

1 **Harmful Algal Blooms and their impacts on shellfish mariculture follow regionally distinct patterns**  
2 **of water circulation in the western English Channel during the 2018 heatwave**

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15

16 **ABSTRACT**

17 Harmful algal blooms (HABs) can have severe ecological, societal and economic impacts upon marine  
18 ecosystems, human health and the seafood industry. We evaluated changes in marine plankton  
19 communities with prevailing physico-chemical conditions throughout an exceptionally warm summer  
20 (2018), to elucidate key factors governing HABs and their impacts on shellfish mariculture in the  
21 western English Channel. Despite warm, stable weather conditions and widespread seasonal  
22 stratification throughout the summer, divergent plankton community compositions were observed at

23 two rope-grown mussel (*Mytilus edulis*) farms (St Austell Bay and Lyme Bay) and a long-term ecological  
24 research LTER site (Plymouth L4). There were significant differences between sites in the abundances  
25 of HAB species, including *Dinophysis* spp. and *Karenia mikimotoi*, whose cell counts bloomed in excess  
26 of UK Food Standards Agency (FSA) advisory ‘trigger’ levels at Plymouth L4 and St Austell Bay, but not  
27 at the Lyme Bay site. The *K. mikimotoi* bloom occurred over two weeks in August and comprised up  
28 to 88% of the standing phytoplankton biomass in St Austell Bay. *Dinophysis* spp. also bloomed here  
29 from May to September, constituting up to 28% of phytoplankton biomass. This protracted bloom  
30 resulted in concentrations of Dinophysis toxins 1 & -2 and pectenotoxins and okadaic acid in shellfish,  
31 which closed shellfish harvesting operations on farms located in St Austell Bay, and other shellfish  
32 sites in the west of the western English Channel (but not in the east of the region). Inter-site  
33 differences in the abundances of these and other HAB species were associated with variations in water  
34 circulation and co-occurring phytoplankton and zooplankton communities. Furthermore, plankton  
35 monitoring data obtained from the L4 site over the past 3 decades showed HAB species (including  
36 *Dinophysis* spp.) with abundances commonly occurring above advisory trigger levels during warmer  
37 periods, such as that coinciding with our study. Under projected climate warming these blooms are  
38 likely to continue to be governed by regionally distinct patterns of water circulation, which need to be  
39 taken into account in marine spatial planning, when assessing the suitability of new shellfish  
40 mariculture sites.

41

42 **Key words:** climate change; HABs; environmental factors; shellfish poisoning; spatial planning; tidal  
43 front

## 44 1) INTRODUCTION

45

46 Mariculture (marine aquaculture, including shellfish, finfish and macroalgal culture) is vitally  
47 important for global food security, and production from aquaculture has now overtaken capture  
48 fisheries (FAO, 2018). Mariculture, in particular, is expected to expand in the UK, with production  
49 predicted to double over the next two decades (Defra, 2017; SeaFish, 2019). Whilst the UK has an  
50 extensive coastline, with the potential to accommodate mariculture, there are numerous constraints  
51 on spatial planning/licensing (e.g. Marine Protected Areas, fishing areas, shipping routes and  
52 recreational areas) and on economic productivity (e.g. local primary production, storm exposure risk  
53 and ease of access). The increasingly frequent and widespread occurrences of harmful algal blooms  
54 (HABs) is a further major constraint on mariculture in NW European shelf seas and other HAB hotspots  
55 relating to mariculture around the globe (Glibert et al., 2014; Weisberg et al., 2019; Trainer et al.,  
56 2020a; Wells et al., 2020).

57

58 HABs can have significant detrimental impacts on mariculture, with an annual cost of >€0.03 billion in  
59 the UK (ASIMUTH, 2014) and €0.9-1.2 billion in the EU (S-3 EuroHAB, 2019; Trainer et al., 2020b).  
60 These costs result from direct losses and from mandatory, pre-emptive harvesting closures or product  
61 recalls to prevent human poisonings from HAB phycotoxins that accumulate in shellfish. HAB species  
62 such as *Dinophysis acuminata* and *Dinophysis acuta* are particularly prevalent and problematic in  
63 European regional seas (Manfrin et al., 2012; Diaz et al., 2019). Above low threshold densities of 100  
64 cells L<sup>-1</sup> specified in the UK (FSA, 2021), the accumulation of Dinophysis toxins (okadaic acid, PTX and  
65 DTX derivatives) in shellfish meat can cause diarrhetic shellfish poisoning (DSP) in human consumers  
66 (Reguera et al., 2014). *Dinophysis* spp. regularly bloom in the summer in sheltered coastal  
67 embayments (Raine, 2014; Schmidt et al., 2018b), and in coastal upwelling zones (Reguera et al., 2014;  
68 Diaz et al., 2019). *Dinophysis* blooms can also occur regularly offshore, for example at the Western  
69 Channel Observatory's L4 site (Widdicombe et al., 2010).

70

71 High biomass blooming HAB species ( $\geq 10^5$  cells L<sup>-1</sup>), such as *Karenia mikimotoi*, are also harmful to  
72 marine life, particularly to caged finfish or sedentary shellfish, which are unable to avoid intoxication  
73 by *Karenia* and/or deoxygenation of the water column, as the blooms decay (Raine et al., 2001; Silke  
74 et al., 2005; Mitchell & Rodger 2007; Coates et al., 2009; Davidson et al., 2009). *Karenia mikimotoi*  
75 often forms major summer blooms along the frontal boundary of the seasonally stratified western  
76 English Channel, extending from Ushant (France) to Lands End (UK), and these blooms can be advected  
77 inshore (Pingree, 1975, Holligan, 1979, Garcia and Purdie, 1994; Widdicombe et al., 2010; Barnes et  
78 al., 2015).

79

80 The increasing prevalence of warm, thermally stratified, and nutrient-limited conditions, typical of hot  
81 summers in European shelf seas, corresponding to high North Atlantic Oscillation (NAO) index values  
82 (Smyth et al., 2010; Hinder *et al.* 2011; Barton *et al.* 2015; Barnes et al., 2015) is likely to select for  
83 HAB species (e.g. dinoflagellate species), whose physiologies and life-history strategies are adapted to  
84 these conditions (Gobler et al., 2020; Wells et al., 2020). For example, motile dinoflagellate HAB  
85 species, including *Dinophysis spp.* and *Karenia mikimotoi*, are able to exploit stable stratified  
86 conditions, by actively seeking light and inorganic nutrients for photosynthesis, and also preying upon  
87 other plankton (mixotrophy) (Anderson et al., 2012; Zhang et al., 2013; Lucas et al., 2016). Increased  
88 sea surface warming can also alter the position and intensity of tidal mixing fronts dividing mixed and  
89 stratified water masses (Sharples and Simpson, 2019), with the potential to expand niches for HAB  
90 species into otherwise well mixed coastal and shelf sea areas, not previously considered to be bloom  
91 hotspots. Understanding the degree to which environmental warming may expand niches for HABs  
92 both spatially and temporally will be critically important for predicting and mitigating future HAB  
93 impacts on existing mariculture operations and for marine spatial planning for enabling the  
94 sustainable growth of the industry (Brown et al., 2019; Wells et al., 2015; 2020). HAB occurrences may  
95 be driven by multiple additional factors, some potentially relating to mariculture, including habitat

96 disturbances and coastal eutrophication (Hallegraeff, 2010; Anderson, 2012; Gowen et al., 2012;  
97 Davidson et al., 2014; Brown et al., 2019). Therefore, discerning climate-driven changes in HAB risk for  
98 shellfish growing areas ideally requires analysis of multi-decadal data (Barton et al., 2015; Dees et al.,  
99 2017). Some understanding of future HAB risk can also be gained from studying extreme events (e.g.  
100 exceptionally warm periods), representing significant departures from long-term means and  
101 resembling possible future climate scenarios under which HABs could develop (Trainer et al., 2020a).

102

103 Here, our broad aim was to examine the potential impact of warming on the occurrence of HABs at  
104 shellfish aquaculture sites in SW England. To do this, we opportunistically surveyed two shellfish  
105 aquaculture sites in St Austell Bay (SAB) and Lyme Bay (LB), and a long-term ecological research (LTER)  
106 site (Plymouth L4), during the unusually warm summer of 2018. The decade 2009-2018 was the  
107 warmest on record in the UK, i.e. 0.3°C warmer than the 1981–2010 average and 0.6°C warmer than  
108 1961–1990 (Kendon et al., 2019). Summer 2018 coincided with the highest summer North Atlantic  
109 Oscillation (NAO) index since 1955, which led to the northward displacement of Atlantic storm tracks,  
110 exceptionally calm conditions and elevated sea surface temperatures around the UK and across the  
111 NW European shelf (Kendon et al., 2019). These conditions resemble future climate change scenarios  
112 for the region (Tinker *et al.* 2016; UKCP018; Kendon et al., 2019). The sites surveyed in our study span  
113 a frontal region around Start Point (~4°W, Figure 1), which separates predominantly summer-stratified  
114 water to the west and predominantly mixed waters to the east (Pingree *et al.* 1983, Boalch 1987).  
115 Historically, these shellfish sites have shown contrasting patterns of HAB exposure, suggesting that  
116 the frontal region may present a boundary for dispersal of bloom forming species in the region.  
117 Consequently, our first aim was to examine the physio-chemical properties, plankton community  
118 composition, and occurrence of HABs at each site in order to assess the degree of  
119 similarity/dissimilarity between sites during the exceptionally warm and stable period from May to  
120 August 2018. To place the survey in a broader regional and temporal context, we examined HAB cell

121 counts and/or biotoxin concentrations recorded by the UK Food Standards Agency (FSA) for the region  
122 during the 2018 sampling period - to assess the prevalence of HABs across the Start Point frontal  
123 region. In addition, we examined the abundance of HAB species at the long-term L4 monitoring site  
124 over a ~30 year period - to assess whether extended periods of summer stratification are typically  
125 associated with increases in the abundance or persistence of dinoflagellate HAB species, which are  
126 known to exploit warm water conditions (Hallegraeff, 2010; Hinder et al., 2011; Glibert et al., 2014;  
127 Wells et al., 2015; Gobler et al., 2017).

128

## 129 **2) METHODS**

### 130 **2.1) 2018 survey**

131 **2.1.1) Sampling points** - Surveys were conducted at three sites; St Austell Bay (SAB), Plymouth (L4)  
132 and Lyme Bay (LB) located on the South coast of SW England (Figure 1). SAB and LB are shellfish  
133 mariculture sites for rope-grown mussels (*Mytilus edulis*). The following is a brief description of the  
134 sites (for detailed site descriptions refer to Table 1). The SAB and LB sites are located 2.5 km and 8 km  
135 from shore, respectively. Both are within UK territorial waters (22.2 km  $\approx$  12 nautical miles) and are  
136 considered coastal mariculture sites (Buck et al., 2018). The third site (L4), part of the Western Channel  
137 Observatory (WCO), is a long-term ecological research (LTER) site (where no mariculture is practised),  
138 located 7.6 km off Penlee Point at the entrance to Plymouth Sound ([WCO, 2020](#)). SAB is a relatively  
139 sheltered site and is less exposed to mixing by prevailing SW winds and tidal streams compared to L4  
140 & LB. Sampling at each site was conducted at paired stations (Stations 1 and 2, see Table 1). Station 1  
141 corresponded to the FSA-designated Representative Monitoring Point for each mariculture site and  
142 the WCO-designated monitoring point at L4. Station 2 was sampled to provide additional data on local  
143 (1-10 km) spatial variation in physico-chemical parameters (Sections 2.1.2 and 2.1.3). Sampling was  
144 conducted for 15 consecutive weeks, from week 21 in May to week 35 at the end of August in 2018.

145 Sampling at L4 corresponded with scheduled WCO monitoring, while sampling at the mariculture sites  
146 LB and SAB corresponded with scheduled HAB and phycotoxin monitoring coordinated by the FSA.

147

148 **2.1.2) Sampling methods** - At paired sampling stations, at each shellfish site, profiles of temperature  
149 and salinity with water depth were obtained using a hand-deployed CastAway™ (SonTek, San Diego,  
150 CA) conductivity temperature depth (CTD) probe. The intensity of stratification was estimated as the  
151 difference in density at water column depths of 2 m and 10 m. On each sampling occasion, the time  
152 of high water, weather conditions (cloud cover, wind speed, direction), Secchi depth, sea state (wave  
153 height), and tidal height were recorded. Water samples were collected from depths of 2 m and 10 m  
154 using a hand-deployed 5 L Niskin bottle (General Oceanics, Miami, FL). Each water sample was split  
155 into aliquots for inorganic nutrient, chlorophyll-*a*, and phytoplankton analysis. Chlorophyll and  
156 nutrient samples were kept refrigerated for up to 24 h before filtration and storage at -20°C.  
157 Phytoplankton samples were preserved directly in 2% (final concentration) acid Lugol's iodine, in  
158 amber glass bottles and stored in the dark. Samples for zooplankton community analysis were  
159 collected (Station 1 only) using vertically-hauled 500 mm diameter WP2-style ring net (200 µm mesh  
160 size) (NHBS, Totnes, UK) from approximately 2 m from the sea bed to the surface. Zooplankton  
161 samples were washed off the 200 µm mesh collector with seawater and immediately preserved in 4%  
162 formaldehyde (final concentration) in a 250 mL bottle. At the Plymouth L4 site, sampling was  
163 conducted as part of the regular WCO monitoring programme according to WCO protocols (Smyth et  
164 al., 2015).

165

166 **2.1.3) Nutrient and chlorophyll analysis** - Nutrient samples were analysed by the UK Environment  
167 Agency National Laboratory Service (Starcross, UK): nitrate, nitrite, ammonium, silicate and total  
168 phosphate were determined colorimetrically using a continuous flow (CF) autoanalyser (EA, 2019).  
169 Chlorophyll-*a* was measured by fluorescence spectrophotometry, following the protocol of Holm-

170 Hansen et al. (1965) using 90% ice-cold acetone as a solvent. Excitation/emission (430/664 nm)  
171 measurements were made using Spectromax M5 spectrophotometer (Molecular Devices, UK) and Chl-  
172 *a* distinguished from pheopigments using the HCl addition method. Chl-*a* concentrations were  
173 estimated against known standards made from pure Chl-*a* (CAS Number 479-61-8, obtained from  
174 Sigma-Aldrich, UK).

175

176 **2.1.4) Phytoplankton and zooplankton enumeration** - Plankton samples were analysed at Plymouth  
177 Marine Laboratory using the same WCO protocols for all sites. Phytoplankton counts were performed  
178 using the Utermöhl technique (Utermöhl, 1958) following the British and European Standard protocol  
179 (BS EN 15204:2006). 50 mL sub-samples were obtained after gently stirring each bulk sample (to  
180 ensure homogeneity) and then settled (for 24 h) prior to examination using an inverted microscope  
181 (100× magnification) and identifications were made to species level where possible. Species  
182 abundances were expressed per mL of water and as carbon biomass ( $\text{mg C m}^{-3}$ ) following Menden-  
183 Deuer and Lessard (2000).

184 Zooplankton were identified to the lowest practicable taxonomic resolution and enumerated under  
185 an inverted microscope (100× magnification). Subsamples were extracted with a Hensen-Stempel  
186 pipette achieving between 200-400 individuals. Larger subsamples were checked for larger and/or  
187 rarer species. Abundance was expressed as numbers of organisms per cubic meter (abundance  $\text{m}^{-3}$ ).  
188 The HAB species *Noctiluca scintillans* was quantified in zooplankton as well as phytoplankton samples,  
189 due to these large dinoflagellates (>200  $\mu\text{m}$  diameter) being caught in the zooplankton net.

190

191 **2.1.5) Survey data analysis** - Statistical analyses were performed on the 2018 survey data primarily  
192 using Primer-E (v.6) statistical software (Clarke *et al.* 2014) and R v3.6.3 (R Core Team, 2017). To  
193 examine the degree of similarity in the physico-chemical environmental characteristics of each site, a

194 principle component analysis (PCA) was performed on normalised salinity, temperature, density, Chl-  
195  $a$  and Secchi depth (a proxy for turbidity) data recorded each week at both 2 m and 10 m depth over  
196 the course of the 15 week monitoring period.

197 Plankton community composition at each site, and differences between sites, were examined using  
198 abundance and carbon biomass data. Briefly, the following multivariate statistical analyses were  
199 performed following square-root transformation of the data to reduce bias from high abundance (or  
200 high biomass) species on the analytical results. We tested dissimilarities in plankton community  
201 composition between sampling sites using Bray Curtis similarity-based cluster analysis and Multi-  
202 Dimensional Scaling ordination. Permutational Multivariate Analysis of Variance (PERMANOVA, 2-way  
203 analysis with weekly samples nested within sites and accounting for random effects associated with  
204 repeated measures) was used to test *a priori* for significant differences between sampling sites (SAB,  
205 L4 and LB). Contribution of key taxa to % similarity of time-series data for each sampling site and %  
206 dissimilarity between sites was assessed *post hoc* using SIMPER.

207

## 208 **2.2) Analysis of temporal and wider spatial variations in HABs and oceanographical conditions**

209

### 210 **2.2.1) Plankton monitoring data**

211 The UK Food Standards Agency HAB monitoring data from SAB, LB and other designated shellfish sites  
212 in SW England (FSA, 2019) were used to evaluate spatial variations in HAB species abundance during  
213 the summer of 2018 and in preceding years. Long-term plankton monitoring data (1993-2018) from  
214 the Western Channel Observatory's L4 site (WCO, 2020) were used to evaluate temporal variations in  
215 HAB species abundance in relation to local variations in sea surface temperature measured every week  
216 via CTD profiling. HAB species (cell) abundances recorded each week were compared to UK Food  
217 Standards Agency (FSA) advisory trigger levels indicative of elevated concentrations of phycotoxins in

218 shellfish that may poison human consumers (FSA, 2021). We determined how frequently trigger levels  
219 were breached for individual HAB species each year leading up to 2018. Although there is a lack of  
220 scientific understanding of phycotoxin production in *K. mikimotoi*, an arbitrary trigger level of 150,000  
221 cells L<sup>-1</sup> is adopted for this species (FSA, 2021). HAB species (cell) abundances were also compared  
222 with water temperature at 10 m depth - using paired-sample Pearson correlations based on  
223 untransformed (normal) data from 2002-2018, during which cell abundances and water temperature  
224 have been sampled concurrently.

225

### 226 **2.2.2) Satellite monitoring data and coastal circulation model outputs**

227 The extent of major plankton blooms in the western English Channel in spring and summer 2018 was  
228 defined by Sentinel-3A ocean and land colour images (OLCI) presented in enhanced colour (Level 2)  
229 by the NERC Earth Observation Data Acquisition and Analysis Service (NEODAAS), hosted at Plymouth  
230 Marine Laboratory and overseen by NERC's National Centre for Earth Observation (NCEO)  
231 (<https://neodaas.ac.uk/Home>). To help identify possible links between the distribution of major  
232 (visible) plankton blooms and water circulation patterns in the western English Channel, daily mean  
233 surface current velocities (net flows at 0 m and 15 m water depth) were obtained from a REP L4 global  
234 total velocity field (0.25° regular grid), derived by Rio et al. (2014) and available from the EU  
235 Copernicus Marine Service Information (CMEMS, 2020). Velocities combined CMEMS REP satellite  
236 Geostrophic surface currents and modelled Ekman currents (using ECMWF ERA5 wind stress). These  
237 velocity data inherently include large-scale thermohaline circulation and wave-driven Stokes drift, and  
238 exclude oscillating tidal flows. Data from each site were aggregated in weeks or months (as required)  
239 and were plotted on a compass rose using 'windRose' in the R package 'openair' v.2.7-2  
240 (<http://davidcarslaw.github.io/openair/>) built in R version 3.6.3. A regional-scale assessment of the  
241 surface current velocities (based on the CMEMS data) was made using the European Space Agency's  
242 Ocean Virtual Laboratory (<https://ovl.oceandatalab.com/>).

243

244

### 245 **3) Results**

#### 246 **3.1) 2018 survey campaign**

##### 247 **3.1.1) Physico-chemical conditions**

248 PCA showed that 32.5% of variation in the combined physico-chemical data was captured in PC1, while  
249 25.9% was captured in PC2. PC1 reflects similar temporal changes across all three sampling sites in  
250 terms of water temperature, salinity and density (Figure 2). The intensity of stratification at each site  
251 was measured as the differential between lower density surface water at 2 m and higher density  
252 deeper water at 10 m (i.e. delta density @ 10m–2m). During the period from week 21 (beginning of  
253 May) until Week 31 (beginning of August) stratification intensified with increasing sea surface  
254 temperature (2 m depth), rising from 12°C to >18.5°C at SAB and LB and from 12°C to >19°C at L4.  
255 Stratification was (apart from week 29) amplified when tidal mixing was reduced during neap tidal  
256 cycles (Figure 2). The depth of the thermocline at each site varied between 5 and 15 m (depending on  
257 tidal cycles) and occurred most frequently at a water depth of around 10 m (SI Figure S1).

258

259 PC2 reflects temporal changes characterised for the most part by reducing Chl-*a* concentration (from  
260 1-0.5 to 0.1 mg Chl-*a* m<sup>-3</sup>) and increasing Secchi depth, which reached maxima of 13.5 m depth at SAB,  
261 12 m at L4 and 17.5 m at LB (SI Figure S2). Chl-*a* concentration and stratification intensity were  
262 generally greatest at SAB, followed by L4 and then LB (Figure 2). Greatest stratification at SAB  
263 coincided with reduced surface salinity, following rainfall events in weeks 24 and 29, and  
264 corresponded with elevated nutrient (ammonium and phosphate) concentrations in near-surface  
265 water samples (SI Figure S2, Table 2). Other than these occasional brief increases in concentrations,  
266 nutrients remained for the most part at or below detectable levels throughout the survey period and

267 were therefore excluded from the PCA. Concordant with low nutrient levels, Chl-*a* concentrations (at  
268 both 2 m and 10 m) were generally low (< 1 mg m<sup>-3</sup>) for the majority of the monitoring period.  
269 However, Chl-*a* concentrations rose sharply at the two western-most sites in mid-August (week 33),  
270 coinciding with a sudden reduction in water temperature and a noticeable increase in nutrient  
271 concentrations at L4 (Table 2).

272

### 273 **3.1.2) HAB occurrence and abundance**

274 The spike in Chl-*a* concentrations in mid-August (week 33) coincided with a high biomass *K.*  
275 *mikimotoi* bloom at SAB (457 mg C m<sup>-3</sup>) and at L4 (128 mg C m<sup>-3</sup>); corresponding cell counts for *K.*  
276 *mikimotoi* exceeded advisory trigger levels of 150,000 cells L<sup>-1</sup> (L4 = 151,000 cells L<sup>-1</sup>; SAB = 737,000  
277 cells L<sup>-1</sup>) (Figure 3). High biomass blooms of *Noctiluca scintillans* (>150,000 cells L<sup>-1</sup>) were also  
278 recorded at L4 and SAB in late July and during August (weeks 30-34). Low biomass blooming  
279 dinoflagellate species (*Dinophysis acuminata* followed by *Dinophysis acuta*) breached trigger levels  
280 of 100 cells L<sup>-1</sup> at L4 (up to 3300 cells L<sup>-1</sup>) and SAB (up to 6900 cells L<sup>-1</sup>) over the entire monitoring  
281 period (Figure 3), leading to the accumulation of *Dinophysis* toxins (okadaic acid, PTX and DTX  
282 derivatives) in shellfish and the closure of mussel farms in SAB throughout the summer. Another low  
283 biomass dinoflagellate HAB species *Prorocentrum cordatum* bloomed in late May/early June and  
284 breached trigger levels of 100 cells L<sup>-1</sup> at L4 (up to 1480 cells L<sup>-1</sup>), SAB (up to 3560 cells L<sup>-1</sup>) and LB (up  
285 to 480 cells L<sup>-1</sup>) (Figure 3). Diatom HABs *Pseudo-nitzschia* spp. were also recorded all three sampling  
286 sites and in late June/early July (week 26 and week 27) at modest biomasses of 0.8 to 1.2 mg C m<sup>-3</sup>  
287 and abundances of 25,000 to 35,000 cells L<sup>-1</sup>, but these were substantially below advisory trigger  
288 levels of 150,000 cells L<sup>-1</sup> (FSA, 2021).

289 High biomass blooms were absent at LB (SI Figure S2); here phytoplankton biomass remained low (6-  
290 57 mg C m<sup>-3</sup>) and was attributable mainly to the diatom *Proboscia alata* (SI Table S1a).

291

292

293 **3.1.2) Plankton community structure**

294 Phytoplankton communities at SAB and L4 were dominated in terms of biomass by dinoflagellates,  
 295 including *Karenia mikimotoi* and *Dinophysis* spp. The short-lived *K. mikimotoi* bloom at SAB and L4  
 296 followed a notable increase in dinoflagellate:diatom ratio taking place two weeks earlier in week 21  
 297 at both SAB and L4 (SI Figure S3). The longer-term *Dinophysis* spp. bloom at SAB and L4 involved the  
 298 sequential blooming of *D. acuminata* in May (week 21) followed by *D. acuta* in August (week 32);  
 299 while their abundances at LB remained low (<100 cells L<sup>-1</sup>). The key ciliate prey species for  
 300 *Dinophysis* spp., *Mesodinium rubrum*, was on average more abundant (>200 cells L<sup>-1</sup>) at SAB and L4  
 301 compared to LB (<100 cells L<sup>-1</sup>), but abundance declined notably at the onset of the *D. acuta* bloom  
 302 in week 32 (Figure 4). This time point marked the depletion of *M. rubrum* at SAB, where a significant  
 303 negative correlation was found between *D. acuta* and *M. rubrum*; Spearman rank correlation  $S =$   
 304 859.56,  $\rho = -0.5349324$ ,  $p\text{-value} = 0.03991$ .

305 Phytoplankton species abundance was dominated by micro-flagellates (diameter  $\sim 2 \mu\text{m}$ ,  $\sim 5$   
 306  $\mu\text{m}$ ), which constituted 80 to 90% of total cell counts at all three sites (SI Table S1a). In particular,  
 307 the non-HAB micro-flagellate *Emiliania huxleyi* reached significant numbers (up to  $3.7 \times 10^6$  cells L<sup>-1</sup>)  
 308 at L4 and SAB in week 27 (2<sup>nd</sup> July), but this species did not bloom at LB. Spatial and temporal  
 309 variations in the biomass and abundance of phytoplankton species were evaluated by multivariate  
 310 statistical analysis, employing Bray Curtis similarity analysis, followed by MDS ordination (SI Figure  
 311 S3). Significant differences between sampling sites and sampling weeks were detected using pseudo  
 312 F-tests in PERMANOVA and PERMDISP, respectively. Pairwise comparisons made in PERMANOVA ( $p$   
 313  $= 0.001$ ) confirmed that SAB, L4 and LB were all significantly different from each other with respect  
 314 to phytoplankton species composition throughout the summer. According to SIMPER, sites were  
 315  $\geq 28\%$  dissimilar based on species  $\times$  abundance (mainly micro-flagellate species) and  $\geq 50\%$  dissimilar

316 based on species  $\times$  biomass, with dinoflagellates including *K. mikimotoi* and *Gyrodinium spirale*, and  
317 diatoms including *Proboscia alata* and *Chaetoceros socialis* accounting for the biggest differences  
318 between sites (SI Table S1b). Environmental matching (BEST) for all three sampling sites found  
319 significant correlations between time-series data for phytoplankton community composition and  
320 environmental parameters: sea surface temperature; density; Secchi depth and Chl-*a* (Spearman  
321 rank correlation (n= 45, two tailed) = 0.386,  $p < 0.05$ ).

322

323 Zooplankton species abundance increased substantially over the course of the 2018 monitoring study  
324 at all three sampling sites. Maximum zooplankton abundance was recorded during a *Noctiluca*  
325 *scintillans* bloom in late July/August (weeks 30-34) at SAB and L4, whereas peaks in zooplankton  
326 abundance at LB were attributable to the copepods *Acartia clausi* and *Temora longicornis* (Figure 4).  
327 Variation in zooplankton species abundance between sites and sampling weeks was evaluated by MDS  
328 ordination (SI Figure S4) and then confirmed using PERMANOVA and PERMDISP, respectively (Site  
329  $F_{\text{pseudo}}(2,33) = 4.10$ ,  $p = 0.001$ ; Week  $F_{\text{pseudo}}(2,33) = 2.21$ ,  $p = 0.173$ ). Pairwise comparisons made in  
330 PERMANOVA ( $p < 0.01$ ) confirmed that zooplankton species composition differed significantly  
331 between all sites. According to SIMPER, sites were  $\geq 56\%$  dissimilar, and the abundance of *Noctiluca*  
332 *scintillans*, *Acartia calusii*, *Harpacticoida longipedia*, *Appendicularia* spp., Cirripede nauplii and *Podon*  
333 *spp.* accounted for the biggest differences between sites (SI Table S2). LB was the most dissimilar site  
334 (62% dissimilar to both L4 and SAB). Biota and Environmental matching (BEST) for all three sampling  
335 sites highlighted significant correlations between time-series data for zooplankton community  
336 composition and environmental parameters: sea surface temperature; density; Secchi depth and  
337 chlorophyll-*a* (Spearman rank correlation (n= 36, two tailed) = 0.365,  $p < 0.05$ ).

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341

## 342 **3.2) Analysis of temporal and wider spatial variations in HABs and oceanographical conditions**

### 343 **3.2.1) Historical occurrence of HABs and impacts at shellfish production sites**

344 HAB events have occurred repeatedly at the SAB and LB shellfish sites since they opened; since 2010  
345 for SAB and since 2015 for LB (Table 3). HAB frequencies (expressed as % of comparable weeks from  
346 2015-2017, in which cell counts in surface water (2 m depth) exceeded advisory trigger levels) have  
347 been higher at SAB versus LB for *K. mikimotoi* (13% versus 0%), *Dinophysis* spp. (15% versus 10%),  
348 *Prorocentrum cordatum* (11% versus 6%), *Pseudo-nitzschia* spp. (3% versus 1%) and for *Alexandrium*  
349 spp. (3% versus 1%). HAB frequencies are under-represented by the above FSA monitoring data  
350 (from 2015 onwards), because when cell counts in water exceed trigger levels, monitoring effort  
351 focusses primarily on the measurement of phycotoxins in shellfish and HAB cell counts are not  
352 reported during this time (FSA, 2019). According to both HAB species abundance and phycotoxin  
353 data, *Dinophysis* blooms are responsible for most HAB events in the region (FSA, 2019). Bloom  
354 intensities (cell abundances) have also been greater at SAB (and L4) in recent years compared to LB,  
355 most notably for *Dinophysis* spp. (Figure 5). Furthermore, the frequency at which *Dinophysis* toxin  
356 concentrations in shellfish meat have exceeded EU regulatory action levels (% of comparable weeks  
357 from 2015-2017, in which action levels (160 µg kg<sup>-1</sup> okadaic acid equivalents) were exceeded) has  
358 also been higher at SAB (22%) compared to LB (11%) (Table 4). The levels of intoxication have also  
359 been substantially greater at SAB, consistent with higher *Dinophysis* spp. bloom intensities (Figure  
360 5). There have been no other toxin breaches in relation to other HAB species at SAB or LB (SI Table  
361 S3).

362

### 363 **3.2.2) Long-term trends in HAB occurrence and abundance at L4**

364 Long-term time series data for L4 (sampled each week from 1993-2018) show that several HAB species  
365 have bloomed regularly, with abundances generally peaking in the summer months (May to  
366 September) (SI Figure S5). *Dinophysis* spp. in particular has exceeded advisory trigger levels most  
367 often, i.e. 63% of weekly sampling events during summer months (May-August inclusive) in 2002-  
368 2017, and rising to 73% in 2018 ( Table 3). Other dinoflagellate HAB species have also frequently  
369 exceeded trigger levels during the summers of 2002-2017 and in 2018 frequencies broke these  
370 historical records: *K. mikimotoi* (2.3% increasing to 6.7%); *Noctiluca scintillans* (1% to 20%);  
371 *Protoceratium reticulatum* (16% to 20%). Frequencies of trigger level exceedance for *Prorocentrum*  
372 *cordatum* reached 30% in summer 2018, equalling historic records, while frequencies for the diatom  
373 HAB genus *Pseudo-nitzschia* spp. declined from a baseline of 10% to 0% in 2018 (Table 3). The bloom  
374 intensities (abundances) of some of these HAB species (particularly *Prorocentrum cordatum*) were  
375 also substantially higher in 2018 than previously recorded (SI Figure S5); this HAB species is epi-  
376 benthic, therefore routine water column sampling may underestimate bloom densities. It is also  
377 important to note that the toxigenic mechanism(s) of *Prorocentrum cordatum*, including shellfish  
378 poisoning mechanisms, remain largely unknown (Khanaychenko et al., 2019). For the majority of HAB  
379 species, there are significant positive correlations between cell abundances and water temperature  
380 at 10 m depth. This is according to Pearson correlations of untransformed (normal) data from the  
381 recent L4 time series (2002-2018), in which cell abundances and water temperature have been  
382 sampled concurrently (SI Figure S5). For *Dinophysis* spp. and *Dinophysis acuta*, the frequency of HAB  
383 events (i.e. number of weeks per year in which HAB cell abundances exceeded advisory trigger levels)  
384 were found to show significant positive correlations with periods of elevated water temperature (i.e.  
385 weeks >15°C at 10 m depth) (Figure 6). Furthermore, the decadal data from L4 (2002-2018) showed a  
386 significant negative correlation between the increasing abundance of *Dinophysis acuta* and declining  
387 abundance of its key prey species *Mesodinium rubrum* (Spearman correlation (paired samples):  $S =$   
388 261.21,  $\rho = 0.616$ ,  $p\text{-value} = 0.011$ ).

389

### 390 **3.2.3) Regional variation in HAB occurrence and surface water circulation patterns**

391 The abundances of dinoflagellates, representing the majority of HAB species re-occurring regularly  
392 along the western English Channel coast, have been greater overall to the west compared to the east  
393 of Start Point (Figure 3). The Start Point frontal region (Figure 1) limited the extent of the eastward  
394 progression of the *K. mikimotoi* bloom along the Channel coast in August 2018, according to data from  
395 the FSA's wider monitoring network (SI Figure S6). Surface current velocities (net flows at 0 m and 15  
396 m water depth) at the three study sites were generally found to be dominated by west to east  
397 components from 8 - 14 August one week prior to the *K. mikimotoi* bloom at SAB and L4 (SI Figure S7).  
398 Wider visualisation of surface currents (<https://ovl.oceandatalab.com/>) during this period showed the  
399 breakdown of cyclonic circulation (typical of seasonal thermohaline circulation) in western English  
400 Channel (Fernand et al., 2004; Hill et al., 2008; SI Table S4), leading to net directional surface flows  
401 from west to east between Lands End and Start Point. During the same period, cyclonic circulation  
402 broke down partially at 1m and remained at 15m depth in Lyme Bay (SI Figure S7).

403

404 Start Point was also clearly shown by Sentinel-3A OLCI to mark the eastern boundary of a major bloom  
405 of the non-HAB micro-flagellate coccolithophore *Emiliana huxleyi* in the western English Channel in  
406 the first two weeks of July (SI Figure 8). *E. huxleyi* was also detected in high numbers (up to 700 000  
407 cells L<sup>-1</sup>) in water samples obtained from L4 in week 27 (2 July 2018) and was also detected at SAB in  
408 week 27 and week 28 (3 and 10 July 2018). Although *E. huxleyi* is not a HAB species, the extent of its  
409 influx is indicative of water circulation and the potential transport of other plankton species in the  
410 region.

411

## 412 **4) DISCUSSION**

413 Our study coincided with the warmest, and one of the calmest, summers ever recorded in the UK and  
414 NW Europe. Sea surface temperatures rose throughout the summer to >18.5°C at LB and SAB and  
415 >19°C at L4, reaching the highest temperature ever recorded at the Western Channel Observatory  
416 (WCO) in over 100 years ([WCO, 2020](#)). These exceptional conditions provided an ideal opportunity  
417 (see Trainer et al., 2020a) to investigate whether or not increased warming and thermal stratification  
418 in the western English Channel, projected under future climate change (UKCP18, Tinker *et al.* 2016),  
419 have the potential to expand niches for HABs both temporally and spatially. Our study found evidence  
420 of higher magnitude, more frequent and/or prolonged seasonal blooms of warm water dinoflagellates  
421 at two sites, SAB and L4, to the west of Start Point, but not at LB to the east. By employing  
422 standardised methods at established WCO and FSA monitoring sites, our study was able to build on  
423 substantial multi-decadal evidence of changes in plankton communities in the region, including  
424 increasing dinoflagellate:diatom ratios (Bedford et al., 2020) and the occurrence and impact on  
425 shellfish cultivation of dinoflagellate HABs, under increasingly prolonged stable, seasonally stratified  
426 conditions (Smyth et al., 2010; Hinder et al., 2011; Glibert et al., 2014;; Gobler et al., 2017; Schmidt et  
427 al., 2018a).

428

#### 429 **4.1) Variation in HABs in relation to physical conditions**

430 Despite intense sea surface warming across all three survey sites in summer 2018, there were  
431 significant differences in plankton assemblages, including more frequent occurrences and higher  
432 abundances of dinoflagellate HAB species (exceeding trigger levels) at SAB and L4 compared to LB. In  
433 particular, the dinoflagellates *Dinophysis acuminata* and *D. acuta* formed blooms which were the  
434 largest and most persistent recorded to date at SAB and L4, and the accumulation of *Dinophysis* toxins  
435 in farmed mussels at SAB led to an 18 week shellfish harvesting ban, costing >£1 million in lost sales.  
436 Greater prevalence of *Dinophysis* spp., and several other dinoflagellate HAB species at SAB and L4,  
437 was consistent with increased water column density stratification (see Barton et al. 2015; Lucas et al.,

438 2016), which is known to occur to the west of the tidal mixing front located off Start Point (Pingree *et*  
439 *al.* 1983, Boalch 1987). To the east of this frontal system, in Lyme Bay, greater tidal mixing is more  
440 favourable for diatom blooms (Smayda and Trainer, 2010). These contrasting hydrodynamic regimes  
441 and associated phytoplankton communities were evident in 2018, according to environmental survey  
442 data for our three study sites. In addition, other more extensive spatial data confirmed that Start Point  
443 (~4°W) marked the eastward extent of high biomass blooms of the non-HAB micro-flagellate  
444 coccolithophore *E. huxleyi* detected in early June by Sentinel 3A satellite imagery, and the  
445 dinoflagellate HAB species *K. mikimotoi* detected in mid-August by the FSA's network of monitoring  
446 stations along the western English Channel. According to a regional-scale assessment of the surface  
447 current velocities, based on the CMEMS data (CMEMS, 2020), the *K. mikimotoi* bloom to the west of  
448 Start Point coincided with the temporary reversal of seasonal thermohaline circulation (typically  
449 running east to west) and the incursion of cooler, nutrient enriched water from the Western  
450 Approaches to the English Channel. Meanwhile to the east of Start Point at LB, sea surface  
451 temperature remained elevated at 17.7-18.5°C and *K. mikimotoi* did not bloom there.

452

453 Our results are consistent with previous studies, which have shown considerable spatial heterogeneity  
454 in HAB occurrence in the region in association with frontal systems (Pingree *et al.*, 1975; Holligan *et*  
455 *al.*, 1979; Hartman *et al.*, 2014; Barnes *et al.*, 2015). For example, *K. mikimotoi* most often blooms  
456 along the western boundary of the seasonally stratified western English Channel, (Pingree, 1975,  
457 Holligan, 1979, Garcia and Purdie, 1994; Widdicombe *et al.*, 2010; Barnes *et al.*, 2015). Another factor  
458 which has been associated with increasing occurrence of HAB, including *K. mikimotoi* and *Dinophysis*  
459 *spp.*, is their physical advection and concentration against the coast in sheltered stratified areas  
460 (Raine, 2014; Gillibrand *et al.*, 2015; Schmidt *et al.*, 2018b). However, our survey data build on  
461 accumulating evidence that *Dinophysis spp.* and other HABs can also bloom regularly offshore along  
462 the western English Channel (Widdicombe *et al.*, 2010), in the wider English Channel, North Sea

463 (Edwards et al., 2019) and elsewhere along the NW European shelf, for example along the Galician  
464 coast (Diaz et al., 2019). The regular offshore occurrence of HAB cell counts above advisory trigger  
465 levels at L4 and wider English Channel indicates a notable risk for future offshore expansion of shellfish  
466 mariculture in the region.

467

468

469

#### 470 **4.2) Variation in HABs in relation to bio-geochemical conditions**

471 Nutrient levels (and chlorophyll concentrations of  $<1 \text{ mg Chl-}a \text{ m}^{-3}$ ) were below the long-term seasonal  
472 average in the summer of 2018 (Smyth et al. 2010) and in this respect conditions were uniform across  
473 our three survey sites for much of the summer. These conditions favoured low biomass, motile  
474 dinoflagellate HABs, including *Dinophysis* spp., with the ability to exploit available light and inorganic  
475 nutrients for photosynthesis, and also to prey upon other plankton (mixotrophy) (Anderson et al.,  
476 2012; Zhang et al., 2013; Lucas et al., 2016). As well as greater stratification favouring more intense  
477 and more prolonged *Dinophysis* blooms at SAB and L4, the greater abundance of a key prey species  
478 *Mesodinium rubrum* ( $\geq 100 \text{ cells L}^{-1}$  at SAB and L4 compared to  $\leq 20 \text{ cells L}^{-1}$  at LB) also likely contributed  
479 to the enhanced survival and population growth of *Dinophysis* spp. (via acquisition of chloroplasts for  
480 autotrophic growth) (Park et al., 2006, 2008). Significant correlation between *Dinophysis acuta* (but  
481 not *Dinophysis acuminata*) and *Mesodinium rubrum* abundance in the long-term data (1992-2018)  
482 from L4 provided further evidence of the importance of this trophic relationship. Elsewhere  
483 *Mesodinium* spp. has been associated with *D. acuminata*, but not with *D. acuta*, for example in coastal  
484 fjords of southern Chile. However, in this alternative example other factors also contributed to niche  
485 differentiation between these *Dinophysis* species; *D. acuta* was associated with higher salinity  
486 compared to *D. acuminata* (i.e. 23-25 psu compared to 17-20 psu), and with lower levels of turbulence

487 and Photosynthetically Active Radiation (PAR) (Baldrich et al., 2021). At each of our coastal survey  
488 sites salinity remained within 33.5-35 psu throughout the water column, so the environmental niches  
489 at our sites were not comparable with those in Chile. Discriminating niches for these species is  
490 important in shellfish waters, since *D. acuta* and *D. acuminata* may produce different profiles of DSP  
491 toxins (OA, DTX and PTX toxins) and profiles have been shown to vary between geographical  
492 regions (Reguera et al., 2014; Baldrich et al., 2021).

493 Plankton grazing and parasitism can also play key roles in regulating the abundance of marine  
494 planktonic micro-algae, including HAB species (Chambouvet et al., 2008; Jones et al., 2011; Montagnes  
495 et al., 2008; Sun et al., 2018). Spatial and temporal variations in phytoplankton and zooplankton  
496 grazers were detected in our study. At LB, there were substantially higher numbers of copepod  
497 grazers, such as *Acartia clausi*, and *Temora longicornis* (Figure 4), which can exert considerable grazing  
498 pressure on phytoplankton, such as *Dinophysis* spp., in European shelf seas, including the western  
499 English Channel (Carlsson et al., 1995; Maneiro et al., 2000; Kozlowsky-Suzuki et al., 2006). The diet of  
500 *A. clausii*, in particular, may contain up to 30% *D. acuminata* (Carlson et al., 1995). Shellfish such as  
501 mussels (*Mytilus edulis*), farmed in SAB and LB, can also exert considerable grazing pressure on both  
502 phytoplankton and zooplankton, removing up to 30% of total plankton biomass in embayed sites with  
503 extended water residence times, such as SAB (Newell, 2004; Lucas et al., 2016; Nielsen et al., 2016;  
504 Cranford, 2019). Biomass removal by shellfish is estimated to be substantially less (~5%) in deeper,  
505 more open coastal waters with shorter residence times, such as LB (Torres pers. comm.). Under  
506 conditions of low primary productivity in summer 2018, farmed mussels at LB showed substantially  
507 lower growth and condition compared to those at SAB (J. Holmyard, G. Rawle pers. comms.). Higher  
508 mussel growth at SAB did not appear to inhibit the blooming of *Dinophysis* spp. or *K. mikimotoi*, nor  
509 did these blooms appear to have a negative effect on mussel growth. The effects of filter feeding  
510 shellfish on plankton community composition, including the abundance of HAB species, (and *vice*  
511 *versa*), are generally poorly understood (Newell, 2004; Petersen et al., 2008; Lucas et al., 2016).  
512 Nevertheless, some bivalve shellfish, including blue mussels (*Mytilus edulis*), can show preferential

513 uptake of HAB cells and may deposit intact live cells or dormant cysts to underlying sediments, from  
514 which they may be re-suspended (Hégaret et al., 2007). The comparative abundance of *Dinophysis*  
515 spp. and other HAB cells or cysts in underlying sediments at SAB and LB has not been quantified to  
516 date.

517

## 518 **CONCLUSIONS**

519 Gaining insights on the likely frequency and extent of HABs under future climate change scenarios,  
520 particularly in rapidly warming NW European shelf seas, is critically important for planning the  
521 expansion of mariculture for the sustainable production of healthy, nutritious seafood. Our study  
522 coincided with the exceptionally warm summer of 2018 and provided an ideal opportunity to  
523 investigate if increased warming and thermal stratification in the western English Channel has the  
524 potential to expand niches for HABs. Despite widespread warm and stable conditions, coupled with  
525 low levels of inorganic nutrients throughout the region, favouring warm water dinoflagellate HAB  
526 species, we detected distinct differences in the magnitude, spatial extent and duration of HABs. HABs  
527 were more pronounced and prolonged in coastal and offshore areas to the west compared to the east  
528 of the Start Point tidal mixing front ( $\sim 4^\circ\text{W}$ ). Differences either side of this frontal system in water  
529 circulation patterns and plankton assemblages, including zooplankton grazers, were linked to the  
530 observed variations in the extent and duration of HAB events. Furthermore, the increasing magnitude  
531 and duration of HABs with rising sea surface temperature to the west of Start Point was highlighted  
532 by long-term data from Plymouth L4. Here dinoflagellate HABs, including *Dinophysis* spp.,  
533 *Prorocentrum cordatum*, *Protoceratium reticulatum*, *Noctiluca scintillans* and *Karenia mikimotoi*,  
534 formed the most prominent blooms recorded since records began in 1992. These contemporary  
535 trends and survey data for 2018 provide a glimpse into possible future climate change scenarios.  
536 However, should warming of over  $3^\circ\text{C}$  occur, as projected from 1960-1989 to 2069-2089 in UK shelf  
537 seas (Tinker et al. 2016), thermal niches for some HABs may be confined below thermocline in the

538 summer, to other seasons or to higher latitudes, allowing other species to take their place. Therefore,  
539 even in a warmer more stable future, changes in plankton species distributions, phenologies and  
540 interactions are likely to continue to make HAB prediction challenging.

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561



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787 **TABLES**

788

789 **Table 1: Physical characteristics of the study sites at St Austell Bay (SAB), Plymouth (L4) and Lyme**  
790 **Bay (LB)**791 <sup>1</sup> Offshore defined by water depth >30m (Froehlich *et al.* 2017). Lyme Bay could be defined as  
792 offshore based on current speed (>0.2m/s), but based on water depth (<30m) it is considered a  
793 coastal site (Froehlich *et al.* 2017).

<i>Site</i>	<i>St Austell Bay (SAB)</i>	<i>Plymouth (L4)</i>	<i>Lyme Bay (LB)</i>
<i>Location (lat, long)</i>			
<i>Station 1</i>	50.315 N, 4.717 W	50.250 N, 4.217 W	50.573 N, 3.214 W
<i>Station 2</i>	50.309 N, 4.735W	50.316 N, 4.174 W	50.639 N, 3.184 W
<i>Type</i>	Shellfish production site (1.5 km <sup>2</sup> , 500-600 tonnes mussels/yr)	Long-Term Ecological Records (LTER) site	Shellfish production site (12 km <sup>2</sup> , 2000 tonnes mussels/yr)
<i>Category</i> <sup>1</sup>	Coastal	Offshore	Coastal
<i>Distance</i>	2.5 km from shore	7.6 km from shore	8.5 km from shore
<i>Depth</i>	~21 m	~55 m	~25 m
<i>Circulation</i>	Weak wind-driven circulation (up to 0.02-0.06 ms <sup>-1</sup> ) Sherwin & Jonas (1994)	Strong tidal currents (up to 0.6 ms <sup>-1</sup> ) Smyth et al. (2010)	Strong tidal currents (up to 0.49 ms <sup>-1</sup> ) Pingree et al. (1983)
<i>OSPAR region</i>	II – Greater North Sea	II – Greater North Sea	II – Greater North Sea
<i>UK Env Agency region</i>	West Inshore region	<i>Not monitored</i>	East Inshore region
<i>OSPAR stratification</i>	Indeterminate density	Indeterminate density	Intermittent density
<i>Thermal stratification</i>	Seasonal	Seasonal	Seasonal

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796 **Table 2: Nutrient concentrations at the sampling sites of Plymouth L4, Lyme Bay and St Austell Bay**

797 Concentrations represent average values for 2 m and 10 m water depth in each calendar month

Site	Date	Nitrite $\mu\text{mol L}^{-1}$	Nitrate $\mu\text{mol L}^{-1}$	Ammonium $\mu\text{mol L}^{-1}$	Silicate $\mu\text{mol L}^{-1}$	Phosphate $\mu\text{mol L}^{-1}$
SAB	May	<0.087	<0.323	<0.554	<2.629	<0.211
SAB	June	<0.087	<0.323	1.109	<2.629	0.390
SAB	July	<0.087	<0.323	0.665	<2.629	<0.211
SAB	August	<0.087	<0.323	0.554	<2.629	<0.211
L4	May	<0.011	0.031	0.100	0.499	0.100
L4	June	<0.011	0.050	0.200	0.499	0.100
L4	July	<0.011	0.050	0.299	0.100	0.100
L4	August	0.011	0.100	0.499	2.000	0.100
LB	May	<0.087	<0.323	<0.554	<2.629	<0.211
LB	June	<0.087	<0.323	0.998	<2.629	<0.211
LB	July	<0.087	<0.323	1.109	<2.629	<0.211
LB	August	<0.087	<0.323	0.665	<2.629	<0.211

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799 **Table 3: Exceedance of cell count trigger levels for HABs according to historical monitoring data for study sites and results from our 2018 study (in bold)**

800 \*From 2015 cell counting undertaken for the Food Standards Agency (FSA) at UK shellfish sites was not continuous; monitoring effort switched to toxin  
 801 monitoring in shellfish, after advisory trigger levels were breached. Therefore the frequency of cell count exceedances are under-reported at SAB and LB.

802 Frequency (%) calculated as number breaches (weeks) / total time period (weeks) x 100.

803

HAB species	Trigger level (cells L <sup>-1</sup> )	Number of weeks exceeding trigger level (%)							
		L4 - all year (1993-2017) /1300 weeks	L4 - summer (2002-2017) /256 weeks	L4 - summer (2018) /15 weeks	SAB - all year (2010-2017) /416 weeks	SAB - all year (2015-2017) /156 weeks	SAB - summer (2018) /15 weeks	LB - all year (2015-2017) /156 weeks	LB - summer (2018) /15 weeks
<i>Karenia mikimotoi</i>	150,000	22 (1.7%)	6 (2.3%)	<b>1 (6.7%)</b>	0 (0%)	0 (0%)	2 (13%) <b>2 (13%)</b>	0 (0%)	0 (0%) <b>0 (0%)</b>
<i>Pseudo-nitzschia</i> spp.	150,000	54 (4.2%)	28 (10.9%)	<b>0 (0%)</b>	15 (4%)	5 (3.2%)	0 (0%) <b>0 (0%)</b>	1 (<1%)	0 (0%) <b>0 (0%)</b>
<i>Noctiluca scintillans</i>	150,000	16 (1.2%)	2 (0.8%)	<b>3 (20%)</b>	0 (0%)	0 (0%)	0 (0%) <b>2 (13%)</b>	0 (0%)	0 (0%) <b>0 (0%)</b>
<i>Phaeocystis globosa</i>	150,000	52 (4.0%)	4 (1.6%)	<b>0 (0%)</b>	0 (0%)	0 (0%)	0 (0%) <b>0 (0%)</b>	0 (0%)	0 (0%) <b>0 (0%)</b>
<i>Dinophysis</i> spp.	100	223 (17%)	162 (63%)	<b>11 (73%)</b>	42* (10%)	23* (15%)	5* (33%) <b>13 (87%)</b>	15* (10%)	9 (60%) <b>3 (20%)</b>
<i>Prorocentrum cordatum</i>	100	185 (14%)	85 (33%)	<b>5 (33%)</b>	28 (6.7%)	17 (11%)	4 (27%) <b>4 (27%)</b>	9 (5.8%)	2 (13%) <b>2 (13%)</b>

<i>Protoceratium reticulatum</i>	100	28 (2.2%)	41 (16%)	<b>3 (20%)</b>	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
							<b>1 (6.7%)</b>		<b>0 (0%)</b>
<i>Alexandrium</i> spp.	40	8 (0.6%)	2 (0.8%)	<b>0 (0%)</b>	12 (3%)	4 (2.6%)	3 (20%)	2 (1%)	0 (0%)
							<b>0 (0%)</b>		<b>0 (0%)</b>

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806 **Table 4: Historical monitoring data for *Dinophysis* spp. cell count breaches versus toxins detected above action levels**

807 Official Control monitoring was administered for SAB and LB by the UK Food Standards Authority, under EU regulations (EC/854/2004).

808 SAB was licenced and opened in October 2009, LB was licenced in 2015.

809 \*From 2015 cell counting performed by CEFAS/FSA was not continuous; monitoring effort switched to toxin monitoring in shellfish, after toxin threshold  
810 was breached (>160 µg okadaic acid equivalents per kg shellfish flesh). Therefore frequencies of cell count exceedances are under-reported at SAB and LB.

811 #Data obtained from this research study. Frequency (%) calculated as number breaches (weeks) / total time period (weeks) x 100.

Year	Plymouth (L4)		St Austell Bay (SAB)				Lyme Bay (LB)			
	Period	Cell count breaches (weeks)	Period	Cell count breaches (weeks)	Toxin breaches (weeks)	Toxin detects below action level (weeks)	Period	Cell count breaches (weeks)	Toxin breaches (weeks)	Toxin detects below action level (weeks)
2010	Feb-Aug	8	Jun	1	2	0				
2011	Mar-Aug	11	Aug	2	2	0				
2012	Mar-Aug	5	Apr-Jul	3	0	0				
2013	May-Nov	23	Jul-Aug	4	3	14				
2014	Jun-Oct	15	Jul-Sep	12	12	7				
2015	Mar-Sep	12	Jun-Oct	8*	16	5	Aug	2*	3	4
2016	Mar-Oct	11	Jul-Oct	11*	17	7	Jul-Sep	10*	10	3
2017	Mar-Oct	12	May-Jun	3	0	10	Jun-Jul	3*	4	6
2010-17	-	86 (24%)	-	44 (10%)	52 (13%)	44 (11%)	-	-	-	-
2015-17	-	24 (15%)	-	22 (14%)	33 (22%)	22 (14%)	-	15 (9%)	17 (11%)	13 (8%)
2018	Apr-Aug	11 (21%)	Apr-Aug	5* (10%), 14# (27%)	18 (35%)	13 (25%)	Apr-Sep	9 (17%), 5# (10%)	1 (2%)	14 (27%)

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## FIGURES

### Figure 1: Sampling site locations - St Austell Bay (SAB), Plymouth (L4) and Lyme Bay (LB)

Note: All three study sites exhibit seasonal stratification of the water column, including LB, which is relatively sheltered from wind and tide in an otherwise generally mixed region.

### Figure 2: Variation in physical parameters characterising the water column and chlorophyll concentrations at each survey site from week 21 to 35

Data represent Station 1 at each survey site: St Austell Bay (SAB) time series indicated by triangles, Plymouth (L4) indicated by circles and Lyme Bay (LB) indicated by squares.

Principal Components Analysis (PCA): PC1 captures temporal changes across all three sampling sites in terms of water temperature, salinity and density. PC2 captures reduction in Chl-*a* concentration and increase in Secchi depth at each site.

### Figure 3: Variation in phytoplankton diversity abundance and biomass at each survey site from week 21 to 35

Data represent Station 1 at each survey site: St Austell Bay (SAB) time series indicated by triangles, Plymouth (L4) indicated by circles and Lyme Bay (LB) indicated by squares.

### Figure 4: Prey and Predator abundance for *Dinophysis* spp. at each survey site from week 21 to 35

Data represent Station 1 at each survey site: St Austell Bay (SAB) time series indicated by triangles, Plymouth (L4) indicated by circles and Lyme Bay (LB) indicated by squares.

Prey: *Mesodinium rubrum* (ciliate). Predators: *Acartia clausii*; *Temora longicornis* (copepods).

### Figure 5: Intensities of *Dinophysis* spp. blooms and Okadaic Acid (OA) accumulation in shellfish in St Austell Bay and Lyme Bay according to FSA monitoring records for 2016 to 2018

Data represent Station 1 at each survey site in weeks 1-52 each year

**Figure 6: Correlations between incidences of *Dinophysis* species exceeding cell count trigger levels and corresponding periods of elevated water temperature at Plymouth (L4) from 2002-2018**

Cell count trigger level = 100 cells L<sup>-1</sup>