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The benthic toxic dinoflagellate *Ostreopsis* cf. *ovata* in the NW Mediterranean Sea: Relationship between sea surface temperature and bloom phenology

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Abstract :

Blooms of the toxic benthic dinoflagellate Ostreopsis cf. ovata can induce ecological and human health issues in certain temperate areas. In order to prevent these negative effects, long-term monitoring studies of O. cf. ovata blooms have been conducted in several impacted areas to have a comprehensive understanding of bloom dynamics and efficient tools for risk management.

O. cf. ovata blooms were monitored every summer (from mid-June to the end of August) on five identified sites in Larvotto beach (Monaco, NW Mediterranean Sea), between 2007 and 2019. This time-series represents one of the largest time-series in the world describing blooms of this species.

Bloom phenological features (timing, duration, maximum cell abundance and growth rate), were found to be highly variable throughout the studied period, and were analyzed as a function of different hydroclimatic parameters, including sea surface temperature (SST). The highest net growth rates were related to temperatures ranging between 21°C and 25°C, and did not coincide with maximal temperature records (27.5°C). Such results suggest that, although global warming possibly influences the expansion of O. cf. ovata from tropical to temperate waters, the definite impact of temperature on bloom dynamics might be more complex than a simple facilitation factor for algal growth, at least in NW Mediterranean waters.

Furthermore, monthly SST anomalies calculated over this 13-year survey showed a strong positive correlation between spring SST positive anomalies and the bloom starting date, indicating that blooms occurred earlier in the season when spring SSTs were warmer than usual.

Overall results provide tools to modelers and managers who are facing crucial challenges to predict the distribution and phenology of O. cf. ovata blooms in European coastal waters, moreover in a context of global warming.

Highlights

► Long-term monitoring showed variability in bloom dynamics of *O.* cf. *ovata* in NW Mediterranean Sea. ► A strong positive correlation was observed between spring sea surface temperatures and bloom timing. ► Highest growth rates did not coincide with highest sea surface temperatures. ► Sea surface temperature, nutrient loads, wind regimes and rainfall were the main factors affecting *O.* cf. *ovata* bloom phenology.

Keywords : Benthic HABs, Long-term monitoring, Environmental factors, SST anomalies, Temperature niche, Mediterranean Sea

1. Introduction

Over the past decades, worldwide reports of Harmful Algal Blooms (HABs) have increased and suggest that these events are more intense and frequent in some areas, and may also be extending to new regions (Hallegraeff, 2010; Wells et al., 2020; Hallegraeff et al., 2021). The causes behind this trend are not clear yet; they may be the result of a combination of changing climate factors (Glibert et al., 2014; Kibler et al., 2015; Moore et al., 2008; Tester et al., 2020; Wells & Karlson, 2018), anthropogenic forcing (Anderson et al., 2002; Glibert et al., 2005; Heisler et al., 2008; Fu et al., 2012; Davidson et al., 2014) and the implementation of worldwide monitoring programs which have improved the capacity of HAB detection (Van Dolah, 2000; Anderson et al., 2012; Hallegraeff et al., 2021).

Amongst the organisms causing harmful events, the toxic species belonging to the marine dinoflagellate genus *Ostreopsis* Schmidt (1901) are found in a large variety of environments, from tropical and sub-tropical environments to temperate areas (Faust et al., 1996; Rhodes, 2011). *Ostreopsis* spp. was reported in the Mediterranean Sea for the first time in 1972 in Villefranche-sur-Mer, France (Taylor, 1979), and regularly detected thereafter along the Mediterranean coastlines (e.g. Mangialajo et al., 2011; Accoroni and Totti, 2016), with three identified species so far, namely, *Ostreopsis* cf. *ovata* (Fukuyo), *Ostreopsis* cf. *siamensis* (Schmidt) and *Ostreopsis fattorussoi* (Accoroni, Romagnoli & Totti). The available data suggest that *O.* cf. *ovata* is the most common species in Mediterranean waters. In this area, the first bloom of *O.* cf. *ovata* was observed off the Tuscany coast in 1998 (Sansoni et al., 2003). Since then, recurrent blooms have been documented in many other Mediterranean coastal areas

(Blanfuné et al., 2015; Accoroni and Totti, 2016). Moreover, this species was identified to cause noxious episodes reported along the Northern (Brescianini et al., 2006; Barroso García et al., 2008; Vila et al., 2008, 2016; Pfannkuchen et al., 2012) and Southern (Illoul et al., 2012) coasts of the Mediterranean Sea. Indeed, *O.* cf. *ovata* blooms were linked to human health symptoms including skin irritations after direct contact with the seawater (Tichadou et al., 2010; Tubaro et al., 2011; Pfannkuchen et al., 2012) or respiratory problems from inhalation of aerosols (Durando et al., 2007; Vila et al., 2016). *Ostreopsis* blooms also have an ecological impact involving mass mortalities of certain invertebrates (Sansoni et al., 2003; Totti et al., 2010) caused either by oxygen limitation due to the excess of microalgal biomass or specific ecotoxic compounds. In Mediterranean Sea, *Ostreopsis* species produce different toxins that can be transferred in some fish and invertebrates (Aligizaki et al., 2008; Biré et al., 2013, 2015; Brissard et al., 2014) and pose a potential risk of food poisoning in humans too. The *Ostreopsis*-produced toxins are palytoxin analogues (Ciminiello et al., 2006, 2012, 2014) and have been related, although not proven yet, to rare and fatal intoxications in the tropics (Tubaro et al., 2011). Luckily, such problems have not been reported in the Mediterranean yet, but the recurrence of the *Ostreopsis* blooms have stimulated intense research and monitoring of this taxon in order to prevent human and environmental health risks.

In the NW Mediterranean Sea, *O.* cf. *ovata* blooms are highly seasonal and occur during the summer to autumn season (Vila et al., 2001; Mangialajo et al., 2008, 2011; Totti et al., 2010). The existence of such a temporal window suggests that a combination of specific environmental conditions during this period may favor the development of the blooms. Several studies have shown the importance of hydrodynamics on the development of *O.* cf. *ovata* blooms (Barone, 2007; Shears and Ross, 2009; Totti et al., 2010). Slight to moderate waves enable cells to settle (Vila et al., 2001), while rough seas and currents would rather favor cell dispersion, which reduces the cell population growth. Relatively low wind intensities (2-4 m s^{-}

[1]) were registered concurrently to some blooms in the NW Mediterranean (Vila et al., 2016). Concerning nutrient availability, its role on the dynamics of *Ostreopsis* blooms is still a matter of debate. Indeed, the ability of *O*. cf. *ovata* to exploit the full spectrum of mixotrophy has still not been determined, given the large variety of potential sources of inorganic and organic matter which could contribute to *Ostreopsis* growth (Accoroni et al., 2017; Jauzein et al., 2017; Lee and Park, 2018). For instance, no direct relationship was found between inorganic nutrient concentrations and cell abundances during bloom periods (Vila et al., 2001; Cohu et al., 2011; Pistocchi et al., 2011; Accoroni et al., 2012), although variations of nitrate to phosphate (N:P) ratios may be involved in the onset of the bloom (Accoroni et al., 2015a). Regarding salinity, laboratory scale studies showed that *O.* cf. *ovata* grew better under high salinity conditions (Pezzolesi et al., 2012), but others suggested that salinity preferences was strain-specific (Tawong et al., 2015). Field observations indicated that *O.* cf. *ovata* blooms were associated with *in situ* salinity values between 37 and 38 in the NW Mediterranean Sea (Vila et al., 2001; Mangialajo et al., 2008) and with a wider range (31 – 39) in the Northern Adriatic Sea (Accoroni et al., 2015a) or in the South-Eastern Mediterranean Sea (Abdennadher et al., 2017). On the other hand, low salinities associated to inflowing freshwater was shown to hinder blooming events (Blanfuné et al., 2015; Carnicer et al., 2015). Sea depth and substratum also appear to be a specific factor when studying the occurrence of blooms, as *Ostreopsis* spp. cells mainly proliferate in shallow waters (Totti et al., 2010; Cohu and Lemée, 2012) and high abundances were also found hosted on macroalgae blades (Cohu et al., 2013; Accoroni et al., 2015b). Indeed, the presence of macroalgae with ramified structures, combined with a sheltered shallow habitat, contributes to the settlement and growth of *O.* cf. *ovata* (Meroni et al., 2018). Among all these environmental factors, it is still unclear if one in particular, or a combination of factors, could have a leading role in *O.* cf. *ovata* bloom seasonality, even though its blooms may depend

120 on the development of macroalgal communities which are also modulated by a seasonal regime
121 in temperate latitudes with clear temperature trends

122 Indeed, temperature is considered as one of the most important environmental factors
123 determining cell biology, growth and reproduction in general terms, and also follows strong
124 seasonal variations that could make it a driver of bloom seasonality. Concerning *Ostreopsis*
125 spp., several studies suggested that relatively high temperatures, as those occurring in summer,
126 favored its growth and bloom development (Hallegraeff, 2010; Granéli et al., 2011). In the
127 Atlantic coastline of the Iberian Peninsula, David et al. (2012) showed that *Ostreopsis* spp.
128 blooms could be triggered when sea surface temperatures (SSTs) exceeded a certain threshold
129 (namely, 19.5°C) over a long enough period (three months). In the NW Mediterranean Sea, the
130 occurrence of *O.* cf. *ovata* blooms have been reported under a wide range of SST, from 16.8°C
131 to 30°C (Mangialajo et al., 2011; Accoroni and Totti, 2016). Even if major proliferation are
132 usually recorded in mid-summer (July) along the coasts of the Ligurian and Catalan Seas coasts,
133 a second bloom often occurs in autumn in these areas (Mangialajo et al., 2008, 2011; Cohu et
134 al., 2011; Vila et al., 2016). In the Northern Adriatic Sea, blooms even appear rather later in
135 autumn, between September and October (Monti et al., 2007; Totti et al., 2010; Ninčević
136 Gladan et al., 2019). Overall, these observations suggest a more underlying and complex role
137 of temperature in the occurrence *O.* cf. *ovata* blooms, beyond a simple increasing facilitation
138 with increasing temperature.

139 In a context of global warming, the investigation of the environmental niche of *O.* cf.
140 *ovata* is key to help predict bloom events and to plan efficient monitoring programs. A long-
141 term monitoring dataset can provide a good comprehension of the potential link between
142 temperature and *O.* cf. *ovata* bloom events. Most well established HAB monitoring programs
143 consist in sampling the plankton community. However, *Ostreopsis* has a main benthic phase
144 attached to surfaces (macroalgae, rocks, pebbles, sand, and invertebrates) with a self-produced

mucilage. Internal biological rhythms (not well understood yet) and hydrodynamics detach *Ostreopsis* cells from the substrate and they are found swimming as part of the plankton or in dense aggregates floating at the sea surface. Benthic cells can be considered as the stock or reservoir of the bloom, while planktonic cells and floating aggregates can be more related to the health symptoms (Totti et al., 2010). So far, some studies have shown good correlations between the *Ostreopsis* populations in the plankton and the benthos (Mangialajo et al., 2011; Giussani et al., 2017) but the uncertainties regarding the factors determining their dynamics recommends the sampling of the two fractions. Such combined plankton and benthos monitoring program was launched in Monaco (Ligurian Sea) in summer 2007, in order to assess the sanitary risk impact of *O.* cf. *ovata* on local recreational waters. This monitoring program is still ongoing and represents the world's largest time-series study ever recorded for *O.* cf. *ovata* bloom events. In addition to the data collected on cells abundance in Monaco waters and on macroalgae, hydroclimatic parameters were also registered on site and in a neighboring station of the Bay of Villefranche-sur-Mer (France), on a weekly basis and over decades. The overall data set enabled to explore the link between biological and ecological information and the local environmental and physical factors in order to describe *O.* cf. *ovata* bloom phenology. Data collected over the first two years of this monitoring program already showed a distinct pattern concerning the timing of the blooms and specific hydroclimatic conditions. In particular, it was noticed that *Ostreopsis* blooms occurred earlier after a warmer spring in 2007, and later following a colder summer in 2008 (Cohu et al., 2011). This observation suggested a new link between hydroclimatic factors and *O.* cf. *ovata* bloom phenology which has been analyzed in the present study, considering the data recorded since 2007 over thirteen years.

2. Materiel and Methods

2.1.Sampling site

Monaco is a sovereign city-state located on the French Riviera coast, in the NW Mediterranean Sea. It is a highly touristic area whose population increases considerably during the summer season. The Larvotto beach (43°44.71' N – 7°26.04' E) is a small sheltered cove surrounded by residential buildings, shops and restaurants. The beach (Fig. 1) is orientated to the South-East and artificial rocky dykes were built as a barrier to protect from waves and swell. Such structures constitute ideal substrates for the development of ramified structured macroalgae, especially Phaeophyceae and Florideophyceae, such as *Halopteris scoparia* Sauvageau, *Dictyota* sp. Lamouroux and *Ellisolandia* sp. Hind & Saunders, which host high densities of benthic microalgae including *O.* cf. *ovata.* Thus, neighbors and tourists can be potentially exposed to the health risks associated to *O.* cf. *ovata* blooms. So far, sporadic skin and mucosal irritations have been observed (Tichadou et al., 2010).

2.2.Sampling process and cell quantification

O. cf. *ovata* blooms occurring in the NW Mediterranean Sea are always observed in early summer, when the SST increases and wind conditions are relatively calm. In order to quantify the abundance of epiphytic *O.* cf. *ovata* cells, a monitoring program started in 2007 and was then conducted every year, generally from mid-June until the end of August. The global estimation of the benthic cell stock in a given area is a complex task as the cell concentration may depend on the presence of certain types of macroalgae and may also vary according to small scale environmental changes. In order to give a reliable estimation of the cell abundance of this area, five different stations were sampled at each sampling date. The sampling campaign was carried out once a week during this period, between 9 am and 11 am, in five stations located on rocky substrate areas within the Larvotto Beach (see Fig. 1). The temporal evolution of the bloom was monitored through the estimation of both benthic cell stock and planktonic cell

194 abundance quantification as described by Cohu et al. (2011). Samples of the most representative
195 macroalgae (usually *Dictyota* sp., *Ellisolandia elongata* and/or *Halopteris scoparia*) were
196 collected at 0.5-meter depth at each sampling station, by using 250 ml plastic flask filled up to
197 the top with the surrounding water. Seawater above the sampled macroalgae, at 0.3-meter depth,
198 was also collected for planktonic cell quantification. Plankton sampling was conducted before
199 collecting the macroalgae in order to avoid releasing *Ostreopsis* benthic cells initially attached
200 to the macroalgae which could overestimate *Ostreopsis* cells in the planktonic phase. All
201 samples were then fixed with acidic Lugol (1% vol./vol.) and kept dark at 4°C. In the laboratory,
202 macroalgae samples were vigorously shaken in the plastic flasks and the seawater was filtered
203 through a 500 µm meshed filter to remove large macroalgal debris and isolate the epiphytic
204 cells. Two additional rinsing of the macroalgae with 100 ml of 0.2 µm filtered seawater were
205 conducted (with additional shaking and percolation steps) to detach as much microalgae cells
206 as possible (Jauzein et al., 2018); all percolated water was merged and the total volume of
207 seawater was noted. Macroalgae were then gently pressed to eliminate excess water and placed
208 onto a tin foil for fresh weight measurement. Cell counts were performed on the percolated
209 water of samples following the Utermöhl method (Utermöhl, 1958), by using a light microscope
210 (Axioscope 5, Zeiss, Oberkochen, Germany). A 1 ml Sedgwick Rafter counting chamber was
211 used for the epiphytic *Ostreopsis* cells and 50 ml sedimentation columns for the planktonic
212 cells. Benthic cell concentrations were expressed as cells per gram of fresh weight of
213 macroalgae (cell g^{-1} FW) and the plankton cells as cell l^{-1}.

214 2.3.Hydroclimatic parameters

215 During the sampling period, seawater temperature (± 0.1°C) was measured *in situ* at each station
216 using a probe. The "Direction de l'Environnement" of Monaco provided hydroclimatic data
217 from their meteorological program, including SST, salinity, pH, wind speed, wind direction and
218 rainfall in Larvotto beach area. Wind speed and direction were used to represent South-North

and West-East wind intensity vectors. In addition, long-term hydrological data including SST, nitrate and nitrite measurements from Point B in Villefranche-sur-Mer (43°41.10' N - 7°18.94' E) were collected by SOMLIT, a French national coastline monitoring network (http://somlit.fr). Located 12 km away from Monaco, Villefranche Bay can be considered as a reference area for the western part of the Ligurian Sea, including Monaco. These data were collected once a week in the bay, all year long, during the whole studied period.

2.4.Calculation and Statistics

Cell abundance for each sampling date was calculated as the mean cell abundance considering the five sampling stations. The difference in cell abundance between two sampling dates (i.e. net growth rate = μ) is the result of the combination of several parameters such as cell growth rate, cell dispersion, cell accumulation, predation and cell mortality rates. Net growth rates were calculated between each sampling week by using the following equation:

$$\mu = \frac{LnN2 - LnN1}{t2 - t1}$$

Where μ is the net growth rate (NGR, d^{-1}) between sampling day 1 and sampling day 2, N1 the mean cell abundance at sampling day 1 (cell g^{-1} FW), N2 the mean cell abundance at sampling day 2 (cell g^{-1} FW), t1 the date in days at the sampling date 1 and t2 the date in days at the sampling date 2. Note that this formula assumes an exponential growth (as defined in Wood et al., 2005) between the two sampling dates, although the detailed dynamics of the cell abundances is not possible to be tracked.

Data from year 2007 were not included in all the analyses as the monitoring started late in the year (early July) while the bloom was already declining. Starting date, maximum abundances and maximum growth rates could not be estimated for this year.

A mean weekly temperature profile was calculated over the thirteen-year monitoring period. Then, for each year, weekly SST anomalies were calculated as differences between temperature values and the mean weekly SST value. Finally, cumulative sums of SST anomalies were performed starting from the first week of each year.

Variations of net growth rate estimated during the phases of bloom development were analyzed as a function of SST using a non-parametric "loess" local polynomial regression model (Cleveland, 1979). The non-parametric Spearman correlation test was used to examine links between the abundance of benthic and planktonic *Ostreopsis* cells, as well as between SST and *O.* cf. *ovata* abundances (in the plankton and the benthos). A Wilcoxon signed-rank (non-parametric) test was applied on SST data collected both in Monaco and Villefranche Bay to ascertain the degree of similarity of the temperatures at both locations. A Principal Component Analysis (PCA) was used to explore the relationships between the different phenological features, namely, timing (starting and finalization dates of the bloom), duration, intensity (characterized by the maximum cell abundances) and maximum growth rate of the bloom, and environmental parameters (seawater temperature, salinity, winds, rainfall and nutrient concentrations). This PCA was performed using seasonal averages (mean of April, May and June) of environmental factors. These mean estimations were considered as representative of the hydroclimatic environment of the spring season, described as a crucial period before the bloom onset. The data set used for the PCA includes the years between 2008 and 2017 since rainfall, wind strength and nutrient concentrations data were not available for the last two years of monitoring. All statistical analyses were performed using R studio (R Core Team, 2019).

3. Results

3.1.Interannual variability

Blooms of *O.* cf. *ovata* occurred every year since 2007 at the same monitored site (Fig. 2). All data obtained over the last thirteen years of monitoring were pooled and the mean cell abundances were calculated over the five sampling stations. Results showed a positive correlation between *O.* cf. *ovata* benthic and planktonic abundances of (Spearman test, N = 147, $r_s = 0.805$, p-value < 0.01) (Fig. 3). However, as explained earlier in the Introduction, *O.* cf. *ovata* an epibenthic species, with the benthic fraction constituting the reservoir of the bloom. Therefore, the following analysis will focus exclusively on benthic abundances.

The highest abundance levels of *O.* cf. *ovata* blooms were constantly observed in summer (between June and August). Only two events within the thirteen-year time series showed two successive blooms in the same year: a first maximum peak of benthic cell abundance in summer followed by a second and smaller peak in late summer were observed in 2012 and 2013 (Fig. 2). Highly variable phenological features of the blooms were observed from one year to another (Fig. 2). Nevertheless, three main parameters enabled to distinguish one bloom from another: the timing, the duration and the maximum cell abundance of blooms.

A concentration of 200,000 cells g^{-1} FW was estimated as the threshold above which the presence of *O.* cf. *ovata* was defined as a bloom. Indeed, this level refers to the lowest value of the overall maximum annual abundances measured during the thirteen blooms (212,300 cells g^{-1} FW measured in 2015). Since samples were collected only once a week, it was difficult to set the exact starting date of the bloom. The average starting day of a bloom was defined in the present study using the abundance threshold (200,000 cells g^{-1} FW) criterion and was defined on Julian day 191 (± 10.6). Delays occurred depending of the year, with blooms appearing as early as 15 days prior to this average starting day (Julian day 177, in 2015), while the latest bloom occurred 25 days later (Julian day 214, 2016).

292 The duration of the event was also variable over the years. When more than 200,000
293 cells g^{-1} FW were quantified during two consecutive sampling dates, the event was defined as
294 a two-week bloom. When abundance values above this threshold were registered only once,
295 then the event was defined as a one-week bloom. The blooms lasted in average 18.7 days (±
296 10.5), of which years 2011 and 2017 presented the longest blooming times (35 and 42 days
297 respectively), and years 2007, 2009 and 2015 the shortest blooming times (7 days).
298 The highest annual maximum abundance values leveled to an average value of 570,878
299 (± 391,871) cells g^{-1} FW. However, the highest value ever recorded was 1,565,514 cells g^{-1} FW
300 (174 % more than the average) in 2007 and the lowest value reached 212,300 cells g^{-1} FW (63
301 % less than the average) in 2013.

302

303 3.2.Relationship between environmental factors and interannual variability of *Ostreopsis*
304 cf. *ovata* blooms

305 A multivariate analysis (PCA) was performed on data collected between April and June from
306 the monitoring of environmental parameters, including physico-chemical measurements of
307 water masses (SST, salinity, nutrients) as well as rainfall and wind intensity vectors
308 (Supplementary Material 1). The two first axis forming the first factorial space explained 70%
309 of the total inertia of projected variables (Fig. 4), indicating a relatively good representation of
310 the relationship between the different environmental parameters. The most important variables
311 for the construction of the first factorial axis of the PCA (46.5 % of the total inertia) were South-
312 North winds (0.90), SST (-0.84) and West-Est winds (0.79). The second axis was driven by
313 nitrates (0.80), salinity (-0.62) and nitrites (0.57) and captured 23.6% of the variation. These
314 results indicate that the first factorial axis of the PCA discriminates the years with bloom events
315 according to the SST during the spring season. Indeed, years with high SST during spring seem

316 to be related to low wind conditions. The second factorial axis highlights the nutrient loading
317 of the area and discriminates years according to the nutrient availability during the spring
318 seasons. Indeed, years which experience a high level of rainfall are related to high nitrate
319 concentration and low salinity values. Among the phenological features, the timing of the
320 bloom event (bloom starting day) and the maximum annual growth rate are both correlated to
321 the first axis of the PCA (0.71 and 0.39, respectively), while the intensity of the bloom
322 (maximum cell concentration) is correlated to the second axis (0.41). No clear relation was
323 found between environmental factors and the bloom duration.

324 Throughout the entire time series, the presence of *O.* cf. *ovata* benthic cells was
325 observed when SST ranged between 18.2°C and 27.9°C, with an overall temperature average
326 of 24.3 ± 1.8°C. When processing the entire dataset provided by the thirteen-year survey,
327 blooming periods (i.e. when benthic cell abundance exceeded 200,000 cells g^{-1} FW) were
328 identified when the mean SST reached 25.0 ± 1.5 °C. When focusing more specifically on each
329 individual year, mean SST values measured during blooming periods ranged between 24.0 ±
330 1.5°C and 25.2 ± 1.7°C. At the very beginning of a bloom event, when cell densities first
331 exceeded the threshold of 200,000 cells g^{-1} FW, the average SST was estimated at 24.9 ±1.4°C.

332 Positive net growth rates (NGR) of *O.* cf. *ovata* were recorded when the SST varied
333 between 18.2°C and 27.9°C. A negative correlation was found between the temperature and the
334 NGR (Spearman, N = 133, r_s = -0.27, p-value < 0.01), but the relation was not linear and highest
335 positive NGRs were not associated to maximal temperature records (Fig. 5). Indeed, the
336 maximum NGR (0.53 d^{-1}) occurred at a temperature of 23.9°C. These variations are confirmed
337 by the local regression loess model, defining the optimal growth temperature at 23.5°C. In these
338 terms, when considering each maximum NGR for each year, the window of optimal growth
339 temperature was estimated between 21.0°C and 24.7°C (Fig. 5).

No significant differences were found by comparing summer SST values measured in Larvotto and in Villefranche Bay (Wilcoxon signed-rank test: N = 125, W = 3869, p-value = 0.645). Therefore, SST values recorded in Villefranche Bay were used as a proxy for estimating the SST of Monaco area. In contrast to data collected in Monaco, SST measurements in Villefranche Bay were collected weekly and throughout the year, which enabled to describe the annual general hydroclimatic conditions of the area. Between 2007 and 2019, the annual mean SST was estimated at 18.8°C (± 4.3) and the respective mean values of the lowest and the highest annual temperatures were estimated at 13.4°C (±0.4) and 26.3°C (±0.9), respectively. Annual SST anomalies were cumulated in order to compare the heat accumulated in surface waters between each surveyed year (Fig. 6). Years with high values of SST anomalies were considered as warmer, while years with low values of SST anomalies were considered as cooler. Profiles of cumulated SST anomalies were different between the years but were also found to be different at a seasonal and monthly scale, thereby differentiating years with a warmer spring season from years with a cooler spring. Amongst the previously detailed phenological features of interest, strong positive correlations were found only between the bloom timing (starting of the event) and the cumulative sum of SST anomalies (Fig. 7A). This was observed for monthly averaged cumulative sum of SST anomalies over the months of April, May and June (prior to the bloom event) and during the whole spring season (April-May-June averaged values), but not before then (Fig. 7B). Thus, blooms of *O.* cf. *ovata* tend to start earlier in the season when SST anomalies are high. No other significant correlations were observed between SST anomalies and the duration of the bloom nor the maximum abundance of the bloom.

4. Discussion

Understanding the relationship between environmental parameters and the phenology of *O.* cf. *ovata* proliferations in the NW Mediterranean Sea can help predict either the timing, duration or intensity of blooms and hence support the management and mitigation of benthic HAB

365 impacts. Such knowledge cannot be gained by observing one single bloom event (e.g. Vila et
366 al., 2001; Battocchi et al., 2010; Totti et al., 2010; Accoroni et al., 2011; Illoul et al., 2012) but
367 requires pluri-annual time series enabling to study the variability of occurring blooms along
368 several years. Furthermore, long-term surveys as currently presented in this study enabled to
369 characterize the *in situ* environmental niche of the target organism, *O.* cf. *ovata*, in the NW
370 Mediterranean Sea. Such a set of data is of great interest for both modelers and managers,
371 focusing on the prediction of HABs in the context of global change and warming of seawater
372 surfaces.

373 In the present study, a multi-parametric approach and the analysis of environmental
374 control parameters for algal growth were both assessed by using the benthic cell number data
375 from *O.* cf. *ovata* abundance measurements. Indeed, as already reported by several studies
376 conducted in NW Mediterranean regions (Mangialajo et al., 2008; Cohu et al., 2011; Jauzein et
377 al., 2018), a strong correlation was found between concentrations of epiphytic and planktonic
378 cells of *O.* cf. *ovata*. *Ostreopsis* is recognized as a benthic organism adapted to the benthic life
379 which is proven by its morphology and ecology (e.g., Hoppenrath et al., 2014). Due to the
380 combination of possible internal biological rhythms and very local sea hydrodynamics, cells
381 can detach from the benthos and circulate as pelagic cell, which explains the observed
382 correlation between benthic and pelagic cell abundances. Epiphytic cells nevertheless
383 represents the main stock, or reservoir, of the *O.* cf. *ovata* population able to sustain bloom
384 events. In terms of toxic risks, both benthic and planktonic pools can be involved in direct
385 contact skin irritations, but planktonic cells only would rather be the agents of intoxication
386 events promoted by inhalation (Totti et al., 2010). In this case, *Ostreopsis*-produced toxic
387 compounds would be spread by aerosolization and wind transport (Ciminiello et al., 2014).
388

Two main results emerge from the analysis of this long-term dataset and shall be discussed hereafter: (1) Spring SST were driving the timing of the bloom (starting date) and (2) the highest recorded temperatures were not correlated to the highest net growth rates of *O*. cf. *ovata*.

4.1.Interannual variations in bloom phenology

The monitoring of *O.* cf. *ovata* blooms which occurred in Monaco during thirteen successive summer seasons, revealed strong yearly variations in terms of phenological features. These variations, such as bloom timing, bloom length and bloom intensity, highlight the complexity behind the formation of *O.* cf. *ovata* blooms and the possible interactions between environmental parameters which are able to shape bloom events. The PCA analysis carried out on this data-set showed that the interannual variability in bloom timing and bloom maximum intensity could be explained by the combination of SSTs, nutrient loadings and wind regimes occurring in the spring season prior to the bloom initiation. Indeed, years which experience high SSTs during the spring season are likely to see *O.* cf. *ovata* densities exceed the 200,000 cells g^{-1} FW threshold early in the summer. High nutrient concentrations, prior and during the bloom onset, is also likely to favor intense bloom episodes. Rainfall and freshwater inflows obviously provided a high nutrient load and decreased water salinity, as shown in the PCA. The combined action of SST and nutrient concentrations on *O.* cf. *ovata* bloom phenology has also been investigated by Accoroni et al. (2015) when studying a time-series of *O.* cf. *ovata* blooms in the Northern Adriatic Sea. These authors suggested that the bloom onset could be triggered when the SST reached a certain threshold and simultaneously coinciding with an inflow of P-riche waters which occurred after a period of relatively high N:P ratio. Similar interconnections were observed by Bucci et al. (2020) regarding the phenology of *Alexandrium catenella* blooms which occurred in the Bay of Fundy (Gulf of Maine, NW Atlantic). The study showed that the

bloom timing and the date exhibiting the maximum cell density (bloom intensity) varied between the years and suggested that both parameters could be linked to a high input of freshwater during the spring and that warmer years were likely to earlier initiate the timing of blooms. In our study, spring season hydrodynamics induced by the strength and the direction of winds did not significantly impact the variability of *O.* cf. *ovata* phenological features. This latter observation was described at least at the interannual scale, although it may play a more important role in the bloom development at the seasonal scale. However, these environmental parameters were shown to be related to high SSTs. Indeed, in the NW Mediterranean seas, wind regimes coming from the South are generally warm and thereby increase the water temperature. Our analysis also highlights the importance of the spring season regarding the phenology of recurrent summer bloom events. Even though environmental factors strongly impact the phenology of the bloom when it is occurring, less is known about how hydroclimatic parameters are affecting the bloom phenology prior to its development.

Further investigations of factors initiating the bloom revealed a strong positive correlation between cumulated SST anomalies and the starting day of the bloom. This relation confirms that *O.* cf. *ovata* blooms are likely to occur earlier in the year, when spring SST are warmer than usual. This correlation is even stronger and more significant when approaching the summer season. Indeed, from April onwards, temperature anomalies can be cumulated to predict the most favorable period for epiphytic *O.* cf. *ovata* abundances to reach the 200,000 cells g^{-1} FW threshold. However, variations in SST during the months of May and June have a strong impact on the bloom timing and may reject the prediction from April. It hence appears that the accuracy for predicting the bloom with SST parameter gets stronger when approaching the bloom event.

The occurrence of an early bloom can be explained by an early germination of resting *O.* cf. *ovata* cysts and/or by a higher division rate favored by optimal environmental conditions

for algal growth. For instance, Lau et al. (2017) showed that an intense bloom of *Alexandrium minutum,* which occurred in the northeast of the Peninsular Malaysian waters, was presumably initiated by an active excystment process. Indeed, several environmental parameters have already shown to trigger dinoflagellate cyst germination such as light exposure (Anderson et al., 1987; Moore et al., 2015), nutrient availability (Bravo and Anderson, 1994; Binder and Anderson, 2004) and a mandatory exposed period to dark-cold conditions (Montresor and Lewis, 2006). Temperature also appears to be one of the main factors controlling excystment of resting dinoflagellate cells (Anderson, 1980; Bravo and Anderson, 1994; Ní Rathaille and Raine, 2011; Moore et al., 2015) as dinoflagellate cysts require a certain SST threshold in order to induce excystment. For *O*. cf *ovata* blooms in the Mediterranean Sea, no relationship between the bloom starting date and neither SST nor nutrient concentrations was found. Instead, only cumulated temperature anomalies (illustrations of heat accumulation in surface waters) showed effects on the bloom timing. Accoroni et al. (2014) indicated that cysts of *O.* cf. *ovata,* sampled from the N Adriactic Sea, needed a temperature of 25°C to germinate, which could explain why blooms occurring in this area are observed from late summer to beginning of fall, after recording the highest temperatures. Another study conducted by Accoroni et al. (2015a) suggested that the combination of optimal temperature and Nitrate/Phosphate ratio could favor both the initiation of cell excystment and cell proliferation, therefore triggering the bloom onset. In this study monitoring *O.* cf. *ovata* blooms in the Conero Riviera (N Adriatic Sea) between 2007 and 2012, cells were never observed below 25°C prior to the bloom onset. Conversely, in Monaco, cells of *O.* cf. *ovata* have been observed at temperatures as low as 18.2°C, and blooms usually start before the maximum SSTs are reached. These variable results seem to indicate that depending on the geographical location, different SST thresholds might be necessary for triggering the cyst germination process which leads to an *O.* cf. *ovata* bloom.

463 *O.* cf. *ovata* bloom events also varied in duration and in intensity across the years.
464 During the bloom events, the highest measured abundance of epiphytic cells reached more than
465 1,500,000 cells g^{-1} FW (in 2007) while the lowest maximum abundance barely exceeded
466 200,000 cells g^{-1} FW (in 2013). The blooms lasted from less than one week (only one sampling
467 day, in 2009 and 2015) up to 4 weeks (5 consecutive sampling days, in 2011). Length and
468 intensity of blooms are the results of a balance between production of biomass (gross growth
469 rate) *versus* induction of cell quiescence (encystment) and cell loss. Diverse factors can induce
470 a limitation of microalgal growth or activation of encystment or lysis. These factors can either
471 be abiotic, such as strong hydrodynamics, nutrient depletion or extreme temperatures, or biotic
472 (e.g., grazing, parasitic interactions). Therefore, long lasting and intense bloom episodes could
473 be the result of persisting optimal hydroclimatic conditions over a long enough period which
474 enhances the production of biomass, and this combined to low biotic (grazers, parasites) and
475 abiotic (hydrodynamics) pressures which are responsible for cell loss. Temporary cyst
476 formation could be a strategy leading to maintain blooms throughout time. Indeed, *O.* cf. *ovata*
477 can form temporary cysts from vegetative cells (Accoroni et al., 2014) when biotic or abiotic
478 pressures emerge in order to overcome short periods of stress. This mechanism has already been
479 shown to help maintain blooms of other harmful dinoflagellate such as *Alexandrium taylori*
480 (Garcés, 2002). Another strategy would be the fueling of the bloom by resting cysts throughout
481 the bloom event, as observed in *Alexandrium* species (Anglès et al., 2012; Lau et al., 2017). By
482 undergoing a slow and wide excystment process, the resting cyst stock would hence
483 continuously provide new vegetative cells to the blooming population, and *in fine* enable a
484 longer bloom episode.

485 In addition to the numerous environmental factors responsible for *O.* cf. *ovata* bloom
486 phenology, part of the variability observed in bloom dynamics over the years may be the result
487 of the strong small-scale repartition of cells on the benthos. Variations observed in the *O.* cf.

488 *ovata* bloom phenology could be related to a high variability of cell abundances measured over
489 small spatial scales. Indeed, the patchy distribution of epiphytic *O.* cf. *ovata* cells, directly
490 linked to the distribution of their biotic substrate, makes the accurate estimation of the benthic
491 cell stock of a given area challenging. This has already been observed by Cohu et al. (2011),
492 who carried out the first two years of this present monitoring program, and suggested that bloom
493 phenology could be related to the spatial and temporal evolution of the diversity of biotic
494 substrates (Totti et al., 2010), as well as local hydrodynamic conditions.

495 Finally, although SST is recognized as a determinant factor for the development of
496 benthic dinoflagellate cells (Pistocchi et al., 2011; Parsons et al., 2012), *O.* cf. *ovata* abundances
497 and growth rates measured during the bloom events are also under the control of other
498 environmental parameters (Carnicer et al., 2015; Accoroni and Totti, 2016). It is generally
499 agreed that *O.* cf. *ovata* blooms are favored by low hydrodynamic conditions, since the highest
500 abundance levels are rather recorded in sheltered areas, even though blooms have also been
501 observed in exposed sites (Barone, 2007; Totti et al., 2010; Accoroni and Totti, 2016). By
502 comparing bloom events throughout the years, the PCA analysis in this present study showed
503 no straight forward relation between environmental parameters and maximum annual growth
504 rates of *O.* cf. *ovata*.
505

506 4.2.Net growth rate

507 Throughout the recurrent *O.* cf. *ovata* summer bloom episodes, the highest positive net growth
508 rates did not coincide with the highest recorded SST. This indicates that relatively high
509 temperatures are not necessarily optimal for the growth of *Ostreopsis*, at least in the Monaco
510 area. Instead, the loess regression model indicated that a moderate temperature (23.5°C) was
511 most suitable for *O.* cf. *ovata* growth. Numerous *in situ* studies have already tried to understand
512 the relation between SST and bloom development, often resulting in different conclusions

513 which seem to depend on the actual studied location (Accoroni and Totti, 2016). For instance,
514 in the NW Mediterranean Sea, the highest abundances of *O.* cf. *ovata* were recorded when
515 temperatures were either higher than 26°C (e.g., in the Ligurian Sea (Mangialajo et al., 2008)
516 and in Greece ((Aligizaki and Nikolaidis, 2006)) or below 23°C (e.g., in the Northern Adriatic
517 Sea (Totti et al., 2010; Accoroni et al., 2011)). In most of these studies, the monitored data were
518 reported as cell abundances and did not show any direct correlation between SST and cell
519 concentration (Vila et al., 2001; Totti et al., 2010; Cohu et al., 2011). On the other hand, by
520 estimating the maximum growth rate of *O.* cf. *ovata* over successive bloom events in this
521 present study focusing on the NW Mediterranean Sea, a narrower range of optimal growth
522 temperatures was defined between 21.0°C and 24.7°C. This temperature range is in agreement
523 with results obtained from laboratory scale studies, which reported that optimal growth
524 temperatures could be strain specific and part of such a strain specificity referring to a thermal
525 niche could depend on the studied area. For instance, Pezzolesi et al. (2012) showed that strains
526 collected in the Tyrrhenian Sea showed maximum growth rates at 20°C whereas highest growth
527 rates were observed at 24°C and 30°C when studying strains isolated from the Catalan coast
528 (Spain, Carnicer et al., 2016) and the Adriatic Sea (Granéli et al., 2011), respectively. However,
529 even within the same region of the Mediterranean Sea, temperature niches enabling optimal
530 growth seem to vary depending on the strain. Indeed, a laboratory study carried out by Scalco
531 et al., (2012) on strains collected in the Tyrrhenian and Adriatic seas showed that the optimal
532 temperature for algal growth was strain-specific, varying between 22°C and 26°C depending
533 on the clone. Since *O.* cf. *ovata* niche temperatures are strongly variable depending on the
534 location but also depending on the strains across Mediterranean Sea, the impact of temperature
535 on the development of blooms are likely to vary depending on local environmental parameters
536 and clonal diversity. In addition, the highest growth rates of *O.* cf. *ovata* do not coincide with
537 the highest observed SSTs, as also reported in most of the *in situ* and laboratory studies

538 conducted in the Mediterranean Sea. This suggests a more complex role of temperature
539 conditions on the phenology of the blooms than a simple increasing bloom facilitation due to
540 increasing temperature. Exceeding too high SST values might even limit the development of
541 the bloom. In the context of ocean warming, this has to be taken into account in the view of
542 implementing long-term previsions of *O.* cf. *ovata* bloom events in the future.

543 4.3.Spring SST anomalies and *in situ* thermal niche: a tool for modelers and managers

544 Relationships between the phenology of *O.* cf. *ovata* blooms and environmental parameters
545 described in this present study are of great interest for predicting and managing HABs. Indeed,
546 the correlation between spring SST anomalies and bloom timing represents a useful tool for
547 predicting future *O.* cf. *ovata* HABs in the Monaco area. Using SST data recorded during the
548 beginning of the year enabled to predict a temporal window for the beginning of a bloom event
549 which can be useful to guide the monitoring effort (Fig. 7A). The *in situ* thermal niche,
550 determined by the relationship between SST and net growth rates during bloom episodes, could
551 also be used by modelers to forecast the future evolution of both the bloom phenology and
552 distribution which can be notably impactful when facing increasing sea temperatures.

553 Modeling the dynamics of coastal HABs is crucial, especially in a context of climate
554 change where the occurrence of HABs seems to be increasing in numbers and expanding in
555 space. Many authors are trying to understand and to predict blooms of toxic dinoflagellates
556 (Maguire et al., 2016; Moita et al., 2016; Ruiz-Villarreal et al., 2016) and toxic cyanobacteria
557 (Hamilton et al., 2009; Rigosi et al., 2015) by using models based on ecological observations.
558 Until now, the accuracy in modelling and predicting such complex phenological events seems
559 to be limited by the lack of available data describing both the species itself and the
560 environmental parameters, but also by the numerous pending questions regarding the ecology
561 of *O.* cf. *ovata* (Asnaghi et al., 2012). Although our study provides data on the actual
562 temperature niche of *O.* cf. *ovata* in the NW Mediterranean Sea and the relations between the

563 bloom phenology and spring SST temperatures, more models describing *O.* cf. *ovata* blooms
564 still need to be designed, improved and adapted to local environmental variables in order to
565 minimize the risks to be exposed to such events. The determination of the thermal niche of *O.*
566 cf. *ovata* in the NW Mediterranean Sea could help forecasting potential long-term variations in
567 the phenology of the blooms but also a possible evolution of the distribution of blooms. On the
568 other hand, the short-term prediction of bloom timing could provide a substantial support to
569 local sanitary authorities in charge of toxic outbreaks, as this could be used to estimate potential
570 risks of exposure weeks before the beginning of the bloom and hence to gain precious time for
571 deploying management strategies.

572 Regarding the impact of climate change, many studies consider global warming as a
573 potential enhancement factor for benthic HABs species to expand their geographical areas,
574 increase the seasonal occurrences and bloom windows (Wells et al., 2015; Gobler et al., 2017;
575 Nakada et al., 2018; Gobler, 2020; Tester et al., 2020). In the Mediterranean Sea, climate
576 projections foresees an increase in SSTs, with an average of 0.45°C per decade by 2050
577 (Alexander et al., 2018). Geographical expansion towards higher latitudes in the Mediterranean
578 Sea is not possible, since *O.* cf. *ovata* is already found in the northern parts of the NW
579 Mediterranean Sea. Moreover, an increase in SST temperature may not necessarily result in
580 more intense blooms since this present study has shown that the highest SSTs do not coincide
581 with the highest growth rates. Therefore, the assumption that ocean warming shall favor the
582 development and the expansion of *O.* cf. *ovata* species and blooms in the future, seems more
583 complex than previously thought. On the other hand, global warming could favor an earlier
584 bloom, as optimal temperature conditions would be reached earlier in the season. Global
585 warming is not the only consequence of climate change and more specific studies between *O.*
586 cf. *ovata* and future ecological conditions in the Mediterranean Sea are needed.

587

5. Conclusion

The phenology of *O.* cf. *ovata* blooms is governed by a complex assemblage of environmental factors and is still lacking specific knowledge able to describe how these environmental parameters interact and affect the progress of toxic blooms. The present study is based on a 13-year time-series of *O.* cf. *ovata* blooms in Monaco and reveals that part of the interannual variability of bloom phenological features, such as the bloom timing and the maximum intensity of the bloom, could be explained by a combination of environmental parameters, including SST and nutrient concentrations, especially during the spring season. The optimal growth temperature which favors the *O.* cf. *ovata* blooms in Monaco waters has been estimated between 21°C and 25°C. In addition, this study revealed a clear relation between spring SSTs and the timing of the bloom of *O.* cf. *ovata* occurring in the NW Mediterranean region. By processing data from this longest time series dedicated to *O.* cf. *ovata* blooms, results suggest that the accumulation of positive SST anomalies induces an early start of the bloom. Considering the increasing trend of SST observed worldwide, due to global climatic changes, such results could be of a great interest for the prediction and management of *O.* cf. *ovata* blooms in recreational waters. Further data collection in the scope of this time series is needed to improve the present knowledge and to deepen investigations regarding the effect of combined environmental parameters on *O.* cf. *ovata* bloom phenology.

Authors' contribution

K.D., A-S.P., S.M. V.D-S. and R.L. designed and contributed to the conduction of the monitoring campaign. K.D., A-S.P. and S.M. analyzed the samples. K.D. and S.G. designed and performed the modelling and statistical analyses. K.D., S.G., E.B., C.J., R.S. and R.L. analyzed the results and prepared the figures. K.D. and R.L. wrote the first version of the manuscript. All authors reviewed and accepted the final version of the manuscript.

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Figure 1

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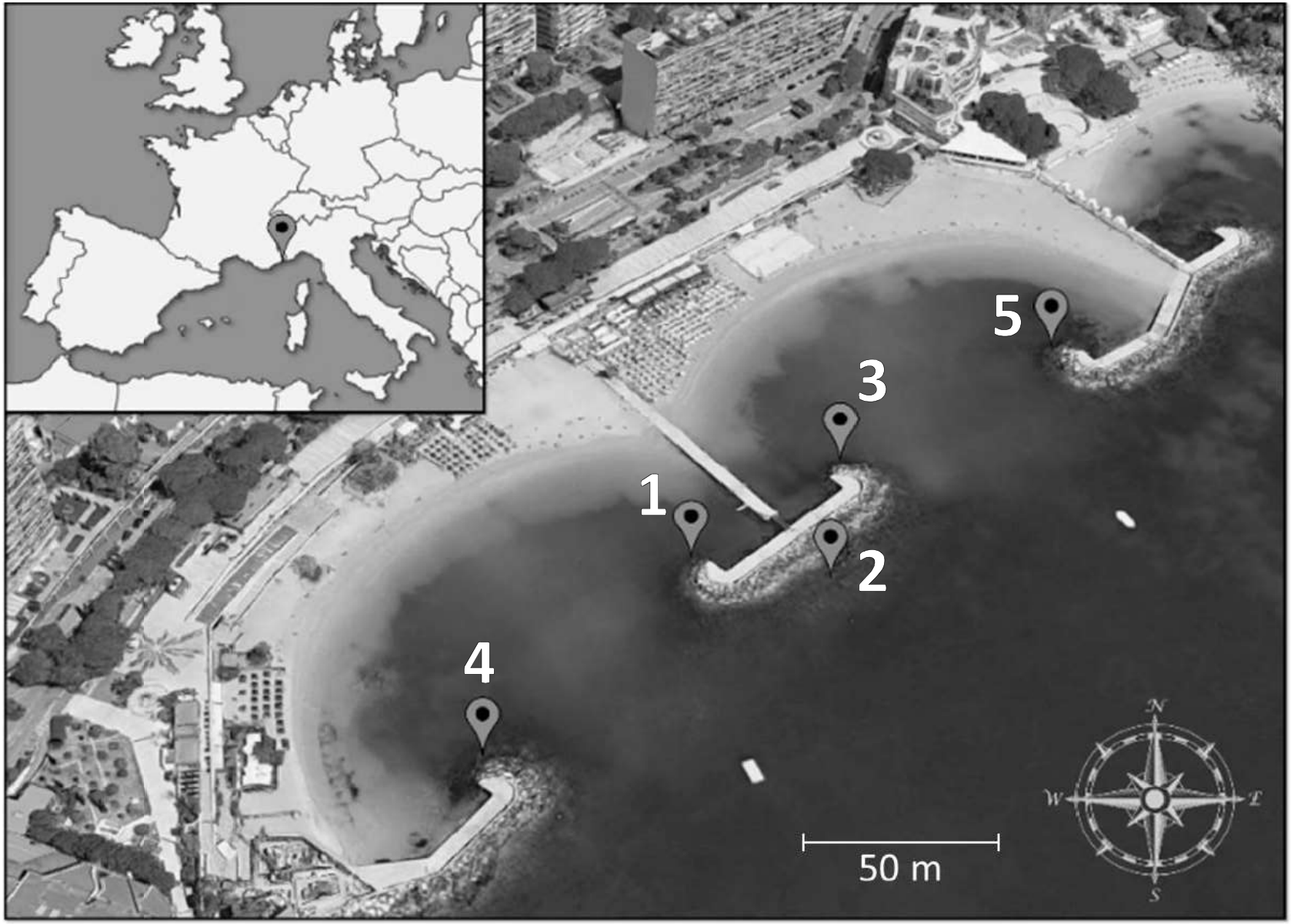

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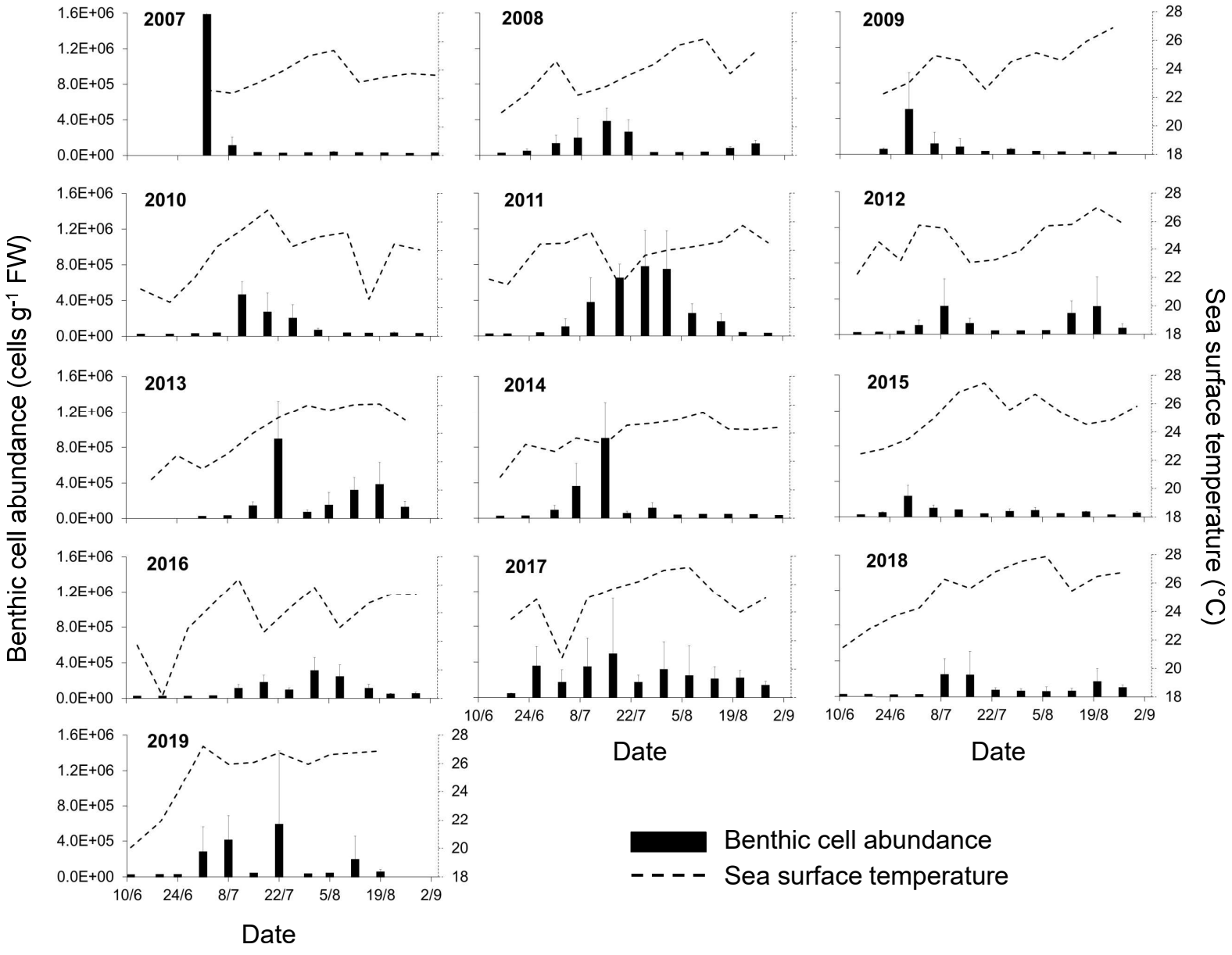

Figure 3

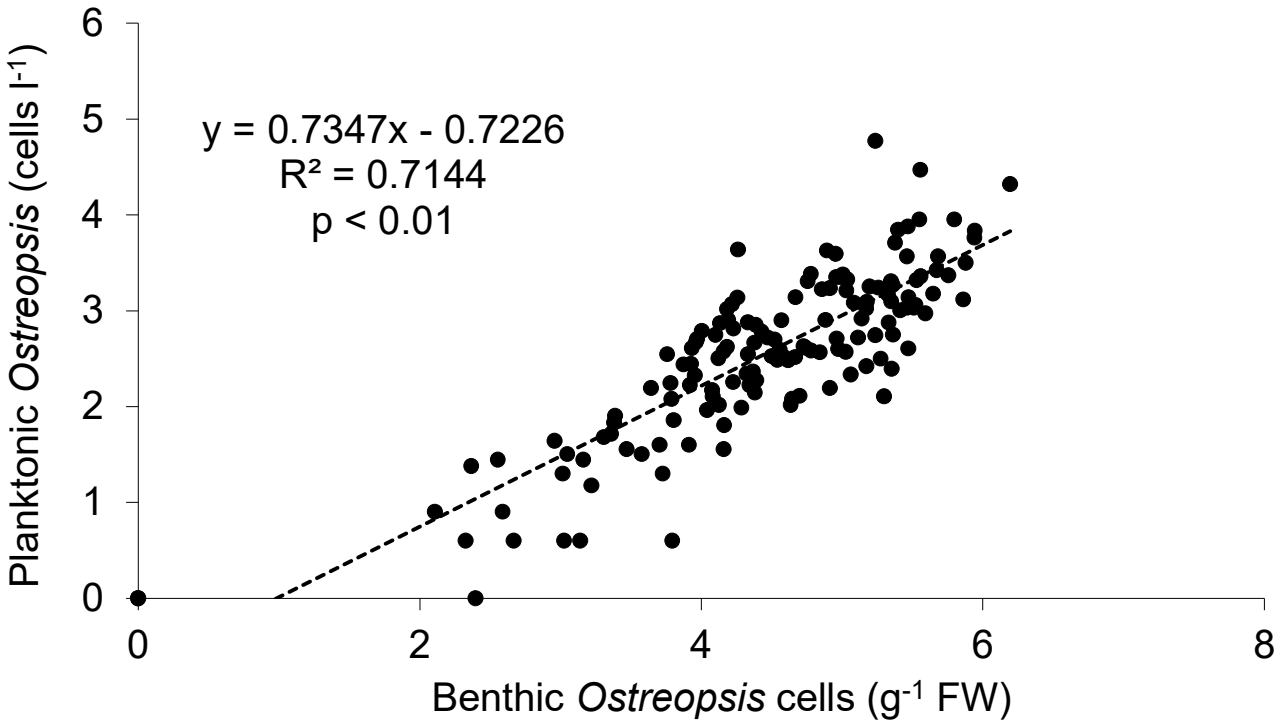

Figure 4

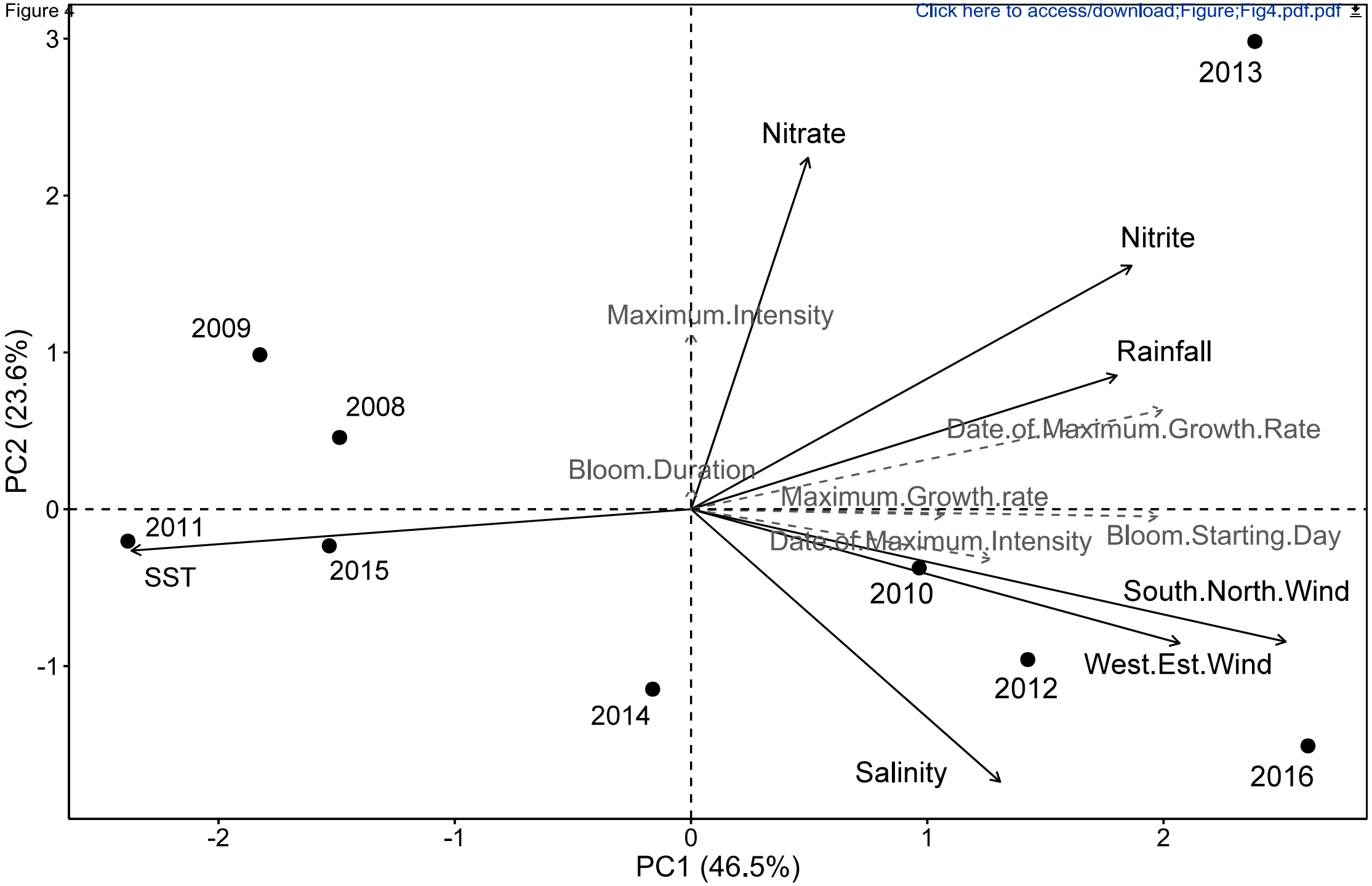

Figure 5

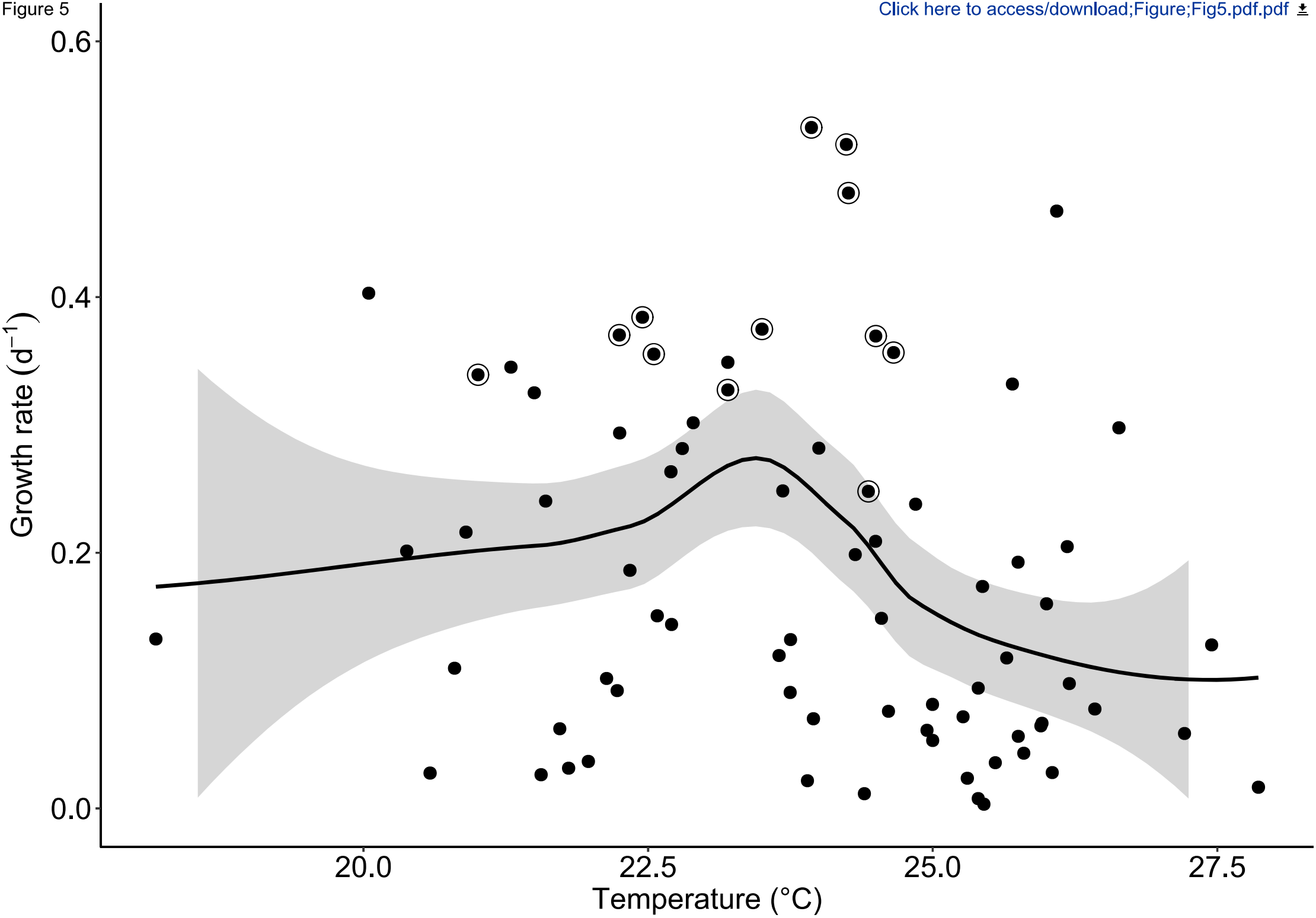

Figure 6

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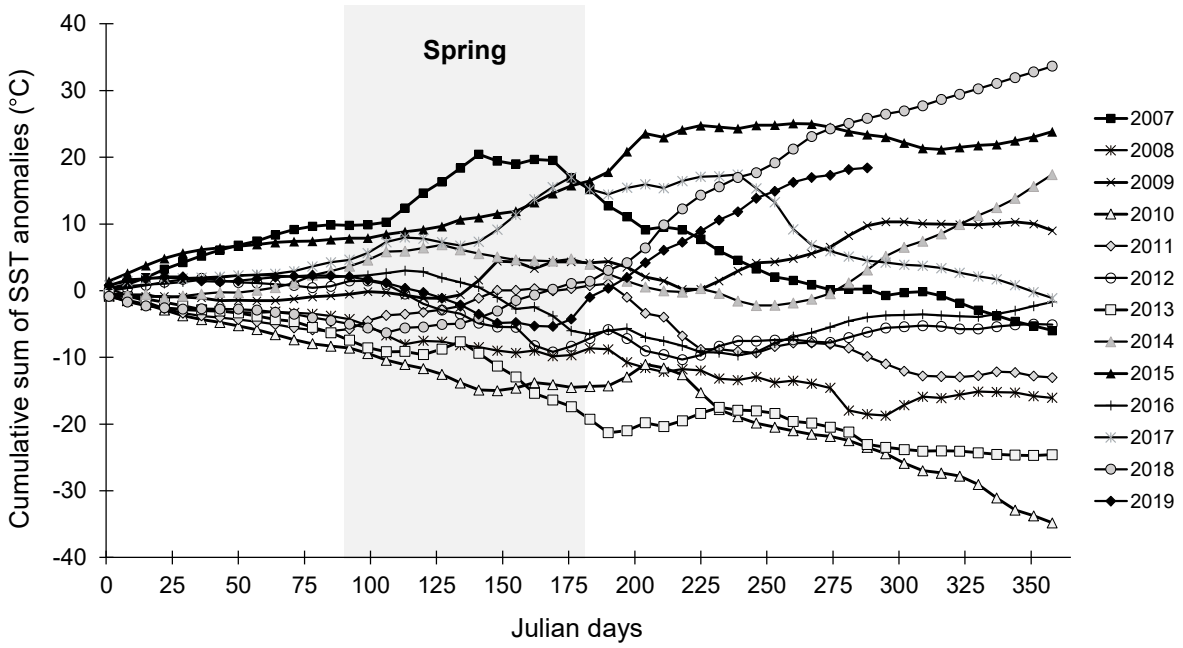

Figure 7

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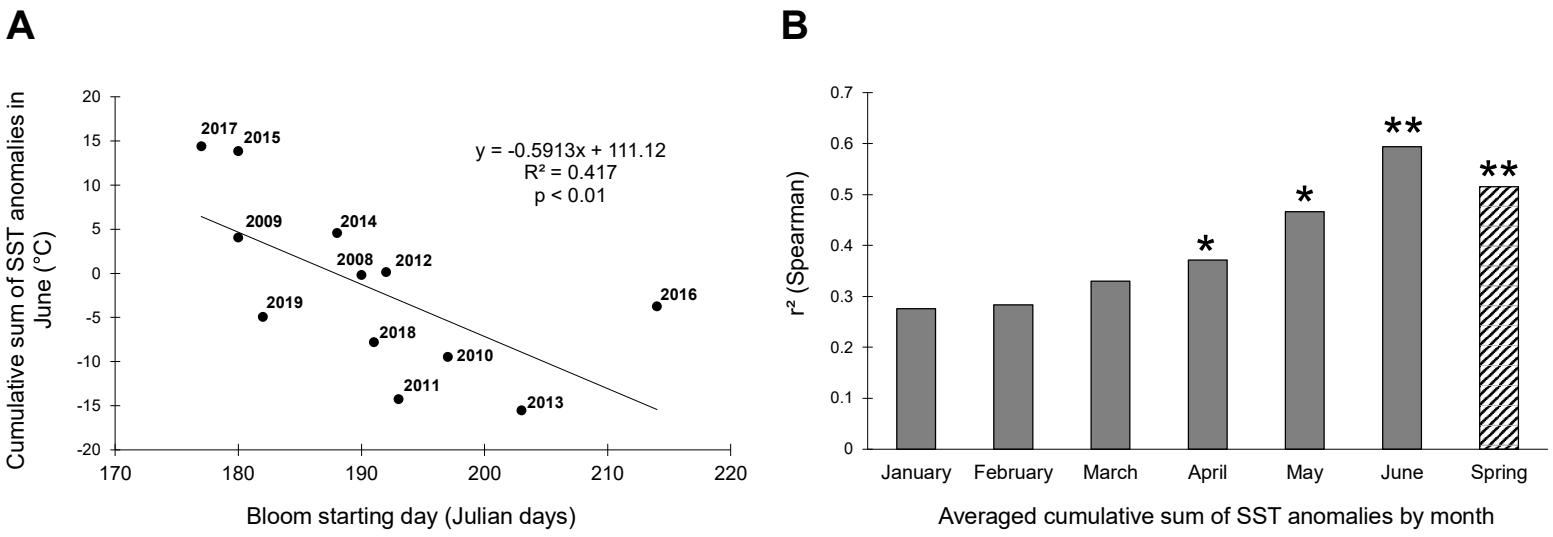

Supplementary Material 1

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☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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