

1 Interannual variability of the initiation of the phytoplankton 2 growing period in two French coastal ecosystems

3 *Main manuscript modifications are highlighted in red.*

4 Coline Poppeschi¹, Guillaume Charria¹, Anne Daniel², Romaric Verney³, Peggy Rimmelin-
5 Maury⁴, Michaël Retho⁵, Eric Goberville⁶, Emilie Grosstefan⁴, Martin Plus²

6 ¹Ifremer, Univ. Brest, CNRS, IRD, Laboratory for Ocean Physics and Satellite remote sensing (LOPS), IUEM,
7 29280 Brest, France.

8 ²Ifremer, DYNECO, Pelagic Ecology Laboratory (PELAGOS), 29280 Brest, France.

9 ³Ifremer, DYNECO, Hydrosedimentary Dynamics Laboratory (DHYSED), 29280 Brest, France.

10 ⁴OSU-European University Institute of the Sea (IUEM), UMS3113, 29280 Plouzané, France.

11 ⁵Ifremer, Morbihan-Pays de Loire Environment Resources Laboratory (LERMPL), 56100 Lorient, France.

12 ⁶Unité Biologie des Organismes et Ecosystèmes Aquatiques (BOREA), Muséum National d'Histoire Naturelle,
13 CNRS, IRD, Sorbonne Université, Université de Caen Normandie, Université des Antilles, Paris, France

14 *Correspondence to:* Coline Poppeschi (coline.poppeschi@ifremer.fr)

15 **Abstract.** Decadal time series of chlorophyll-*a* concentrations sampled at high and low frequencies are explored
16 to study climate-induced changes on the processes inducing interannual variations in the Initiation of the
17 Phytoplankton Growing Period (IPGP) in early spring. In this study, we specifically detail the IPGP in two
18 contrasting coastal temperate ecosystems under the influence of rivers highly rich in nutrients: the Bay of Brest
19 and the Bay of Vilaine. A large interannual variability in the IPGP is observed in both ecosystems in connection
20 with variations of environmental factors (available light depending from solar radiation, chlorophyll concentration
21 and turbidity - sea temperature - turbulence driven by currents, wind direction and intensity and tidal mixing -
22 nutrients from river flow). We show that the IPGP is delayed by around 30 days in 2019 in comparison with 2010.
23 *In situ* observations and a one-dimensional vertical model coupling hydrodynamics, biogeochemistry, and
24 sediment dynamics show that the IPGP generally depends on the interaction between several environmental
25 factors. IPGP is mainly conditioned, at the local scale, by sea surface temperature and available light conditions,
26 controlled by the turbidity of the system before first blooms. While both bays are hydrodynamically contrasted,
27 the processes that modulate IPGP are similar. In both bays, IPGP can be delayed by cold spells and flood events
28 at the end of winter if these extreme events last several days.

29 30 **Keywords**

31 Phytoplankton biomass, Long-term *in situ* observations, Coastal temperate ecosystems, Extreme events, Climate
32 change.

33 **1 Introduction**

34 Although studied for 70 years (Sverdrup, 1953), the optimal conditions that trigger the Initiation of
35 Phytoplankton Growing Period (IPGP) in ocean waters in early spring are not well understood (Sathyendranath *et*
36 *al.*, 2015). Three main theories are proposed to date: the Critical Depth Hypothesis (Sverdrup, 1953), the Critical
37 Turbulence Hypothesis (Huisman *et al.*, 1999) and the Disturbance-Recovery Hypothesis (Banse, 1994;
38 Behrenfeld, 2010; Behrenfeld *et al.*, 2013). These hypotheses, determined with specific scales (*e.g.* mixed layer
39 depth dynamics and annual evolution) and ecosystems, are still regularly debated owing to the use of more efficient
40 models and new observation systems that allow the collection of large *in situ* datasets (Boss and Behrenfeld, 2010;
41 Rumyantseva *et al.*, 2019; Caracciolo *et al.*, 2021). Coastal waters remain highly dynamic and productive
42 ecosystems at the interface between land and sea and are distinguished from the waters of the open sea (*e.g.* Gohin
43 *et al.*, 2019; Liu *et al.*, 2019). Because coastal systems are directly influenced by anthropogenic inputs from rivers,
44 no nutrient limitation is observed in late winter. A myriad of factors and mechanisms can then affect the IPGP in
45 coastal areas (Townsend *et al.*, 1994; Cloern, 1996) but the incident light at the air/sea interface (Glé *et al.*, 2007)
46 and the sea surface temperature (Trombetta *et al.*, 2019) are the main forcings. Low water turbidity also plays a
47 major role and allows deeper light penetration (Iriarte and Purdie, 2004). This occurs by low vertical mixing
48 conditions in shallow waters (Ianson *et al.*, 2001), *i.e.* limited advective exchanges, weak wind (Tian *et al.*, 2011),

49 neap tide (Ragueneau *et al.*, 1996) and in absence of flooding events (Peierls *et al.*, 2012). Depending on the
50 morphology and hydrodynamics of coastal zones (estuaries, bays, lagoons), the importance of controlling factors
51 can be variable (Cloern, 1996). The variability of IPGP plays a major role on several biological compartments in
52 coastal ecosystems: change in the timing of IPGP can impact zooplankton and fish by inducing species
53 replacements (Sommer *et al.*, 2012), or phytoplankton itself by changing species composition or the succession of
54 species (Ianson *et al.*, 2001; Edwards and Richardson, 2004; Chivers *et al.*, 2020).

55 By amplifying or modifying environmental forcings, it is now well-documented that global climate
56 change may influence the IPGP in coastal areas (Smetacek and Cloern, 2008; Barbosa *et al.*, 2010; Pearl *et al.*,
57 2014; IPCC, 2021). Heat waves, as opposed to cold spells, have become more frequent in recent years and can
58 advance or delay the IPGP respectively (Gomez and Souissi, 2008). Wind storms, by inducing vertical mixing and
59 sediment resuspension, can have a significant effect on water turbidity which in turn limits light penetration and
60 therefore influences the IPGP. Floods, following heavier rainfall, may increase continental erosion, land-based
61 transfers and ultimately nutrient inputs to coastal ecosystems. Because coastal ecosystems are strongly influenced
62 by changes in land use, detecting long-term climate-induced signals is challenging (Kromkamp and Van
63 Engeland, 2010).

64 Our study is based on two geographically close but **hydrodynamically different nearshore ecosystems**:
65 (1) the Bay of Brest, a shallow semi-enclosed bay with well-mixed waters (Le Pape and Menesguen, 1997) and
66 (2) the Bay of Vilaine, a shallow open bay with long water residence times (Chapelle *et al.*, 1994). These two
67 coastal ecosystems are strongly impacted by anthropogenic pressures, such as intensive agriculture (Ragueneau *et*
68 *al.*, 2018; Ratmaya *et al.*, 2019). **The river influence induces waters highly rich in nutrients.** Most studies dealing
69 with IPGP are mainly based on discrete water sampling (Iriarte *et al.*, 2004; Tian *et al.*, 2011) or modeling
70 (Townsend *et al.*, 1994; Philippart *et al.*, 2010). Only few studies investigate long-term high-frequency
71 observations (Gomez and Souissi, 2008; Iriarte and Purdie, 2004) to assess interannual variability of the IPGP and
72 to identify the triggering and controlling factors.

73 In this study, we aim to better understand interannual local changes in the IPGP in coastal temperate
74 ecosystems in the current context of global climate change over the last 20 years. We first detect and analyze the
75 temporal variability of the IPGP and we then quantify how environmental forcings influence its dynamics. To
76 detect and analyze IPGP in coastal environments, we develop a method, combining high-frequency decadal *in situ*
77 observations and modeling, based on a 1DV hydro-sedimentary and biogeochemical coupled numerical model.
78 The potential impact of hydro-meteorological extreme events, such as cold waves, flood events and wind bursts,
79 on the IPGP is then investigated.

80 2 Data and methods

81 2.1 Study areas

82 The study focuses on two northwestern French **coastal temperate ecosystems**, the Bay of Brest and the
83 Bay of Vilaine, which are both impacted by excessive nutrient inputs from watersheds, but exposed to different
84 hydrodynamic conditions.

85 The Bay of Brest is a semi-enclosed bay (180 km^2) with 50% of the surface shallower than 5 m depth.
86 The Bay is connected with the Atlantic Ocean (Iroise sea) through a narrow and shallow strait. Tidal variation
87 reaches 8 m during spring tides, which represents an oscillating volume of 40 % of the high tide volume.
88 Freshwater inputs are essentially from the Aulne river (catchment area 1875 km^2 , mean river flow $26 \text{ m}^3 \text{ s}^{-1}$), and
89 also from two smaller rivers, the Elorn (catchment area 385 km^2 , mean river flow $6 \text{ m}^3 \text{ s}^{-1}$) and the Mignonne
90 (catchment area 111 km^2 , mean river flow $1.5 \text{ m}^3 \text{ s}^{-1}$). Because of the macrotidal regime, the high nitrate
91 concentrations do not generate important green tides (Le Pape *et al.*, 1997) and the strong decreases in the Si:N
92 and Si:P ratios did not exhibit dramatic phytoplankton community shifts from diatoms to non-siliceous species in
93 spring (Del Amo *et al.*, 1997) according to the high Si recycling (Ragueneau *et al.*, 2002; Beucher *et al.*, 2004).

94 The Bay of Vilaine is a mesotidal open bay (69 km^2) under the influence of the Vilaine (catchment area
95 $10\ 500 \text{ km}^2$, mean river flow $70 \text{ m}^3 \text{ s}^{-1}$) and the Loire (catchment area $117\ 000 \text{ km}^2$, mean river flow $850 \text{ m}^3 \text{ s}^{-1}$)
96 river discharges, with tidal ranges varying between 4 and 6 m (Merceron, 1985). The Loire river plume tends to
97 spread northwestward with a dilution of 20- to 100-fold by the time it reaches the Bay of Vilaine (Ménesguen *et*
98 *al.*, 2018). The Vilaine river plume tends to spread throughout the bay before moving westward (Chapelle *et al.*,
99 1994). The water residence time varies seasonally between 10 and 20 days (Chapelle *et al.*, 1994). The water
100 circulation is mainly driven by tides, winds and river flows (Lazure and Jegou, 1998). This bay is well known as
101 one of the most sensitive European Atlantic coastal ecosystems to eutrophication (Ménesguen *et al.*, 2019). The
102 Bay of Vilaine has undergone eutrophication over recent decades mainly due to high nutrient inputs from the
103 Vilaine and Loire rivers (Rossignol-Strick, 1985; Ratmaya *et al.*, 2019).

109 **2.2 In situ observations**

110
111 COAST-HF-Iroise (Rimmelin-Maury *et al.*, 2020) and COAST-HF-Molit (Retho *et al.*, 2020) are two high-
112 frequency monitoring buoys of the French national observation network COAST-HF¹ (Répécaud *et al.*, 2019;
113 Farcy *et al.*, 2019; Cocquempot *et al.*, 2019; Poppeschi *et al.*, 2021) located respectively in the Bay of Brest
114 (4.582°W; 48.357°N) and in the Bay of Vilaine (2.660°W; 47.434°N) (Fig. 1). COAST-HF-Iroise has been
115 operating in the strait between the Bay of Brest and the Iroise sea since 2000. COAST-HF-Molit buoy has been
116 sampling the plume of the Vilaine river since 2008. Buoys are deployed during the whole year except for COAST-
117 HF-Molit only available for part of the year prior to 2018 (from mid-February to early September, i.e. from day
118 50 to 250 for the period 2008-2017). Depending on the tide, the depth at the mooring sites ranges from 11 to 17 m
119 for both COAST-HF buoys. Environmental parameters (temperature, salinity, turbidity, dissolved oxygen and Chl-
120 *a* fluorescence) are measured at 2 m (COAST-HF-Iroise) and 1.3 m (COAST-HF-Molit) below the surface, every
121 20 and 60 minutes. The Chl-*a* fluorescence is measured by a Turner CYCLOPS-7 Sensor (precision \pm 5%) and
122 is considered as a proxy of phytoplankton biomass (unit FFU).

123 Sub-surface Chl-*a* concentrations are provided from two French marine monitoring networks, the SOMLIT
124 coastal observation network² and the REPHY (French Observation and Monitoring program for Phytoplankton
125 and Hydrology in coastal waters)³. They are collected bimonthly respectively at the SOMLIT-Brest (4.552°W;
126 48.358°N) and the REPHY-Loscolo (2.445°W; 47.496°N) stations which are close to the COAST-HF stations.
127 Chlorophyll-*a* concentrations are measured with either spectrophotometric or fluorimetric methods (Aminot and
128 Kérouel, 2004).

129 Daily river flows are measured at gauging stations (French hydrology “Banque Hydro” database⁴), located
130 close to the main river mouths [Aulne-Gouezec (4.093°W; 48.205°N), Loire-Montjean (1.78°W; 47.106°N)]. The
131 Vilaine river flow is controlled by a dam, and data were provided by the Vilaine Public Territorial Basin
132 Organization⁵ (Fig. 1).

133 The tide gauge stations (Shom⁷) at Brest (4.495°W; 48.382°N) and Crouesty (2.895°W; 47.542°N) record the
134 sea level every minute.

135 Precipitation, air temperature, wind direction and intensity, and the solar flux data are retrieved every 6 minutes
136 from two meteorological stations from the Météo-France observation network⁶: Guipavas (4.410°W; 48.440°N)
137 and Vannes-Séné (2.425°W; 47.362°N) (Fig. 1). The solar flux can be used here as a proxy for subsurface PAR
138 (Photosynthetically Available Radiation).

139 **2.3 MARS3D-1DV modeling experiments**

140 **2.3.1 MARS3D-1DV model**

141
142 A 1DV (one-dimensional vertical) model configuration is implemented to simulate changes in biogeochemical
143 variables due to hydrodynamics and sediment dynamics in both bays.

144
145 The hydrodynamical model is based on the MARS3D (3D hydrodynamics Model for Applications at Regional
146 Scale) code (Lazure and Dumas, 2008). This model is a primitive equation model with a free surface and uses the
147 Boussinesq and hydrostatic pressure assumptions. Here, we use the 1DV configuration of the model, with 10
148 vertical sigma levels for 15 m depth. The time step is 30 s.

149 The sediment model (MUSTANG - Le Hir *et al.*, 2011; Grasso *et al.*, 2015; Mengual *et al.*, 2017) is designed
150 to simulate the transport and changes in different sediment mixtures. In the sediment, 50 layers (refined near the
151 surface) for a total thickness of 40 cm are implemented. Four sediment classes are considered: muds (diameter 10
152 μm), fine sand (diameter 100 μm), medium sand (diameter 200 μm) and coarse sand (diameter 400 μm). The
153 sediment dynamics (transport in the water column, exchanges at the water/sediment interface, erosion/deposition

¹ www.coast-hf.fr, data available on www.coriolis-cotier.org

² <https://sommli.fr>

³ <https://doi.org/10.17882/47428>

⁴ www.hydro.eaufrance.fr/

⁵ <https://www.eptb-vilaine.fr/>

⁶ <https://donneespubliques.meteofrance.fr/>

⁷ <http://data.shom.fr>

154 processes) are driven by an advection/dispersion equation for each sediment class (refer to Le Hir et al., 2011 for
155 a detailed description of the sediment model).

156 The biogeochemical model BLOOM (BiogeochemicaL cOastal Ocean Model) is derived from the ECO-
157 MARS model (Cugier et al., 2005; Ménesguen et al., 2019) adding major processes of early diagenesis. Nitrogen,
158 phosphorus, and silica cycles are studied considering four nutrients, respectively nitrate, ammonium, soluble
159 reactive phosphorus, silicic acid (sorption/desorption of phosphate on suspended sediment and
160 precipitation/dissolution of phosphate with iron processes are also included). The model is also represented by
161 three phytoplankton classes (microphytoplankton, dinoflagellates, pico-nano-phytoplankton), two zooplankton
162 classes (micro- and meso-zooplankton), and exchanges at the water/sediment interface and inside the sediment
163 compartment.

164 2.3.2 MARS3D-1DV model sensitivity experiments

165 These three models (hydrodynamical, sediment and biogeochemical) are coupled online during simulations
166 and allow the nutrient and phytoplankton dynamics in both bays to be reproduced. The simulation for the Bay of
167 Brest does not include nutrient inputs from the sediment because it is considered to be negligible around the
168 COAST-HF-Iroise station.

169 Dissolved and particulate variables are defined in the water column and in the sediment. Initial values for both
170 bays are uniform over the initial vertical profile (Table 1) and are based on a 3D realistic coupled simulation during
171 the year 2015 the 15th of February extracted at the position of COAST-HF-Iroise for the Bay of Brest and at the
172 position of COAST-HF-Molit station for the Bay of Vilaine (Plus et al., 2021).

173 To evaluate the sensitivity of the biogeochemical dynamics to environmental conditions, sensitivity
174 experiments are then performed using the coupled MARS3D/BLOOM/MUSTANG 1DV model configuration. All
175 simulations are started at the end of winter (15th February) and run until the end of the year. The range of values
176 used in the sensitivity experiments are derived from the minimum and maximum observed *in situ* data. Each
177 parameter is tested with a constant value for the whole simulation.

178 Three parameters are individually explored in both bays:

- 179 - The air temperature in sensitivity experiments ranges from 4 to 14°C and is controlled by the intensity of
180 solar radiations. Air temperature represents the main controlling parameter of Sea Surface Temperature in
181 the 1DV model. This parameter drives the radiative fluxes in the model and then constrains the SST.
- 182 - Wind intensity effect on the IPGP is explored for values between 0 and 10 m s⁻¹. In the 1DV model, wind
183 is a source of vertical mixing in the simulation.
- 184 - The Cloud Coverage (CC) sensitivity experiments ranged in value between 0 and 100% CC. This
185 parameter is a driver of Photosynthetic Available Radiation (PAR) in the ocean. For the formulation of
186 radiative fluxes in the 1DV MARS3D model, 100% cloud coverage allows an inflow of 38% of the total
187 solar radiation in the water column. Each individual experiment is associated with a constant CC applied
188 to the seasonal solar radiation.

189 As the sediment plays a role on the light penetration and acts as an active source of nutrients mainly in the Bay
190 of Vilaine, the mud erosion rate (values between 2.10^{-5} and 2.10^{-7} kg m⁻² s⁻¹) is explored only in that bay (sand
191 erosion rate fixed to 0.0001 kg m⁻² s⁻¹). For the sensitivity experiments, it drives a mass of sediment eroded
192 and resuspended and a bottom input of nutrients in the water column.

193 A second set of experiments is conducted combining the effect of these environmental parameters in order to
194 explore the cumulative or opposite effect on the IPGP. The upper and lower bounds of the range of
195 environmental parameters are taken into account. Experiments are detailed in Table 5.

200 2.4 Data processing

201 2.4.1 Chl-*a* fluorescence data

202 To analyze high-frequency time series of *in situ* Chl-*a* fluorescence, the Quenching effect (Lehmuskero
203 et al., 2018), a decrease in fluorescence in the presence of light (Fig. 2), is removed by analyzing only night-time
204 data as reported in Carberry et al. (2019). Chl-*a* fluorescence data are studied on a daily basis, i.e. averaged from
205 10 pm to 5 am. Years with less than 75% of valid data (i.e. 2005, 2006, 2008, 2009 and 2018 in the Bay of Brest)
206 are not considered.

209 **2.4.2 Detection of the IPGP**

210
211 We apply methods from the literature (Kromkamp *et al.*, 2010; Philippart *et al.*, 2010; Brody *et al.*, 2013)
212 to calculate annual IPGP values (not shown). Kromkamp *et al.* (2010) set an arbitrary beginning and end of the
213 phytoplankton growing period at 20% and 80% of the cumulative Chl-a fluorescence measured from January 1st
214 to December 31st. Similarly, Brody *et al.* (2013) consider a threshold of 5% above the yearly median chlorophyll.
215 Philippart *et al.* (2010) considers the beginning of the growing period as the maximum daily difference in Chl-a
216 fluorescence.

217 Because we obtain unrealistic IPGP dates from our dataset when using the methods proposed by Kromkamp *et al.*
218 (2010 - i.e. too late IPGP; Brody *et al.* (2013 - i.e. too early IPGP) and Philippart *et al.* (2010 - i.e. multiple
219 IPGP), we propose an alternative detection method based on discontinuities of the Chl-a fluorescence signal (Fig.
220 3): daily FFU slopes are calculated based on a linear regression over a +/-2 day window for each day, from 1st
221 January to 31st December, and each year. The IPGP date is identified when the slope exceeds a threshold value,
222 defined as the median of the daily slopes, for the first time in the year for at least 20 days. The end of the
223 phytoplankton growing period is determined when the slope stabilizes below the threshold for at least 20 days for
224 the last time in the year. The cumulative Chl-a fluorescence corresponds to the duration of the growing period.

225 **2.4.3 Pattern of the phytoplankton growing period**

226
227 The k-means method (Hartigan and Wong, 1979) is used to characterize the annual patterns of the
228 phytoplankton growing period.

229 We exclude the year 2013 from the analysis of the Bay of Vilaine because of a large number of missing
230 data. When the interval over which consecutive data are missing is no longer than one week, we perform a linear
231 interpolation to replace the missing data. A 5-day running average is applied to the Chl-a fluorescence signal and
232 the data are then normalized by the maximum value. We analyze Chl-a fluorescence every year for 150 days after
233 the IPGP.

234 Time series from both bays are merged before application of the k-means and the number of clusters (or
235 centroids) is set at 2 to distinguish the dominant patterns of the phytoplankton growth period at both sites. The use
236 of a larger number of clusters is investigated and does not produce a pattern representing a large number of
237 observed growing periods.

238 **2.4.4 Detection of extreme events**

239
240 The peak over threshold method (see Oliver *et al.*, 2018 and Poppeschi *et al.*, 2021 for further details) is
241 used to detect hydro-meteorological extreme events such as cold waves, flood events and wind bursts. An event is
242 considered as extreme if values are higher than a given statistical threshold for at least 3 consecutive days. In the
243 present study, the 90-percentile threshold is selected to detect floods and wind bursts and the 10-percentile to
244 detect cold waves. Seasonal anomalies are calculated over at least 20 years, by subtracting raw data from the winter
245 average value (cold spells) or from the spring average value (wind bursts and floods).

246 **3. Results**

247 **3.1 Characterization of the phytoplankton growing period**

248
249 The high-frequency Chl-a fluorescence time series at both sites show an intense seasonal cycle with low
250 values from November to February and high values from March to October (Fig. 4). Focusing on the period from
251 2010 to 2019 in the Bay of Brest, the minimum Chl-a fluorescence is observed during the years 2012 and 2013
252 and does not exceed 7 FFU. In contrast, years such as 2010, 2014, 2015 or 2019 show Chl-a fluorescence values
253 above 15 FFU but can be up to 20 FFU. In the Bay of Vilaine, a similar seasonal pattern is observed with higher
254 values reaching 50 FFU in 2013. Small (< 20 FFU) and high (> 35 FFU) Chl-a fluorescence amplitude are observed
255 occasionally (in 2014 and 2017 and in 2013 and 2016, respectively). The Chl-a fluorescence is higher, almost
256 double, in the Bay of Vilaine compared to the Bay of Brest with a mean cumulative Chl-a fluorescence around
257 580 FFU and 360 FFU, respectively (Table 2). The high phytoplankton biomass of the Bay of Vilaine is
258 corroborated by the concentrations measured by low-frequency observation programs (SOMLIT and REPHY).

260 The phytoplankton growing period ranges from approximately March 10th to September 30th in both regions
261 (Table 2). The average duration of the phytoplankton growing period is 179 days in the Bay of Vilaine and 200
262 days in the Bay of Brest (Table 2). The phytoplankton growing period is characterized by successive blooms,
263 whose number and intensity are variable from year to year (Fig. 4).

264
265 The main patterns of the phytoplankton growing period are identified by the two clusters (Fig. 5). Cluster 0
266 includes the phytoplankton growing period with two successive marked blooms in early spring and in summer,
267 the intensity of the second bloom being highly variable. Cluster 1 is characterized by a plateau during the two first
268 months of the phytoplankton growing period. Most of the patterns of the Bay of Vilaine are in cluster 0 while those
269 of the Bay of Brest are in cluster 1 (Table 3). The years that stand out in the Bay of Brest (2002, 2010, 2014)
270 correspond to years with the highest cumulative *Chl-a* fluorescence (≥ 450 FFU). The atypical years in the Bay
271 of Vilaine (2011, 2017 and 2019) show the lowest cumulative *Chl-a* fluorescence (≤ 450 FFU).

272 **3.2 Variability of the Initiation of the Phytoplankton Growing Period (IPGP)**

273
274 Calculations performed to determine the IPGP for high- and low-frequency data yield comparable results (Fig.
275 6). The mean differences between the IPGP calculated with the high and low-frequency data are 5 and 8 days for
276 the Bay of Brest and the Bay of Vilaine, respectively. A difference of only 4 and 6 days between the model
277 simulations (reference year = 2015) and the high-frequency *in situ* data is observed in the Bay of Brest and the
278 Bay of Vilaine, respectively.

279
280 A decadal variability of the IPGP is recorded from mid-February to mid-April in both ecosystems (day 50 to
281 day 102 in the Bay of Brest and day 53 to day 93 in the Bay of Vilaine; Fig. 6). In the Bay of Brest, early IPGPs
282 (day < 53) are observed in 2010 and 2013 whereas late IPGP (day > 93) are observed in 2001, 2017 and 2019. In
283 the Bay of Vilaine, the earliest IPGP is detected in 2012 (day 53) and the latest in 2019 (day 93).

284
285 The variability of IPGP in the Bay of Brest shows two linear trends (Fig. 6a), with a decrease of 52 days from
286 2001 to 2010 (observed in both high- and low-frequency datasets), followed by an increase (+48 days) from 2011
287 to 2019, a decline also observed in the Bay of Vilaine (Fig. 6b). Over the period 2011-2019, the IPGP is shifted
288 towards a later date by +3.5 days per year in the Bay of Vilaine and +3.7 days per year in the Bay of Brest.

289 **3.3 Analysis of environmental conditions driving the IPGP**

290 **3.3.1 Impact of environmental conditions on the IPGP**

291
292 We next quantify the influence of environmental drivers on the date of IPGP (Fig. 7). These drivers
293 represent the major limiting factors of the phytoplankton growth and comprise input of nutrients (river flow), PAR
294 (incident light), Sea Surface Temperature - SST - (air temperature, incident light) and turbidity in the water column
295 (river flow, wind intensity).

296
297 The median values of the environmental drivers observed at the date of each annual IPGP are very close
298 in both bays (Table 4) : temperate SST (10 °C), weak wind (3 m.s⁻¹), a medium PAR (1360 W m⁻²), a low turbidity
299 (7 NTU) and a weak tidal amplitude (semi-amplitude of 1.6 m in the Bay of Brest and 0.9 m in the Bay of Vilaine).
300 The IPGP occurs mainly during neap tides, at 68 % and 77 % in the Bay of Brest and in the Bay of Vilaine,
301 respectively. The river flow is low during the IPGP with a runoff of 46 m³ s⁻¹ for the Aulne, 96 m³ s⁻¹ for the
302 Vilaine and 1196 m³ s⁻¹ for the Loire.

303
304 To assess how environmental drivers may impact (i.e. advance or delay) the IPGP, we focus on the 15
305 days before the mean day of the IPGP (day 68) and of each annual IPGP. The considered 15 days length is related
306 to the typical water residence time in both bays (Frere *et al.*, 2017; Poppeschi *et al.*, 2021 for the Bay of Brest -
307 Chapelle *et al.*, 1994; Ratmaya *et al.*, 2019 for the Bay of Vilaine).

308 The earliest IPGP dates (IPGP $<$ day 55) are associated with earlier occurrence of favorable
309 environmental conditions than the other years. Earliest IPGP which occurred before day 55 are in 2010 and 2013
310 in the Bay of Brest and in 2012 in the Bay of Vilaine (Fig. S1f, 7c - S2a). Early IPGP between day 55 to 60, also
311 associated with favorable environmental conditions, are found in 2002 and 2016 in the Bay of Brest (Fig. S1b,
312 S1j).

313 In the same way, the latest IPGP dates (IPGP > day 90) are associated with unfavorable environmental
314 conditions until the date of the IPGP. Latest IPGP occurring after day 90 are observed in 2001, 2003, 2017 and
315 2019 in the Bay of Brest and in 2019 in the Bay of Vilaine (Fig. S1a,c,k,l - S2g). For example, the delay detected
316 in 2017 in both bays is due to strong wind and a lack of PAR until the day of IPGP (Fig. S1k - Fig. S2e). Late
317 IPGP between day 70 to 90 are recorded in 2004, 2007 and 2012 in the Bay of Brest, and in 2014, 2017 and 2018
318 in the Bay of Vilaine (Fig. S1d,e,g, 7d - S2e,f).

319
320 The interannual variability of the date of the IPGP is therefore not controlled by a unique environmental
321 driver. When the values of the environmental drivers responsible for the IPGP (Table 4) are compared to the mean
322 values of the environmental drivers over a period of 30 days around the IPGP (Table S1), threshold values are
323 observed in both bays: river flow is lower than usual (between 10 and 30 $\text{m}^3 \text{s}^{-1}$), temperature is close to the
324 expected value (10°C), wind is weak (0.5 to 1.5 m s^{-1}), PAR is stronger ($>300 \text{ W m}^{-2}$), and turbidity is low (about
325 1.5 NTU). IPGP starts around day 68 (± 3 days) on average (Fig. 7a,b).

326 3.3.2 Modeling the importance of the environmental drivers

327
328 The relative contribution of each environmental driver on the IPGP is determined by MARS-1DV simulations
329 starting on February 1st (Fig. 8). Environmental drivers tested in the model are controlling:

- 330 - the sea temperature - explored in the model by perturbing air temperature (as a controlling driver in the
331 model of the Sea Surface Temperature evolution),
- 332 - the level of water turbulence - through wind intensity,
- 333 - the available light - controlled by Cloud Coverage (CC, as a sea surface PAR proxy) and turbidity (erosion
334 rate as a proxy) limiting light penetration in the water column.

335 Model results show that early IPGP are associated with air temperature higher than 9 °C (resulting in a SST higher
336 than 8 °C), low wind intensity, weak CC and low turbidity. Environmental drivers responsible for early or late
337 IPGP are similar in both bays. Air temperature is the main driver with a potential deviation from the mean IPGP
338 of 25 days in the Bay of Brest and 40 days in the Bay of Vilaine (Fig. 8). Wind, CC and turbidity have a lower
339 impact on the IPGP (around 6 days in the Bay of Brest and 13 days in the Bay of Vilaine). In the Bay of Vilaine,
340 the environmental drivers can simulate later IPGP than in the Bay of Brest.

341
342 In the Bay of Brest (Fig. 8a), only the air temperature variations have a real impact on the IPGP. If the air
343 temperature is low (< 8°C), the IPGP is not triggered before day 74 (Table 5, Exp 1). If the air temperature is high
344 (> 13°C), the IPGP can start on day 49 (Table 5, Exp 2).

345 In the Bay of Vilaine, the air temperature and the erosion rate are the two main drivers impacting the IPGP
346 (Fig. 8b). Similarly to the Bay of Brest, if the air temperature is low (< 6°C), the IPGP is late and appears only
347 after day 80 (Table 5, Exp 1). If temperature is equal or above 13°C, the IPGP is early and appears on day 45
348 (Table 5, Exp 2). If the erosion rate is low ($2.10^{-7} \text{ kg m}^{-2} \text{s}^{-1}$), then the IPGP takes place on day 76 (Table 5, Exp
349 7). If the erosion rate is high ($2.10^{-5} \text{ kg m}^{-2} \text{s}^{-1}$), the IPGP occurs late after day 87 (Table 5, Exp 8).

350 The variations of wind and CC induce weaker shifts in the date of the IPGP, i.e. about one week at the most
351 (Table 5, Exp 3,4,5,6). However, wind and CC can still explain variations of IPGP. For example, early IPGPs, in
352 2010 in the Bay of Brest and in 2012 in the Bay of Vilaine, due to low wind conditions (around 2 m s^{-1} , Fig. S2a
353 - S1f) are observed in *in situ* measurements and also confirmed by the model (Fig. 8b).

354
355 The combined effect of the environmental factors can also be explored from the MARS-1DV model
356 simulations (Fig. 9). The modeling conditions (hereafter called “Exp”) are detailed in Table 5 and compared to the
357 mean IPGP date (day 68).

358 The simulations confirm the observations, late IPGP correspond to the most extreme unfavorable combined
359 environmental values (temperature of 4°C, wind intensity of 10 m s^{-1} , CC of 100% and erosion rate of 2.10^{-5} kg
360 $\text{m}^{-2} \text{s}^{-1}$ - Exp A). In the Bay of Brest and the Bay of Vilaine, IPGP occurs 9 days (i.e. twice as late as for any
361 individual driver simulation) and 64 days later respectively. Late IPGP can also be linked to the combined effect
362 of only two factors such as: “temperature and wind” and “temperature and CC” with a delay of 5 and around 22
363 days respectively (Exp B,C). In contrast, no delay is observed for the combination “wind and CC” (Exp D) in both
364 bays.

365 Same as previously, early IPGP are found in the simulations as in the observations when conditions correspond to
366 a high temperature (14°C), no wind intensity and CC, and a low erosion rate ($2.10^{-7} \text{ kg m}^{-2} \text{s}^{-1}$) - Exp K. All the
367 combined scenarios permit the occurrence of an earlier IPGP (by at least 5 additional days) compared to
368 experiments that consider a single modified parameter.

370 This analysis enables environmental parameters to be classified with respect to their impact on the IPGP.
371 In both bays, the temperature appears to be the key factor driving the IPGP. By combining the environmental
372 drivers, the IPGP can occur even later or earlier than with a single forcing. In both bays, the combination of wind
373 and CC has no impact on the IPGP, which occurs near the median day (Exp D and N). The extreme couplings of
374 Exp A,E,F,G,J delay the date of IPGP later than detected in the observations for the Bay of Vilaine. All simulations
375 show a higher impact on the date of IPGP in the Bay of Vilaine than in the Bay of Brest (Fig. 9, Table 5).

376 **3.4 Impact of extreme hydro-meteorological events on the IPGP**

377 **3.4.1 Cold spells**

378 The impact of cold spells on the IPGP is simulated with the MARS-1DV model based on two criteria: (i)
379 the period of occurrence of the event, set in mid- or end February, (ii) the duration and intensity of the cold spell,
380 which can be either short and weak (8 days, 7°C) or long and intense (20 days, 5°C) (Fig. 10).

381 In both bays, when the cold spell appears in mid-February, the IPGP is not impacted. However, it is
382 delayed by about 15 days when occurring at the end of February. The duration of the cold spell, when longer than
383 15 days, also has an impact on the IPGP, with a delay of 13 and 12 days in the Bay of Brest and in the Bay of
384 Vilaine, respectively.

385 Eight cold spells are detected in February in both bays between 2001 and 2019. In 2011, both sites are
386 impacted simultaneously with cold spells. Long cold spells (30 days) are observed in 2009 and 2018, leading to
387 an anomaly of more than -1.9°C.

388 The cold spell observed in 2018 in the Bay of Vilaine may explain the later IPGP. There is no change in
389 the IPGP in 2011 and 2013, despite the cold spell, the period of occurrence being too early during winter 2011,
390 and the duration too short in 2013 (only 10 days).

391 In the Bay of Brest, the cold spells in 2003 and 2004 may explain the delay of the IPGP (respectively
392 days 93 and 85). The presence of long and intense cold spells in 2010 and 2011 do not shift the IPGP (days 50 and
393 67) because they occur too early (before day 20).

394 **3.4.2 Wind bursts**

395 Based on our model simulations, the wind bursts that occur during at least three continuous days have no
396 impact on the IPGP in both bays, whatever the duration, the period and the intensity (+/- 1 day). In the Bay of
397 Vilaine, only one wind event is detected in 2018 (3 days long and 6 m.s⁻¹). In the Bay of Brest, several events are
398 detected, but no significant impact is observed on the IPGP.

400 **3.4.3 Flood events**

401 River floods can delay the IPGP by resuspending sediment in the water column and therefore limiting
402 light penetration in the water column. Inputs of nutrients have no impact during the late winter period because
403 nutrient concentrations are maximal, with no limitation on phytoplankton growth. Flood events are analyzed with
404 observation data collected in the month prior to the IPGP date because the 1DV modeling approach does not allow
405 the sensitivity to hydrological events to be simulated (*i.e.* it is necessary to simulate horizontal advection
406 processes).

407 In the Bay of Brest, the impact of flood events depends on their duration and intensity: when the flood
408 exceeds 15 days, a delay in the IPGP is detected. Shorter and more intense floods (> 300 m³ s⁻¹) do not impact the
409 IPGP.

410 In the Bay of Vilaine, only two flood events are observed close to the IPGP date in 2014 and 2015. The
411 2015 flood event, which is 10 days longer and more intense (> 100 m³ s⁻¹) than the 2014 one, delays the IPGP date
412 by 10 days.

4 Discussion

418 4.1 Comparison of the phytoplankton growing period in both bays

419
 420 Despite their contrasting hydrodynamics (e.g. Petton *et al.*, 2020; Poppeschi *et al.*, 2021; Lazure and Jegou, 1998; Ratmaya *et al.*, 2019; Menesguen *et al.*, 2019), the median dates of the start and the end of the phytoplankton growing period are the same in the Bay of Brest and in the Bay of Vilaine whether they are calculated from high- and low- frequency datasets and from model simulations. The phytoplankton growing period occurs from March to September and lasts about 190 days in both bays. This concordance is related to a similar seasonality of the environmental drivers.

421
 422
 423
 424
 425 The observed cumulative fluorescence is almost double in the Bay of Vilaine compared with the Bay of Brest. This difference in the amount of chlorophyll produced in surface waters from both bays is also recorded by the low-frequency observation programs and by satellite observations (Menesguen *et al.*, 2019). It can be explained by the difference of the hydrodynamics and the influence of different watersheds. The Bay of Brest is a semi-enclosed bay with a macro-tidal regime influenced by two local rivers (Aulne and Elorn) whereas the Bay of Vilaine has a weaker tidal regime, is open on the continental shelf and is widely influenced by a large river (Loire river).

426
 427 Two different patterns of the phytoplankton growing period are identified by the k-means classification
 428 in both bays. The flattened, weak and long bloom highlighted in the Bay of Brest can be explained by assuming
 429 that nutrients are not limiting the phytoplankton growth during spring. The maintenance of the diatom succession
 430 throughout spring since the 1980's (Quéguiner 1982; Del Amo *et al.*, 1997) can be explained by the combination
 431 of increasing N and P loads, intense Si recycling and a macrotidal regime (Ragueneau *et al.*, 2019). The
 432 phytoplankton growing period in the bay of Vilaine is characterized by several successive peaks including two
 433 main ones. Nutrients here drive the seasonal evolution of the phytoplankton growing period through periods of
 434 nutrient-limited conditions. These fluctuations are governed by phosphorus and nitrate loads from Vilaine and
 435 Loire rivers (Ratmaya *et al.*, 2019), but probably also by the stoichiometry of recycled elements in the water and
 436 at the water-sediment interface (Ratmaya *et al.*, 2022). **However, at the beginning of the phytoplankton growing**
 437 **period (IPGP), the system is not nutrient limited in terms of nitrate, phosphorus and silicates.**

444

445

446 4.2 Identification of the environmental conditions supporting the IPGP

447

448 The method that we developed to detect IPGP on both high-frequency and low-frequency *in situ*
 449 observations shows comparable results and detects similar initiation dates for some years, while a time lag between
 450 high- and low-frequency observations can be observed for other years. This difference is mainly explained by the
 451 difference in the sampling frequency. The late deployment of the buoy in the Bay of Vilaine (i.e. not deployed
 452 until mid-February before 2018) can also explain some differences between both sites. High-frequency data
 453 provide a more accurate detection of the day of the IPGP, while an uncertainty of about ± 7 days is observed with
 454 low-frequency observations. This comparison between high- and low-frequency based IPGP detection highlights
 455 the sensitivity of sampling strategy in the observation of phytoplankton growing periods (Bouman *et al.*, 2005;
 456 Serre-Fredj *et al.*, 2021) related to the response of the ecosystem within a few hours after an environmental change
 457 (Lefort and Gasol, 2014; Thyssen *et al.*, 2008).

458

459

460 The modeled IPGP, based on the year 2015, is coherent with high-frequency observations (around 5 days
 461 of difference between modeled and observed IPGP). Considering the idealized framework for modeling
 462 computations (1DV model instead of a realistic 3D model configuration), the agreement between observations and
 463 simulations validates the 1DV approach to explore IPGP dynamics. With the 1DV configuration, the vertical
 464 dynamics in the water column, coupled with biogeochemistry and sediment dynamics are well reproduced.
 465 Atmospheric forcings and interactions with the bottom layer are the main environmental drivers. The full range of
 466 impacts related to the horizontal advection (e.g. in considered regions, rivers advected plumes can change the
 467 hydrodynamics and the biogeochemical contents) are not evaluated, however. In the Bay of Brest and in the Bay
 468 of Vilaine, such advected sources exist (e.g. Poppeschi *et al.*, 2021; Lazure and Jegou, 1998) but inputs from rivers
 469 are not main drivers of the IPGP in nutrient-rich environments. Nutrient loads advected by rivers may impact the
 470 phytoplankton community later during the growing period rather than at IPGP (e.g. Ratmaya *et al.*, 2019).

471

472

473

474

475

476 We characterize similar environmental conditions in both bays as the IPGP is mainly driven and limited
 477 by similar **local** conditions. The ideal temperature ($> 10^\circ\text{C}$) and PAR (1300 W m^{-2}) for the IPGP are in agreement
 478 with those from previous studies conducted in similar coastal ecosystems (e.g. Glé *et al.*, 2007; Townsend *et al.*,
 479 1994; Trombetta *et al.*, 2019). Neap tidal conditions, weak wind (lower than 3 m s^{-1}) and weak river flow can also
 480 play a positive role to observe earlier IPGP according to the previous study of Ragueneau *et al.*, 1996.

476 As also shown in the German Bight (Tian *et al.*, 2011), wind intensity is a driver of turbidity in the water column
477 which inhibits phytoplankton growth. The impact of wind direction on the IPGP is estimated to be negligible.
478 Local changes in those features (temperature, incident radiation, tidal conditions, wind conditions and river flow)
479 induce differences in detected IPGP. **Indeed, in this coastal temperate ecosystem, we observe that the beginning**
480 **of the growing period is limited by light (controlled by incident radiation, turbidity at this season), and water**
481 **temperature. The IPGP also occurs during low vertical mixing conditions.**

482
483 The comparison of the individual importance of each environmental driver shows that temperature and
484 light penetration are the key environmental drivers in both bays. Similarly in the North Sea, Wiltshire *et al.* (2015)
485 highlight the importance of the light availability in the timing and intensity of the spring bloom. **Similarly**, too
486 high turbidity (due to sediment resuspension) can also limit the production and delay IPGP in the bay of Vilaine.
487 Similar limitations are observed in the German Bight (Tian *et al.*, 2009) or along the UK South Coast (Iriarte and
488 Purdie, 2004). The combined effect of surface incident radiation and turbidity can amplify the delay of the IPGP.
489 However, with the existence of minimum mandatory conditions, an earlier IPGP can not be observed or modeled,
490 except if thresholds are reached earlier (e.g. warmer temperature earlier during the year).

491 492 4.3 Interannual evolutions of the IPGP

493
494 The IPGP in these two bays shows a strong interannual variability with initiation dates varying from late
495 winter to spring. A mean difference of 50 days between the earliest and latest IPGP dates is observed. Each year
496 has a different date of IPGP related to different environmental conditions. However, the beginning of the
497 phytoplankton growing period is always dominated in both bays by the same centric diatoms, genera *Chaetoceros*
498 and *Skeletonema*, whose abundance varies from year to year depending on climatic conditions (REPHY, 2021).

499 The earliest IPGP are observed and related to favorable environmental conditions early in the year. For
500 example, the IPGP can occur before day 50, associated with exceptionally weak wind and river flow in addition
501 to a sufficient PAR and nearly-optimal temperature of around 10°C (e.g. 2010 in the Bay of Brest and 2012 in the
502 Bay of Vilaine). But if the environmental conditions are not favorable (e.g. 2017 and 2019 in both bays), the IPGP
503 is delayed. This can be due to a strong wind during several days (not a single wind burst) and a weak PAR and
504 sometimes also because of turbidity events limiting the light penetration.

505 However, the reason to have early or late IPGP is not always the same. Late IPGP can be due to low
506 temperature conditions rather than a strong wind or a lack of PAR as seen previously (e.g. 2003 in Bay of Brest).
507 Also, the IPGP can be different from one bay to another in the same year, almost half of the years studied from
508 2012 to 2016. For example, the 2012 IPGP is early in the Bay of Vilaine (day 53) while it is late in the Bay of
509 Brest (day 80), related to strong wind activity and low PAR. This difference between the two bays indicates a
510 local, not regional, effect of the processes affecting the IPGP.

511
512 The analysis of the IPGP over the last two decades has highlighted its evolution through two trends, one
513 per decade. The IPGP occurs earlier each year until 2010 when the trend is reversed. At a larger scale, this change
514 in trends is not directly observed for the same years. For example, using hourly data, Hunter-Cervera *et al.* (2016)
515 show earlier blooms of picophytoplankton on the New England Shelf during 2003-2012 due to warming spring
516 periods, and later blooms in 2013-2015 for cooler spring temperatures. The similarity between these observations
517 and those found here in our study on the other side of the Atlantic basin for a slightly later breaking year (2012
518 instead of 2010) suggests a large-scale impact of the warming waters in spring. On the eastern part of the Atlantic,
519 we also know that 2010 was an atypical year, with an important accumulation of phytoplankton biomass as
520 observed by Bedford *et al.* (2020) on the North-West European shelf. However, limited indicators do not allow
521 conclusions to be drawn regarding the impact of large-scale forcings on observed shifts in phytoplankton blooms.

522
523 As the climate warms, earlier phytoplankton blooms are expected (Friedland *et al.*, 2018) but not later
524 IPGP as observed in our study regions. However, the mechanisms that trigger blooms in coastal ecosystems -
525 especially eutrophic ones - are not similar to the processes that influence blooms in the open ocean. For example,
526 by investigating long-term (1975-2005) daily data, Wiltshire *et al.* (2008) observe later phytoplankton blooms in
527 the German bight, but with no link to global warming. Henson *et al.* (2018) model a bloom shift of 5 days per
528 decade from 2006 to 2025, with later blooms. A possible explanation may involve the lower spring sea surface
529 temperatures, as observed in recent years (Hunter-Cervera *et al.* 2016), which could cause a delay of the IPGP.
530 We do not detect significant trends in environmental conditions over the last 20 years at either site, and therefore
531 do not establish direct links with the trends observed in the IPGP timing. In the southern California Bight, similar
532 changes in IPGP are observed from 1983 to 2000, but no link with environmental drivers has been identified (Kim
533 *et al.*, 2009).

534 535 4.4 Extreme events

536
537
538
539
540
541

We show that a cold spell is likely to delay the IPGP if it occurs at the end of winter (after 20th February) or/and if the cold spell lasts long enough (> 15 days). This is in accordance with the study of Gomez and Souissi (2008) in the English Channel where cold spells can affect the date of IPGP by increasing the water column mixing. In both bays, the drop in temperature related to the cold spell prevents the IPGP. Cold spells may also drive local patterns by influencing the phytoplankton communities (Gomez and Souissi, 2008; Schlegel *et al.*, 2021).

542 Flood events have an influence on the phytoplankton biomass when they occur in spring due to the supply
543 of nutrients. When they occur in late winter, nutrients are already at their maximum. The impact of floods on IPGP
544 is consequent only if they are at least 15 days long. This scheme is also observed by Saeck *et al.* (2013) along a
545 river-estuary-bay continuum and explained by a shortened water residence time and a limited light due to flood-
546 induced turbidity in the coastal zone.

547 No relationship is observed between wind events and IPGP in both bays because they are weakly stratified
548 contrary to open seas (*i.e.* Black Sea, Mikaelyan *et al.*, 2017). In coastal stratified regions (e.g. under the influence
549 of river plumes), strong wind and tidal mixing can enhance the mixing and break down stratification thus
550 distributing phytoplankton (Joordens *et al.*, 2021). During the IPGP, except during floods, both regions are weakly
551 stratified and are then less sensitive to combined wind/tidal short events.

552 5 Conclusions

553
554
555
556
557
558
559
560
561
562
563

This study provides a new understanding of the IPGP dynamics in coastal temperate areas by using both high and low-frequency *in situ* data, in combination with simulations from a 1DV model. Strong similarities are found in both bays. An important interannual variability of the IPGP is observed, with a trend towards a later IPGP over the last decade (2010-2020). We quantify the importance of environmental conditions on the IPGP. When we compare observed IPGP with favorable environmental conditions and following sensitivity experiments with the 1DV model, water temperature and turbidity (limiting light penetration in the water column) appear as the main drivers explaining interannual IPGP variability. The IPGP is a complex mechanism, usually triggered by more than one environmental parameter. The analysis of the influence of extreme events reveals that cold spells and floods have a strong impact by delaying the IPGP when episodes are long enough and occur after winter. No effect of wind bursts is detected.

564
565
566
567
568
569
570
571
572
573
574

While this study shows comparable IPGP dynamics when based on 1DV model simulations or *in situ* observations, we will next investigate the effect of a fully realistic hydrodynamics (including horizontal and vertical advections; mixing processes; remote sources of nutrients from rivers) on phytoplankton dynamics using a 3D model. We will focus on exploring the variability of phytoplankton communities during IPGP to assess whether community change is occurring, as observed in other studies and for other ecosystems (Ianson *et al.*, 2001; Edwards and Richardson, 2004; Chivers *et al.*, 2020). When interannual evolutions in the phytoplankton growth are explored, the detection and the understanding of harmful algal bloom dynamics can also be addressed based on similar approaches. Further studies will be dedicated to the simulation of the coastal ecosystem in the future based on numerical simulation based on climate scenarios. The investigation of other contrasting coastal environments will allow us to better understand and anticipate the expected impact of global change on coastal phytoplankton dynamics.

575 Author contributions

576
577
578
579

CP, GC, AD, RV, PR-M and EGo conceptualized the study. PR-M, EGr and MR collected data. MP and GC developed the model configuration. CP, GC, AD and RV drafted the first versions of the paper. CP carried out all the analyses and wrote the final version of the paper. All authors contributed to the discussions and revisions of the study.

580 Acknowledgements

581
582
583
584
585

We would like to acknowledge COAST-HF (<http://www.coast-hf.fr>), SOMLIT (<http://sommelit.epoc.u-bordeaux1.fr>) and REPHY (<https://doi.org/10.17882/47248>) national observing networks, for providing data flux readily available. COAST-HF and SOMLIT are components of the National Research Infrastructure ILICO. We would like to thank the Shom for tidal data and also Météo-France for wind and solar flux products. We also thank Dr Claire Labry for fruitful discussions and Dr Sally Close for her proofreading.

586 **Financial support**

587 This study is part of the State-Region Plan Contract ROEC supported in part by the European Regional
588 Development Funds and the COXTCLIM project funded by the Loire-Brittany Water Agency, the Brittany region
589 and Ifremer.

590 **References**

591
592 Aminot, A., and Kerouel, R.: Hydrologie des écosystèmes marins. Paramètres et analyses, Editions de l'Ifremer,
593 336 p., ISBN 2-84433-133-5, 2004.

594
595 Banse, K.: Grazing and zooplankton production as key controls of phytoplankton production in the open
596 ocean, *Oceanography*, 7(1), 13-20, <https://www.jstor.org/stable/43925524>, 1994.

597
598 Barbosa, A., Domingues, R., and Galvão., H.: Environmental forcing of phytoplankton in a Mediterranean estuary
599 (Guadiana estuary, south-western Iberia): A decadal study of anthropogenic and climatic influences, *Estuaries and
Coasts*, doi:10.1007/s12237-009-9200-x, 2010.

600
601 Bedford, J., Ostle, C., Johns, D. G., Atkinson, A., Best, M., Bresnan, E., ... and McQuatters-Gollop, A.: Lifeform
602 indicators reveal large-scale shifts in plankton across the North-West European shelf, *Global Change Biology*,
26(6), 3482-3497, doi:10.1111/gcb.15066, 2020.

603
604 Behrenfeld, M. J.: Abandoning Sverdrup's critical depth hypothesis on phytoplankton blooms, *Ecology*, 91(4),
977-989, doi:10.1890/09-1207, 2010.

605
606 Behrenfeld, M. J., Doney, S. C., Lima, I., Boss, E. S., and Siegel, D. A.: Annual cycles of ecological disturbance
607 and recovery underlying the subarctic Atlantic spring plankton bloom, *Global biogeochemical cycles*, 27(2), 526-
608 540, doi:10.1002/gbc.20050, 2013.

609
610 Beucher, C., Treguer, P., Corvaisier, R., Hapette, A. M., and Elskens, M.: Production and dissolution of biosilica,
611 and changing microphytoplankton dominance in the Bay of Brest (France), *Marine Ecology Progress Series*, 267,
57-69, doi:10.3354/meps267057, 2004.

613
614 Boss, E., and Behrenfeld, M.: In situ evaluation of the initiation of the North Atlantic phytoplankton bloom,
615 *Geophysical Research Letters*, 37(18), doi:10.1029/2010GL044174, 2010.

616
617 Bouman, H., Platt, T., Sathyendranath, S., and Stuart, V.: Dependence of light-saturated photosynthesis on
618 temperature and community structure, *Deep Sea Research Part I: Oceanographic Research Papers*, 52(7), 1284-
619 1299, doi:10.1016/j.dsr.2005.01.008, 2005.

620
621 Brody, S. R., Lozier, M. S., and Dunne, J. P.: A comparison of methods to determine phytoplankton bloom
622 initiation, *Journal of Geophysical Research, Oceans*, 118(5), 2345-2357, doi:10.1002/jgrc.20167, 2013.

623
624 Caracciolo, M., Beaugrand, G., Hélaouët, P., Gevaert, F., Edwards, M., Lizon, F., ... and Goberville, E.: Annual
625 phytoplankton succession results from niche-environment interaction, *Journal of Plankton Research*, 43(1), 85-
626 102, doi:10.1093/plankt/fbaa060, 2021.

627
628 Chapelle, A., Lazure, P., and Ménèsguen, A.: Modelling eutrophication events in a coastal ecosystem. Sensitivity
629 analysis, *Estuarine, Coastal and Shelf Science*, 39(6), 529-548, doi:10.1016/S0272-7714(06)80008-9, 1994.

630
631 Chivers, W. J., Edwards, M., and Hays, G. C.: Phenological shuffling of major marine phytoplankton groups over
632 the last six decades, *Diversity and Distributions*, 26(5), 536-548, doi:10.1111/ddi.13028, 2020.

633
634 Cloern, J. E.: Phytoplankton bloom dynamics in coastal ecosystems: a review with some general lessons from
635 sustained investigation of San Francisco Bay, California, *Reviews of Geophysics*, 34(2), 127-168,
636 doi:10.1029/96RG00986, 1996.

637

638 Cocquempot, L., Delacourt, C., Paillet, J., Riou, P., Aucan, J., Castelle, B., Charria, G., Claudet, J., Conan, P.,
639 Coppola, L., Hocdé, R., Planes, S., Raimbault, P., Savoie, N., Testut, L., and Vuillemin, R.: Coastal Ocean and
640 Nearshore Observation: A French Case Study, *Frontiers in Marine Science*, 6(324), 1-17,
641 doi:10.3389/fmars.2019.00324, 2019.

642

643 Cook, P. L., Holland, D. P., and Longmore, A. R.: Effect of a flood event on the dynamics of phytoplankton and
644 biogeochemistry in a large temperate Australian lagoon, *Limnology and Oceanography*, 55(3), 1123-1133,
645 doi:10.4319/lo.2010.55.3.1123, 2010.

646

647 Cugier, P., Billen, G., Guillaud, J. F., Garnier, J., and Ménesguen, A.: Modelling the eutrophication of the Seine
648 Bight (France) under historical, present and future riverine nutrient loading, *Journal of Hydrology*, 304(1-4), 381-
649 396, doi:10.1016/j.jhydrol.2004.07.049, 2005.

650

651 Del Amo, Y., Le Pape, O., Tréguer, P., Quéguiner, B., Ménesguen, A., and Aminot, A.: Impacts of high-nitrate
652 freshwater inputs on macrotidal ecosystems. I. Seasonal evolution of nutrient limitation for the diatom-dominated
653 phytoplankton of the Bay of Brest (France), *Marine Ecology Progress Series*, 161, 213-224, doi:10.5194/bg-16-
654 1361-2019, 1997.

655

656 Edwards, M., and Richardson, A. J.: Impact of climate change on marine pelagic phenology and trophic
657 mismatch, *Nature*, 430(7002), 881-884, doi:10.1038/nature02808, 2004.

658

659 Farcy, P., Durand, D., Charria, G., Painting, S.J., Tamminem, T., Collingridge, K., Grémare, A.J., Delauney, L.,
660 and Puillat, I.: Toward a European coastal observing network to provide better answers to science and to societal
661 challenges; the JERICO research infrastructure, *Frontiers in Marine Science*, 6, 1-13,
662 doi:10.3389/fmars.2019.00529, 2019.

663

664 Frère, L., Paul-Pont, I., Rinnert, E., Petton, S., Jaffré, J., Bihannic, I., Soudant, P., Lambert, C. and Huvet, A.:
665 Influence of environmental and anthropogenic factors on the composition, concentration and spatial distribution
666 of microplastics : a case study of the Bay of Brest (Brittany, France), *Environ. Pollut.*, 225, 211-222,
667 doi:10.1016/j.envpol.2017.03.023, 2017.

668

669 Friedland, K. D., Mouw, C. B., Asch, R. G., Ferreira, A. S. A., Henson, S., Hyde, K. J., ... and Brady, D. C.:
670 Phenology and time series trends of the dominant seasonal phytoplankton bloom across global scales, *Global
671 Ecology and Biogeography*, 27(5), 551-569, doi:10.1111/geb.12717, 2018.

672

673 Glé, C., Del Amo, Y., Bec, B., Sautour, B., Froidefond, J. M., Gohin, F., Maurer, D., Plus, M., Laborde, P., and
674 Chardy, P.: Typology of environmental conditions at the onset of winter phytoplankton blooms in a shallow
675 macrotidal coastal ecosystem, Arcachon Bay (France), *Journal of plankton research*, 29(11), 999-1014,
676 doi:10.1093/plankt/fbm074, 2007.

677

678 Gohin, F., Van der Zande, D., Tilstone, G., Eleveld, M. A., Lefebvre, A., Andrieux-Loyer, F., Blauw, A. N.,
679 Bryère, P., Devreker, D., Garnesson, P., Hernández Fariñas, T., Lamaury, Y., Lampert, L., Lavigne, H., Menet-
680 Nedelec, F., Pardo, S., and Saulquin, B.: Twenty years of satellite and in situ observations of surface chlorophyll-
681 a from the northern Bay of Biscay to the eastern English Channel. Is the water quality improving ? *Remote Sensing
682 of Environment*, 233(September), 111343, doi:10.1016/j.rse.2019.111343, 2019.

683

684 Gomez, F., and Souissi, S.: The impact of the 2003 heat wave and the 2005 cold wave on the phytoplankton in the
685 north-eastern English Channel, *Comptes Rendus Biologies*, 331(9), 678-685, doi:10.1016/j.crvi.2008.06.005,
686 2008.

687

688 Grasso F., Le Hir P., and Bassoullet P.: Numerical modelling of mixed-sediment consolidation, *Ocean Dynamics*,
688 65(4), 607- 616, doi:10.1007/s10236-015-0818-x, 2015.

689

690 Hartigan, J., and Wong, M.: Algorithm AS 136: A K-Means Clustering Algorithm. *Journal of the Royal Statistical
691 Society, Series C (Applied Statistics)*, 28:1, 100-108, doi:2346830, 1979.

692

693 Henson, S. A., Cole, H. S., Hopkins, J., Martin, A. P., and Yool, A.: Detection of climate change-driven trends in
phytoplankton phenology, *Global Change Biology*, 24(1), e101-e111, doi:10.1111/gcb.13886, 2018.

694
695 Huisman, J. E. F., van Oostveen, P., and Weissing, F. J.: Critical depth and critical turbulence: two different
696 mechanisms for the development of phytoplankton blooms, *Limnology and oceanography*, 44(7), 1781-1787,
697 doi.org/10.4319/lo.1999.44.7.1781, 1999.
698
699 Hunter-Cevera, K. R., Neubert, M. G., Olson, R. J., Solow, A. R., Shalapyonok, A., and Sosik, H. M.:
700 Physiological and ecological drivers of early spring blooms of a coastal phytoplankton, *Science*, 354(6310), 326-
701 329, doi:10.1126/science.aaf8536, 2016.
702
703 Husson, B., Hernández-Fariñas, T., Le Gendre, R., Schapira, M., and Chapelle, A.: Two decades of *Pseudo-*
704 *nitzschia* spp. blooms and king scallop (*Pecten maximus*) contamination by domoic acid along the French Atlantic
705 and English Channel coasts: Seasonal dynamics, spatial heterogeneity and interannual variability, *Harmful*
706 *Algae*, 51, 26-39, doi:10.1016/j.hal.2015.10.017, 2016.
707
708 Ianson, D., Pond, S., and Parsons, T.: The spring phytoplankton bloom in the coastal temperate ocean: growth
709 criteria and seeding from shallow embayments, *Journal of oceanography*, 57(6), 723-734,
710 doi.org/10.1023/A:1021288510407, 2001.
711
712 IPCC: Summary for Policymakers. In: *Climate Change 2021: The Physical Science Basis. Contribution of*
713 *Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Masson-
714 Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis,
715 M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu and B. Zhou
716 (eds.)], Cambridge University Press, In Press, 2021.
717
718 Iriarte, A., and Purdie, D. A.: Factors controlling the timing of major spring bloom events in an UK south coast
719 estuary, *Estuarine, Coastal and Shelf Science*, 61(4), 679-690, doi:10.1016/j.ecss.2004.08.002, 2004.
720
721 Joordens, J. C. A., Souza, A. J., & Visser, A.: The influence of tidal straining and wind on suspended matter and
722 phytoplankton distribution in the Rhine outflow region. *Continental Shelf Research*, 21(3), 301-325,
723 doi:10.1016/S0278-4343(00)00095-9, 2001.
724
725 Kromkamp, J. C., and Van Engeland, T.: Changes in phytoplankton biomass in the western Scheldt estuary during
726 the period 1978-2006, *Estuaries and Coasts*, 33(2), 270-285, doi:10.1007/s12237-009-9215-3, 2010.
727
728 Kim, H. J., Miller, A. J., McGowan, J., and Carter, M. L.: Coastal phytoplankton blooms in the Southern California
729 Bight, *Progress in Oceanography*, 82(2), 137-147, doi:10.1016/j.pocean.2009.05.002, 2009.
730
731 Lazure, P., and Dumas, F.: An external-internal mode coupling for a 3D hydrodynamical model for applications
732 at regional scale (MARS), *Advances in water resources*, 31(2), 233-250, doi:10.1016/j.advwatres.2007.06.010,
733 2008.
734
735 Lazure, P., and Jégou, A. M.: 3D modelling of seasonal evolution of Loire and Gironde plumes on Biscay Bay
736 continental shelf, *Oceanologica acta*, 21(2), 165-177, doi:10.1016/S0399-1784(98)80006-6, 1998.
737
738 Lefort, T., and Gasol, J. M.: Short-time scale coupling of picoplankton community structure and single-cell
739 heterotrophic activity in winter in coastal NW Mediterranean Sea waters, *Journal of plankton research*, 36(1),
243-258, doi:10.1093/plankt/fbt073, 2014.
740
741 Le Hir P., Cayocca F., and Waeles B.: Dynamics of sand and mud mixtures: A multiprocess-based modelling
strategy, *Continental Shelf Research*, 31(10), S135- S149, doi:10.1016/j.csr.2010.12.009, 2011.
742
743 Lehmuskerö, A., Skogen Chauton, M., and Boström, T.: Light and photosynthetic microalgae: A review of
744 cellular- and molecular-scale optical processes, *Progress in Oceanography*, 168(September), 43-56,
doi:10.1016/j.pocean.2018.09.002, 2018.
745
746 Le Pape, O., and Menesguen, A.: Hydrodynamic prevention of eutrophication in the Bay of Brest (France), a
747 modelling approach, *Journal of Marine Systems*, 12(1-4), 171-186, doi:10.1016/S0924-7963(96)00096-6, 1997.

748 Liu, X., Dunne, J. P., Stock, C. A., Harrison, M. J., Adcroft, A., and Resplandy, L.: Simulating water residence
749 time in the coastal ocean: A global perspective, *Geophysical Research Letters*, 46(23), 13910-13919, doi:
750 10.1029/2019GL085097, 2019.

751

752 Ménèsguen, A., Dussauze, M., and Dumas, F.: Designing optimal scenarios of nutrient loading reduction in a
753 WFD/MSFD perspective by using passive tracers in a biogeochemical-3D model of the English Channel/Bay of
754 Biscay area, *Ocean & Coastal Management*, 163, 37-53, doi:10.1016/j.ocecoaman.2018.06.005, 2018.

755

756 Ménèsguen, A., Dussauze, M., Dumas, F., Thouvenin, B., Garnier, V., Lecornu, F., and Répécaud, M.: Ecological
757 model of the Bay of Biscay and English Channel shelf for environmental status assessment part 1: Nutrients,
758 phytoplankton and oxygen, *Ocean Modelling*, 133, 56-78, doi.org/10.1016/j.ocemod.2018.11.002, 2019.

759

760 Mengual B., Le Hir P., Cayocca F., and Garlan T.: Modelling fine sediment dynamics: Towards a common erosion
law for fine sand, mud and mixtures, *Water*, 9, 564, doi:10.3390/w9080564, 2017.

761

762 Mikaelyan, A., Chasovnikov, V., Kubryakov, A., and Stanichny, S.: Phenology and drivers of the winter-spring
763 phytoplankton bloom in the open Black Sea: The application of Sverdrup's hypothesis and its refinements,
Progress in Oceanography, 151, 163-176, doi:10.1016/j.pocean.2016.12.006, 2017.

764

765 Moncheva, S., Gotsis-Skretasb, O., Pagoub, K., and Krasteva, A.: Phytoplankton Blooms in Black Sea and
766 Mediterranean Coastal Ecosystems Subjected to Anthropogenic Eutrophication: Similarities and
767 Differences, *Estuarine, Coastal and Shelf Science*, 53, 281-295, doi:10.1006/ecss.2001.0767, 2001.

768

769 Oliver, E., Donat, M., Burrows, M., Moore, P., Smale, D., Alexandra, L., Benthuysen, J., Feng, M., Sen Gupta, A.,
770 Hobday, A., Holbrook, N., Perkins-Kirkpatrick, S., Scannell, H., Straub, S. and Wernberg, T.: Longer and more
771 frequent marine heatwaves over the past century, *Nature communications*, 9 :1324, doi:10.1038/s41467-018-
772 03732-9, 2018.

773

774 Paerl, H. W., Hall, N. S., Peierls, B. L., and Rossignol, K. L.: Evolving paradigms and challenges in estuarine and
775 coastal eutrophication dynamics in a culturally and climatically stressed world, *Estuaries and coasts*, 37(2), 243-
776 258, doi.org/10.1007/s12237-014-9773-x, 2014.

777

778 Peierls, B. L., Hall, N. S., and Paerl, H. W.: Non-monotonic responses of phytoplankton biomass accumulation to
779 hydrologic variability: a comparison of two coastal plain North Carolina estuaries, *Estuaries and coasts*, 35(6),
1376-1392, doi.org/10.1007/s12237-012-9547-2, 2012.

780

781 Petton, S., Pouvreau, S., and Dumas, F. Intensive use of Lagrangian trajectories to quantify coastal area dispersion,
782 Ocean Dynamics, 70(4), 541-559, doi.org/10.1007/s10236-019-01343-6, 2020.

783

784 Philippart, C. J. M., van Iperen, J. M., Cadée, G. C., and Zuur, A. F.: Long-term field observations on seasonality
785 in chlorophyll-a concentrations in a shallow coastal marine ecosystem, the Wadden Sea, *Estuaries and Coasts*,
786 33(2), 286-294, doi:10.1007/s12237-009-9236-y, 2010.

787

788 Plus, M., Thouvenin, B., Andrieux, F., Dufois, F., Ratmaya, W., Souchu, P. Diagnostic étendu de l'eutrophisation
789 (DIETE). Modélisation biogéochimique de la zone Vilaine-Loire avec prise en compte des processus
790 sédimentaires. Description du modèle Bloom (BiogeochemicaL cOastal Ocean Model). RST/LER/MPL/21.15.
791 <https://archimer.ifremer.fr/doc/00754/86567/>, 2021.

792

793 Poppeschi, C., Charria, G., Goberville, E., Rimmelin-Maury, P., Barrier, N., Petton, S., Unterberger, M.,
794 Grosssteffan, E., Repecaud, M., Quéméner, L., Le Roux, J.-F., and Tréguer, P.: Unraveling salinity extreme events
795 in coastal environments : a winter focus on the bay of Brest, *Frontiers in Marine Science*, 8, 705403, doi:10.3389/fmars.2021.705403, 2021.

796

797

798 Quéguiner, B., and Tréguer, P.: Studies on the Phytoplankton in the Bay of Brest (Western Europe), Seasonal
799 Variations in Composition, Biomass and Production in Relation to Hydrological and Chemical Features (1981—
800 1982), *Botanica Marina*, 27, 449-459, 1984.

801

802 Ragueneau, O., Quéguiner, B. and Tréguer, P.: Contrast in biological responses to tidally-induced vertical mixing
803 for two macrotidal ecosystems of western Europe, *Estuarine, Coastal and Shelf Science*, 42, 645-665,
804 doi:10.1006/ecss.1996.0042, 1996.

805
806 Ragueneau, O., Chauvaud, L., Leynaert, A., Thouzeau, G., Paulet, Y. M., Bonnet, S., Lorrain, A., Grall, J.,
807 Corvaisier, R., Le Hir, M., Jean, F., and Clavier, J.: Direct evidence of a biologically active coastal silicate pump:
808 ecological implications, *Limnology and Oceanography*, 47(6), 1849-1854, doi.org/10.4319/lo.2002.47.6.1849,
809 2002.
810
811 Ragueneau, O., Raimonet, M., Mazé, C., Coston-Guarini, J., Chauvaud, L., Danto, A., Grall, J., Jean, F., Paulet
812 Y.-M., and Thouzeau, G.: The impossible sustainability of the Bay of Brest ? Fifty years of ecosystem changes,
813 interdisciplinary knowledge construction and key questions at the science-policy-community interface, *Frontiers*
814 in *Marine Science*, 5, 124, doi.org/10.3389/fmars.2018.00124, 2018.
815
816 Ratmaya, W., Soudant, D., Dalmon-Monviola, J., Plus, M., Cochennec-Laureau, N., Goubert, E., Andrieux-Loyer,
817 F., Barillé, L. and Souchu, P.: Reduced phosphorus loads from the Loire and Vilaine rivers were accompanied by
818 increasing eutrophication in the Vilaine Bay (south Brittany, France), *Biogeosciences*, 16:1361-1380,
819 doi:10.5194/bg-16-1361-2019, 2019.
820
821 Ratmaya, W., Laverman, AM., Rabouille, C., Akbarzadeh, Z., Andrieux-Loyer, F., Barillé, L., Barillé, A-L., Le
822 Merrer, Y., and Souchu, P.: Temporal and spatial variations in benthic nitrogen cycling in a temperate macro-tidal
823 coastal ecosystem : Observation and modeling, *Continental Shelf Research*, doi:10.1016/j.csr.2022.104649, 2022.
824
825 Répécaud, M., Quemener, L., Charria, G., Pairaud, I., Rimmelin, P., Clauquin, P., Jacqueline, F., Lefebvre, A.,
826 Facq, J.V., Retho, M., and Verney, R.: National observation infrastructure: an example of a fixed-platforms
827 network along the French Coast: COAST HF, OCEANS IEE, pp. 1-6, doi:10.1109/OCEANSE.2019.8867451,
828 2019.
829
830 REPHY: French Observation and Monitoring program for Phytoplankton and Hydrology in coastal waters,
831 REPHY dataset - French Observation and Monitoring program for Phytoplankton and Hydrology in coastal waters.
832 Metropolitan data, SEANOE, doi:10.17882/47248, 2021.
833
834 Retho, M., Quemener, L., Le Gall, C., Repecaud, M., Souchu, P., Gabellec, R. and Manach, S.: MOLIT Vilaine
835 data and metadata from Coriolis Data Centre, SEANOE, doi:10.17882/46529, 2020.
836
837 Rimmelin-Maury, P., Charria, G., Repecaud, M., Quemener, L., Beaumont, L., Guillot, A., Gautier, L., Prigent, S.,
838 Le Becque, T., Bihannic, I., Bonnat, A., Le Roux, J-F., Grossteffan, E., Devesa, J., and Bozec, Y.: Iroise buoys
839 data from Coriolis data center as core parameter support for Brest Bay and Iroise sea studies, SEANOE, 2020.
840
841 Rossignol-Strick, M.: A marine anoxic event on the Brittany coast, July 1982, *Journal of Coastal Research*, 11-
842 20, https://www.jstor.org/stable/4297005, 1985.
843
844 Rumyantseva, A., Henson, S., Martin, A., Thompson, A. F., Damerell, G. M., Kaiser, J., and Heywood, K. J.:
845 Phytoplankton spring bloom initiation: The impact of atmospheric forcing and light in the temperate North
846 Atlantic, *Oceanography*, 178, 102202, doi:10.1016/j.pocean.2019.102202, 2019.
847
848 Saeck, E. A., Hadwen, W. L., Rissik, D., O'Brien, K. R., and Burford, M. A.: Flow events drive patterns of
849 phytoplankton distribution along a river-estuary-bay continuum, *Marine and Freshwater Research*, 64(7), 655-
850 670, doi:10.1071/MF12227, 2013.
851
852 Sathyendranath, S., Ji, R., and Browman, H. I.: Revisiting Sverdrup's critical depth hypothesis, *ICES Journal of*
853 *Marine Science*, 72(6), 1892-1896, doi:10.1093/icesjms/fsv110, 2015.
854
855 Schlegel, R. W., Darmaraki, S., Benthuyzen, J. A., Filbee-Dexter, K., and Oliver, E. C.: Marine cold-
856 spells, *Progress in Oceanography*, 198, 102684, doi.org/10.1101/2021.10.18.464880, 2021.
857
858 Serre-Fredj, L., Jacqueline, F., Navon, M., Izabel, G., Chasselin, L., Jolly, O., ... and Clauquin, P.: Coupling high
859 frequency monitoring and bioassay experiments to investigate a harmful algal bloom in the Bay of Seine (French-
860 English Channel), *Marine Pollution Bulletin*, 168, 112387, doi:10.1016/j.marpolbul.2021.112387, 2021.
861

862 Smetacek, V., & Cloern, J. E.: On phytoplankton trends, *Science*, 319(5868), 1346-1348, doi:
863 10.1126/science.1151330, 2008.

864

865 Sommer, U., Adrian, R., De Senerpont Domis, L., Elser, J. J., Gaedke, U., Ibelings, B., Jeppesen, E., Lürling, M.,
866 Molinero, J. C., Mooij, W. M., van Donk, E., and Winder, M.: Beyond the Plankton Ecology Group (PEG) model:
867 mechanisms driving plankton succession, *Annual review of ecology, evolution, and systematics*, 43, 429-448,
868 doi:10.1146/annurev-ecolsys-110411-160251, 2012.

869

870 Stockwell, J. D., Doubek, J. P., Adrian, R., Anneville, O., Carey, C. C., Carvalho, L., ... and Wilson, H. L.: Storm
871 impacts on phytoplankton community dynamics in lakes, *Global change biology*, 26(5), 2756-2784,
872 doi:10.1111/gcb.15033, 2020.

873

874 Sverdrup, H.: On vernal blooming of phytoplankton, *Conseil Exp. Mer*, 18, 287-295, 1953.

875

876 Thyssen, M., Tarhan, G. A., Zubkov, M. V., Holland, R. J., Grégori, G., Burkhill, P. H., and Denis, M.: The
877 emergence of automated high-frequency flow cytometry: revealing temporal and spatial phytoplankton variability,
878 *Journal of plankton research*, 30(3), 333-343, doi:10.1093/plankt/fbn005, 2008.

879

880 Tian, T., Merico, A., Su, J., Staneva, J., Wiltshire, K., and Wirtz, K.: Importance of resuspended sediment
881 dynamics for the phytoplankton spring bloom in a coastal marine ecosystem, *Journal of Sea Research*, 62(4), 214-
882 228, doi:10.1016/j.seares.2009.04.001, 2009.

883

884 Tian, T., Su, J., Flöser, G., Wiltshire, K., and Wirtz, K.: Factors controlling the onset of spring blooms in the
885 German Bight 2002–2005: light, wind and stratification, *Continental Shelf Research*, 31(10), 1140-1148,
886 doi:10.1016/j.csr.2011.04.008, 2011.

887

888 Townsend, D. W., Cammen, L. M., Holligan, P. M., Campbell, D. E., and Pettigrew, N. R.: Causes and
889 consequences of variability in the timing of spring phytoplankton blooms, *Deep Sea Research Part I: Oceanographic
890 Research Papers*, 41(5-6), 747-765, doi:10.1016/0967-0637(94)90075-2, 1994.

891

892 Trombetta, T., Vidussi, F., Mas, S., Parin, D., Simier, M., and Mostajir, B. : Water temperature drives
893 phytoplankton blooms in coastal waters, *PLoS one*, 14(4), e0214933, doi:10.1371/journal.pone.0214933, 2019.

894

895 Wiltshire, K. H., Malzahn, A. M., Wirtz, K., Greve, W., Janisch, S., Mangelsdorf, P., ... and Boersma, M.:
896 Resilience of North Sea phytoplankton spring bloom dynamics: An analysis of long-term data at Helgoland
897 Roads, *Limnology and Oceanography*, 53(4), 1294-1302, doi:10.4319/lo.2008.53.4.1294, 2008.

898

899 Wiltshire, K. H., Boersma, M., Carstens, K., Kraberg, A. C., Peters, S., and Scharfe, M.: Control of phytoplankton
900 in a shelf sea: determination of the main drivers based on the Helgoland Roads Time Series, *Journal of Sea
901 Research*, 105, 42-52, doi:10.1016/j.seares.2015.06.022, 2015.

902

903

904

905

906

907

908

909

910

911

912

913

914

915

916

917

918

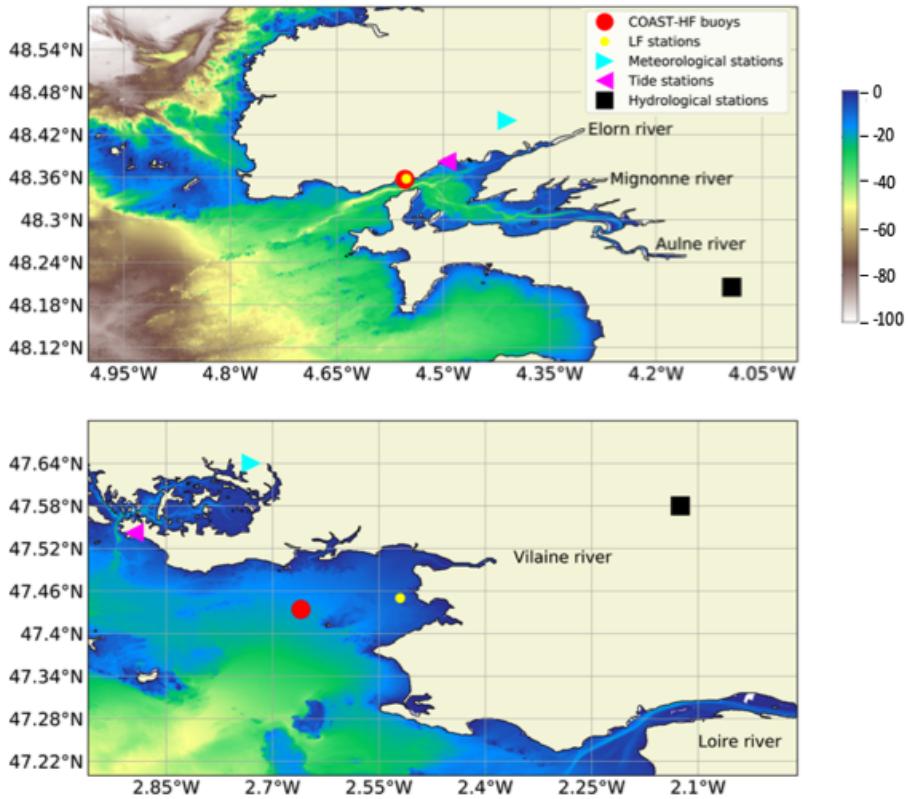
919

920

921

922

923



924
925
926
927
928
929
930
931
932
933
934
935
936
937
938
939
940
941
942
943
944
945
946
947
948
949
950
951
952
953
954
955
956
957
958
959
960
961

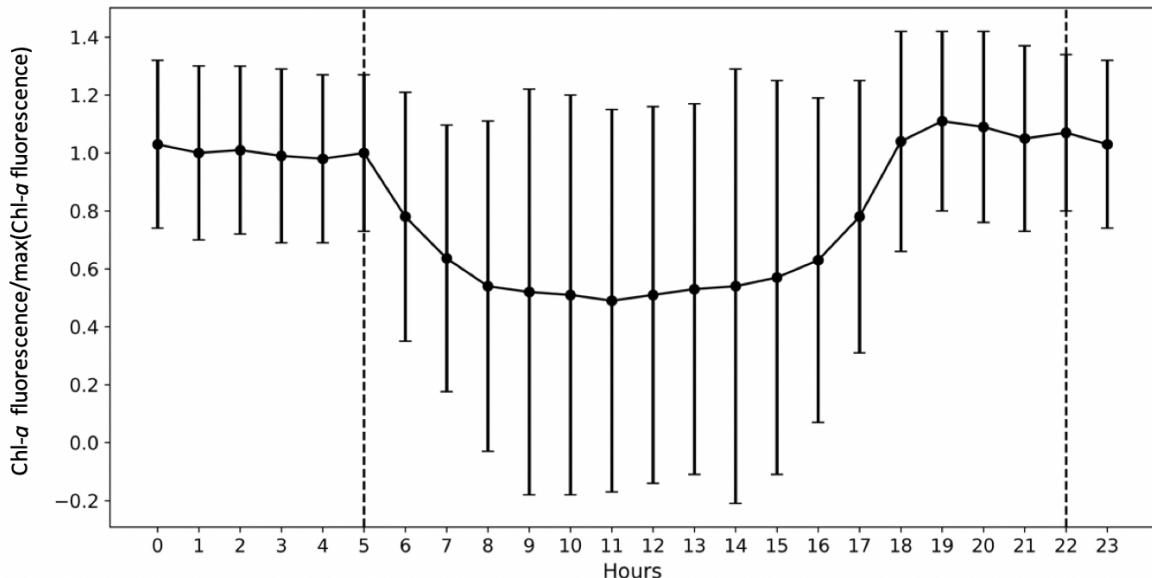
Figure 1: Location of the sampling sites: COAST-HF-Iroise and COAST-HF-Molit buoys (red circles); SOMLIT-Brest and REPHY-Loscolo sampling stations (yellow circles); Brest and Croesty tide gauge stations (blue triangles); Guipavas and Vannes-Séné meteorological stations (purple triangles); hydrological stations of the Aulne and Vilaine rivers (black squares) with the Loire station off the map.

Parameters	Bay of Brest	Bay of Vilaine
Dissolved O ₂ (mg L ⁻¹)	9	10
Mesozooplankton (μmolN L ⁻¹)	0.05	0.1
Microzooplankton (μmolN L ⁻¹)	0.05	0.05
Dinoflagellates (μmolN L ⁻¹)	0.05	0.1
Diatoms (μmolN L ⁻¹)	0.5	0.5
Soluble reactive phosphorus (μmol L ⁻¹)	0.5	0.8
Silicic acid (μmol L ⁻¹)	10	30
Nitrate (μmol L ⁻¹)	16	30
Ammonium (μmol L ⁻¹)	0.5	0.25
Coarse sand (g L ⁻¹)	0	0
Fine sand (g L ⁻¹)	0	0

Mud ($g L^{-1}$)	0.03	0.05
--------------------	------	------

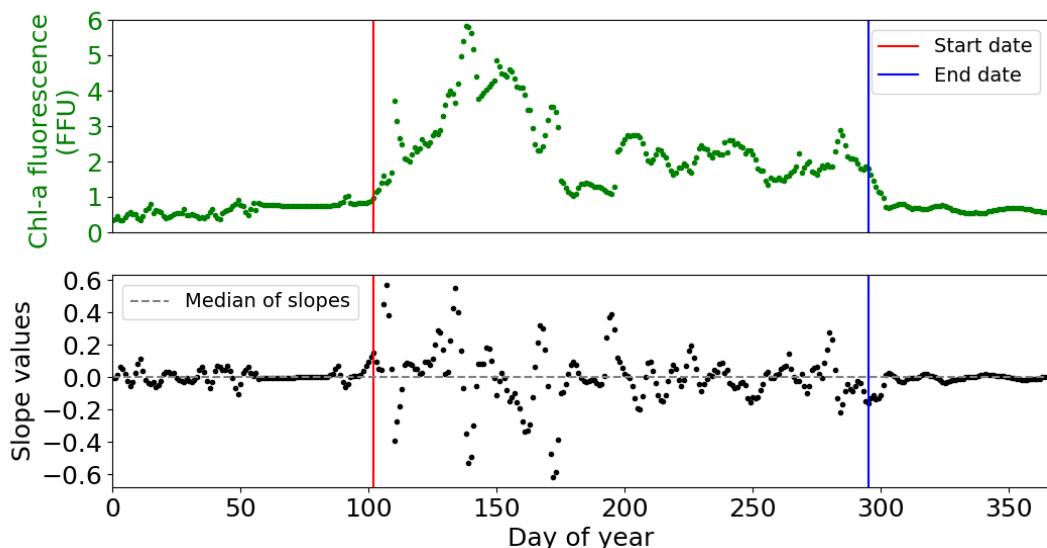
962
963
964
965

Table 1: Initial conditions in the water column for the MARS-1DV model for the beginning of the simulation on the February 15th.



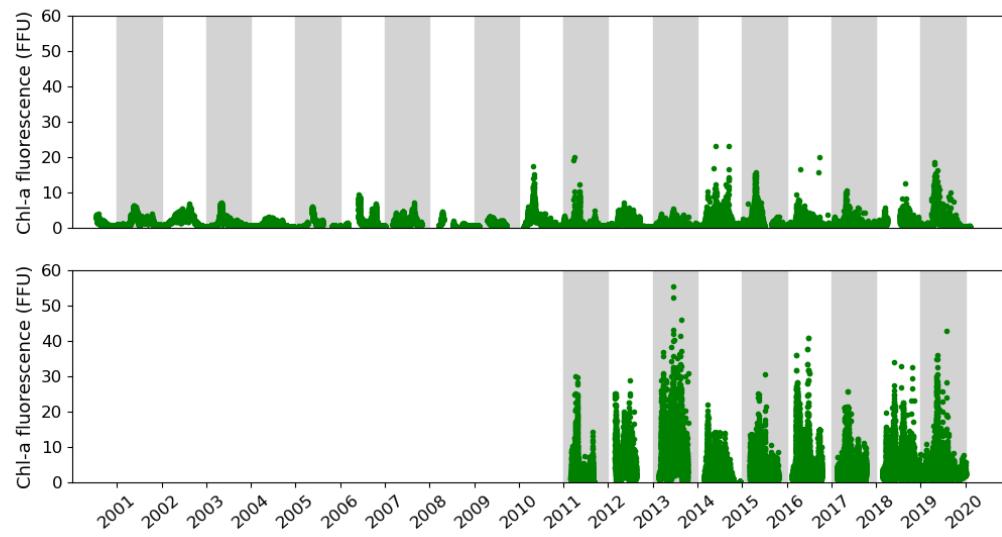
966
967
968
969
970

Figure 2: Importance of the Quenching effect on Chl-a fluorescence is represented by COAST-HF-Iroise data from 2000 to 2019. The standard deviation is represented by vertical black bars. The dashed lines represent the beginning and end of the selected values for the rest of the study from 10 pm to 5 am.



971
972
973
974

Figure 3: Example of detection of the start (red line) and end (blue line) of the phytoplankton growing period in 2001 at COAST-HF-Iroise. The threshold value - median of slopes - is represented by a dotted grey line.

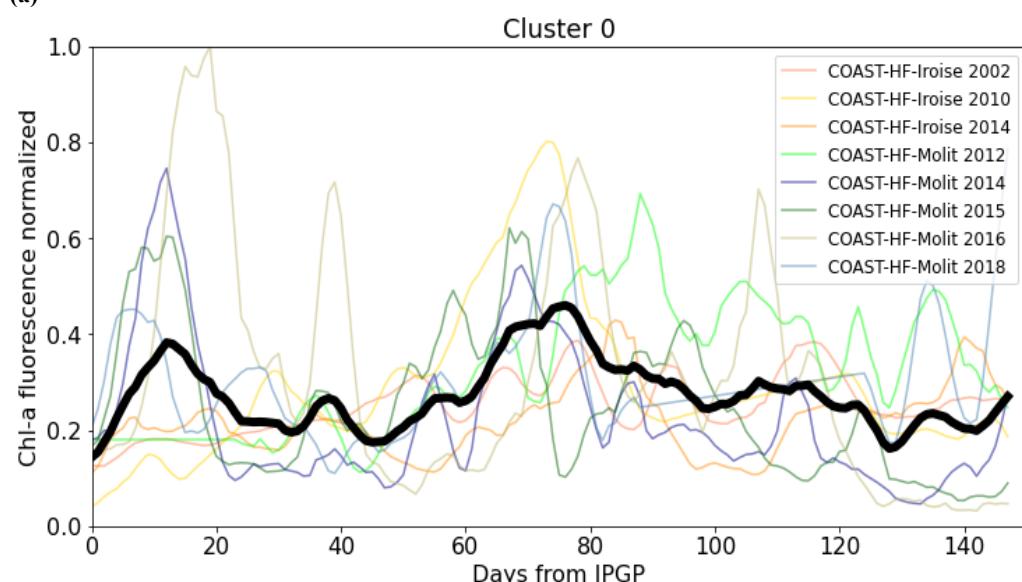


975
976
977 **Figure 4: Temporal changes in the *in situ* Chl- a fluorescence measured in the Bay of Brest (top) and the Bay of Vilaine**
978 (bottom).
979
980

	Start date (Day of year)	End date (Day of year)	Duration (Days)	Cumulative Chl- a fluorescence (FFU)
Bay of Brest (2001-2019)	50 - 69 - 102	253 - 274 - 308	165 - 200 - 256	217 - 364 - 567
Bay of Vilaine (2011-2019)	53 - 68 - 93	218 - 269 - 316	165 - 179 - 239	276 - 582 - 1406

981
982
983 **Table 2: Global characteristics of the phytoplankton growing period in the Bay of Brest and in the Bay of Vilaine.**
984
985
986
987

(a)



988
989
990

991
992

(b)

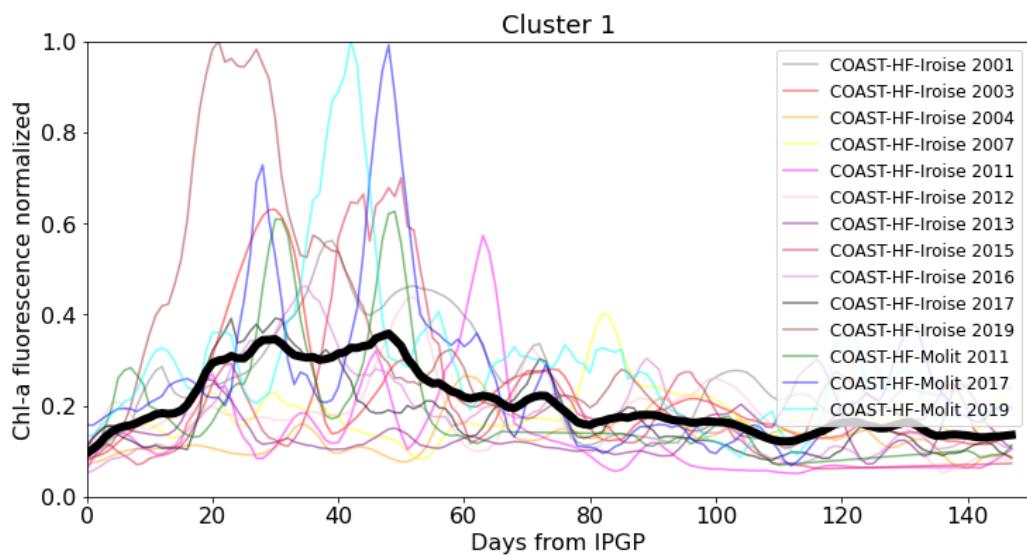
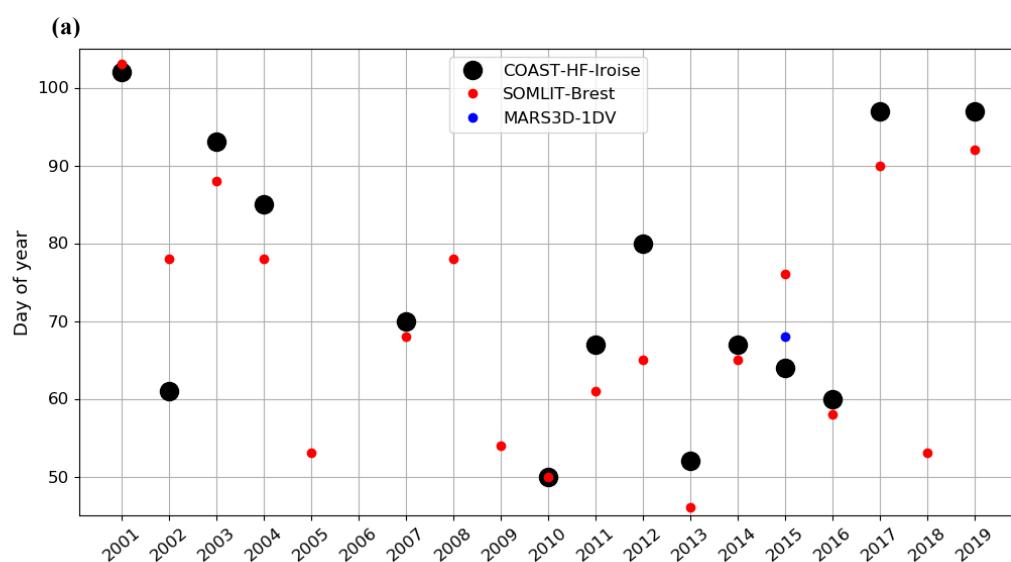


Figure 5: (a) Cluster 0 and (b) cluster 1 representative of the patterns of the phytoplankton growing period observed in both bays. The median pattern is drawn in bold.

993
994
995
996
997
998
999

Year	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
Bay of Brest COAST-HF-Iroise	1	0	1	1			1			0	1	1	1	0	1	1	1		1
Bay of Vilaine COAST-HF-Molit											1	0	X	0	0	0	1	0	1

Table 3: Cluster group assigned to each annual phytoplankton growing period on both sites. Grey boxes represent years with missing data. The cross represents the year 2013 of the Bay of Vilaine not considered.



(b)

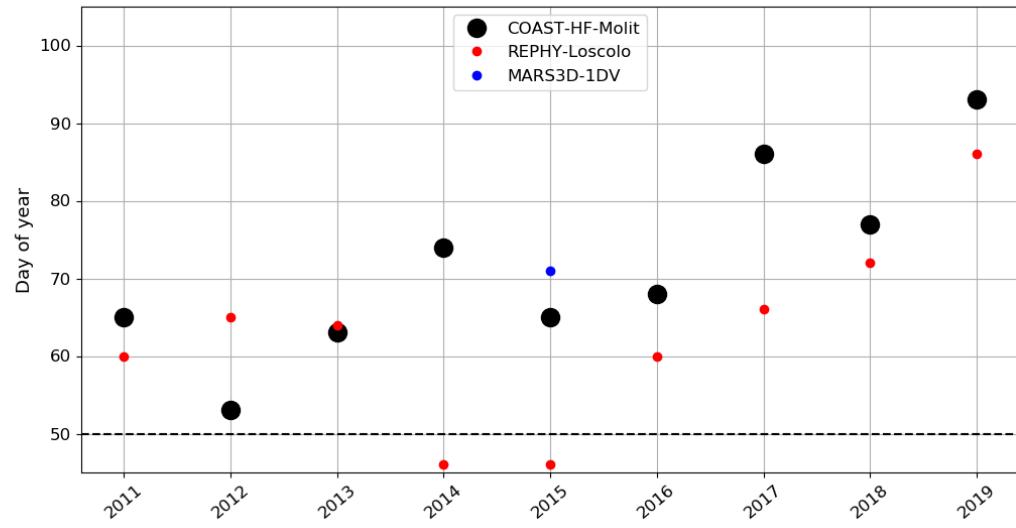
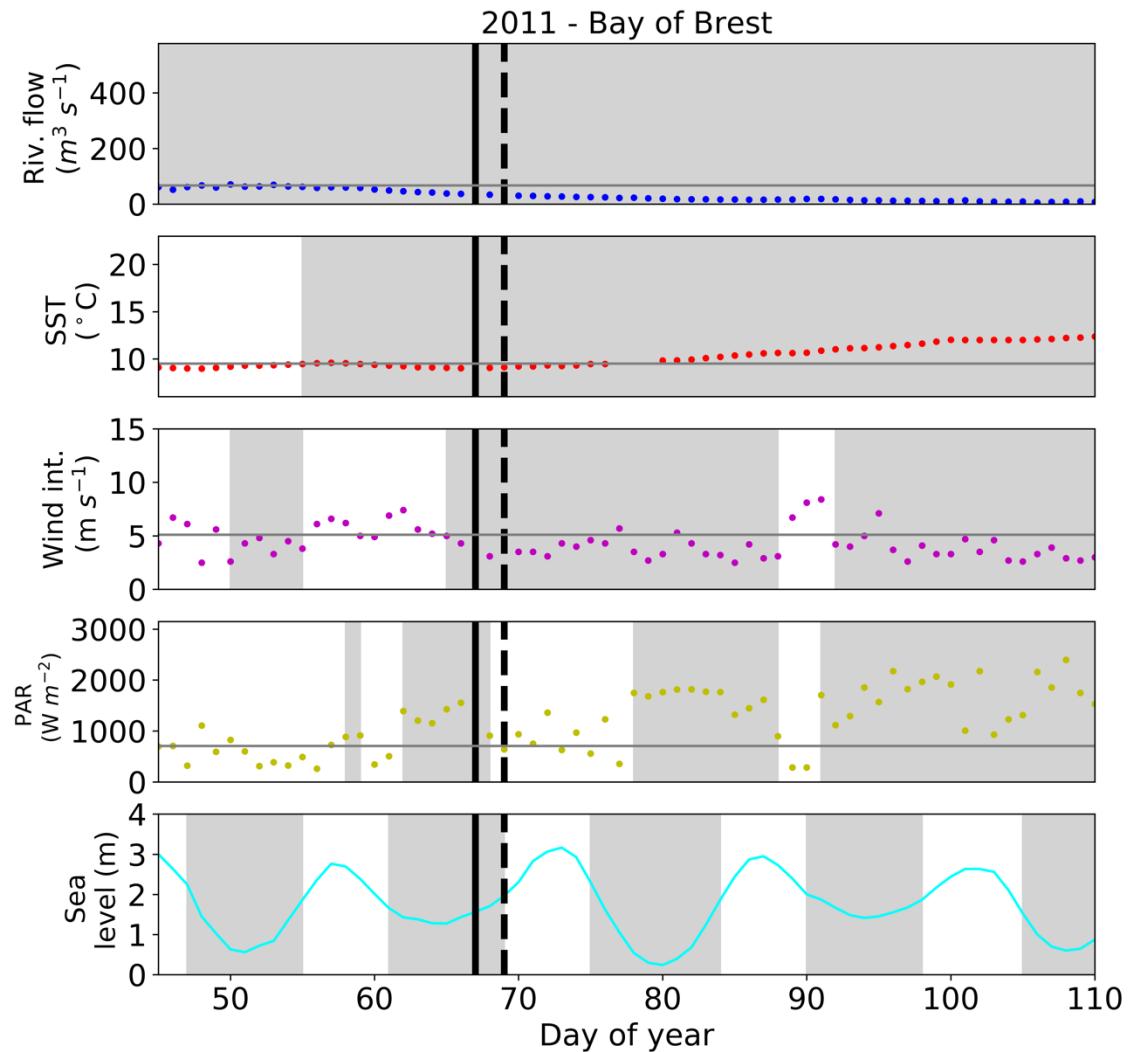


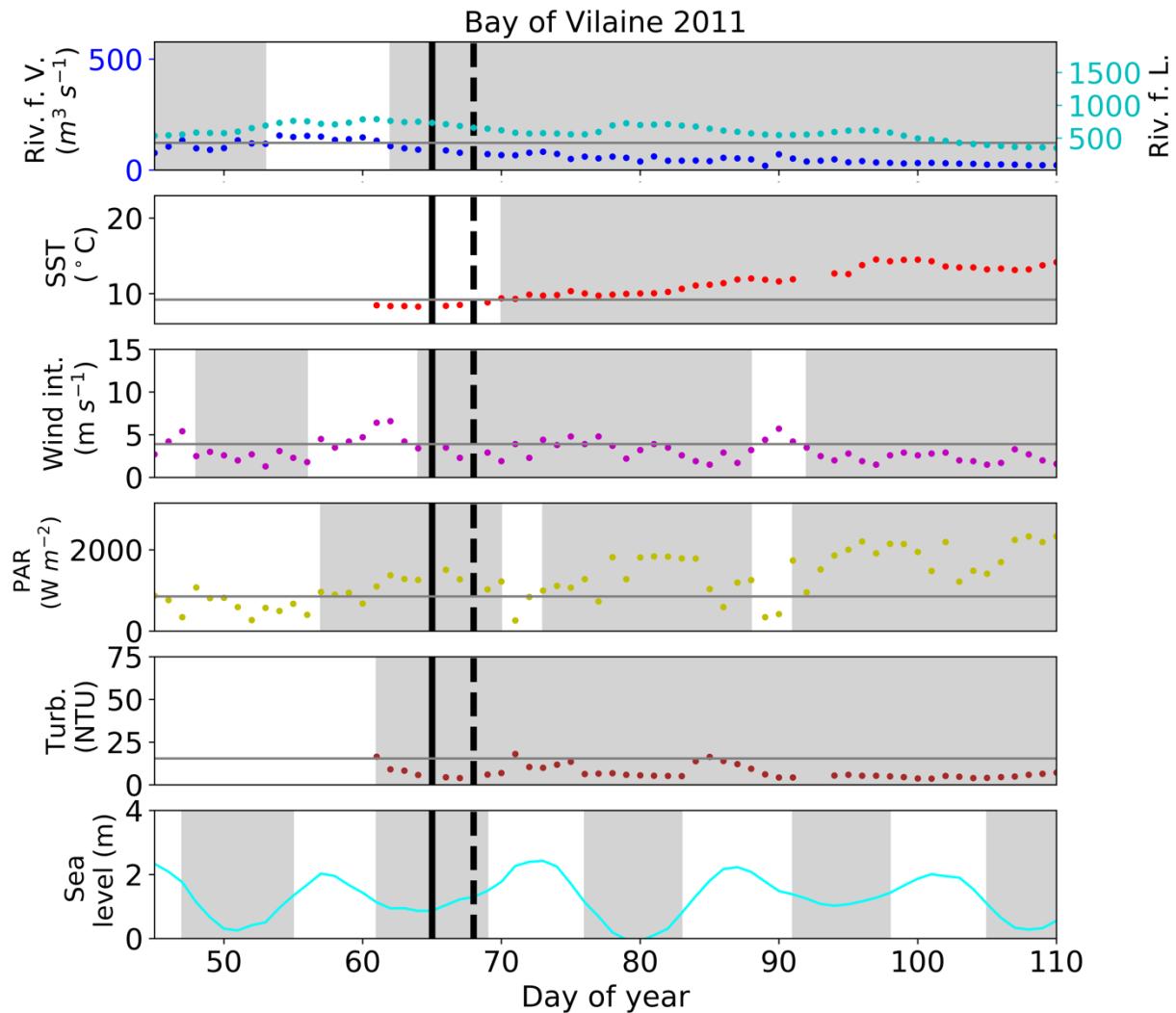
Figure 6: Changes in the IPGP date in (a) the Bay of Brest and (b) the Bay of Vilaine are determined with high-frequency time series (black circles), low-frequency time series (red circles) and with the model (blue circle). The dotted black line represents the date of the COAST-HF-Molit buoy deployment.

1011
 1012
 1013
 1014
 1015
 1016
 1017
 1018
 1019
 1020
 1021
 1022
 1023
 1024
 1025
 1026
 1027
 1028
 1029
 1030
 1031
 1032
 1033
 1034
 1035
 1036
 1037
 1038
 1039
 1040
 1041
 1042
 1043
 1044
 1045
 1046
 1047
 1048
 1049
 1050
 1051
 1052
 1053
 1054
 1055
 1056
 1057
 1058
 1059



1061
1062
1063
1064
1065
1066
1067
1068
1069
1070
1071
1072
1073
1074
1075
1076
1077
1078
1079
1080
1081
1082
1083

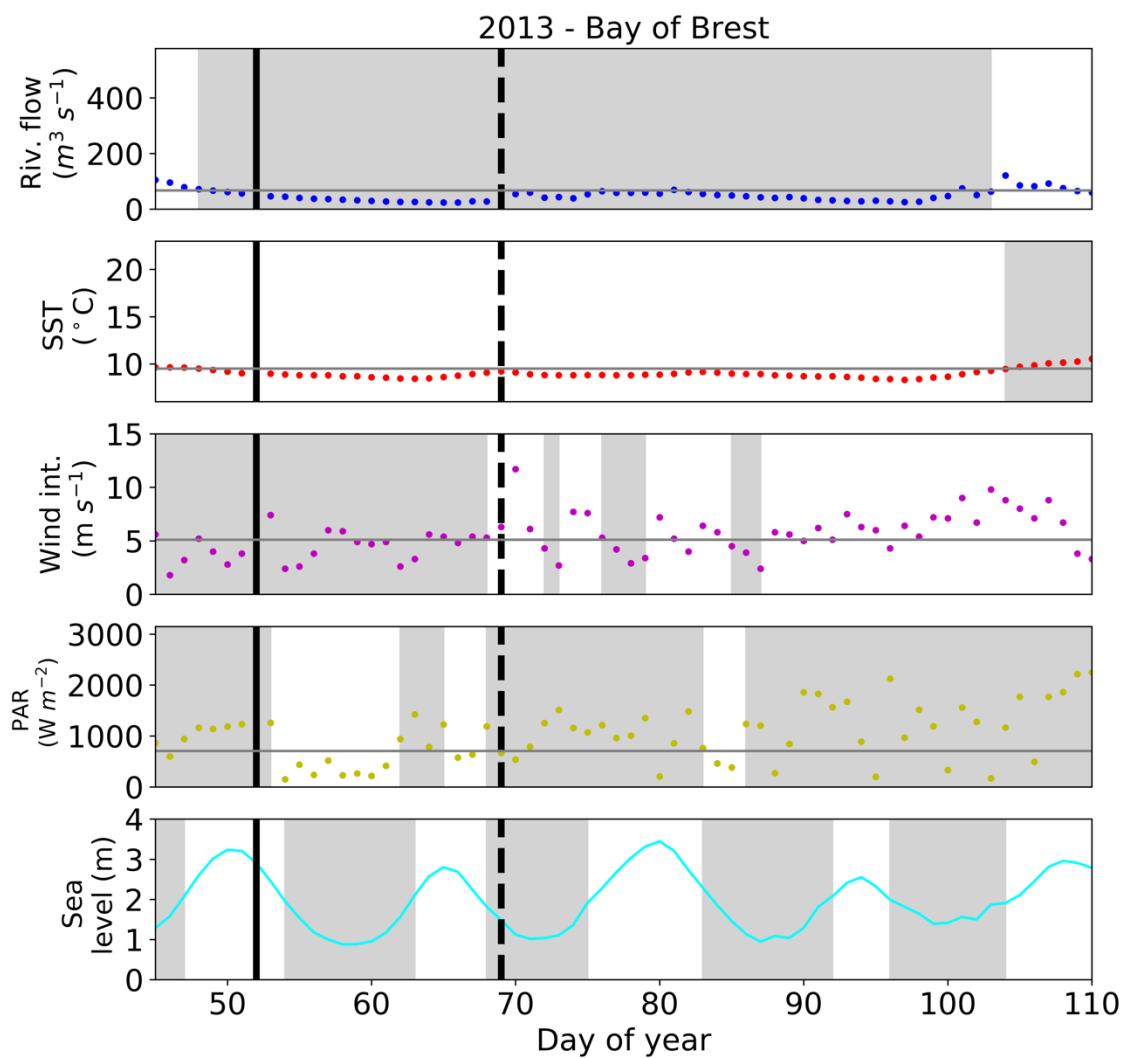
(b)



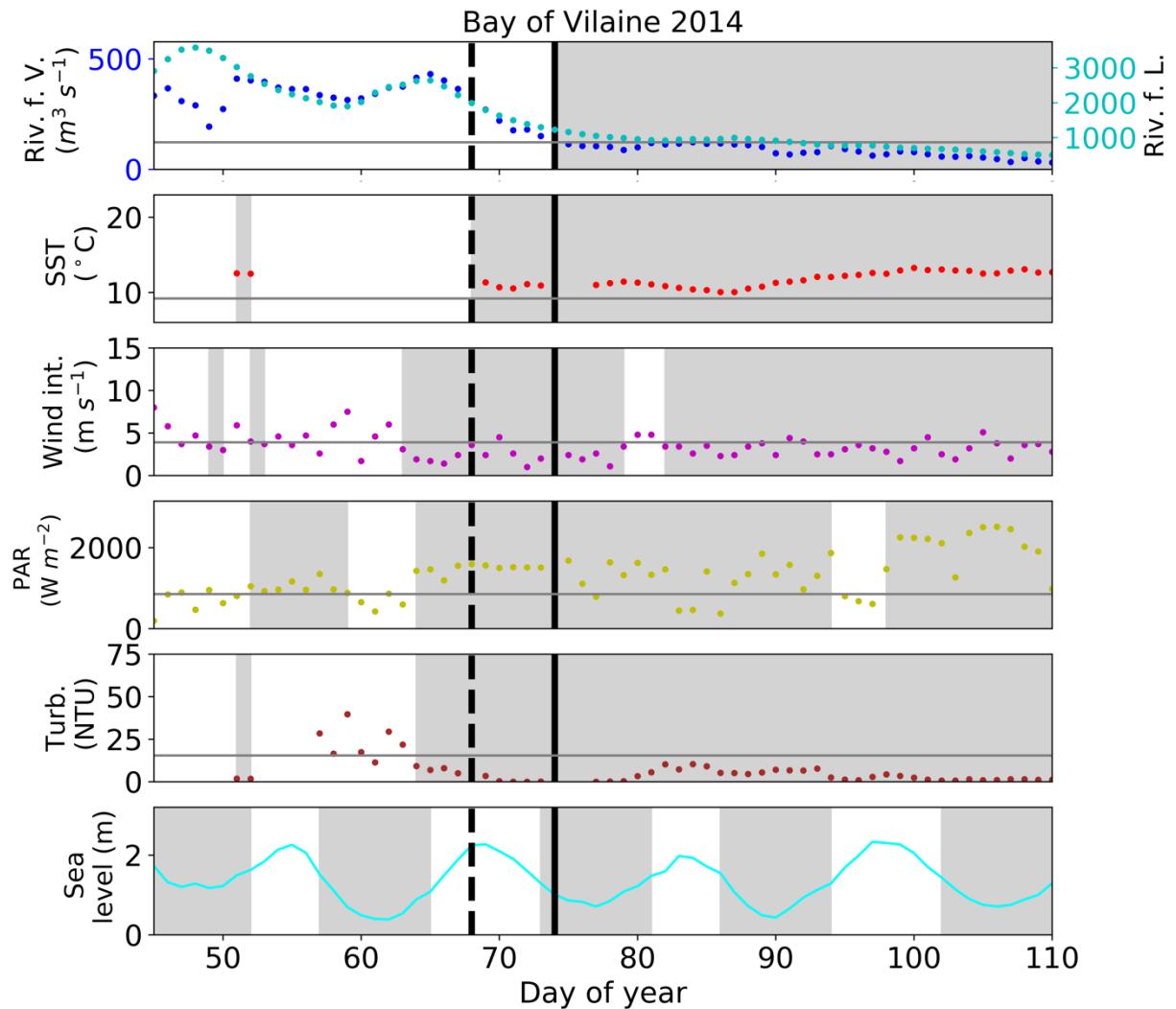
1085
1086
1087
1088
1089
1090
1091
1092
1093
1094
1095
1096
1097
1098
1099
1100
1101
1102
1103
1104
1105
1106
1107

1108
1109
1110

(c)



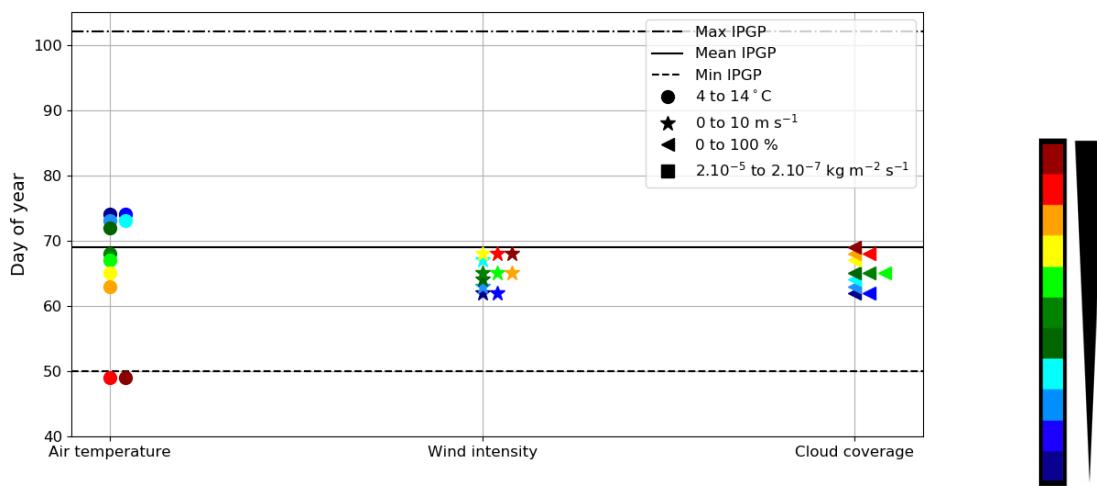
1111
1112
1113
1114
1115
1116
1117
1118
1119
1120
1121
1122
1123
1124
1125
1126
1127
1128
1129
1130
1131

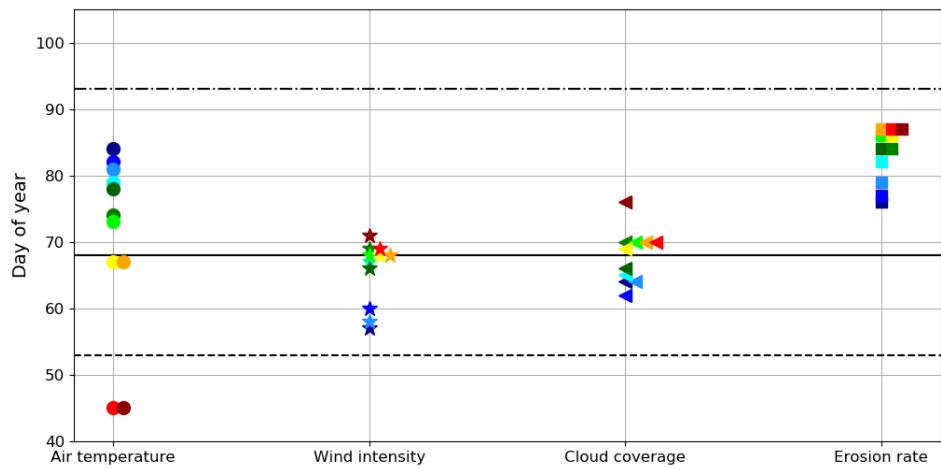


1133
1134 **Figure 7: IPGP dates and environmental drivers: flow of the Aulne, Vilaine and Loire rivers, Sea Surface Temperature**
1135 **(SST), wind intensity, PAR, turbidity and sea level at high tide. Illustrations in 2011 for a mean IPGP date in (a) the**
1136 **Bay of Brest and (b) the Bay of Vilaine; in 2013 for an early IPGP date in (c) the Bay of Brest; in 2014 for a late IPGP**
1137 **date in (d) the Bay of Vilaine. The mean IPGP date of each bay is represented by a dotted black line and the IPGP date**
1138 **of the year is represented by a straight black line. Thresholds of each environmental driver are represented by grey**
1139 **vertical lines corresponding to the mean conditions calculated 30 days around the IPGP date. Grey areas are time**
1140 **periods favorable to IPGP.**

	Bay of Brest (2001-2019)	Bay of Vilaine (2011-2019)
	Min - Median - Max	Min - Median - Max
River flow ($\text{m}^3 \text{s}^{-1}$)	13 - 46 - 100	36 - 96 - 205
SST ($^{\circ}\text{C}$)	8 - 10 - 12	8 - 10 - 11
Wind intensity (m s^{-1})	1 - 3 - 6	1 - 3 - 4
PAR (W m^{-2})	915 - 1373 - 2220	814 - 1341 - 1939
Turbidity (NTU)	1 - 7 - 21	0 - 7 - 22
Sea level (m)	0.5 - 1.6 - 2.9	0.6 - 0.9 - 1.6
PO₄ ($\mu\text{mol/L}$)	0.1 - 0.4 - 0.6	0.1 - 0.8 - 1.4
DIN ($\mu\text{mol/L}$)	8 - 20 - 38	25 - 57 - 244
Si(OH)₄ ($\mu\text{mol/L}$)	4 - 8 - 16	8 - 38 - 112

1144
1145
1146 **Table 4:** Characteristics of environmental drivers at the date of IPGP in the Bay of Brest and in the Bay of Vilaine.
1147
1148
1149 (a)
1150

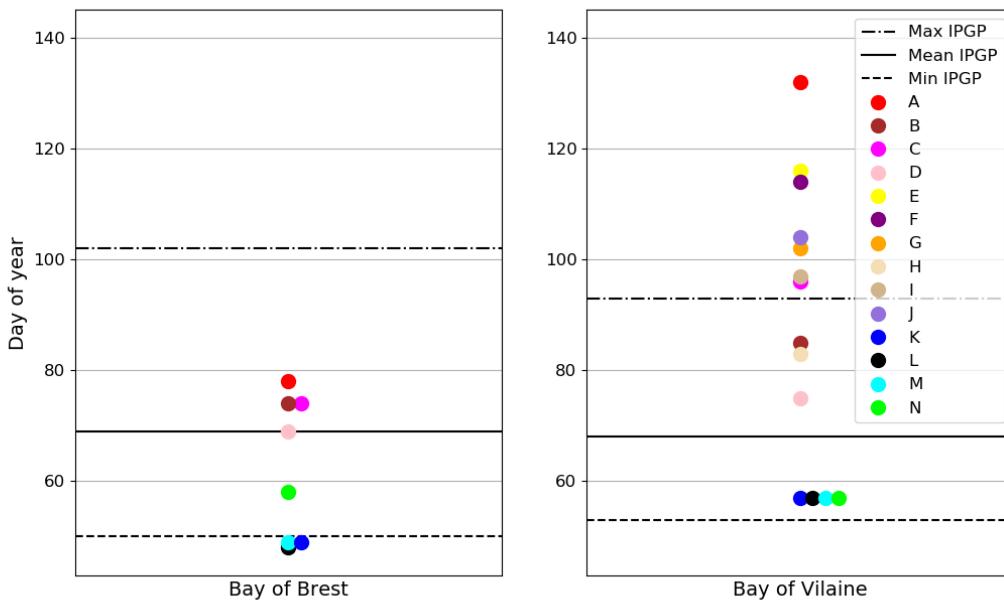




1154
 1155
 1156 Figure 8: Impact of the variation of environmental drivers on the date of IPGP in (a) the Bay of Brest and (b) the Bay
 1157 of Vilaine. Steps of: 1°C for the air temperature, 1 m s⁻¹ for the wind intensity, 10 % for the cloud coverage and
 1158 0.0000036 kg m⁻² s⁻¹ for the erosion rate equivalent to a variation of suspended matter between 0.02 and 0.08 mg L⁻¹ at
 1159 IPGP.
 1160
 1161

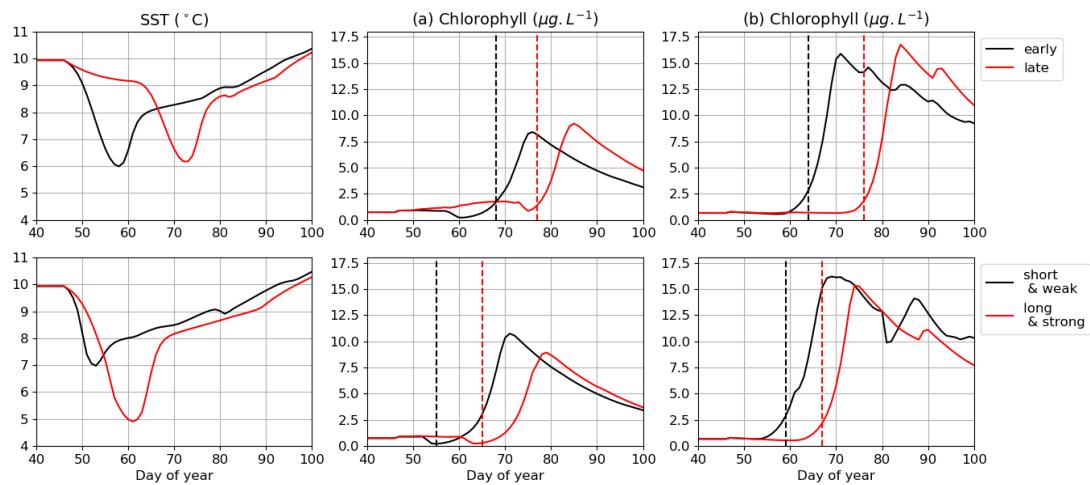
Experiment	Air temperature (°C)	Wind intensity (m s ⁻¹)	Cloud coverage (%)	Erosion rate (kg m ⁻² s ⁻¹)	Simulated IPGP Bay of Brest (days)	Simulated IPGP Bay of Vilaine (days)
1	4	3	70	2.10 ⁻⁶	+5	+16
2	14	3	70	2.10 ⁻⁶	-20	-23
3	10	0	70	2.10 ⁻⁶	-1	-11
4	10	10	70	2.10 ⁻⁶	-7	+3
5	10	3	0	2.10 ⁻⁶	=	-4
6	10	3	100	2.10 ⁻⁶	-7	+8
7	10	3	70	2.10 ⁻⁷		+8
8	10	3	70	2.10 ⁻⁵		+19
<hr/>						
A	4	10	100	2.10 ⁻⁵	+9	+64
B	4	10	70	2.10 ⁻⁶	+5	+17
C	4	3	100	2.10 ⁻⁶	+5	+28
D	10	10	100	2.10 ⁻⁶	=	+6
E	4	10	70	2.10 ⁻⁵		+48
F	4	3	100	2.10 ⁻⁵		+46
G	10	10	100	2.10 ⁻⁵		+34
H	10	3	100	2.10 ⁻⁵		+19
I	10	10	70	2.10 ⁻⁵		+29
J	4	3	70	2.10 ⁻⁵		+36
K	14	0	0	2.10 ⁻⁷	-20	-11
L	14	0	70	2.10 ⁻⁷	-21	-11
M	14	3	0	2.10 ⁻⁷	-20	-11
N	10	0	0	2.10 ⁻⁷	-11	-11

1162
 1163 Table 5: Assumptions are explored in the 1DV model for environmental parameters independently (1-8) and with
 1164 combined effect (A-N) with the modified values (grey background) and text in bold for the Bay of Brest only (+ for later
 1165 IPGP, - for earlier IPGP, = for equal IPGP) with IPGP equal the mean observed IPGP of day 68.



1166
1167
1168
1169

Figure 9: Influence of combined environmental parameters for the MARS-1DV model in both bays (Bay of Brest - left and Bay of Vilaine - right) with detailed experiments in Table 2.



1170
1171
1172
1173
1174
1175
1176
1177
1178
1179
1180

Figure 10: Impact of cold spells on the IPGP date simulated in (a) the Bay of Brest and (b) the Bay of Vilaine. Four conditions of cold spells are explored: an early (mid-February), a late (end of February), a short (8 days) and a long (20 days). The IPGP dates are represented by dotted lines.