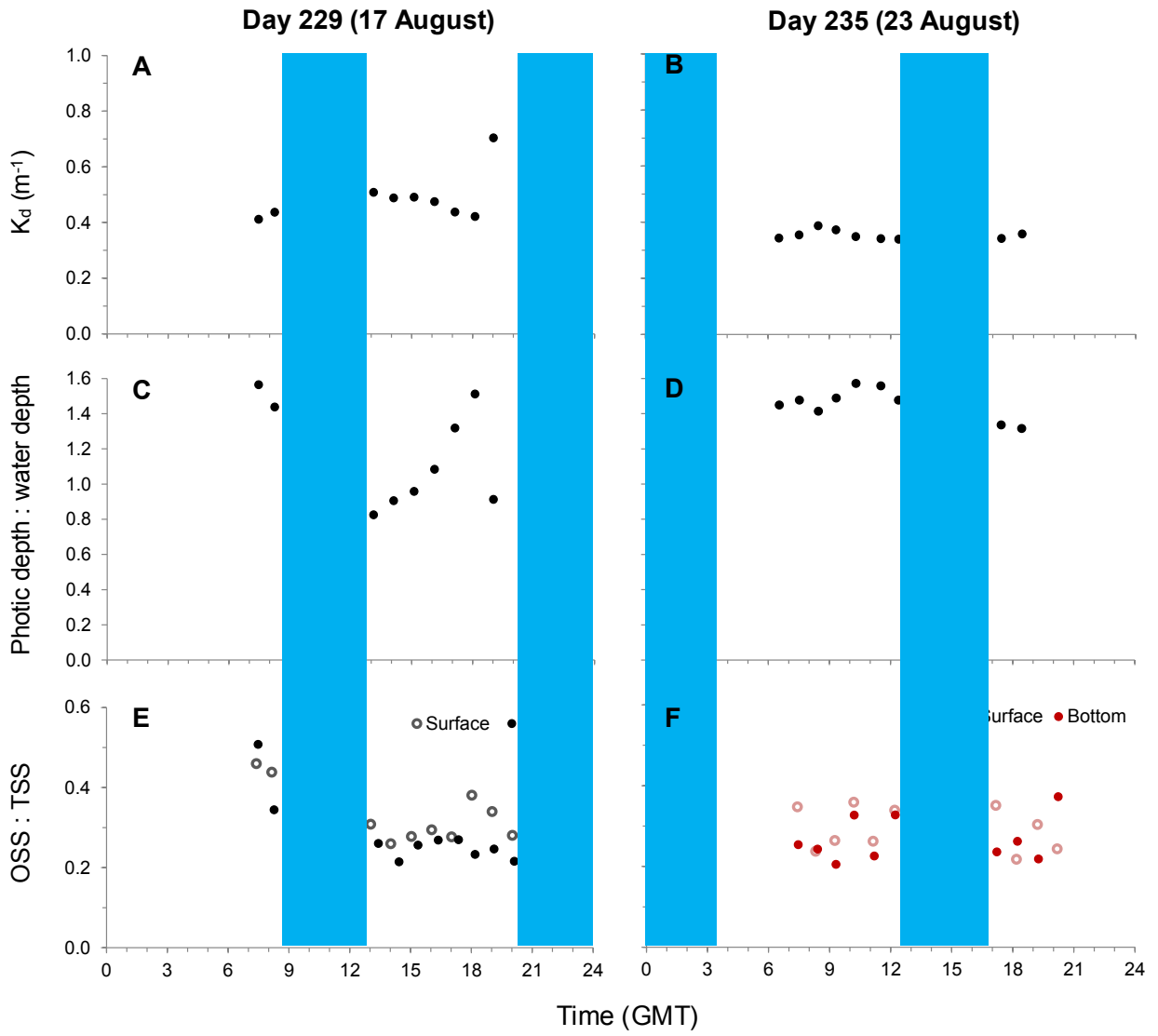
687 (Figure 4)

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689 (Figure 5)

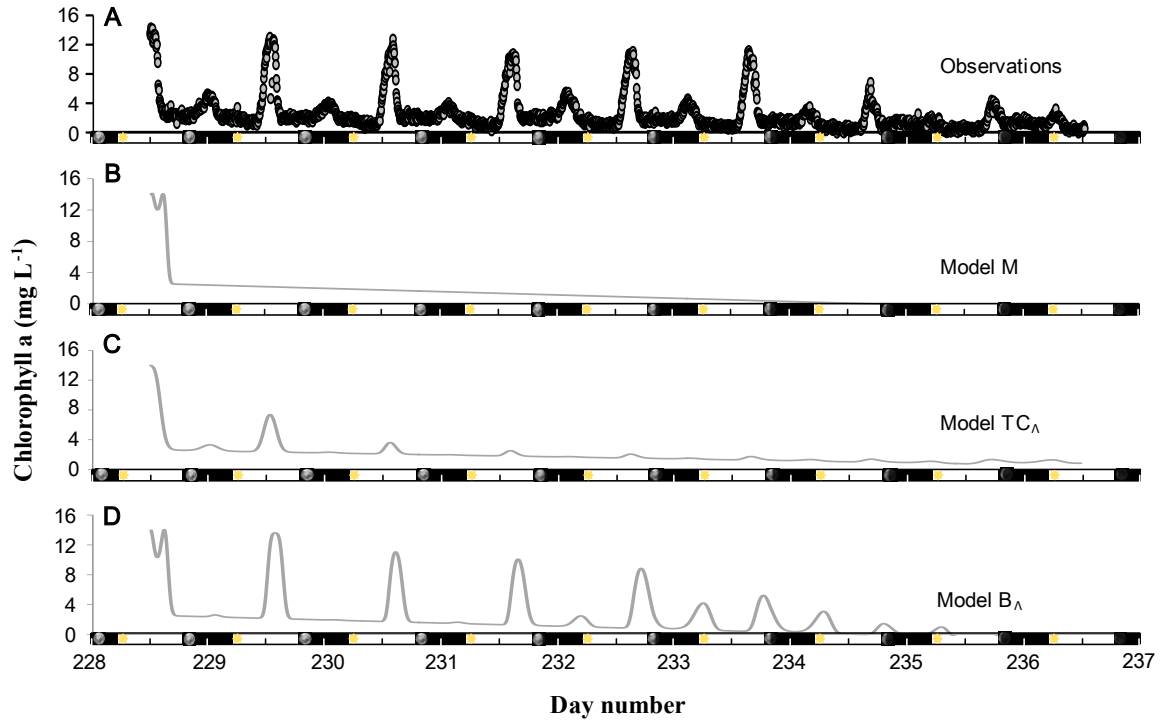
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692 (Figure 6)

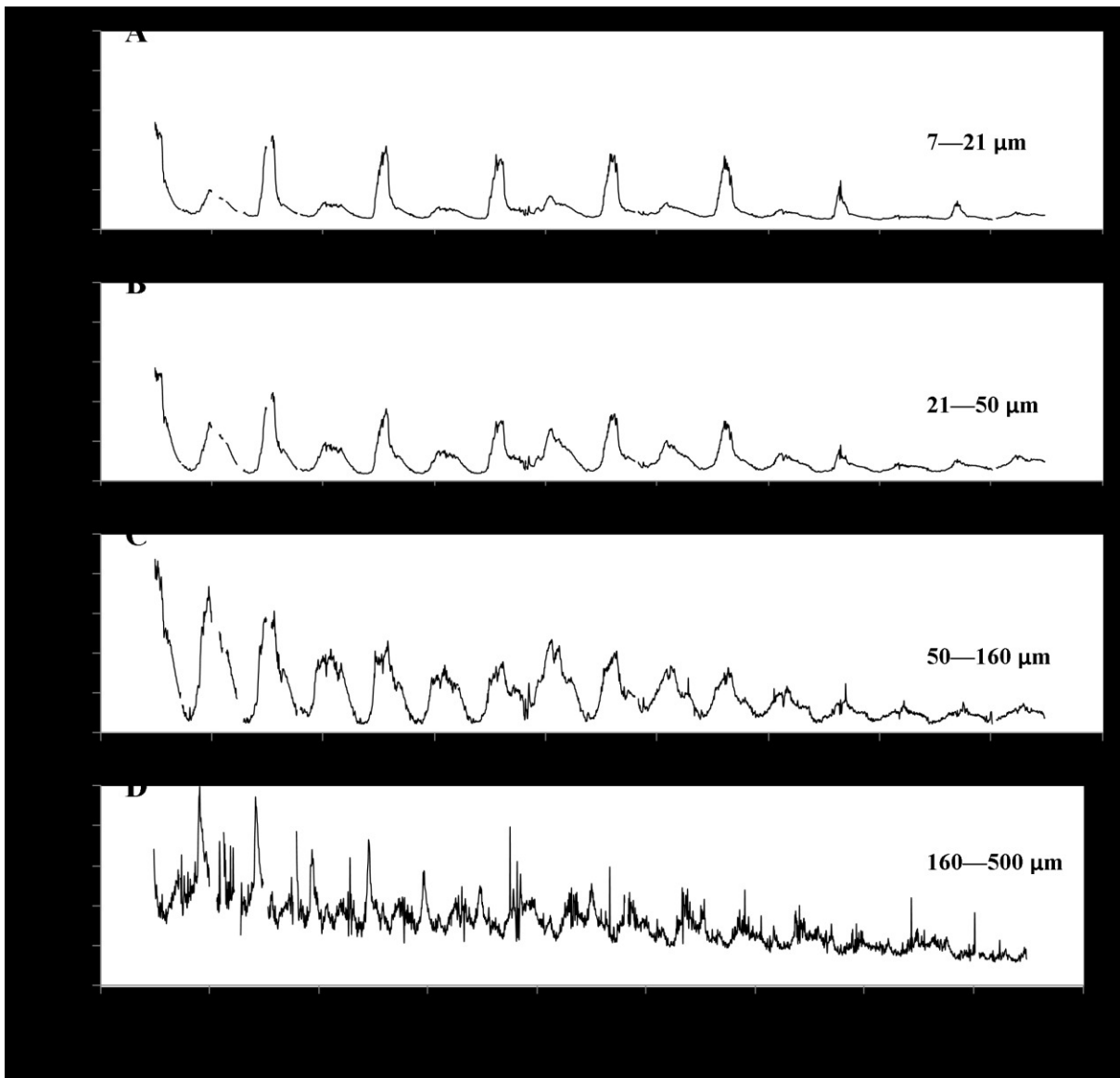
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695 (Figure 7)

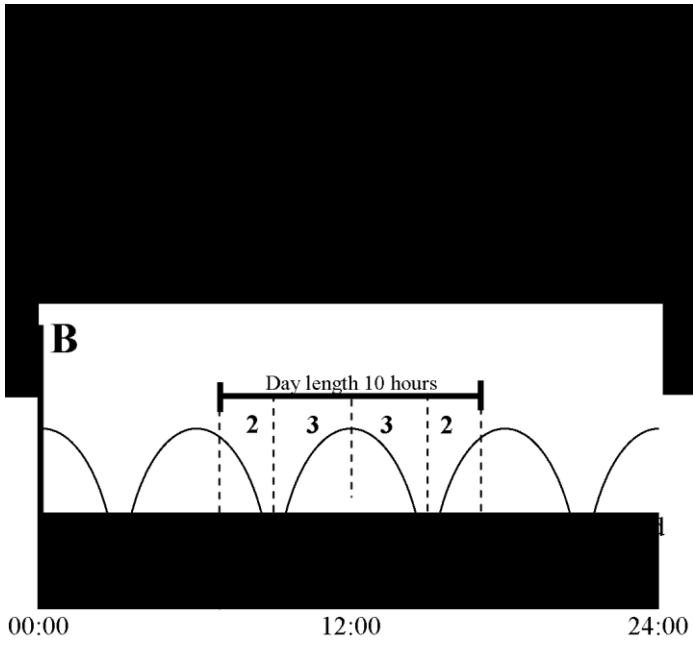
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698 (Figure 8)

699



700

(Figure 9)

702

703 **LIST OF TABLE CAPTIONS**

704

705 Table 1. Taxons that dominated phytoplankton populations in August of a given year. Colour
706 code gives their abundance. Data are derived from ¹Jones & Spencer 1970, ²Kennington
707 1970, ³Al-Hasan et al. (1975), ⁴Blight et al. (1995), ⁵Greenwood et al. (2012). The data
708 represented by white hatching are calculated from volumetric concentrations by inferring
709 spherical-equivalent diameters.

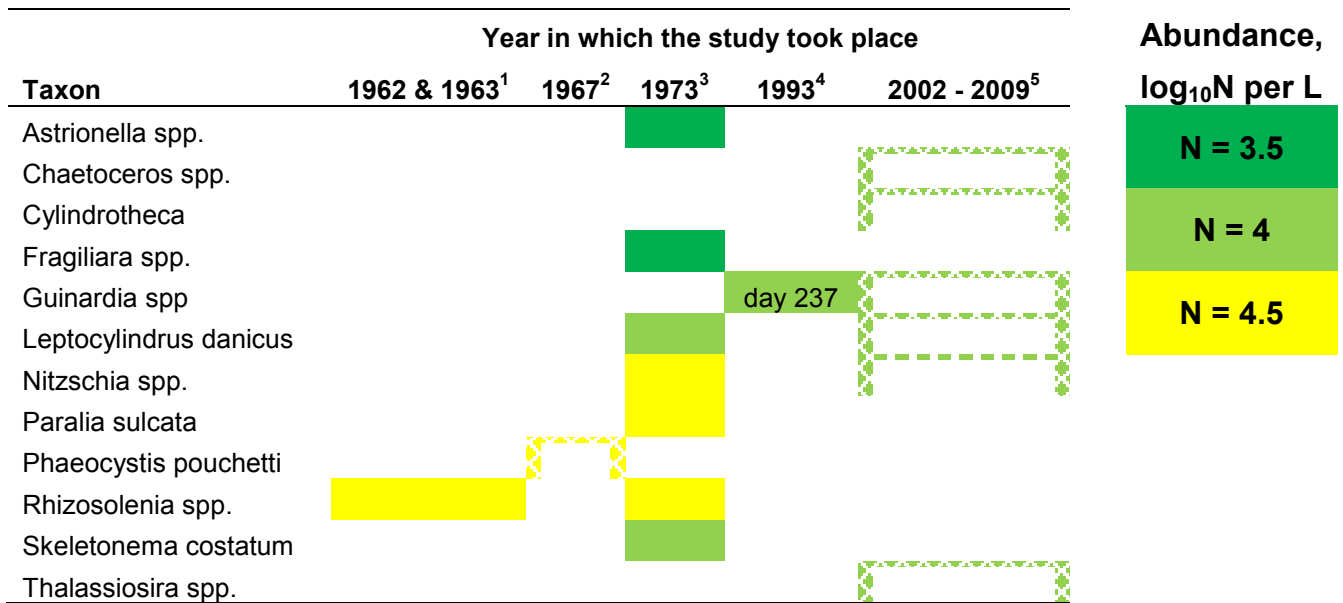
710

711 Table 2. Sizes and achievable speeds of diatoms with buoyant movement. Each of the taxons
712 listed has been recorded to dominate the phytoplankton population in the Menai Strait in
713 August of a given year (Table 1). Data derived from ¹Kennington (1970), ²Al-Hasan et al.
714 (1975), ³Blight et al. (1995), ⁴Ross (2004), ⁵UBC (2012), ⁶Perperzak et al (2003), ⁷Moore &
715 Villareal (1996), ⁸Skreslet (1988), ⁹Smeyda & Boleyn (1965). Size data are from the original
716 works where possible or from the phytoplankton encyclopedia “phyto’pedia” where not
717 (UBC 2012). Recorded sizes and speeds of the same taxons in Southampton Water are given
718 for comparison.

719

720 TABLES

721



722 (Table 1)

723

Taxon	Menai Strait ^{1,2,3}	Size (µm)		W _s ⁴ (µm s ⁻¹)		Number in colony
		Southampton water ⁴	Phyto'pedia ⁵	Individual ^{4,6}	Colonial ⁷⁻⁹	
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	

724 (Table 2)