



# Unusual coccolithophore blooms in Scottish waters

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Abstract. Two unusual blooms were observed in Scottish waters during summer 2021. One was in the Clyde Sea and the other by the east coast of the Shetland Islands. Both had the appearance of coccolithophore blooms. Transmission electron microscopy of a sample from the Clyde Sea confirmed the presence there of the coccolithophore *Emiliania huxleyi*. We examine the conditions that led to these unusual blooms. In situ data are scarce and so we draw inference from satellite data and

- 5 reanalysis. For Shetland, the bloom can be seen to originate further north on the edge of the continental shelf. It is advected south and then west towards the Shetland coast by surface currents exceptionally from the east. For the Clyde Sea region, April 2021 was on average the coldest weather of the last 30 years (National Climate Information Centre). We hypothesize that the cold restricted the usual spring bloom of diatoms. A restricted spring bloom would mean higher than usual concentrations of nutrients in the summer. It might also mean reduced numbers of predators. These factors would provide ideal conditions for
- 10 coccolithophores to flourish as temperatures and sunlight increase.

## Short summary

There were two unusual blooms in Scottish waters in summer 2021. Both turned the sea a turquoise colour visible from space, typical of coccolithophore blooms. We use reanalysis and satellite data to examine the environment that led to these blooms. We suggest unusual weather was responsible in both cases.

## 15 1 Introduction

Summer 2021 saw milky, turquoise coloured waters caused by algal blooms in two locations off Scotland, in the Clyde Sea on the west coast, and also to the east of the Shetland Islands (Fig. 1). These blooms were visually striking and so unusual that they were reported in the news (Bradshaw, 2021). Transmission electron microscope analysis of a water sample from the Clyde (Fig. 1(d)) confirmed the algae to be a morphotype of coccolithophore, *Emiliania huxleyi* (morphotype B). Blooms of

20 this organism are common in spring and early summer in the North Atlantic, and occur in some years in the northern North Sea and the western English Channel. However, coccolithophore blooms which discolour water to this extent are uncommon on the west coast of Scotland, and this is thought to be the first such bloom in the Clyde Sea since 1983.





Coccolithophores belong to a diverse group of phytoplankters (class Prymnesiophyceae) that is widespread in the oceans. The ecological group that includes *Emiliana* is particularly abundant in upwelling and temperate sub-polar regions (Balch

- et al., 2019). Most coccolithophores are not themselves harmful or toxic but they are of ecological importance, particularly for carbon cycling and sequestration (Rost and Riebesell, 2004). They typically produce an exoskeleton consisting of several calcium carbonate plates called coccoliths (Young et al., 1999). These coccoliths are not opaque (phytoplankton require light for photosynthesis) but they scatter and polarise light. The visual effect is to turn the sea a milky turquoise colour, visible to the human eye and in satellite imagery.
- 30 The function of the coccoliths is unclear. They are believed to be protective, either against grazing, against viral or bacterial attack, or as a refractor of light that acts as a sunshade in excessively bright conditions (Monteiro et al., 2016). Müller (2019) suggests that coccolith production may have evolved originally as an efficient mechanism for intracellular  $Ca^{2+}$  detoxification at a time of elevated seawater  $Ca^{2+}$  concentrations (e.g. during the Cretaceous and Jurassic periods).

The conditions that gave rise to these blooms may be indicators of change that will also be relevant to harmful algal blooms, and to the marine ecosystem more generally. In this paper we use observations and reanalysis data to look for unusual environ-

mental conditions that might have allowed these blooms to thrive in Scottish waters.





## 2 North West Shelf reanalysis

The NWS reanalysis (product ref 1 & 2) is a coupled physical and biogeochemical reanalysis for 1993 onwards at 7km horizontal resolution, 51 vertical levels, for a domain that encompasses the North-West European Shelf (Kay et al., 2020). It
uses the physical ocean model NEMO (Madec and Team, 2008) with tides and the biogeochemical model ERSEM (Butenschön et al., 2016). The atmospheric forcing is given by the ERA5 atmospheric reanalysis (Hersbach et al., 2018). The river discharge for years 2018 onwards is from a daily climatology.

ERSEM simultaneously describes pelagic and benthic ecosystems in terms of phytoplankton, bacteria, zooplankton, zoobenthos and the biogeochemical cycling of carbon, nitrogen, phosphorus and silicon. ERSEM uses a functional group approach to

- 45 describe the ecosystem, whereby biota are grouped together according to their trophic level (subdivided according to first size, then trophic role and finally feeding method). Four functional groups of phytoplankton are included, three of zooplankton and one of bacteria. The four Plankton Functional Types (PFTs) are:
  - P1: diatoms, 20-200  $\mu$ m with an affinity for silica
  - P2: nanophytoplankton, 2-20  $\mu$ m
- 50 P3: picophytoplankton,  $0.2-2 \,\mu m$ 
  - P4: flagellates, 20-200  $\mu$ m without silica requirements

The P2 class allows for calcification and so includes coccolithophores. The reanalysis uses NEMOVAR (Mogensen et al., 2012) to assimilate observations of physical variables (satellite SST, in situ temperature and salinity profiles (Waters et al., 2015)). From September 1997 onwards it also assimilates observations of chlorophyll-a partitioned between the 4 PFTs, estimated from ocean colour satellite data (Skákala et al., 2018)).

In data assimilation, the model is adjusted towards the observations. Both observations and model are prone to errors and so the reanalysis does not aim to fit the observations exactly. How closely it fits depends on the statistical errors specified for observations and for model values. The observations here are estimates of chlorophyll-a from the OLCI instrument. The estimation process masks for various factors which could corrupt the estimates, including cloud, sun glint, and coccoliths (OC-

60 CCI, 2020). This means there are few data available for the Clyde during the period of the bloom (12 June to 7 July) and that those data should be treated with caution.

#### 3 Shetland bloom

Figure 1 shows a bloom on the eastern side of Shetland. There is no information on the species present but the satellite imagery has a distinctive appearance associated with coccolithophores. The feature is visible in satellite imagery over the period 26

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June to 15 July 2021. Blooms in the North Sea and as far north as Shetland are not unusual. Satellite imagery (not shown) reveals extensive blooms to the east of Shetland in June 2019 and June 2020. Typically, coccolithophore blooms in the North



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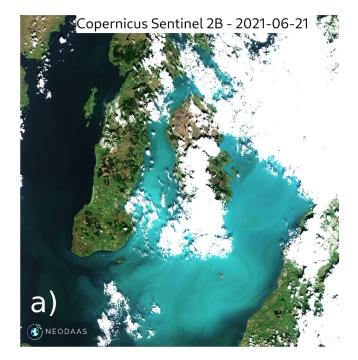


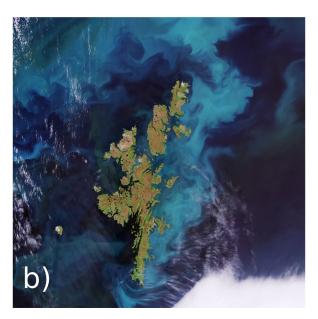
Sea develop to the south of Shetland and are advected by the overall anti-clockwise circulation in the North Sea. They are often visible on satellite imagery in June and July (Kondrik et al., 2019). To the north of Shetland, the continental shelf break is marked by the European Slope Current, an intense eastward-flowing jet bringing North Atlantic water into the Norwegian Sea. Some of this water flows south around the western and eastern sides of Shetland. To trace the origin of the bloom, the

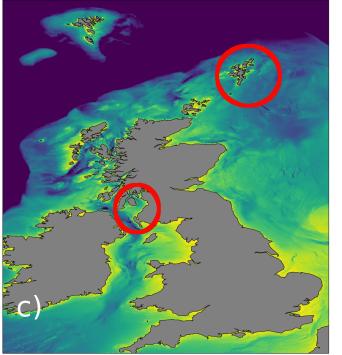
- *OceanParcels* software package (Delandmeter and van Sebille, 2019) was used to advect particles backwards in time from the date and region of the bloom. The advection was driven by daily mean currents from the NWS reanalysis (product ref 1). Figure 2(c) shows virtual particles positioned at approximately the location of the Shetland bloom on 3 July 2021. In Fig. 2(b) and Fig. 2(a) those particles are advected backwards to 18 June and 2 June respectively. These appear to confirm it is the Slope
- 75 Current that brought the bloom to the east of Shetland. This is consistent with the satellite imagery in Fig. 2, where a much larger bloom is seen upstream to the north-east of Shetland.











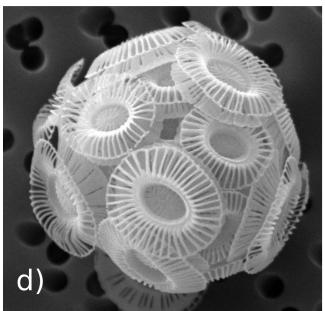


Figure 1. (a) Sentinel-2 MSI image of Clyde Sea on 21 June 2021 11:35 UTC, True Colour with enhanced contrast. Processed by NEODAAS, using ACOLITE atmospheric correction. (b) Sentinel-2 MSI image of Shetland Islands on 1 July 2021, processed by ESA https://www.esa.int/ESA\_Multimedia/Images/2021/11/Shetland\_Islands (c) Bathymetry map with locations of (a) and (b) marked in red. Shelf edge is visible as transition from light blue (less than 200 m depth) to dark blue (deep water). (d) Scanning electron micrograph of sample from the Clyde, June 2021, identified as *E. huxleyi* Morphotype B. Credit: Eileen Bresnan (Marine Laboratory, Aberdeen)





An unusual feature of the 2021 bloom was that it came so close inshore. Examination of imagery for years 2017 to 2020 provided by PML and of a dataset of coccolithophore blooms for 1998 to 2016 in Kondrik et al. (2019) finds no other examples where blooms intrude among the islands and bays on the eastern side of Shetland. May 2021 saw anomalously low atmospheric
pressure over the UK (Weather Magazine, b) bringing easterly winds to the north of the UK. These winds brought cold air over the North Sea and Scotland, consistent with cold SST that month (Fig. 3). The winds also drive surface currents which were, unusually, easterly to the east of Shetland in the NWS reanalysis in May 2021 (Fig. 3). We suggest these anomalous currents brought coccolithophore laden water close inshore.

## 4 Clyde Sea bloom

- The Clyde Sea comprises a large tidal estuary with several islands and fjord-like sea lochs. It is the outlet of the River Clyde and other rivers into the Irish Sea. It has a maximum depth of 164m, with a sill (the 'Great Plateau') of approximately 40m depth where it meets the Irish Sea. Freshwater outflow from rivers and from land drainage tends to maintain stable stratification in the basin (Simpson and Rippeth, 1993). This together with the sill restricts tidal mixing to mostly near-surface waters. Edwards et al. (1986) estimate a residence time of 2 months for surface water in the Outer Firth. Nutrient content in the Clyde tends to
- 90 be higher than adjacent coastal waters (based on measurements of nitrate, in Slesser and Turrell (2013). Tidal currents within the Clyde Sea tend to be weak. Water in the deeper waters below the sill can stagnate, leading to nutrient build-up near the sea bed. Simpson and Rippeth (1993) show that strong winds can sometimes overcome the vertical stability and mix the water column.

### 4.1 Annual cycle of diatoms in the Clyde Sea

95 Marshall and Orr (1927) sampled the Clyde Sea and its lochs extensively, finding that

"There is a well-marked spring diatom maximum which starts at the end of March or the beginning of April."

They also observed a second, smaller, summer maximum but noted that diatoms near the surface were less healthy than those several metres deeper. Tests with samples left in direct sunlight and in shade showed that summer light levels were injurious for these diatoms.

- 100 Hannah and Boney (1983) assessed extensive and more recent surveys (1976-1978) of the Inner Firth. They found rapid growth in diatoms from late March or early April in each year of the study, dominated by *Skeletonema spp.* and *Thalassiosira nordenskioldii*. They also found *Nitschia seriata* (now called *Pseudo-nitzschia 'seriata* type') and *Chaetoceros spp.* at those times present in considerable numbers. During these spring blooms total chlorophyll was dominated by diatoms. For 1977 they found evidence that the *Skeletonema* were being grazed by microzooplankton (*Ebria*). Bresnan et al. (2016) also report an
- 105 intense spring bloom dominated by *Skeletonema* during the monitoring period 2005-2013.





### 4.1.1 Timing and source of 2021 Clyde bloom

Figure 1 shows the Clyde bloom on 21 June 2021. There are earlier visual reports of bright patches in the sea around the Isle of Arran in the centre of the Clyde Sea on 12 June (Evers-King et al., 2021). Enhanced colour imagery from SENTINEL-3 OLCI imagery reveals nothing significant for that day but is much obscured by cloud. Imagery for 13-16 June is almost wholly 110 obscured by cloud, and the first clear satellite image of a bright patch across the whole of the Clyde Sea is from 18 June (Fig. 2(b)). This bright patch persists until 5 July and then fades. Figure 2(c) shows that by this time the bloom is apparent even in the northernmost reaches of Loch Fyne. This sea loch flows into the Clyde Sea but is tidal along its 65km length.

Figure 2(a) shows virtual particles from the Clyde Sea on 18 June (Fig. 2(b)) advected backwards in time to 2 June. Some of the particles stay within the Clyde Sea. Other particles appear to have originated from further south in the Irish Sea. The

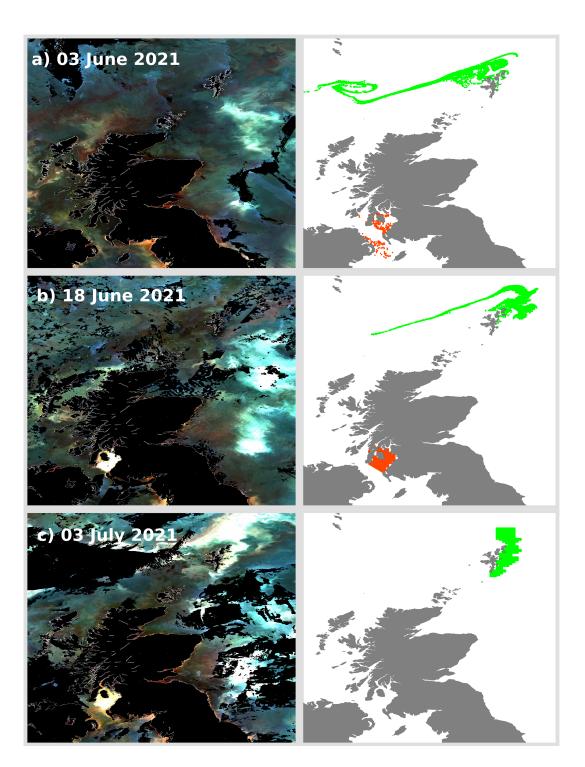
satellite image in Fig. 2(a) reveals no plankton features within the Clyde Sea itself on 2 June but several bright patches in 115 the Irish Sea at that time, indicating the presence of significant concentrations of plankton. It is possible that E. huxleyi was introduced by tidal mixing into the Clyde from the Irish Sea, or that it was already resident in small quantities. The satellite imagery shows the bloom mostly confined to the Clyde Sea. We conclude that conditions within the Clyde basin in early June were particularly favourable for the bloom to thrive in place. We aim here to understand exactly which aspects were favourable and what brought them about. 120

## 4.1.2 Physical environment in 2021 & 1983

Figure 4(a) shows daily values of Sea Surface Temperature (SST) from the NWS reanalysis for a point central in the Clyde Sea, for years 1998-2021. June 2021 values are in the middle of the range. Values for April and May are towards the cold end of the range. Statistics from a high-resolution satellite SST product in Table 1 (product ref 4) confirm this. Monthly means for April, May and June 2021 are, respectively, at the 10<sup>th</sup>, 5<sup>th</sup> and 52<sup>nd</sup> percentiles for those months over the period 1982-2021.



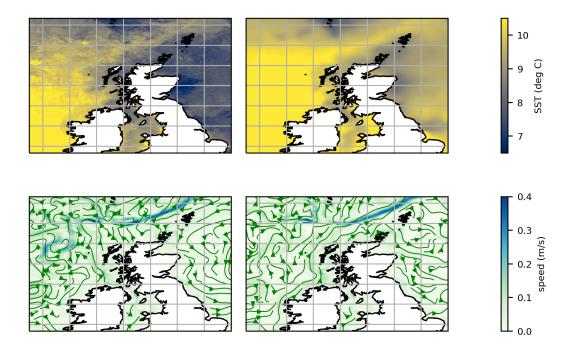




**Figure 2.** Left-hand side: Enhanced ocean colour satellite imagery (provided by PML, product ref 5) from SENTINEL-3 OCLI instrument for dates 3 June 2021, 18 June 2021, 3 July 2021. The brightest pixels are indicative of high numbers of coccoliths. Right-hand side: simulation for the same dates, using particles advected backward in time from the Clyde (orange, 18 June 2021) and from Shetland (green, 03 July 2021)







**Figure 3.** Top: Sea surface temperature monthly mean from CMEMS high-resolution L4 data (product ref 4). Left is May 2021 from near real-time product. Right is 1983-2020 climatology for May from reprocessed product. Bottom: surface current for May from reanalysis (product ref 1). Left is May 2021, right is 1983-2020 May climatology.





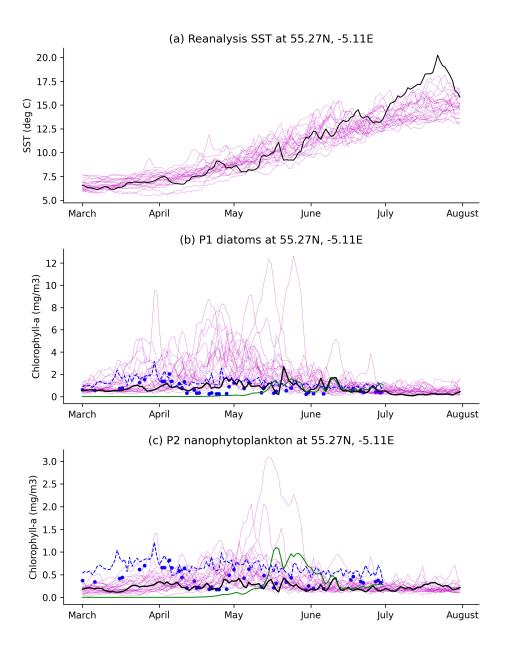


Figure 4. Daily mean values of (a) sea surface temperature (product ref 1) and chlorophyll concentrations (product ref 2) for (b) P1 diatoms, (c) P2 nanophytoplankton. Black line is daily mean values from the NWS reanalysis for 2021. Magenta lines are reanalysis values for the same days in the years 1998-2020. Blue dots are observations of PFT chlorophyll for 2021 from ocean colour data (product ref 3). Dashed blue line is mean values of the observations for the years 1998-2020. Green line is 2021 values from a version of the reanalysis not assimilating the PFT chlorophyll observations.





**Table 1.** Statistics of monthly means from (a) CMEMS European area level 4 SST analysis at 55.27° N, 5.11° W, and (b,c,d) from weather stations in Clyde catchment area (National Climate Information Centre)

a) Sea surface temperature 1983				2021		
	monthly mean (° C)	anomaly (° C)	percentile	monthly mean (° C)	anomaly (° C)	percentile
April	7.93	-0.25	25%	7.53	-0.65	10%
May	9.70	-0.31	22%	8.81	-1.20	5%
June	11.65	-0.54	17%	12.24	0.05	52%
b) Air temperature 1983			2021			
	monthly mean (° C)	anomaly (° C)	percentile	monthly mean (° C)	anomaly (° C)	percentile
April	4.9	-2.0	4%	5.5	-1.4	10%
May	8.4	-1.4	7%	8.4	-1.4	10%
June	11.6	-0.8	26%	13.4	1.0	83%
c) Sunshine hours 1983				2021		
	total	% of climatology	percentile	total	% of climatology	percentile
April	134	90%	38%	236	159%	100%
May	114	60%	5%	151	80%	19%
June	154	98%	59%	174	111%	76%
d) Rai	d) Rainfall 1983			2021		
	total (mm)	% of climatology	percentile	total (mm)	% of climatology	percentile
April	57	73%	28%	16	20%	5%
May	104	124%	69%	96	115%	64%
June	73	82%	36%	42	47%	12%

Anomalies and percentiles are relative to yearly climatology: (a) SST is CMEMS reprocessed level 4 satellite product 1982-2020, (b,c,d) Weather station data are for Clyde catchment area from NCIC for 1980-2021

Table 1(a) includes statistics for 1983, the previous year that such a bloom was seen in the Clyde Sea. SST in April, May and June 1983 was colder than average, with values at the 25<sup>th</sup>, 22<sup>nd</sup> and 17<sup>th</sup> percentiles respectively. The cold SST for both years can be linked to the weather at the time. Table 1(b,c,d) shows weather data for these months in 2021 and 1983, averaged for a set of land-based weather stations chosen by the National Climate Information Centre (NCIC) to represent the Clyde catchment area. For 2021, April and May were unusually cold, but June was warmer than average. April was exceptionally sunny and dry. 1983 and 2021 have in common a cold and dry April, a cold, cloudy and wetter than average May, and a dry June. In both years, May was a month of storms and high winds (Weather Magazine, b, a). The two years differ in that 2021 had a sunny April and a warm June. In 1983 April had average sunshine and June was colder than average.





## 4.1.3 Additional data for 2021 from reanalysis and observations

- 135 Figure 4 shows reanalysis daily values of SST and also of chlorophyll from the ocean colour product for plankton functional types P1 (diatoms) and P2 (nanophytoplankton). These are for a point in the central Clyde Sea (55.27° N, 5.11° E, as for Table 1). Values are shown for 2021 and also for the years 1998-2020. The black line is the 2021 reanalysis, and the green line a 'free run', which is the 2021 reanalysis without assimilation of PFT chlorophyll. The values of the observations are also plotted (product ref 3), as blue dots (2021) and as a blue dashed line for the 1998-2020 daily average.
- For P1, the 1998-2020 reanalysis has spring growth starting variously between end of March to mid May, reaching values between 2 and 10 mg m<sup>-3</sup>, with some later peaks much higher. Observed values for 2021 show limited growth at the end of March and then a decline from early April, as SST cools. Values increase in May to no more than average (2 mg m<sup>-3</sup>). The reanalysis has low values from March to mid-May, and the free run even lower. The reanalysis doesn't rise as far as the observations, but does achieve a compromise between the observations and the free run. ERSEM would appear to expect low growth of diatoms given the environmental conditions. The observed values in April are consistent with that.

For P2, observations peak at around  $1 \text{ mg m}^{-3}$  from mid March to mid April, dip, and then rise to around  $0.7 \text{ mg m}^{-3}$  from late April to mid May, appearing to follow the rise in SST. The free run starts with low values, rises sharply in mid May to around  $1.0 \text{ mg m}^{-3}$ , and falls again in mid June. The reanalysis starts March with values around  $0.2 \text{ mg m}^{-3}$  and stays within  $\pm 0.2 \text{ mg m}^{-3}$  of this for the whole period March to July. In most other years, the reanalysis peaks rather higher ( $0.5 \text{ mg m}^{-3}$ )

150 or higher) at some point in April or May, with 3 years reaching  $2.0 \text{ mg m}^{-3}$  or more. The reanalysis and free run in 2021 do not track the observations closely. Sharp rises in the free run coincide with two storms that passed over northern UK, one on 9, 10 and 11 May and a stronger one on 20 and 21 May. The first storm also appears to cause a rise in P2 for the reanalysis, and a pause in the rate of increase for SST. This suggests the winds are mixing the water column. The second storm coincides with a dip in SST, again consistent with mixing.

#### 155 4.1.4 Diversity of the Clyde bloom

Transmission electron microscopy of a sample from Millport collected at the end of June revealed the bloom to be comprised of liths and cells of *E. huxleyi* - morphotype B (Fig 1(d)), providing the first confirmation of this species in high abundance at this site. *E. huxleyi* morphotypes A and B have been recorded in the waters around Scotland (van Bleijswijk et al., 1991; León et al., 2018). Little is known about the seasonality of *E. huxleyi* morphotypes on the west coast of Scotland. A study at

160 the Marine Scotland Scottish Coastal Observatory (SCObs) monitoring site at Stonehaven on the east coast from 2010-2013 showed a distinct repeated seasonality in the occurrence of different *E. huxleyi* morphotypes (León et al., 2018). Morphotype B was commonly recorded in spring with morphotype A occurring from June to August followed by an overcalcified form of morphotype A (type AO) in autumn and winter months. The dominance of *E. huxleyi* morphotype B in the 2021 Clyde bloom differs in timing from the seasonality recorded on the east coast.





#### 165 4.1.5 Possible causes of Clyde bloom

Mayers et al. (2019) assessed coccolithophore growth and mortality rates based on samples from the Celtic Sea in April 2015. They identified several conditions that favour coccolithophore blooms. These are considered individually below.

- a) Warm, stratified waters SST in June 2021 was close to average for that month (Table 1(a)). June 1983 was unusually cold.
   Vertical profiles of temperature from the reanalysis for 2021 (not shown) are stably stratified but this is typical for June.
- 170 Conclusion: not likely to be a contributory factor for 2021 and even less so for 1983
  - **b**) Sunlight June 2021 was sunnier than average (76<sup>th</sup> percentile, Table 1(c)). June 1983 was close to average.

Conclusion: Sunshine might have been a contributory factor in 2021.

- c) Availability of nutrients We have no direct measurements of nutrients in the Clyde Sea. Reanalysis estimates are of limited use because the reanalysis relies on a climatology for river inputs. Rainfall (and so river flow) in April 2021 and 1983
   175 was much less than climatology (Table 1(d)), which would tend to limit diatom growth in the spring. Rainfall in May was above average for both years. May was also a stormy month for both years, which may have mixed the water column, bringing nutrients from deep water into the photic zone (Pingree et al., 1977). Each of these factors could lead to higher
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at the end of May.

Conclusion: Observations show low chlorophyll mass in spring 2021. This can be explained by the cold air and water temperatures in April 2021, also seen in April 1983. The wet and stormy conditions in May of both years likely increased nutrient levels in near-surface layers in the Clyde. Both these factors would help produce suitable conditions for a bloom.

than usual nutrient availability by the end of May. The observations of chlorophyll and the reanalysis both suggest lower than usual diatom growth in April and May 2021 (Fig. 4). This would also lead to higher than usual nutrient availability

d) Scarcity of predatory microzooplankton Mayers et al. (2019) found that microzooplankton exert strong top-down control
 on coccolithophore populations, grazing up to 80% of daily production in a bloom of *E. huxleyi*. We might hypothesise that fewer diatoms in April and May led to low numbers of microzooplankton during that time, reducing the grazing pressure on *E. huxleyi* in late May and early June. However, growth rates for microzooplankton can be rapid, sometimes more than 3 doublings per day for tintinnids (Verity, 1986).

Conclusion: This could be a contributory factor. We have no evidence. The ability of microzooplankton to multiply rapidly suggests at least that other factors were also involved.

## 5 Discussion

Phytoplankton are of special interest in the waters around Scotland, where aquaculture and fishing are major industries. Through primary production, phytoplankton form the base of a food chain that sustains marine fauna (Frederiksen et al., 2006). Blooms of phytoplankton can be harmful to other marine life and can produce toxins dangerous for human consumers





195 of seafood (Davidson et al., 2011). There is thus increasing interest from policy makers to understand the diversity dynamics of phytoplankton communities in Scotland and other parts of the North West European Shelf (NWS) to understand its influence on industries and diversity status assessments (Siemering et al., 2016; McQuatters-Gollop et al., 2019).

This paper presents hypotheses to explain two unusual blooms. We suggest that the bloom on the eastern side of Shetland originated in Atlantic water brought north of Shetland by the Slope Current, and then steered towards the coast by surface

- 200 currents which were driven by anomalous easterly winds. The bloom within the Clyde Sea appears to have developed in place. We suggest that environmental factors may have combined to create suitable conditions in the Clyde Sea. A cold and dry April could have restricted spring growth of diatoms, leaving nutrients available for a summer bloom of coccolithophores. A wet and stormy May might also have added to the nutrients. Most of these conditions (all but the dry April) were also present in 1983, the last time there was such a bloom.
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- 5 Our suggestions are based on limited evidence (SST and chlorophyll estimates from satellite, modelling by the reanalysis). We do not have in situ measurements from within the blooms to confirm some aspects of our hypotheses.

For both blooms, we propose the weather as a key factor. Other studies also identify the importance of the weather for algal blooms. Whyte et al. (2014) looked at unusually strong blooms of the biotoxin-producing dinoflagellate *Dinophysis* on the western side of the Shetland Islands in the summers of 2006 and 2013. They found these blooms coincided with periods where

210 the winds, usually more southerly, became westerly. They suggested the westerly winds advected *Dinophysis* populations onshore resulting in an increase in Diarrhetic Shellfish Toxin levels in farmed mussels (*Mytilus edulis*).

There is evidence that the distribution of coccolithophores has expanded polewards in recent decades (Beaugrand et al., 2013; Winter et al., 2013; Rivero-Calle et al., 2015), due either to changes in ocean temperature or dissolved inorganic carbon. Changing weather patterns have the potential to influence the occurrence of unusual phytoplankton blooms in coastal waters.

215 These changes have the potential to impact higher trophic levels in the marine ecosystem. A better understanding of the processes and dynamics involved will help in forewarning, preparation and development of adaptation measures for these changes.

Data availability. Data used was as listed in Table 2. Nearly all data are publicly available from the websites referenced there.

Author contributions. R. Renshaw processed the reanalysis data and wrote much of the text. E. Bresnan produced the micrograph of the
 220 *E. huxleyi* sample. P. Miller produced the ocean colour images. Every author contributed to discussion and development of the hypotheses presented. Every author also added to and reviewed the text.

Competing interests. The authors declare that they have no conflict of interest.





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#### Tables





# Table 2. CMEMS and non-CMEMS products used in this study.

Ref. No.	Product name & type	Documentation		
1	NWSHELF_MULTIYEAR_PHY_004_009	PUM: https://catalogue.marine.copernicus.eu/documents		
		/PUM/CMEMS-NWS-PUM-004-009-011.pdf		
		QUID: https://catalogue.marine.copernicus.eu/documents		
		/QUID/CMEMS-NWS-QUID-004-009.pdf		
		https://doi.org/10.48670/moi-00059		
2	NWSHELF_MULTIYEAR_BGC_004_011	PUM: https://catalogue.marine.copernicus.eu/documents		
		/PUM/CMEMS-NWS-PUM-004-009-011.pdf		
		QUID: https://catalogue.marine.copernicus.eu/documents		
		/QUID/CMEMS-NWS-QUID-004-011.pdf		
		https://doi.org/10.48670/moi-00058		
3	OCEANCOLOUR_GLO_BGC_L4_MY	PUM: https://catalogue.marine.copernicus.eu/documents		
	_OBSERVATIONS_009_104	/PUM/CMEMS-OC-PUM.pdf		
		QUID: https://catalogue.marine.copernicus.eu/documents		
		/QUID/CMEMS-OC-QUID-009-101to104-116-118.pdf		
		https://doi.org/10.48670/moi-00281		
4	SST_ATL_SST_L4_REP_OBSERVATIONS_010_026	PUM: https://catalogue.marine.copernicus.eu/documents		
		/PUM/CMEMS-SST-PUM-010-026.pdf		
		QUID: https://catalogue.marine.copernicus.eu/documents		
		/QUID/CMEMS-SST-QUID-010-026.pdf		
		https://doi.org/10.48670/moi-00153		
5	Additional satellite ocean colour data			
	processed by Plymouth Marine Laboratory			