

2015-05-15

The role of advection in the distribution of plankton populations at a moored 1-D coastal observatory

Cross, J

<http://hdl.handle.net/10026.1/3760>

10.1016/j.pocean.2015.04.016

PROGRESS IN OCEANOGRAPHY

Elsevier BV

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

1 The role of advection in the distribution of plankton
2 populations at a moored 1-D coastal observatory

3 Jaimie Cross^{a,*}, W. Alex M. Nimmo-Smith^a, Philip J. Hosegood^a, Ricardo
4 Torres^b

5 ^a*School of Marine Science and Engineering, Plymouth University, Drake Circus,*
6 *Plymouth PL4 8AA, UK*

7 ^b*Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL1 3DH, UK*

8 **Abstract**

9 The degree to which advection modulates the distribution of plankton popu-
10 lations at a 1-D coastal observatory was assessed at station L4 in the western
11 English Channel (50° 15' N 4° 13' W, depth 50 m), part of the Western Chan-
12 nel Observatory (WCO). Five tidal-cycle surveys were conducted, three in
13 spring and two in summer 2010. Observations of the physical characteris-
14 tics of L4 were obtained by using a moored acoustic doppler current profiler
15 (ADCP) and a free-falling microstructure sensor (MSS). The moored ADCP
16 highlighted the presence of vertical shear, with typical values of U during
17 spring tides of $\sim 0.5 \text{ m s}^{-1}$ at the surface and $\sim 0.2 \text{ m s}^{-1}$ at the bed. The
18 distribution of phyto- and zooplankton populations above a size threshold
19 of $200 \mu\text{m}$ were examined using an in-line holographic imaging system, the
20 Holocam. Variability in time as well as depth is a common feature through-
21 out each of the surveys, with examples of recorded numbers of phytoplankton
22 that ranged between 1300 L^{-1} and 2300 L^{-1} at the same depth but at different
23 points within the tidal cycle. Further, at the same points in the tidal cycle
24 the number of recorded zooplankton was also seen to vary, specifically with

*Corresponding author. 3a Reynolds Building, Drake Circus, Plymouth University,
Plymouth PL4 8AA UK

Email address: `jaimie.cross@plymouth.ac.uk` (Jaimie Cross)

1
2
3
4
5
6
7
8
9
10 25 the identification of gelatinous planula in spring that increased the observed
11 26 number to maximums of between 140 L^{-1} and 220 L^{-1} in the upper layer,
12 27 considerably higher than the corresponding WP-2 net counts for a similar
13 28 period. Specific aspects of the movement and transfer of plankton relating
14 29 to advection and interaction with the pycnocline are identified, both across
15 16 tidal cycles and seasons.

17
18
19 30 *Keywords:* Shear; Advection; L4; Plankton dispersal; Holographic
20 31 imaging; Potential Energy Anomaly; WCO; Western English Channel
21
22

23 24 32 **1. Introduction**

25
26 33 The distribution of plankton populations in shelf and coastal regions is of
27 34 major importance in our effort to better understand carbon cycling and the
28 35 temporal and spatial variability of the so-called ‘biological pump’. Shelf seas
29 36 in particular are disproportionate contributors to the export of carbon from
30 37 the atmosphere to the deep ocean, accounting for $>40\%$ of the global total
31 38 (Jahnke, 2010). Phytoplankton play a direct role in the uptake of dissolved
32 39 inorganic carbon (DIC), whilst zooplankton have equal importance within
33 40 the carbon cycle as consumers of phytoplankton and supporting both marine
34 41 ecosystem dynamics and fisheries activity (Caley et al., 1996).

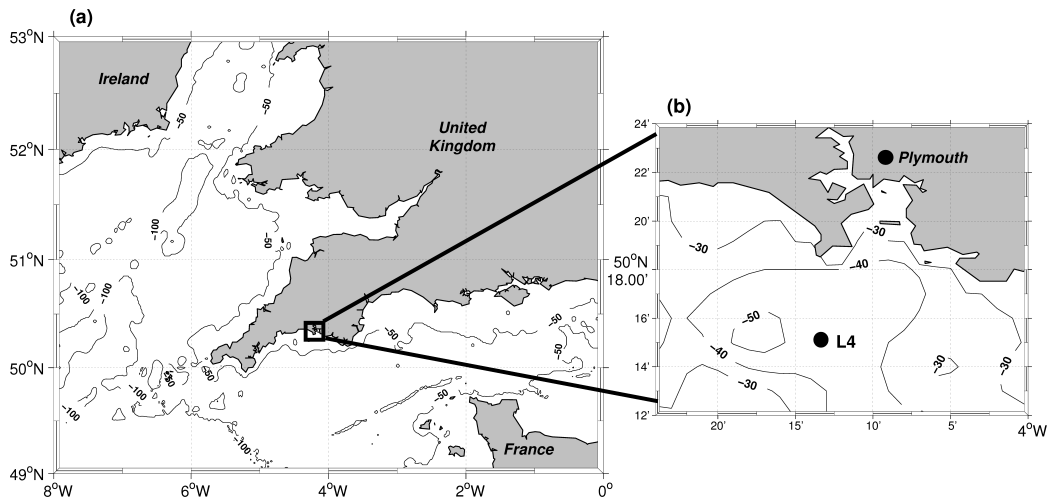
35 42 Quantifying the distribution of plankton populations in energetic, coastal
36 43 environments offers a considerable challenge. Typically, multi-disciplinary
37 44 studies that would take into account plankton dynamics are logistically chal-
38 45 lenging, requiring a suite of instrumentation that is frequently unavailable
39 46 or expensive to operate both in time and finance. Often, measurements of
40 47 fluorescence and optical backscatter (OBS) are taken along with *in situ* wa-
41 48 ter samples to provide insight into the movement and transfer of plankton
42 49 (e.g. Corcoran and Shipe 2011). Relative measures of OBS and fluorescence
43 50 are insufficient, however, when needing to confidently supply quantitative
44 51 information concerning biomass, plankton concentration or number. Deter-
45 52 mining the composition and structure of plankton populations *in situ* poses
46 53
47 54
48 55
49 56
50 57
51 58
52 59
53 60
54 61
55 62
56 63
57 64
58 65

1
2
3
4
5
6
7
8
9
10 53 an even greater challenge, particularly as most, if not all available methods
11 54 to determine distribution rely on disturbing plankton from their natural en-
12 55 vironment (e.g. the Optical Plankton Counter (Herman et al., 2004), and
13 56 the submersible FlowCam (See et al., 2005)).

15 57 The application of an *in situ* instrument that does not directly interfere
16 58 with its sample, the Laser in situ Scattering and Transmissometer (LISST)
17 59 more commonly used for investigations into suspended particulate matter, is
18 60 growing in popularity amongst phytoplankton ecologists (Rzadkowski and
19 61 Thornton, 2012). However, the LISST has been recently shown to be unreli-
20 62 able when attempting to quantify non-spherical natural particulates (Davies
21 63 et al., 2012; Graham et al., 2012). As such, when using this instrument to
22 64 evaluate changes to the distribution of plankton, it is unclear whether the
23 65 LISST is the appropriate tool in light of the range of shapes exhibited by
24 66 plankton in the natural environment (McCandliss et al., 2002; Karp-Boss
25 67 et al., 2007). As demonstrated recently by Cross et al. (2013), the emerging
26 68 technology of holographic imaging offers the benefit of *in situ*, non-destructive
27 69 sampling of the water column, and is used exclusively throughout this work
28 70 to enumerate plankton populations. The flexibility afforded by holographic
29 71 imaging allows for the simultaneous analysis of both phyto- and zooplankton
30 72 distributions.

31 73 The Western Channel Observatory (WCO), maintained and run by Ply-
32 74 mouth Marine Laboratory (PML), is located in the Western English Channel
33 75 and includes a permanent station, L4, where long-term oceanographic and
34 76 biogeochemical observations have been routinely collected on a weekly basis
35 77 since 2002 (available from the WCO website at
36 78 <http://www.westernchannelobservatory.org.uk/data.php>), which supplement
37 79 further historical plankton records collected since the late 1980s (Figure 1).
38 80 Much of the focus of the research at this location has involved long-term char-
39 81 acteristics of biological particle populations, rarely invoking physical forcing
40 82 as the principal driver of change (e.g. Widdicombe et al., 2010). Build-

1
 2
 3
 4
 5
 6
 7
 8
 9
 83 ing on the short-term temporal variability of physical forcing at L4 brought
 84 about by the presence of vertical shear highlighted by [Cross et al. \(2014\)](#),
 85 such variability is invoked as the principle driver of the observed changes
 86 throughout each of the surveys presented in this work. The identification of
 87 advection as being a potentially important contributor to the structure of the
 88 water column at L4 could hold consequences for the measurement of plankton
 89 populations at this and other similar locations, given the likelihood of such
 90 populations to be substantially altered by sheared flow. The principal aim
 91 of this paper then, is to apply a novel method to help quantify and explain
 92 the degree to which the accurate sampling of plankton populations might
 93 be impacted by tidal advection, and also to examine how these populations
 94 might change across the spring-neap cycle and seasons.



46 Figure 1: Map of the southern part of the United Kingdom (a) with exploded section
 47 noting the location of Station L4, approximately 10 km south of Plymouth (b)
 48
 49

95 2. Methods

96 2.1. Survey location

97 Station L4 resides approximately 10 km south of Plymouth at 50° 15' N
 98 4° 13' W where the water depth is around 50 m with a seabed predominantly

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

99 consisting of sand. Long-term data exist for temperature and salinity at
100 L4, in addition to phytoplankton and zooplankton abundance, and forms a
101 central part of the WCO. The long-term data indicates that the site is well-
102 mixed during the winter, and weakly stratified between April and October.
103 When stratified, the water column has an average difference in temperature
104 of 2°C between the upper and lower layers (Cross, 2012). The site is charac-
105 terised by a dominant semi-diurnal tide, experiencing a maximum range of
106 over 5 m that generates currents of 0.5-0.6 m s⁻¹ at the surface.

107 *2.2. Physical measurements*

108 *2.2.1. The Lagrangian surveys*

109 Measurements utilising an array of instruments were undertaken during
110 five surveys in spring and summer 2010 aboard the *RV Plymouth Quest*.
111 Instruments were deployed in a Lagrangian reference frame whilst follow-
112 ing a drifter drogued by a holey sock positioned at 3-12 m. Within the
113 drifter-drogue assembly, a downward-facing 600 kHz Acoustic Doppler Cur-
114 rent Profiler (ADCP) was fixed within a neutrally-buoyant submersible at an
115 approximate depth of 20 m. The ADCP sampled at 2 s intervals with a bin
116 size of 0.5 m, with the depth of the first good bin at 21 m. The device was
117 able to resolve the level of current shear present for the lower part of the wa-
118 ter column. The vessel relocated to the drifter each hour, and measurements
119 were obtained whilst the drifter was no further than 100 m from the ship.
120 A free-fall microstructure profiler, the ISW Wassermesstechnik MSS-90, was
121 utilised to observe the turbulent velocity shear. The number of profiles taken
122 during each hour ranged from 6-8. The MSS-90 contains a number of sensors
123 including optical backscatter (OBS), a fluorometer and conductivity, tem-
124 perature and depth (CTD) probe. The dissipation rate of turbulent kinetic
125 energy was estimated from the small-scale shear and assuming isotropy is
126 defined as:

$$\varepsilon = 7.5\nu\langle(\partial u/\partial z)^2\rangle, \quad (1)$$

1
2
3
4
5
6
7
8
9
10 where ν is the kinematic viscosity, which in seawater takes the value of about
11 $10^{-6} \text{ m}^2 \text{ s}^{-1}$, and $\partial u / \partial z$ represents the spatial derivative of the horizontal
12 current component, u , in the vertical direction, z . The angled brackets denote
13 a suitable time average, and the units of turbulent dissipation are given
14 in W kg^{-1} . MSS-90 profiles begin at a depth of 5 m, due to the potential
15 for contamination from the motion of the boat induced by wave activity
16 (Lozovatsky et al., 2006). The MSS-90 samples at a rate of 1024 Hz with a
17 typical fall speed of 0.5 m s^{-1} . Such high frequency measurements allow for
18 great confidence in the estimate of ε .
19
20
21
22
23

24 2.3. Holographic camera

25
26 An in-line digital holographic imaging system, the Holocam, was also
27 deployed. The Holocam is mounted on a steel frame along with a CTD,
28 and is described fully in Graham and Nimmo Smith (2010). Briefly, the
29 system contains a laser light source that illuminates a sample volume con-
30 taining plankton particles which scatter the light, whereupon an interference
31 pattern is generated and subsequently recorded by a charge-coupled device
32 (CCD). The resulting hologram is then computationally reconstructed post-
33 deployment to give in-focus images of every particle in the sample volume,
34 allowing for the calculation of particle statistics such as volume concentration
35 and size distribution. Each raw hologram has a pixel resolution of $4.4 \mu\text{m}$,
36 and is 1536×1024 pixels in size, yielding a sample volume of 1.65 cm^3 which
37 is later scaled up to one litre during post-processing. In practical terms the
38 minimum particle size resolved by this system is around $25 \mu\text{m}$, with the
39 maximum size limited only by the size of the CCD, here in excess of 6 mm.
40 The Holocam was profiled vertically through the water column once each
41 hour, near-simultaneously with the MSS profiles. The sampling frequency
42 was 5 Hz with a profiling speed typically in the range of $0.2\text{-}0.4 \text{ m s}^{-1}$, thus
43 samples were obtained at a vertical resolution of around 5-6 cm.
44
45
46
47
48
49
50
51
52
53
54

55 The average number of holograms taken during a given profile of the
56 instrument is around 1000; however the number of images for a given section
57
58

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

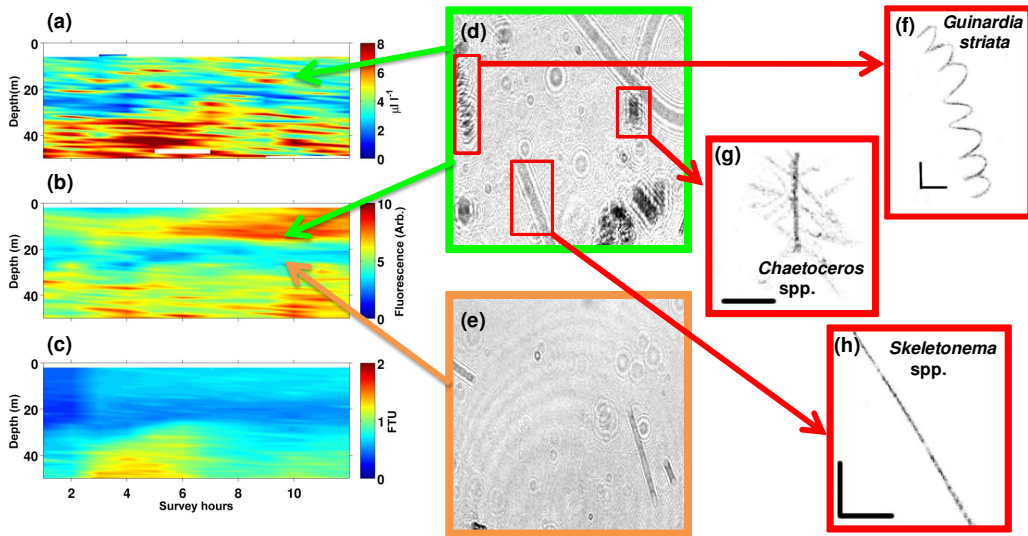


Figure 2: Illustration of the initial particle analysis using signals of interest from the MSS. Part (a) shows the total particle volume concentration (Holocam), (b) and (c) the response from the fluorescence and OBS sensors (MSS). Parts (d) to (h) represent a step-wise view of selecting raw holograms prior to numerical reconstruction in order to establish the type of plankton present. The scale bar in (f) is $200\ \mu\text{m}$, in (g) and (h) $100\ \mu\text{m}$.

of the water column may vary with the minor variation in fall speed range or water column properties. With the sample volume of each image, the total volume of water sampled during each profile would be in the region of 1.5-2 L. An illustration of how the Holocam is used to assess the particle environment is further displayed in Figure 2. The first step of this analysis is to locate the raw holograms that relate to the area of the water column that is of interest. Regions of interest (ROI) may be defined within each hologram and numerically reconstructed, revealing a sharp and in-focus image of planktonic particles (Figure 2f to h).

An additional technique was employed to determine how plankton may be altered by changes to their physical environment, and also where within a tidal cycle their number is shown to vary. Prior to this work, such enumeration of plankton has not been possible *in situ* without disturbing the plankton from their natural environment. Within the size range of phyto-

1
2
3
4
5
6
7
8
9
10 171 plankton that the Holocam may reliably resolve, phytoplankton biomass at
11 172 L4 is dominated by chain-forming phytoplankton (Widdicombe et al., 2010),
12 173 whereby within each image a colony of multiple diatom cells is regarded a
13 174 single suspended particle. Diatom chains are routinely found to grow to sev-
14 175 eral mm in size and are readily identifiable from the image data. However,
15 176 to maximise efficiency when counting individual colonies, only phytoplank-
16 177 ton $\geq 200 \mu\text{m}$ were identified and recorded. The assumption is made that
17 178 this threshold would be sufficient to identify changes to the phytoplankton
18 179 population brought about by changes imposed upon the water column by
19 200 physical processes.

20
21
22
23
24
25 181 A simple, graphical user interface was designed in Matlab which took
26 182 a flattened, reconstructed image of a 1024x1024 ROI as an input. Blocks
27 183 of images were collated within 5 m intervals. Plankton were first identified
28 184 as present through simple observation of each image. Upon identification,
29 185 selection of the plankton was achieved through the click of a computer mouse.
30 186 The interface stored each click as a single piece of plankton, allowing for
31 187 the calculation of the mean number of plankton per unit volume of 1 L.
32 188 Throughout this paper, the term number is used to refer to this metric when
33 189 describing changes to both the phyto- and zooplankton populations.

34 35 36 37 38 39 40 190 *2.3.1. Bedframe deployment*

41
42 191 In addition to the Lagrangian surveys, a further deployment of a moored
43 192 ADCP was conducted for a two-week period from 28th July 2010 to August
44 193 11th 2010. Deployments were also scheduled for the spring and autumn
45 194 seasons but were thwarted by logistical challenges. An upward-facing 600 kHz
46 195 ADCP was placed within a bedframe at the seabed. The ADCP sampled at
47 196 6 s intervals with a bin size of 1 m, with the first good bin at a height of 2 m
48 197 above the bottom (mab). Despite the lack of seasonal coverage, the ADCP
49 198 data would provide the background context with respect to the properties
50 199 of the current and also clearly demonstrates the degree to which shear is
51 200 present at L4.

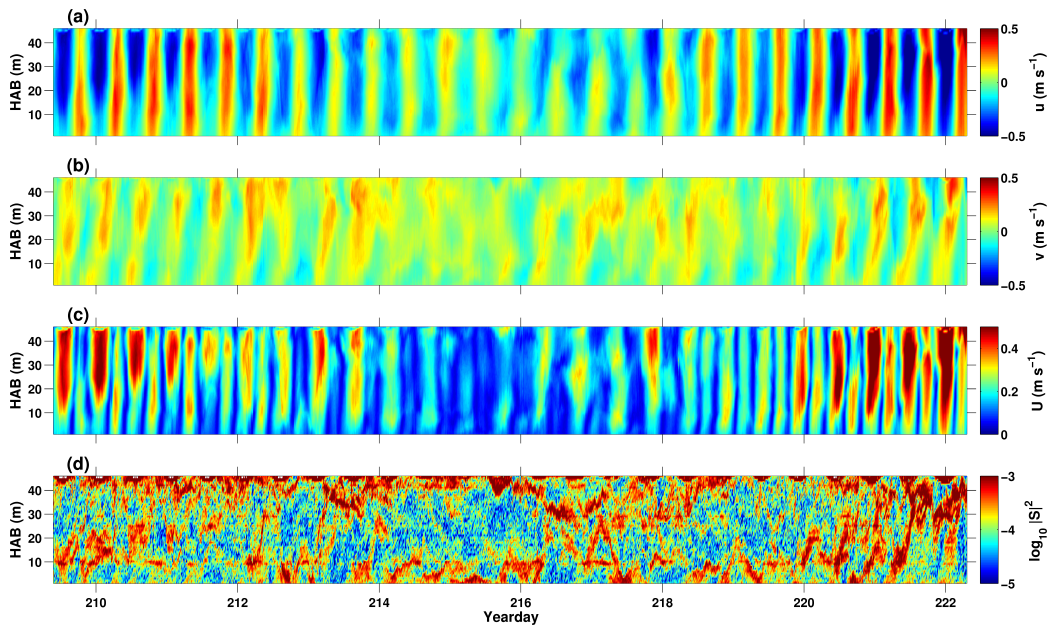


Figure 3: Results from the moored ADCP deployed at L4 during summer 2010. Plots (a) and (b) display the u and v components of velocity, (c) the velocity magnitude, U , and (d) shear, $|S|^2$ (s^{-2}). HAB refers to height above the bottom.

3. Results

3.1. ADCP deployment summer 2010

Placing the Lagrangian surveys into context the deployment of the moored ADCP showed, for summer at least, that the water column at L4 is subjected to varying degrees of current shear (Figure 3c). The tidal current at L4 is dominated by the east-west, or u component with speeds frequently reaching 0.5 m s^{-1} toward the surface during spring tides, and occasionally exceeding this toward the latter part of the deployment. Neap tides, occurring during the middle of the deployment typically yield lower maximum values of around 0.3 m s^{-1} toward the surface. Shear is calculated as $|S|^2 = \sqrt{\left(\frac{\partial u}{\partial z}\right)^2 + \left(\frac{\partial v}{\partial z}\right)^2}$, with the logged values displayed in (Figure 3d). The entire deployment of the bedframe is characterised by patches of elevated $|S|^2$ that frequently exceed 10^{-3} s^{-2} largely toward the surface and closer to the bed, with values in the

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

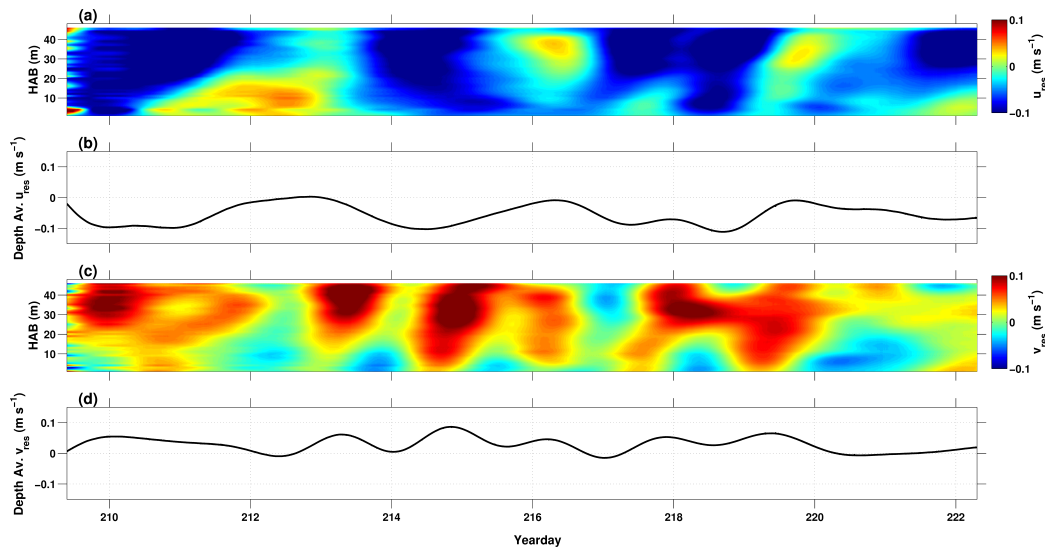


Figure 4: Mean flow at L4 during the bedframe deployment. Plots (a) and (c) show the residual velocity in the u and v directions respectively. The depth-averaged velocity values for each component are displayed in (b) and (d).

middle of the water column an order of magnitude lower. These lower values are more often present during the periods when U is reduced, particularly during neap tides. The general picture presented by the calculated $|S|^2$ is of a site that is regularly exposed to persistent and high levels of sheared flow.

Residual flow is determined by low-pass filtering of the tidal signal with a $0.75 \text{ cycles day}^{-1}$ (cpd) cut-off, yielding the values displayed in Figure 4. As anticipated for this site, the dominant flow is along the west-east (u) axis, with values of this component frequently approaching 0.1 m s^{-1} and directed predominantly to the west. North-south, or flow in the v direction is broadly 50% weaker, predominantly directed to the north. However, the deployment period is short, and likely to be impacted by rapid changes to the meteorological conditions that are occasionally observed. Periods of increased wind forcing are experienced during this deployment, which could influence the direction of the residual flow (e.g. see later Figure 7). The example of the week 5 observations on the 4th August and the days preceding demonstrate

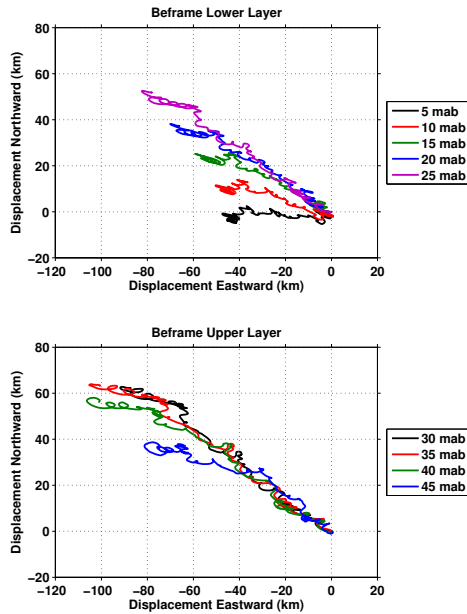


Figure 5: Progressive vector diagrams from the deployment of the moored ADCP. The water column is split into upper and lower layers as labelled, further highlighting the presence of sheared flow.

229 this whereby the wind was directed from the south, likely influencing the
 230 direction of the net flow which is pushed to the north at this time. Whilst
 231 these values offer an indication of the residual flow at this site, it is clear that
 232 a future deployment of greater duration would benefit all users of L4.

233 A further illustration of the vertical shear that dominates the dynamics
 234 of the water column at L4 is given by a progressive vector diagram (Figure
 235 5). Broadly, the water column can be split into two layers, the lower ~ 20 m.
 236 and upper ~ 30 m. The mean displacement for a given water particle for the
 237 lower layer is 61 km on a broad heading of west-north-west. In contrast, for
 238 the upper layer the mean displacement is 99 km directed to the north-west.

239 3.2. Background meteorological data for the tidal surveys

240 Meteorological observations throughout the period of the spring surveys
 241 are shown in Figure 6. The Plymouth University meteorological station pro-

1
 2
 3
 4
 5
 6
 7
 8
 9
 10
 11
 12
 13
 14
 15
 16
 17
 18
 19
 20
 21
 22
 23
 24
 25
 26
 27
 28
 29
 30
 31
 32
 33
 34
 35
 36
 37
 38
 39
 40
 41
 42
 43
 44
 45
 46
 47
 48
 49
 50
 51
 52
 53
 54
 55
 56
 57
 58
 59
 60
 61
 62
 63
 64
 65

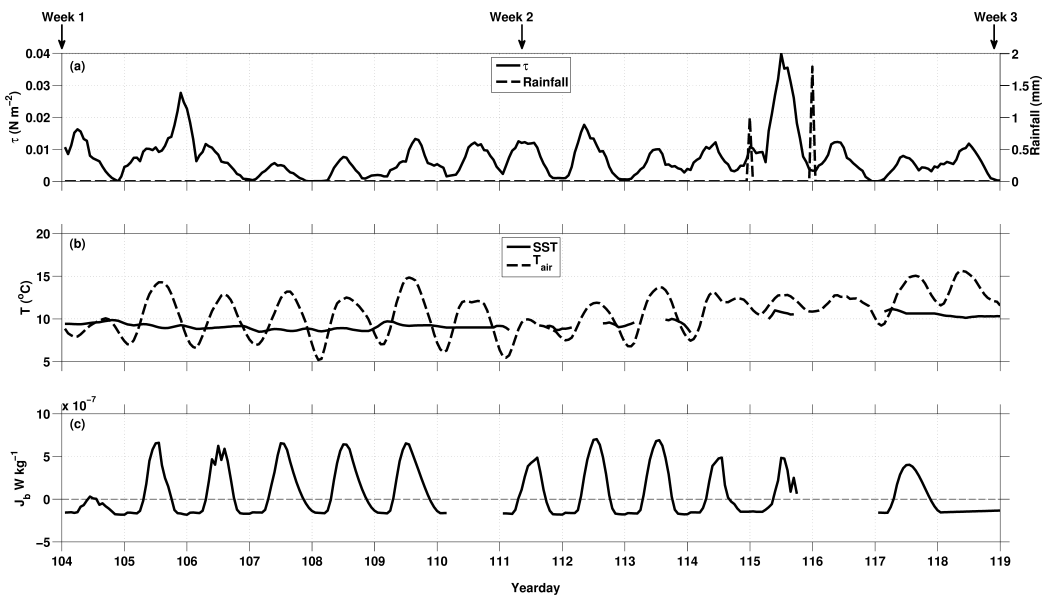
242 vided the observed wind stress, τ , rainfall and air temperature. Winds were
 243 light throughout April 2010, during the survey period yielding a maximum
 244 value for τ of 0.2 N m^{-2} between weeks 1 and 2. The wind stress presented
 245 in plot (a) of Figure 6 indicates that the potential for wind stirring, and
 246 therefore enhanced episodes of turbulent events at the surface, was reduced,
 247 particularly during the dates of the measurement campaigns. Similarly, the
 248 level of precipitation was very low during this month and once again on the
 249 dates of each of the surveys no rainfall was recorded by the met station nor
 250 experienced on board the vessel during the deployment. There was a gradual
 251 increase in air temperature in April, the mean air temperature during week
 252 one was 8.8°C compared with 13.2°C during week 3 (Figure 6b-c). The
 253 observed sea surface temperature (SST) reflects the increase in air temper-
 254 ature with a mean value of 9.2°C during week 1 and 10.3°C for week 3.
 255 There are several missing periods from instances when the L4 buoy was of-
 256 fline which have been supplemented by satellite from the AVHRR pathfinder
 257 dataset. Further limitations with respect to SST came from the amount of
 258 cloud cover present.

A measure of the extent to which the meteorological parameters influence
 the stability of the water column is the buoyancy flux, J_b . Positive values of
 J_b indicate stabilising conditions and *vice versa*. Following Hosegood et al.
 (2008), the buoyancy flux is given by

$$J_b = c_p^{-1} g \rho^{-1} \alpha Q + g \rho^{-1} \beta (E - P) S_{surf} \quad (2)$$

259 in units of W kg^{-1} . Here, $Q = Q_{shortwave} + Q_{longwave} + Q_{latent} + Q_{sensible}$ which
 260 represents the total heat flux (W m^{-2}), c_p is the specific heat of water and g
 261 the acceleration due to gravity. Evaporation and precipitation are given by
 262 E and P respectively, S_{surf} is the surface salinity, with α and β representing
 263 the thermal expansion and haline contraction coefficients. It should be noted
 264 that the gaps that appear in Figure 6c represent periods where the lack of
 265 both SST and S_{surf} meant that J_b could not be computed, and that for days

1
2
3
4
5
6
7
8
9
266 111 to 115 a constant S_{surf} value was required. The terms that dominate
267 J_b are $Q_{shortwave}$ and Q_{latent} , whereby short wave radiation stabilises and
268 the latent heat flux acts to destabilise during periods of strong winds. In
269 the absence of the latter, the general pattern is one of stability with daily
270 maximums of J_b frequently exceeding $5 \times 10^{-7} \text{ W kg}^{-1}$. The largely negative
271 value of J_b during day 104 can be attributed to the lack of solar insolation
272 through increased cloud cover and low air temperature.



41
42 Figure 6: The background meteorological data for the survey period during generated by
43 observations from the PU met station. Plot (a) displays wind stress (τ) and rainfall, (b)
44 air and sea surface temperature, and (c) buoyancy flux (J_b). Both (a) and (b) consist of
45 daily averages. With respect to SST, limited data was available due to the L4 buoy being
46 off-line. Satellite data were used where possible but was also limited due to the presence
47 of cloud-cover. The arrows mark the positions of each of the survey periods.

48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
273 The planned surveys of weeks 4 and 5 were each due to be conducted
274 across 12 hours, in the same manner of those in April, however the meteo-
275 rological conditions experienced throughout these campaigns did not allow
276 for this. The impact of these conditions can be considered in addition to the
277 relative change imparted by seasonal elements such as increased insolation.

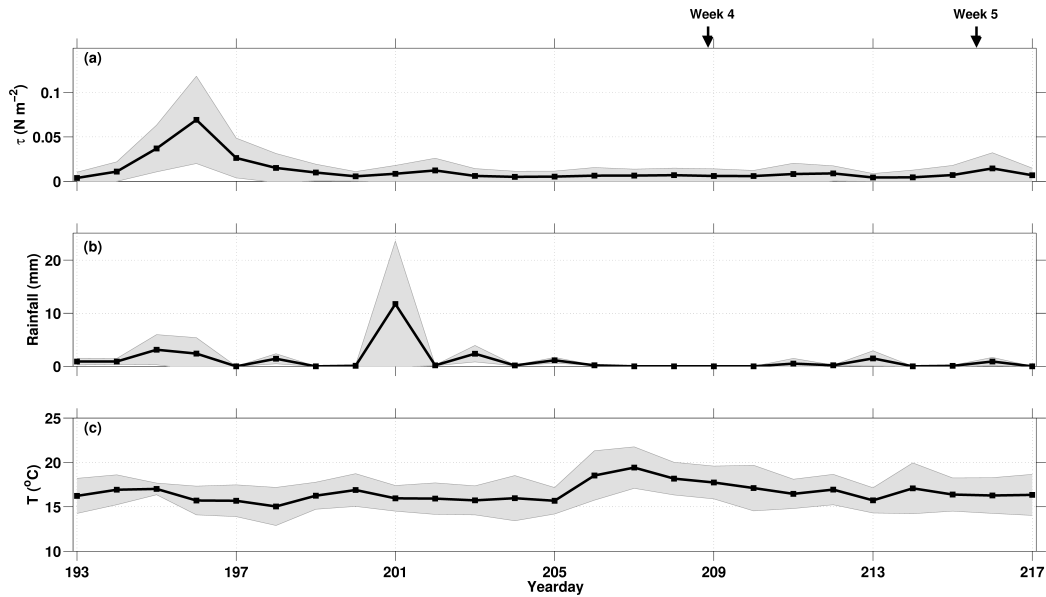


Figure 7: The background meteorological data for the survey period of weeks 4 and 5 generated by observations from the PU met station. Plot (a) displays wind stress (τ), (b) rainfall and (c) air temperature. All plots consist of daily averages, with the shaded region representing 1 S.D about the mean.

By way of context, some of the key meteorological parameters are displayed in Figure 7. Unfortunately, the calculation of the buoyancy flux could not be achieved across this period due to the absence of SST and sea surface salinity (SSS) measurements. The L4 buoy would ordinarily supply this data but was off-line from the 30th July for a period of around one month. Additionally, the satellite data that was used to provide supplementary data as per the previous weeks were not available due to the extent of the cloud cover.

3.3. Spring 2010 surveys

The evolution of several of the measured parameters for each survey is displayed in Figures 8 and 9. Spring tides occurred during weeks 1 and 3 with neaps in week 2 when the minimum tidal range was experienced (≈ 2 m). Each of the plots displays observations across a 12 hour tidal cycle observed

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

in weeks 1, 2 and 3 respectively.

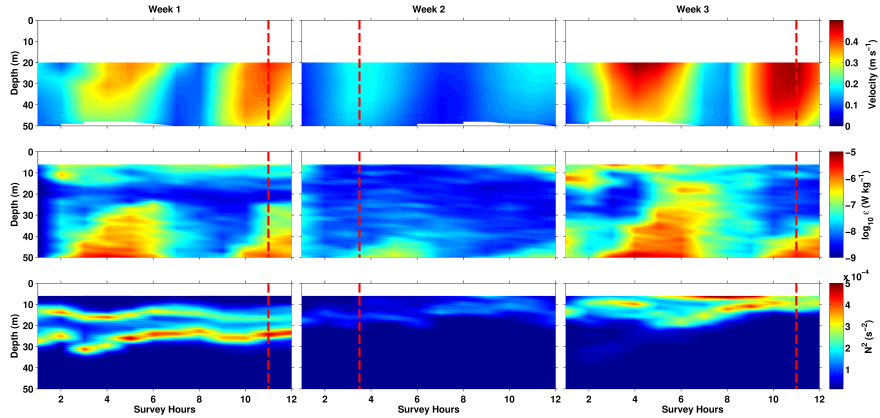


Figure 8: Measurements obtained from the ADCP and MSS for each of the surveys. The uppermost row displays the velocity magnitude observed with the ADCP. The middle row contains the dissipation of turbulent kinetic energy, ε , with the bottom row showing the buoyancy frequency, N^2 . The vertical dashed lines mark the point of high water for each survey.

291

292 During week 1, the peaks in ε occur shortly after the times of peak flow,
 293 whereby the maximum velocities recorded by the ADCP are 0.37 m s^{-1} and
 294 0.42 m s^{-1} for the ebb and flood tides respectively. Maximum values for ε
 295 are experienced between hours four and five, with values approaching 10^{-5}
 296 W kg^{-1} at the seabed. Enhanced dissipation at the bed is broadly coincident
 297 with the peaks in U , though the largest values for ε occur around 1-1.5 hours
 298 following the periods of faster current velocity. The influence of the pycno-
 299 cline on ε is evident, apparently suppressing turbulent activity where values
 300 for N^2 are in excess of 10^{-4} s^{-2} at around 15-30 m. This is also reflected
 301 in the plots of salinity and density, but to a lesser extent in temperature,
 302 illustrating the greater influence of salinity on the water column than tem-
 303 perature for this survey. This is reflected in the density ratio, a parameter
 304 that quantifies the relative influence of temperature and salinity on density,

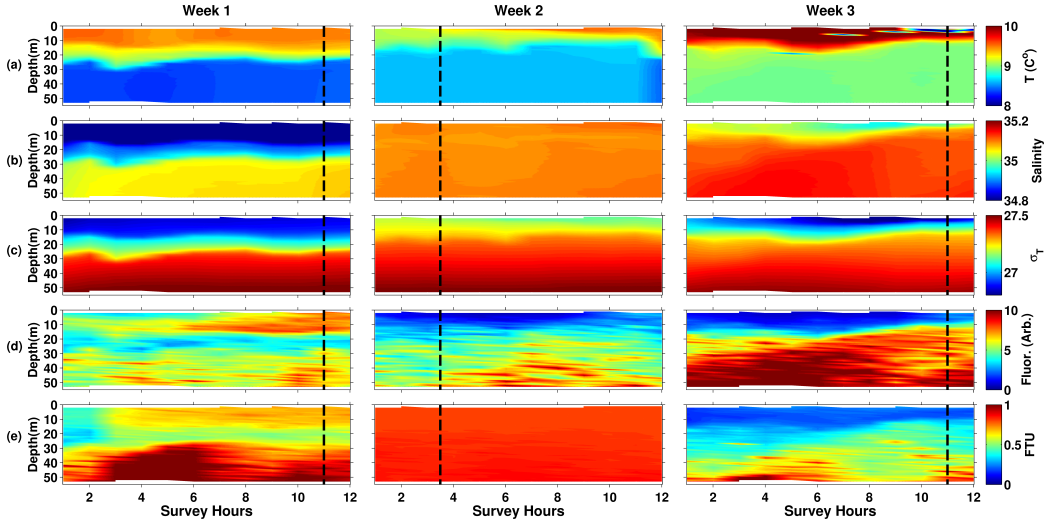


Figure 9: Scalar parameters obtained from the MSS measurements. The top row (a) displays temperature, followed by salinity (row b) and *in situ* density (row c). rows (d) and (e) shows fluorescence and turbidity respectively for each of the surveys as labeled. The vertical dashed lines mark the point of high water for each survey.

where values within the range of -1 to 1 indicate a dominance of salinity and is expressed as

$$R_\rho = \frac{\alpha(\Delta T)}{\beta(\Delta S)} \quad (3)$$

where, as previously, α and β are the thermal expansion and haline contraction coefficients respectively. For this week, the mean $R_\rho = -0.68$ in the upper 25 m of the water column.

The markedly reduced values for ε during week 2 are illustrative of the reduced flow experienced during neap tides. Current velocities were observed to be $< 0.2 \text{ m s}^{-1}$ for both ebb and flood, reflected in maximum dissipation around $10^{-6} \text{ W kg}^{-1}$ in the bottom 3 m of the water column. There is a more marked time-velocity asymmetry when compared with either week 1 or week 3. The lower values of dissipation are evident and decrease to values approaching $10^{-8} \text{ W kg}^{-1}$ at a depth of around 40 m throughout the survey. The apparent absence of stratification in week 2 is consistent with the

1
2
3
4
5
6
7
8
9
10 318 corresponding plots for turbulent dissipation, although a weak pycnocline
11 319 does exist during this time, with $N^2=10^{-6} \text{ s}^{-2}$ at numerous points. Further
12 320 temporal variability is displayed in week 3. Elevated levels of ϵ return as
13 321 a consequence of the spring tides, with increased tidal velocities of close to
14 322 0.5 m s^{-1} during both high and low water generated by a larger tidal range
15 323 ($> 3 \text{ m}$). This results in enhanced values of dissipation which more readily
16 324 exceed $10^{-5} \text{ W kg}^{-1}$, and higher values of $10^{-4} \text{ W kg}^{-1}$ are not uncommon,
17 325 particularly within the bottom 5 m of the water column. The pycnocline is
18 326 shallower here at around 10-20 m and seemingly it is temperature that con-
19 327 trols the water column with the mean $R_\rho = -1.07$ in the upper 25 m. Values
20 328 of N^2 are marginally lower when compared to week 1.

27 329 *3.4. Summer 2010 surveys*

28
29 330 The campaigns of week 4 and 5 were conducted across spring and neap
30 331 tides, respectively. The combination of the downward-facing ADCP to as-
31 332 sess current flow and the MSS to observe the TKE dissipation was again
32 333 employed, illustrating the contrasts between the two tidal regimes (Figure
33 334 10). The dominance of the ebb tide is again prominent in week 4, with peak
34 335 flow magnitudes occasionally exceeding 0.50 m s^{-1} between hours four and
35 336 six. Low water was around hour six, and high water a little before hour 12.
36 337 In the two hours prior to high water the increase in current magnitude is
37 338 smaller than that observed shortly before low water, with values here reach-
38 339 ing no more than around 0.20 m s^{-1} . There is no direct comparison with week
39 340 5 as this survey is conducted over the shorter period of 7 hours. As such,
40 341 the opportunity to observe the flow regime during the ebb tide is lost. The
41 342 strongest flow recorded during neap tide is around 0.14 m s^{-1} , shortly before
42 343 high water during hour 4.

43 344 During week 4, ϵ peaks at $10^{-5} \text{ W kg}^{-1}$ and unlike the corresponding
44 345 surveys in spring, at no point exceed this value. There are striking features
45 346 that mark the evolution of ϵ throughout the tidal cycle here. Broadly, there
46 347 is a marked discontinuity where a sharp reduction in values of dissipation

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

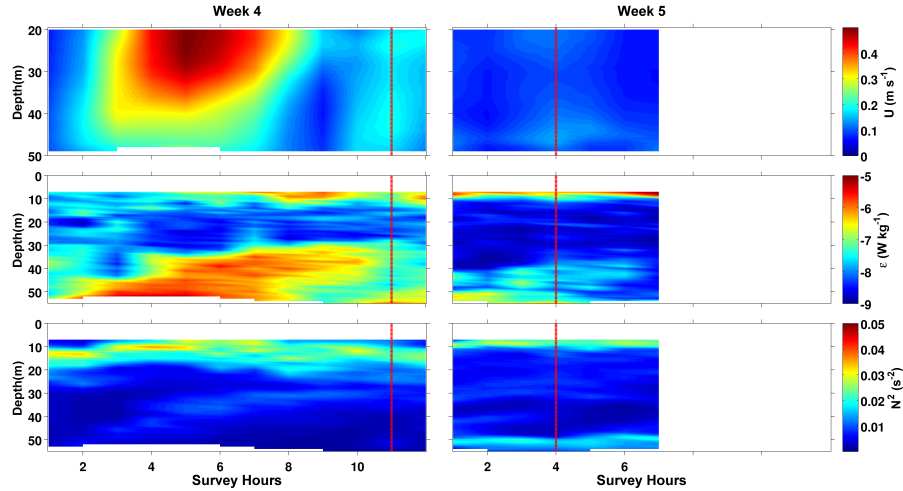


Figure 10: Data from the two surveys of Summer 2010. The top row displays current magnitude (U) from the ADCP, the middle row TKE dissipation (ϵ) with the buoyancy frequency (N^2) comprising the bottom row. The vertical dashed line on each of the plots denotes the time of high water for each survey.

occurs at approximately 30 m, though this is not entirely consistent with the position of the pycnocline which is somewhat shallower at 20 m marked by the peak in N^2 displayed in the lowermost plot of Figure 10, and further highlighted in Figure 11. Week 5 is of course quite different, though there is a noticeable patch of elevated dissipation toward the bed that is sustained throughout much of the duration of this shortened survey. Maximum values of ϵ rarely exceed $10^{-7} \text{ W kg}^{-1}$ save for a smaller region close to the bed during the first two hours. The thin region of increased ϵ closer to the surface is most likely due to the transfer of energy from the additional wind and wave activity at the surface.

The depth of the pycnocline is similar to that observed during the week 1 survey in spring 2010. Naturally, the surface to bottom temperature difference is greater, peaking at 4.3°C , with the maximum temperature at the surface reaching 16.1°C between hours six and eight of the week 4 survey.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

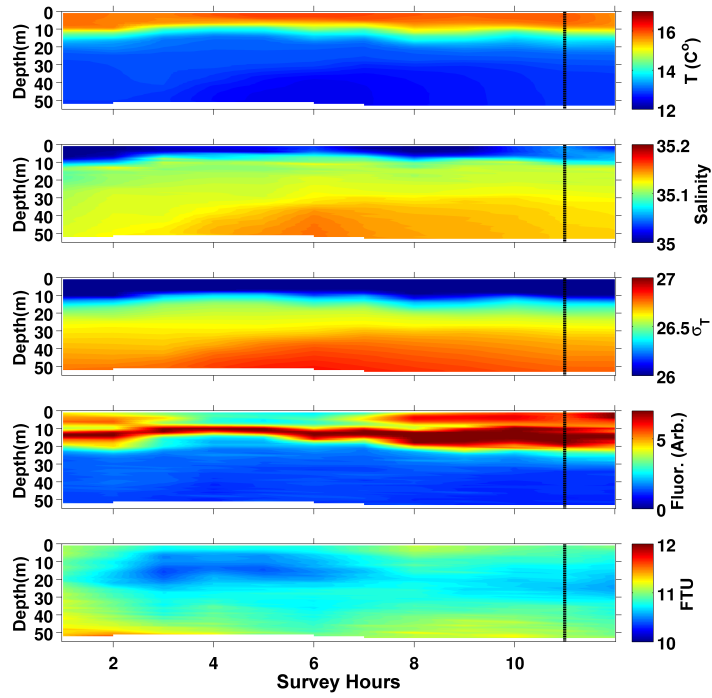


Figure 11: MSS sensor data for week 4. Temperature is the uppermost plot followed by Salinity and σ_T . Fluorescence in arbitrary units to represent relative changes to the sensed voltage follows, with the final plot showing turbidity from the OBS sensor. The vertical dashed line on each of the plots denotes the time of high water for this survey.

1
2
3
4
5
6
7
8
9
10 362 This period corresponded with the middle of the afternoon where air tem-
11 363 peratures were also at their highest. The plot of density in Figure 11 mirrors
12 364 that of N^2 , denoting a somewhat stronger density gradient present here than
13
14 365 seen in the week 1 survey in spring underscoring the influence of seasonal
15 366 change on the physical regime. Whether L4 can be considered subject to a
16
17 367 more permanent thermocline throughout summer is not clear, however, due
18 368 to the competing forces of temperature and salinity at this location and the
19
20 369 propensity for the pycnocline to rapidly erode following increased wind stress
21 370 or enhanced mixing by tidal forcing. This is further illustrated by the ob-
22
23 371 served picture of the water column presented in Figure 12. Here, the plots
24
25 372 of temperature and salinity (and thus density) are much more homogeneous.
26
27 373 With temperature, there are thin regions of warmer water at the surface and
28 374 cooler water at the bottom. Each is of around 5 m in depth, with maxi-
29
30 375 mum and minimum temperatures of 15.7°C and 13.3°C at the surface and
31 376 bottom respectively. The subsequent reduction in surface to bottom temper-
32
33 377 ature difference of 1.7°C implies that thorough mixing has occurred from a
34 378 combination of the meteorological conditions (Figure 7) and that of the tide.

379 3.5. Water column energetics

38
39 380 In explaining the temporal evolution of stratification displayed by Figure
40 381 9, the potential energy anomaly (PEA) was calculated (following the method
41 382 outlined by [Simpson and Bowers 1981](#); [Simpson et al. 1990](#) and also more
42 383 recently by [Cheng et al. 2010](#)), to quantify the degree to which L4 is stratified
43 384 for a given survey and calculate the amount of energy required to bring about
44
45 385 a completely mixed water column.

46
47
48 386 The approach considered by [Simpson and Bowers \(1981\)](#) details the time
49 387 derivative of PEA, when only stirring by tidal and wind forcing and buoyancy
50 388 input from solar heating are important. This is also the case for L4, although
51 389 the extent to which this location is influenced by freshwater outflow from the
52
53 390 nearby rivers Tamar and Plym across short time scales is yet to be explicitly
54
55 391 quantified. Rainfall for the period of April 2010, as shown in Figure 6, is

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

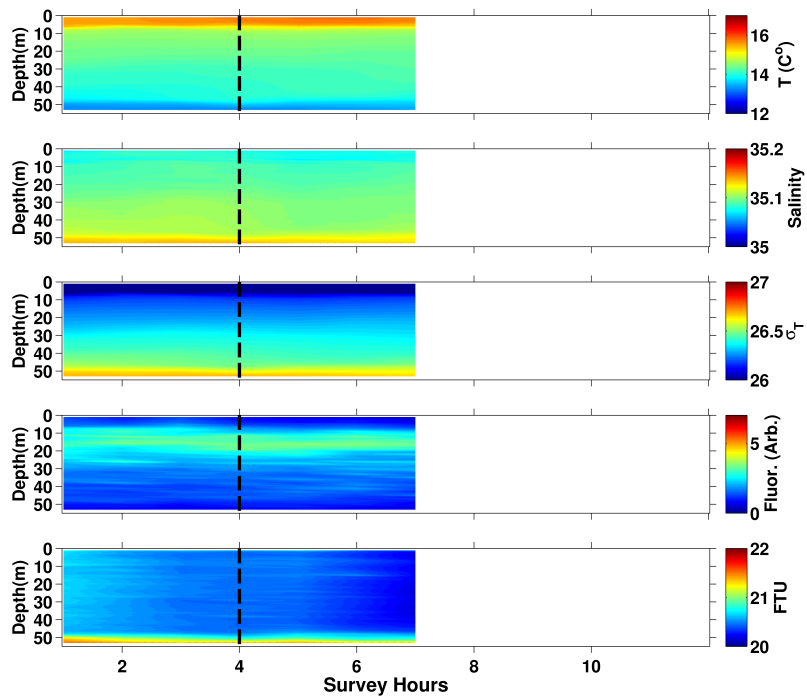


Figure 12: MSS sensor data for week 5. Temperature is the uppermost plot followed by Salinity and σ_T . Fluorescence in arbitrary units to represent relative changes to the sensed voltage follows, with the final plot showing turbidity from the OBS sensor. The vertical dashed line on each of the plots denotes the time of high water for this survey.

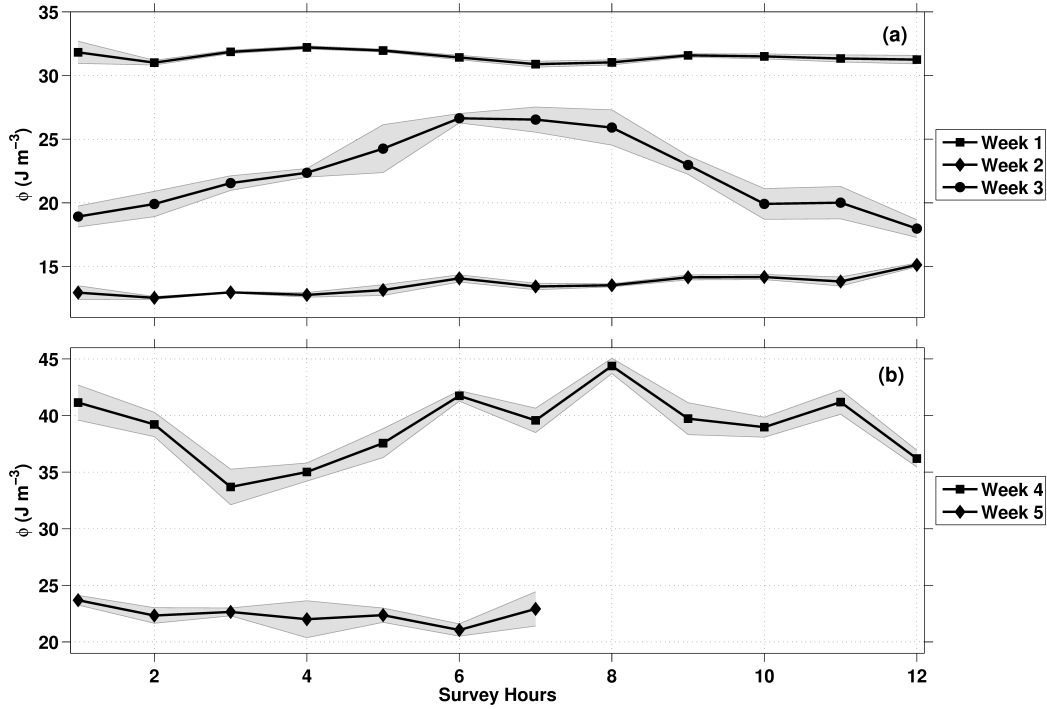


Figure 13: Hourly-averaged Potential Energy Anomaly (PEA) for each of the five surveys. The shaded envelope around the values for each week represent 1 S.D about the mean.

effectively nil so neglecting this as an additional input of buoyancy is valid. [Simpson et al. \(1990\)](#) described the PEA, in units of J m^{-3} , as follows:

$$\phi = \frac{1}{H} \int_{-H}^0 (\bar{\rho} - \rho) g z dz. \quad (4)$$

Here, the overbar defines a depth-averaged value of density, with H representing the total depth of the water column.

The calculated PEA reflects the stratification in each week, with $\phi > 30 \text{ J m}^{-3}$ in the spring tide of week 1, $\phi < 15 \text{ J m}^{-3}$ for week 2 during neaps. Surface heating is a major contributor to stratification, though despite the increase in surface temperature during week 3 maximum values for ϕ reach only 26.5 J m^{-3} , markedly lower than those observed in week 1 (Figure 13a).

1
2
3
4
5
6
7
8
9
401 Winds were light throughout the spring surveys, and with the correspond-
402 ing calm conditions it seems likely that during periods when meteorological
403 conditions are less quiescent the PEA will be lower.

404 The expectation that stratification should be stronger during summer
405 was partially borne-out. As with the spring surveys, though, and in line
406 with the observations displayed in Figures 11 and 12, temporal variability
407 exists between the tidal cycles. Prior to the less favourable meteorological
408 conditions experienced during week 5, it is likely that stratification would
409 have been promoted by light winds and increased levels of solar radiation.
410 This is reflected in the maximum values of PEA of 44.8 J m^{-3} , occurring at
411 hour 8 of the week 4 survey in the middle of the afternoon. The mean for the
412 survey is 39.0 J m^{-3} . The subsequent mixing and/or presence of advection
413 has reduced the observed PEA for week 5. Here, the maximum value for
414 this curtailed survey is 23.6 J m^{-3} with the mean for the seven hours of data
415 collected being 22.4 J m^{-3} . These results compare favourably with those of
416 Groom et al. (2009), who found that in mid-summer L4 values for ϕ were
417 typically in the range of $40\text{-}50 \text{ J m}^{-3}$.

418 3.6. Distribution of Plankton populations

419 3.6.1. Spring surveys

420 The fluorescence data displays strong signals at particular points in the
421 water column, particularly in the upper layer during weeks 1, 3 and 4.
422 Whether these signals accurately reflect changes to larger plankton can be
423 assessed through the manual counting of individual plankton from the im-
424 ages recorded by the Holocam. The images from the casts of three periods
425 during each survey, the time of high, low and slack water were selected and
426 analysed as per the technique described in section 2 and denoted events A,
427 B and C respectively.

428 Qualitative assessment of the phytoplankton for all images showed that
429 *Skeletonema* spp., and *Chaetoceros* spp. dominate, examples of which are
430 illustrated in Figure 2. Higher numbers of phytoplankton are recorded during

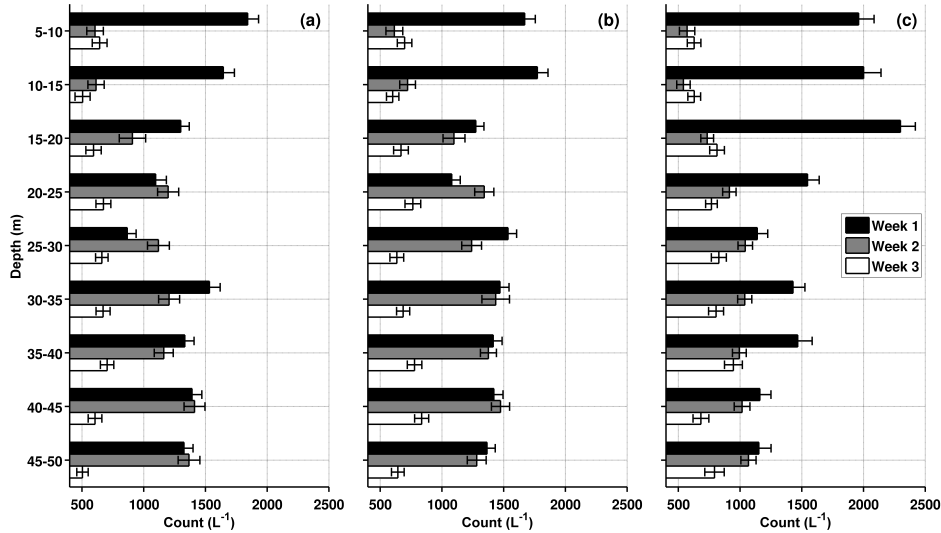


Figure 14: Number counts for the phytoplankton population $\geq 200 \mu\text{m}$ during weeks 1, 2 and 3. Plot (a) represents event A, (b) event B and (c) event C for the three surveys.

week 1, and toward the surface in particular where the recorded count is above 1500 L^{-1} in both of the two uppermost depth intervals throughout the survey (Figure 14). This is not repeated in either of the other surveys, and it is only during week 2 that the count is above 1000 L^{-1} , with counts of around 600 L^{-1} being more common in week 3. It should be noted here that a single phytoplankton particle according to this classification may comprise of a number of individual cells. Comparisons to other studies that employ cell counts as a measure of phytoplankton biomass have not been conducted.

Event C during week 1 displays counts of phytoplankton that are considerably greater than those of weeks 2 and 3, particularly in the upper 20 m of the water column. At no other point during any of the depth intervals does the count exceed 1500 L^{-1} , perhaps indicating that the values identified during the latter part of the week 1 survey are exceptional. The fluorescence signature for this period reflects the count in the upper three depth intervals (Figure 9). This pattern is not repeated for either the week 2 or 3

1
2
3
4
5
6
7
8
9
10 446 survey. The counts for these weeks in the same upper three depth intervals
11 447 are relatively lower and broadly similar, with counts typically in the region
12 448 of 500-850 L⁻¹, frequently a factor of two lower than week 1. The consistent
13 449 domination of diatoms as the most abundant population of larger particles
14 450 continues at this stage of the tidal cycle for each of the three weeks, although
15 451 not without a large degree of inter-tidal variability, which is also the case for
16 452 the other populations under consideration.

17
18
19
20 453 The variability demonstrated during the same period for zooplankton is
21 454 high (Figure 15). The images recorded during week 3 consist of biological
22 455 particles that are very different in character to either of the previous weeks,
23 456 as the presence of what are probable examples of jellyfish planula larvae dom-
24 457 inate the water column (Figure 16). These plankton are present throughout
25 458 each of the surveys, but to a lesser extent. The counts for week 1 above
26 459 30 m contain no planula, returning a selection of other types of zooplank-
27 460 ton (examples of which are shown in Figure 17). Each of the images has
28 461 been extracted from the full, reconstructed hologram following identification
29 462 of the particle of interest. Many more of these animals were captured by
30 463 the Holocam than were returned by WP-2 net trawls throughout the entire
31 464 sampling period (data provided by the WCO), although it should be noted
32 465 that the trawls and Holocam casts were not conducted concurrently. The
33 466 pattern broadly continues for weeks 2 and 3, as the majority of planula are
34 467 found at depths lower than the pycnocline. In week 3 during the event A
35 468 period the zooplankton count reaches its maximum of 312 L⁻¹ at the 35-40 m
36 469 depth interval, the depth-averaged value for this point being 196 L⁻¹. This
37 470 compares to depth-averages of 117 L⁻¹ for week 2 and 55 L⁻¹ for week 1, il-
38 471 lustrating the impact that the increased number of planula have on the total
39 472 zooplankton population.

40
41
42
43
44
45
46
47
48
49
50
51
52 473 For event B, a similar picture is presented. Once more the greatest num-
53 474 ber of particles are seen during week 3, with counts in excess of 200 L⁻¹ for
54 475 all but the uppermost two depth intervals. There are higher numbers of this

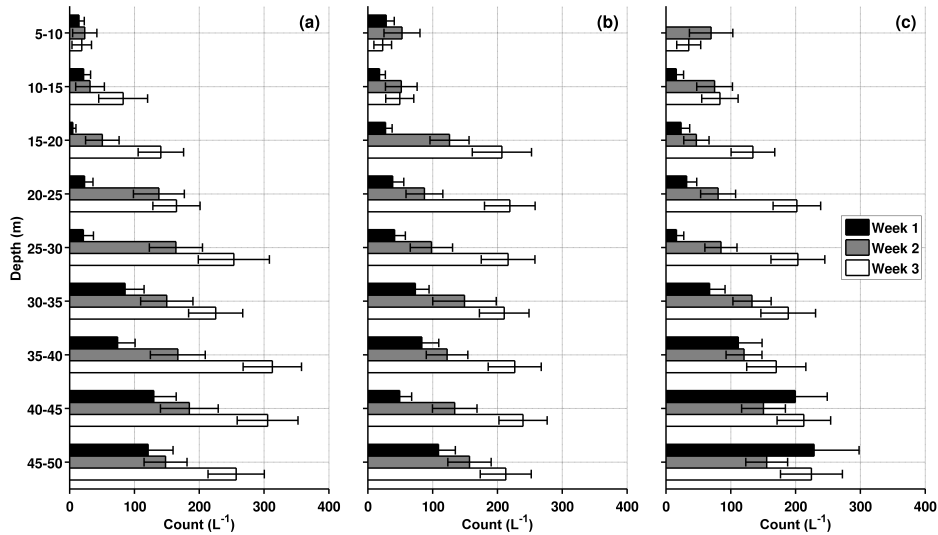


Figure 15: Number counts for the Zooplankton population during April 2010. Plot (a) represents event A, (b) event B and (c) event C for the three surveys.

476 population present in week 2 when compared to week 1, however for both
 477 of these periods counts of less than 150 L^{-1} are more common. A reflection
 478 on the lower number of planula present in week 1, the depth-averaged values
 479 here are 52 L^{-1} . This compares to 109 L^{-1} for week 2 and 178 L^{-1} for week
 480 3.

481 The pattern of zooplankton counts with depth exhibited by events A and
 482 B continues for the third event, as again numbers of this population increase
 483 when below 30 m. Noticeably, however, the maximum number of zooplankton
 484 recorded during this event is lower at 228 L^{-1} , which on this occasion is seen
 485 at the lowest interval of week 1. For week 2, the zooplankton count does
 486 not exceed 160 L^{-1} and remains relatively stable at the shallower intervals,
 487 a feature of this population during this survey across each of the selected
 488 events. Overall, and again a reflection of the presence of planula, it is week
 489 3 with the highest depth-averaged values of 162 L^{-1} , compared to 77 L^{-1} for
 490 week 1 and 102 L^{-1} for week 2.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

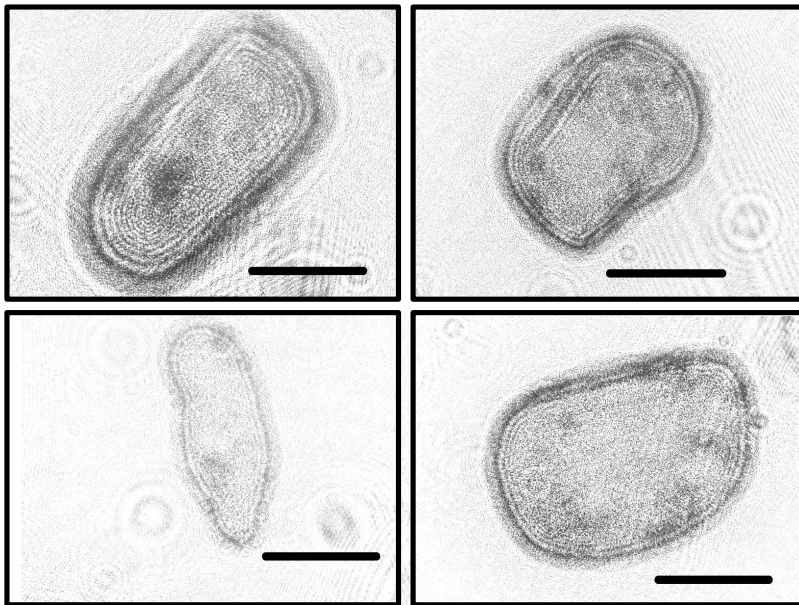


Figure 16: A selection of the probable planula larvae which increased the zooplankton population count in each of the spring surveys, with the scale bar in each image set to $1000\ \mu\text{m}$. These examples are unreconstructed, normalised raw images. Figure adapted from [Cross et al. \(2013\)](#).

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

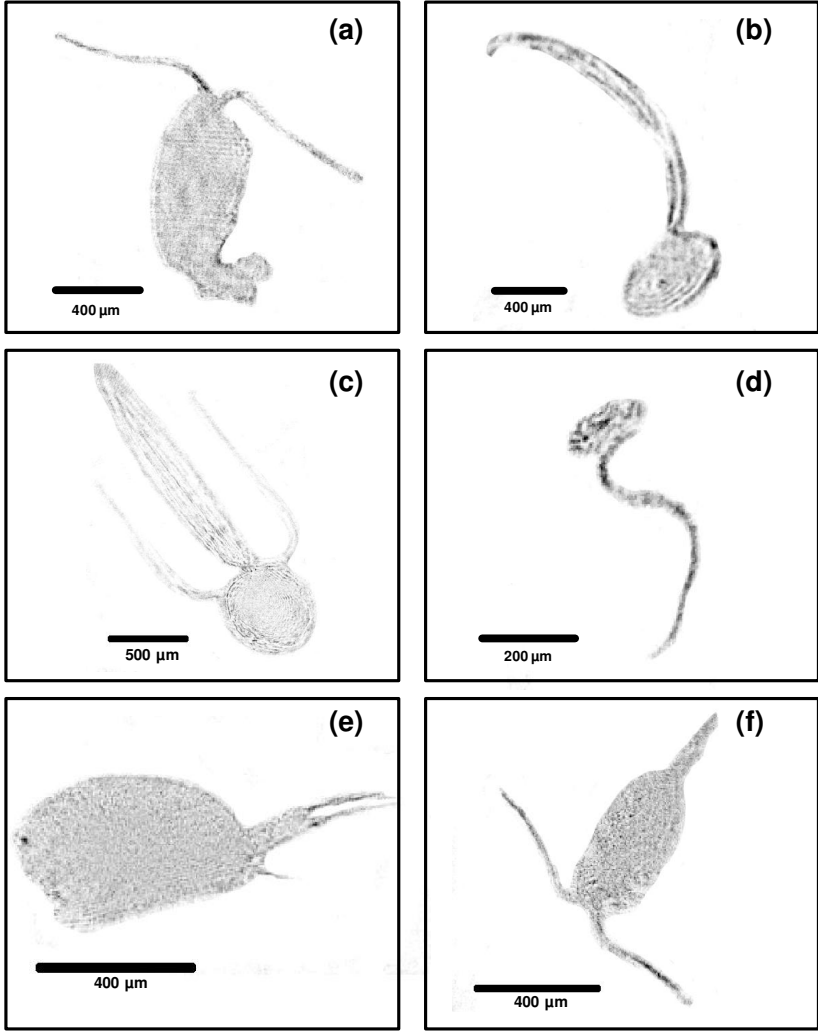


Figure 17: A selection of zooplankton that do not fall into the category of planula. Image (a) shows a copepod; image (b) is a probable example of *Oikopleura* spp.; image (c) an undetermined ascidian larvae; image (d) another example of *Oikopleura* spp. ; image (e) a crustacean larvae; image (f) a further copepod example.

1
2
3
4
5
6
7
8
9
10 Overall, a lower number of zooplankton are observed which is generally
11 the expectation at L4 given the dominance of phytoplankton, although this
12 may be a function of season. Comparisons to the population counts of the
13
14

15 Table 1: Comparison of depth-averaged counts of zooplankton populations across Weeks
16 1, 2 and 3.

	WP-2 Planula (L ⁻¹)	WP-2 Other (L ⁻¹)	Holocam Planula (L ⁻¹)	Holocam Other (L ⁻¹)	Holocam Total (L ⁻¹)
Week 1	0	3.6	47.4	14.0	61.4
Week 2	0	3.7	92.0	17.3	109.3
Week 3	0	2.2	157.2	21.3	178.5
Mean N(L ⁻¹)±S.D	0 (0)	3.2 (0.76)	98.9 (55.2)	17.5 (3.7)	116.4 (58.9)

17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

493
494 WCO assessed by using WP-2 nets for the same period are shown in Table 1.
495 Though there is a lag between the two sampling techniques, differences exist
496 for all three weeks. [Eloire et al. \(2010\)](#) conducted a long-term investigation
497 into zooplankton composition at the L4 site, utilising data from the previous
498 20 years. The peak in zooplankton population occurs in April, with the
499 average number of zooplankton equating to 4.5 L⁻¹ with Copepods making
500 up as many as 90% of this number. With some of the recorded counts in this
501 study indicating a population of many times this, it would appear that the
502 use of a WP-2 net alone may be under-resolving the zooplankton population
503 at L4.

504 For the Holocam data, Table 1 shows the depth-averaged zooplankton
505 count for the three casts relating to each of the events for weeks 1, 2 and
506 3. A distinction has been made between Planula larvae and ‘other’ zoo-
507 plankton, typically the Copepods or Appendicularians that strongly impact
508 upon the ecosystem dynamics of coastal and shelf sea systems ([Gowen et al.,
509 1999](#); [Gallienne and Robins, 2001](#)). This has been done to account for the
510 likely seasonal nature of the planula population, focusing on the zooplankton
511 which are important grazers of phytoplankton and, with respect to the Ap-
512 pendicularians, contributors to particulate organic matter (POM) ([Hopcroft](#)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

513 and Roff, 1998). It is unfortunate that concurrent water samples were not
514 obtained alongside the Holocam casts in order to effect a more explicit com-
515 parison. However, the recorded number of non-planula zooplankton is con-
516 sistently above that captured by the WP-2 net by a factor greater than five
517 and the 20 year average for April reported by Eloire et al. (2010) by almost
518 a factor of four. Further, the reported counts are for the region of the water
519 column from 5-50 m, as opposed to the bed to the surface as would be sam-
520 pled by the WP-2 net. Owing to this artificial shortening of the total sample
521 volume, the depth-averaged Holocam counts shown in Table 1 are likely to
522 under-estimate the total number of zooplankton.

523 3.6.2. Summer surveys

524 For weeks 4 and 5, event A represents hours 4 and 1 respectively, with
525 hours 9 and 5 constituting event B. Differences occur for the phytoplankton
526 population, more notably between events A and B of week 4. The relative
527 measure of fluorescence displayed in Figure 11, it is apparent that a similar
528 increase in the phytoplankton population to that observed during week 1
529 is present. As with week 1, fluorescence increases throughout the survey
530 toward the surface as the survey progresses through the tidal cycle. This
531 is in addition to the marked, elevated region of fluorescence that appears
532 to be consistent with the bottom of the thermocline. Also reflected in the
533 counts, the maximum number of phytoplankton particles exceed 2500 L^{-1}
534 on two occasions at the 10-15 m and 15-20 m depth intervals during week
535 4 (Figure 18b). During event A in week 4, the population counts broadly
536 reflect the fluorescence measurement from the MSS, with enhanced counts in
537 excess of 1000 L^{-1} between 10 and 20 m, before falling considerably below this
538 value as depth increases. A similar pattern exists for week 5, commensurate
539 with the weaker, but nonetheless present, enhanced fluorescence signal at a
540 comparable depth to that of week 4. The same conditions persist for event
541 B, reflected by the counts for this stage of the tide in week 5.

542 For zooplankton, the variability between weeks 4 and 5 is less marked.

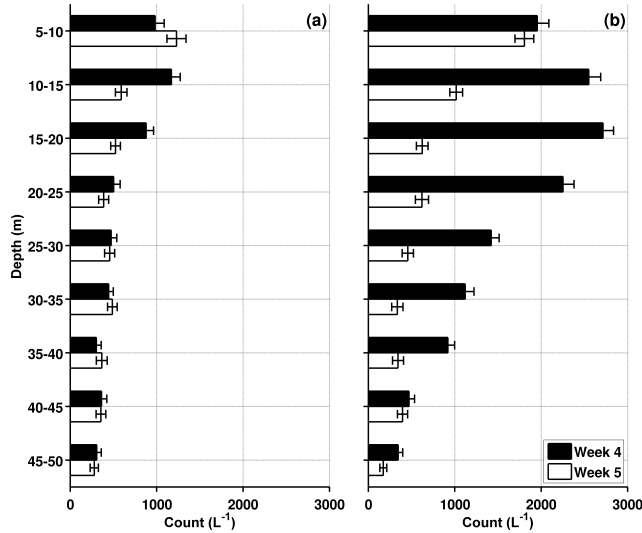


Figure 18: Particle number counts for the Phytoplankton population during July/August 2010. Plot (a) represents event A, and (b) event B for the two surveys.

Of particular note is the absence of the planula larvae that were abundant throughout the Spring surveys of weeks 1, 2 and 3. Thus, the numbers reflected by the counts in Figure 19 represent only those animals illustrated by the examples in Figure 17, that is organisms that are ‘hard-bodied’ such as the Copepods and Appendicularians. The absence of any zooplankton for a given week or interval is marked by a gap at the appropriate depth bin. The largest value for either week, 45 L^{-1} , is observed during event B in week 4, though most of the recorded counts fall below this yielding depth averaged values of 11.2 L^{-1} for week 4 and 10.5 L^{-1} for week 5.

The relatively lower number of zooplankton observed during the summer surveys is closer to the long term average than those of April. The absence of the gelatinous planula is in part responsible for this, though this will now provide a better opportunity to compare with the net trawls of the similar period, given that it is only the harder-bodied organisms that are present.

The comparisons between the two methods are again to be treated with

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

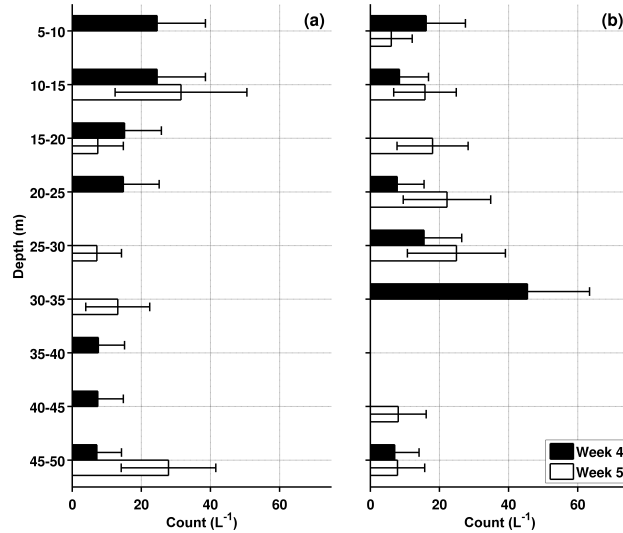


Figure 19: Particle number counts for the Zooplankton population during July/August 2010. Plot (a) represents event A, and (b) event B for the two surveys.

Table 2: Comparison of depth-averaged counts of zooplankton populations across weeks 4 and 5.

	WP-2 count (L^{-1})	Holocam count (L^{-1})
Week 4	13.7	11.2
Week 5	5.7	10.5
Mean $N(L^{-1}) \pm S.D$	7.7 (5.3)	11.8 (1.7)

558 some caution, as the net trawls were conducted two days prior to the tidal
559 station surveys. Table 2 displays the depth-averaged values for both tech-
560 niques, and in the case of the Holocam counts, the values here represent the
561 average for both of the casts of events A and B. Perhaps surprisingly, given
562 the counts observed during the surveys of April, the WP-2 count for week
563 4 of $13.7 L^{-1}$ exceeds that of the Holocam. The monthly average for the
564 20-year time series considered by [Eloire et al. \(2010\)](#) gives close to $3 L^{-1}$ for
565 July and around $3.5 L^{-1}$ for August. Week 5 displays a similar pattern to
566 that seen in weeks 1, 2 and 3, whereby the numbers of zooplankton from the

1
2
3
4
5
6
7
8
9 net trawl is somewhat lower than the counts returned by the Holocam.

10 11 12 568 **4. Discussion**

13 14 15 569 *4.1. Physical characteristics of L4*

16
17 570 L4, whilst being subjected to many wide-ranging and comprehensive sur-
18
19 571 veys dating back to the early part of the last century, has mainly been a
20
21 572 focal point for the study of biological, and to a lesser extent chemical activ-
22
23 573 ity. Comprehensive assessment of the physical characteristics of L4, beyond
24
25 574 that of 1-D observations of temperature and salinity, are rare. However, the
26
27 575 supposition that advection plays a dominant role in the local dynamics of the
28
29 576 water column has been previously suggested by [Pingree and Griffiths \(1977\)](#)
30
31 577 and more recently at L4 by [Cross et al. \(2014\)](#). This potential for advection
32
33 578 at this site, which will generate lateral gradients in density, is invoked as a
34
35 579 possible driver of small-scale inhomogeneities at L4. The temporal variabil-
36
37 580 ity observed here therefore suggests the need for caution when undertaking
38
39 581 investigations across short time-scales at this and other similar locations glob-
40
41 582 ally. It is acknowledged that the presence of advection and the partitioning
42
43 583 of the water column into two layers has restricted the interpretation of the
44
45 584 Lagrangian experiment to the upper layer, within which the drogued drifter
46
47 585 is located. With respect to the distribution of phytoplankton, the striking
48
49 586 changes to this population occur within the upper layer so the emphasis
50
51 587 on the importance of advection in modulating the distribution is arguably
52
53 588 sound. Less confidence is attributed to advection for the somewhat patchy
54
55 589 distribution of zooplankton, though further comment on this is left for the
56
57 590 following section.

58
59 591 The picture of the weakest stratification at neap tides is a function of the
60
61 592 timing of the surveys. Each survey is a 12-hour snapshot, broadly captured
62
63 593 either at the commencement of springs or neaps, therefore leaving little time
64
65 594 for the relevant strengths of the tidal forcing to establish control of the ver-
595
596 595 tical structure prior to each campaign. Therefore, there is the appearance

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

596 of hysteresis at L4 which is perhaps somewhat misleading as the strongest
597 stratification during the week 1-3 surveys appears at spring tides.

598 The temperature-dominated survey of week 3 is in contrast to week 1, as
599 illustrated by the density ratio, R_ρ (Figure ??). The resulting shallower and
600 weaker pycnocline is evidenced by the degree to which a patch of enhanced
601 turbulence is able to breach the pycnocline, possibly transporting nutrients,
602 suspended particles, heat, salt and momentum with it. It has been observed
603 that in temperate shelf seas the onset of stratification in spring can be deter-
604 mined by a combination of the strength of mixing driven by tidal, wind and,
605 to a lesser extent, convective forcing (Sharples et al., 2006; Sharples, 2008).
606 In the absence of any meaningful atmospheric forcing during this period, and
607 given that the strength of the tidal forcing alone is apparently insufficient to
608 entirely overcome the weakly-stratified water column, it is doubtful that mix-
609 ing is exclusively responsible for the rapid temporal change observed between
610 the three surveys.

611 Tidal forcing is often considered to be the dominant contributor to mix-
612 ing at L4 (e.g. Lopez-Urrutia et al. 2005; Lewis and Allen 2009), and this
613 is reasonable in the absence of any previous investigation into the physical
614 drivers of stratification here. Other studies have recognised that quantifying
615 the temporal evolution of stratification as an important part of developing
616 1-D coastal observatories. This has received less attention when the focus
617 has been on assessing long-term change (which is the principal motivation
618 for their existence), however it has perhaps not been considered that such
619 striking differences can occur over such short time-scales. A recent inves-
620 tigation by Groom et al. (2009) observed that mid-summer values of ϕ at
621 L4 compared poorly with sites in the Celtic Sea for the same season, albeit
622 with measurements taken in the latter location from an earlier period. In
623 acknowledging that L4 should be regarded as only exhibiting weak stratifica-
624 tion, and presumably therefore prone to complete mixing from the tidal and
625 atmospheric forcing, it is important to address this potential for variability.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

626 That stratification at L4 never becomes fully established is illustrated well
627 by Figure 13. Mixing between the spring and neap tides for weeks 4 and 5
628 may have reduced ϕ by half, substantially below the assumed average for the
629 summer noted by Groom et al. (2009). A further campaign following week
630 5 would have been advantageous in determining whether the water column
631 would re-stratify to the point which is observed during week 4. Spring-
632 neap modulation of the PEA is often associated with more defined regions of
633 freshwater influence, such as Liverpool Bay and the Rhine ROFI (e.g. Fisher
634 et al., 2002; Polton et al., 2011). In this area, where freshwater input is
635 potentially important but less influential, it is assumed that the alternation
636 between high and low vales of PEA is predominantly brought about by the
637 action of the tide. For the most part, these surveys were carried out in the
638 absence of strong meteorological forcing, which will also have the effect of
639 reducing the PEA further.

640 The sources of the advected properties, in particular the observed salinity
641 structure of week 1, is not altogether certain though one candidate is possibly
642 the freshwater outflow from the River Tamar. As previously noted, the work
643 of Siddorn et al. (2003) modelled the flow from the Tamar and found that
644 the potential exists for freshwater to reach L4. Assuming this has occurred
645 for the week 1 survey, it is particularly striking that it has done so in the
646 absence of any large rainfall events. This suggests that salinity-induced strat-
647 ification of this kind could well be a regular feature at this location, altering
648 the water column properties on a periodic basis and potentially influencing
649 the exchange of nutrients and suspended particulate matter. Further quan-
650 tification is necessary here in the form of more intensive observations across
651 longer periods of time, examining the extent of advection from this source.
652 Additional effort must be given to examining the permanency of this vari-
653 ability, in light of the importance of the L4 station in providing time-series
654 observations that assist in identifying ecosystem and climate-related change.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

655 *4.2. Plankton distribution*

656 Throughout each of the events within each survey there are contrasts in
657 the phytoplankton counts. During week 1, the pattern of greater numbers
658 down to the depth of 20 m exists for all of the events. During event C,
659 there is a noticeable disparity between the three surveys. It is proposed that
660 spatial variability at L4, brought about by the presence of vertical shear
661 and the resulting advection that follows, is responsible for this rapid increase
662 in phytoplankton. Additionally, the formation of blooms of diatoms such as
663 those most commonly seen during this work would typically take of the order
664 of days, not the few hours across which the increase in number was witnessed
665 here (e.g. [Suzuki et al., 2002](#)).

666 A similar increase in phytoplankton is not seen elsewhere during any of
667 the spring campaigns. The counts in the upper part of the water column at
668 depths above 20 m during weeks 2 and 3 are lower, in the case of the upper
669 two depth intervals by a factor of three. Across each of the selected events for
670 these latter two weeks the pattern is of increasing numbers of phytoplankton
671 with depth at all intervals below the pycnocline. This is perhaps not entirely
672 expected in light of studies focusing on phytoplankton distribution that have
673 both observed and modelled maximum biomass at the base of the thermocline
674 (e.g. [Sharples et al., 2001](#); [Ross and Sharples, 2008](#)). However, given the
675 observations here are taken during the onset of stratification, rather than
676 late summer when stratification is stronger as is the case for the [Sharples
677 et al. \(2001\)](#) study, the summer surveys show that this pattern is not typical
678 for L4 across all seasons.

679 The advantages of multi-cast sampling above point measurements are
680 considerable when attempting to improve estimates of the distribution of
681 plankton populations. There is great importance placed on accurate assess-
682 ments of plankton in informing models related to the transfer of carbon across
683 the air-sea interface. As shown here, sampling the water column at one point
684 during a given tidal cycle could lead to substantial over or under-estimates

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

685 of their number. Whilst the assumption may be that long-term means of
686 population density will account for these short-term fluctuations, if the de-
687 gree to which this variability is present is unknown, then the margin of error
688 associated with such measurement strategies may need to be revised.

689 It is important to ensure that a suite of techniques are available when
690 investigating plankton dynamics in the shallow shelf environment. Obvious
691 limitations of the Holocam are that an image is not always able to identify a
692 precise species, or that the camera resolution is insufficient to provide detail
693 on the size range of interest. The advantages of the non-destructive nature of
694 operation though are considerable, and although chain phytoplankton com-
695 munities can also be disrupted when sampled using nets or bottles, operating
696 the Holocam in conjunction with traditional water sampling will offer more
697 accurate information into the size of plankton populations.

698 The differences between the number of zooplankton particles observed, in
699 comparison to both the long term average and net trawls conducted across
700 the same period, is largely a result of the inability of the nets to accurately
701 record gelatinous planula. Concerns over the under-representation of WP-2
702 nets have been previously raised a number of times in the past ([Henroth, 1987](#);
703 [Hopcroft et al., 1998](#)), and more recently by [Gallienne and Robins \(2001\)](#),
704 [Remsen et al. \(2004\)](#) and [Riccardi \(2010\)](#). Frequently, these concerns
705 are largely related to the potential for the population of smaller organisms
706 to be under-resolved by using nets. However, with the results presented here
707 it would seem that the problem is not restricted to smaller size classes alone,
708 but throughout a range of sizes, and also by the fact that the counts are only
709 concerned with those particles that are greater than 200 μm . Possible causes
710 preventing nets from adequately sampling zooplankton populations range
711 from avoidance, clogging and destruction of individual organisms. Each of
712 these is somewhat difficult to quantify, though nonetheless seem reasonable in
713 light of the evidence produced here. If the true population of zooplankton is
714 substantially underestimated, then current ecosystem models that rely upon

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

715 the accuracy of such data will need to take this uncertainty into account.

716 The results with respect to the under sampling of zooplankton should
717 be treated with caution. The lack of concurrent sampling ensures that the
718 only comparison can be between the long-term average and the effectively
719 point-sampled casts of the Holocam. Further work is planned to test this
720 more accurately, and will be reported on in due course. However, that the
721 WP-2 nets do not capture a single planula larvae throughout this period is
722 striking. The short-term temporal variability of the zooplankton is consid-
723 erable, though, and there remains the possibility that at the point in time
724 that the sampling occurred that few, or perhaps none at all were present.
725 What is perhaps more likely, is that the gelatinous nature of the particles
726 themselves has led to their destruction upon capture by the net, which has
727 been previously noted in similar studies using the same sampling methods
728 (Halliday et al., 2001; Warren et al., 2001). The ecological importance of
729 these planula, and the significance of their presence or absence, needs to be
730 given further attention.

731 The importance of stratification to the existence of planktonic species is
732 well documented, with both the timing of the onset of stratification (Sharples
733 et al., 2006), and also when it becomes established in later months, particu-
734 larly with respect to continued growth, and access to a favourable light and
735 nutrient climate (Cianelli et al., 2009). Stratification is variable at L4, clearly
736 being continually influenced by advective forces, placing a degree of stress
737 upon each of the organisms through periodic adjustment and/or erosion of
738 the thermocline (Ross and Sharples, 2008). Evidence of the establishment
739 of stronger stratification is shown in Figure 11 for week 4, albeit subse-
740 quently undergoing partial erosion observed in the following week (Figure
741 12). Perhaps in response to the enhanced opportunity for access to nutri-
742 ents, the concurrent streak of increased fluorescence at the same position of
743 the thermocline during week 5 indicates that species of phytoplankton are
744 present, as has been observed frequently in other shelf sea locations (Sharples

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

745 [et al., 2001](#)). This suggests that during summer advection may not lead to
746 the wholesale change in water column structure observed in spring over the
747 course of a spring-neap cycle, assuming that the local temperature-salinity
748 field remains similar across spatial scales relative to the tidal excursion.

749 Throughout the tidal cycle in week 4, the fluorescence signal displays some
750 asymmetry and appears to encompass a wider region of the water column
751 toward the latter part of the survey than at the beginning. This is matched by
752 an equivalent rise in the number of phytoplankton at the same point (Figure
753 [18](#)). For many of the depth intervals, the difference between the two events is
754 striking, as the counts are often a factor of two, and sometimes three, greater
755 than the earlier part of the survey. For the following week 5, albeit only half a
756 tidal cycle, the counts are more homogeneous and the disparity is not present.
757 During week 1, the similar difference was attributed to advection, whereby a
758 larger population was brought into the sampling field by variable current flow
759 in the upper part of the water column, as observed in similar locations (e.g.
760 [Hill et al., 2005](#)), and it is likely that the same process occurs for week 4.
761 This further demonstrates the importance of acknowledging that advection
762 at L4 is an active process when assessing inter- and intra-tidal variability.
763 This short term variability in the plankton population is demonstrated by
764 the contrast between the surveys of week 4 and 5. Near the surface, numbers
765 of phytoplankton are similar between the spring and neap tidal cycles, but
766 very quickly the number of phytoplankton falls as depth increases, as implied
767 by the fluorescence signal. Plankton variability across spring-neap cycles in
768 shelf seas has been demonstrated previously ([Domingues et al., 2010](#)), further
769 emphasising the need for more frequent sampling to take this into account.

770 When examining the changes to zooplankton populations, there are no-
771 table differences displayed between the seasons, largely in response to the
772 absence of the jellyfish planula. For both surveys in the summer, the count
773 at no time exceeds 50 L^{-1} , considerably lower than the counts observed in
774 spring. In line with the reduction in phytoplankton during summer months,

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

775 however, this is perhaps expected and has been shown to occur several times
776 previously (e.g. [Coyle and Pinchuk, 2005](#); [Eloire et al., 2010](#)). Once more,
777 the agreement between the results of the Holocam and those of the net counts
778 is poor, although the discrepancy is not as striking as for the earlier surveys.
779 The long term average (around 3.5 L^{-1}) is also supportive of the general trend
780 for the number of zooplankton species to be reduced during this time of year.

781 5. Conclusions

782 At present, a range of parameters are collected from the L4 station by ei-
783 ther the automated L4 buoy or weekly via research vessel. Both mechanisms
784 are point measurements, yielding useful but limited data as no appreciation
785 is given for how the biological and chemical samples of choice interact with
786 physical forcing. As has been identified by the present study, temporal vari-
787 ability exists with respect to the evolution of stratification and the develop-
788 ment of the seasonal pycnocline. In the event that data from this 1-D moored
789 observatory is utilised in investigations of shorter weekly or intra-seasonal ac-
790 tivities, the continuing measurement programme may need to address this as
791 an ongoing concern.

792 The campaigns undertaken for this research were the most comprehen-
793 sive physical investigation into the mechanics of L4 to date. That L4 is
794 regarded to be weakly-stratified is well understood, but the degree to which
795 the presence of advection might alter the vertical structure of current flow
796 was previously unknown. The process whereby the water column moves from
797 mixed to stratified during spring has been demonstrated to be complex and
798 delayed by inter-tidal variability. The influence of freshwater run-off remains
799 something of an unknown, although it has been shown previously through
800 the long term time series that river outflow does contribute to the salinity
801 structure here. Parcels of water that vary in temperature and salinity are
802 likely to be responsible for altering the density of the water column through
803 advection. The lowered salinity of week 1 is a potential example of this,

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

804 though in the absence of any meaningful rain in the weeks leading to that
805 campaign, it is unlikely to have been the river run-off providing the source.
806 The subsequent influence on plankton populations is clear, and the degree to
807 which such changes occur at L4 must now be considered as frequent.

808 The manual count of the images provided by the Holocam has provided
809 strong evidence for the need to conduct further work in the area of zoo-
810 plankton identification and enumeration. With respect to phytoplankton,
811 the mechanism used to count these particles is not readily transferred to
812 existing studies, which typically prefer to use a cell count. There is the pos-
813 sibility that individual cells can be counted using the reconstructed images
814 in the same way as for entire colonies of diatom chains. This is, however,
815 likely to be a very time-consuming task and would need to be given thought.
816 A potential solution would be concurrent water sampling, with the tradi-
817 tional method of enumerating cells married to the manual counts, which
818 may provide some indication of the extent to which the two techniques are
819 in agreement.

820 The requirement for inter-disciplinary studies to increase in number at
821 L4, and at similar 1-D coastal observatories, is clear. Future work at this
822 site may need to be equally well resolved. This is particularly important
823 when identifying the extent to which the presence of temporal variability
824 will impact upon current estimates of the distribution of plankton, and by
825 what margin the difficulty of inter-year comparisons will increase as a result.

826 **6. Acknowledgements**

827 This work was supported by NERC grant (NE/G52388X/1), and also by
828 EU MyOcean (218812) R&D PB-LC 10-103. Many thanks to the crew of the
829 *RV Quest*, to Emlyn Davies, Dan Buscombe and Bob Brewin for additional
830 labour. Thanks also to Dr. Emily Baxter who provided assistance in the
831 identification of the planula larvae.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

832 **References**

833 Caley, M.J., Carr, M., Hixon, M., Hughes, T., Jones, G., Menge, B., 1996.
834 Recruitment and the Local Dynamics of Open Marine Populations. Annual
835 Review of Ecology and Systematics 27, 477–500.

836 Cheng, P., Valle-Levinson, A., Winant, C.D., Ponte, A.L.S., Gutierrez de Ve-
837 lasco, G., Winters, K.B., 2010. Upwelling-enhanced seasonal stratification
838 in a semiarid bay. Continental Shelf Research 30, 1241–1249.

839 Cianelli, D., Sabia, L., d’Alcala, M.R., Zambianchi, E., 2009. An individual-
840 based analysis of the dynamics of two coexisting phytoplankton species in
841 the mixed layer. Ecological Modelling 220, 2380–2392.

842 Corcoran, A., Shipe, R., 2011. Inshoreoffshore and vertical patterns of phy-
843 toplankton biomass and community composition in Santa Monica Bay, CA
844 (USA). Estuarine Coastal and Shelf Science 94, 24–35.

845 Coyle, K., Pinchuk, A., 2005. Seasonal cross-shelf distribution of major
846 zooplankton taxa on the northern gulf of alaska shelf relative to water
847 mass properties, species depth preferences and vertical migration behavior.
848 Deep Sea Research II 52, 217–245.

849 Cross, J., 2012. The Dynamics of Suspended Particles in a Seasonally Strat-
850 ified Coastal Sea. Ph.D. thesis. University of Plymouth.

851 Cross, J., Nimmo Smith, W.A.M., Torres, R., Hosegood, P., 2013. Biological
852 controls on resuspension and the relationship between particle size and
853 the Kolmogorov length scale in a shallow coastal sea. Marine Geology 343,
854 29–38.

855 Cross, J., Nimmo Smith, W.A.M., Torres, R., Hosegood, P., 2014. The
856 dispersal of phytoplankton populations by enhanced turbulent mixing in
857 a shallow coastal sea. Journal of Marine Systems 136, 55–64.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

858 Davies, E., Nimmo-Smith, W., Agrawal, Y., Souza, A., 2012. Lisst-100 re-
859 sponse to large particles. *Marine Geology* 307-310, 117–122.

860 Domingues, R., Anselmo, T., Barbosa, A., Sommer, U., Galvao, H., 2010.
861 Tidal variability of phytoplankton and environmental drivers in the fresh-
862 water reaches of the Guadiana estuary (SW Iberia). *International Review*
863 *of Hydrobiology* 95, 352–369.

864 Eloire, D., Somerfield, P., Conway, D., Halsband-Lenk, C., Harris, R., Bon-
865 net, D., 2010. Temporal variability and community composition of zoo-
866 plankton at station L4 in the western channel: 20 years of sampling. *Jour-*
867 *nal of Plankton Research* 32, 657–679.

868 Fisher, N.R., Simpson, J.H., Howarth, M.J., 2002. Turbulent dissipation in
869 the rhine rofi forced by tidal flow and wind stress. *Journal of Sea Research*
870 48, 249–258.

871 Gallienne, C., Robins, D., 2001. Is oithona the most important copepod in
872 the worlds oceans? *Journal of Plankton Research* 23, 1421–1432.

873 Gowen, R., McCullough, G., Kleppel, G., Houchin, L., Elliott, P., 1999.
874 Are copepods important grazers of the spring phytoplankton bloom in the
875 western irish sea? *Journal of Plankton Research* 21, 465–483.

876 Graham, G., Davies, E., Nimmo-Smith, W., Bowers, D., Braithwaite, K.,
877 2012. Interpreting lisst-100x measurements of particles with complex shape
878 using digital in-line holography. *Journal of Geophysical Research* 117,
879 C05034.

880 Graham, G., Nimmo Smith, W.A.M., 2010. The application of holography to
881 the analysis of size and settling velocity of suspended cohesive sediments.
882 *Limnology and Oceanography - Methods* 8, 1–15.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

883 Groom, S., Martinez-Vicente, V., Fishwick, J., Tilstone, G., Moore, G.,
884 Smyth, T., Harbour, D., 2009. The Western English Channel observa-
885 tory: Optical characteristics of station L4. *Journal of Marine Systems*
886 77, 278–295. Workshop on Coastal Observatories - Best Practice in the
887 Synthesis of Long-Term Observations and Models, Liverpool, ENGLAND,
888 OCT 16-19, 2006.

889 Halliday, N., Coombs, S., Smith, C., 2001. A comparison of lhpr and opc
890 data from vertical distribution sampling of zooplankton in a norwegian
891 fjord. *Sarsia* 86, 87–99.

892 Henroth, L., 1987. Sampling and filtration efficiency of two commonly used
893 plankton nets. a comparative study of the nansen net and the unesco wp
894 2 net. *Journal of Plankton Research* 9, 719–728.

895 Herman, A., Beanlands, B., Phillips, E., 2004. The next generation of optical
896 plankton counter: the laser-opc. *Journal of Plankton Research* 26, 1135–
897 1145.

898 Hill, V., Cota, G., Stockwell, D., 2005. Spring and summer phytoplankton
899 communities in the chukchi and eastern beaufort seas. *Deep Sea Research*
900 II 52, 3369–3385.

901 Hopcroft, R., Roff, J., 1998. Production of tropical larvaceans in kingston
902 harbour, jamaica: are we ignoring an important secondary producer?
903 *Journal of Plankton Research* 20, 557–569.

904 Hopcroft, R., Roff, J., Lombard, D., 1998. Production of tropical copepods
905 in kingston harbour, jamaica: the importance of small species. *Marine*
906 *Biology* 130, 593–604.

907 Hosegood, P.J., Gregg, M.C., Alford, M.H., 2008. Restratification of the
908 Surface Mixed Layer with Submesoscale Lateral Density Gradients: Diag-

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

909 nosing the Importance of the Horizontal Dimension. *Journal of Physical*
910 *Oceanography* 38, 2438–2460.

911 Jahnke, R., 2010. A Global Synthesis. Springer-Verlag. chapter In: *Carbon*
912 *and Nutrient Fluxes in Continental Margins: A Global Synthesis*. pp.
913 597–615.

914 Karp-Boss, L., Azevedo, L., Boss, E., 2007. LISST-100 measurements of
915 phytoplankton size distribution: evaluation of the effects of cell shape.
916 *Limnology and Oceanography - Methods* 5, 396–406.

917 Lewis, K., Allen, J.I., 2009. Validation of a hydrodynamic-ecosystem model
918 simulation with time-series data collected in the Western English Channel.
919 *Journal of Marine Systems* 77, 296–311. Workshop on Coastal Observa-
920 tories - Best Practice in the Synthesis of Long-Term Observations and
921 Models, Liverpool, ENGLAND, OCT 16-19, 2006.

922 Lopez-Urrutia, A., Harris, R., Acuna, J., Baamstedt, U., Fyhn, H., Flood,
923 P., Gasser, B., Gorsky, G., Irigoien, X., Martinussen, M., 2005. Response
924 of marine ecosystems to global change: Ecological impact of appendicular-
925 ians. *Contemporary Publishing International*. chapter in: *A comparison*
926 *of appendicularian seasonal cycles in four contrasting European coastal*
927 *environments*. pp. 255–276.

928 Lozovatsky, I., Roget, E., Fernando, H., Figueroa, M., Shapovalov, S., 2006.
929 Sheared turbulence in a weakly stratified upper ocean. *Deep Sea Research*
930 *Part I: Oceanographic Research Papers* 53, 387–407.

931 McCandliss, R., Jones, S., Hearn, M., Latter, R., Jago, C., 2002. Dynamics of
932 suspended particles in coastal waters (southern North Sea) during a spring
933 bloom. *Journal of Sea Research* 47, 285–302. 26th General Assembly of
934 the European-Geophysical-Society, NICE, FRANCE, 2001.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

935 Pingree, R., Griffiths, D., 1977. The bottom mixed layer on the continental
936 shelf. *Estuarine and Coastal Marine Science* 5, 399–413.

937 Polton, J., Palmer, M., Howarth, M., 2011. Physical and dynamical oceanog-
938 raphy of liverpool bay. *Ocean Dynamics* 61, 1421–1439.

939 Remsen, A., Hopkins, T., Samson, S., 2004. What you see is not what
940 you catch: a comparison of concurrently collected net, optical plankton
941 counter, and shadowed image particle profiling evaluation recorder data
942 from the northeast gulf of mexico. *Deep Sea Research Part I: Oceanog-
943 raphic Research Papers* 51, 129–151.

944 Riccardi, N., 2010. Selectivity of plankton nets over mesozooplankton taxa:
945 implications for abundance, biomass and diversity estimation. *Journal of
946 Limnology* 69, 287–296.

947 Ross, O.N., Sharples, J., 2008. Swimming for survival: A role of phyto-
948 plankton motility in a stratified turbulent environment. *Journal of Marine
949 Systems* 70, 248–262.

950 Rzadkowolski, C., Thornton, D., 2012. Using laser scattering to identify
951 diatoms and conduct aggregation experiments. *European Journal of Phy-
952 cology* 47, 30–41.

953 See, J., Campbell, L., Richardson, T., Pinckney, J., Shen, R., 2005. Com-
954 bining new technologies for determination of phytoplankton community
955 structure in the northern gulf of mexico. *Journal of Phycology* 41, 305–
956 310.

957 Sharples, J., 2008. Potential impacts of the spring-neap tidal cycle on shelf
958 sea primary production. *Journal of Plankton Research* 30, 183–197.

959 Sharples, J., Moore, C., Rippeth, T., Holligan, P., Hydes, D., Fisher, N.,
960 Simpson, J., 2001. Phytoplankton distribution and survival in the ther-
961 mocline. *Limnology and Oceanography* 46, 486–496.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

962 Sharples, J., Ross, O., Scott, B., Greenstreet, S., Fraser, H., 2006. Inter-
963 annual variability in the timing of stratification and the spring bloom in
964 the North-western North Sea. *Continental Shelf Research* 26, 733–751.

965 Siddorn, J., Allen, J., Uncles, R., 2003. Heat, salt and tracer transport in
966 the Plymouth Sound coastal region: a 3-D modelling study. *Journal of the*
967 *Marine Biological Association of the United Kingdom* 83, 673–682.

968 Simpson, J.H., Bowers, D.G., 1981. Models of stratification and frontal move-
969 ment in shelf seas. *Deep Sea Research Part I: Oceanographic Research*
970 *Papers* 28, 727–738.

971 Simpson, J.H., Brown, J., Matthews, J., Allen, G., 1990. Tidal straining,
972 density currents and stirring in the control of estuarine stratification. *Es-*
973 *tuaries* 13, 125–132.

974 Suzuki, K., Tsudab, A., Kiyosawac, H., S, T., Nishiokae, J., Sainoa, T.,
975 Takahashif, M., Wong, C., 2002. Grazing impact of microzooplankton on
976 a diatom bloom in a mesocosm as estimated by pigment-specific dilution
977 technique. *Journal of Experimental Marine Biology and Ecology* 271, 99–
978 120.

979 Warren, J., Stanton, T., Benfield, M., Wiebe, P., Chu, D., Sutor, M.,
980 2001. In-situ measurements of acoustic target strengths of gas-bearing
981 siphonophores. *ICES Journal of Marine Science* 58, 740–749.

982 Widdicombe, C.E., Eloire, D., Harbour, D., Harris, R.P., Somerfield, P.J.,
983 2010. Long-term phytoplankton community dynamics in the western En-
984 glish Channel. *Journal of Plankton Research* 32, 643–655.