1	Bottom-up effects of variable winter weather conditions on phytoplankton dynamics in an
2	enclosed bay: implications for ecological responses to climate change
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17 To investigate phytoplankton dynamics in response to variable winter weather conditions along the 18 Sea of Japan, we conducted daily sampling in enclosed Maizuru Bay in five winters and found 19 distinctive differences between 2016/2017 and 2018/2019. A clear diatom bloom occurred through 20 the water column in moderately cold/snowy 2016/2017, whereas in exceptionally warm/snow-free 21 2018/2019 a small peak of dinoflagellates occurred only in the subsurface. Nutrient concentrations 22 changed drastically depending on freshwater discharge and diatom growth in 2016/2017, showing a 23 contrast with constant nutrient concentrations in 2018/2019. Copepod densities were approximately 24 ten times higher in 2016/2017 than in 2018/2019, indicating bottom-up effects in 2016/2017. As the 25 absence of a diatom bloom from 2018/2019 can be attributed neither to nutrient limitation nor to grazing pressure, we hypothesize that wind mixing is a key factor triggering a diatom bloom. 26 27 Within the five winters, clear diatom blooms were found only after strong winds and heavy 28 precipitation including snowfall. Wind mixing would possibly promote the 29 germination/rejuvenation of viable resting stage cells as inocula for a diatom bloom, while the 30 growth and maintenance are supported by nutrient supply through freshwater discharge. In Maizuru 31 Bay, winter production is likely activated by harsh weather conditions characteristic of this region. iner 32

33 INTRODUCTION

34 Ongoing climate change imposes greater stresses upon marine phytoplankton through sea surface 35 warming, ocean acidification, and extreme weather events (Winder and Sommer, 2012). To predict 36 and mitigate adverse effects of climate change, phytoplankton dynamics should be monitored on 37 various spatiotemporal scales. Although global generalizations may be possible in phenology and 38 distribution (Edwards and Richardson, 2004; Ji et al., 2010; Thomas et al., 2012), distinctive 39 responses can occur in coastal phytoplankton communities (Cloern and Jassby, 2008), which are 40 subjected to local conditions (e.g., weather and topography) and human disturbance (e.g., nutrient 41 discharge and toxin contamination). In the US Atlantic coast, the phytoplankton bloom is predicted to diminish with stronger grazing pressure from zooplankton in warmer winters and springs (Keller 42 43 et al., 1999; George et al., 2015). In contrast, the winter-spring phytoplankton bloom is affected 44 primarily by wind in the European Mediterranean coast, although contradictory effects of strong 45 winds were reported even from neighboring areas (Goffart et al., 2002; Zingone et al., 2010). Decadal trends of increasing winter air temperature and decreasing total winter snowfall have been 46 47 found in most of meteorological observatories along the Sea of Japan side of the Japanese 48 archipelago (Takahashi, 2021). Despite large interannual fluctuations, many of these trends are 49 statistically significant from 1961 to 2012. The replacement of snow by rain at higher temperatures 50 may be responsible for the decreasing trends of snowfall, as there is no clear trend in winter 51 precipitation in terms of volume and frequency during this period (Takahashi, 2021). Even with the 52 same water volume, freshwater will flow into the sea more smoothly in rainy winters because of the 53 lack of time lags between snowfall and snowmelt. Additionally, not only winter snowfall but also 54 winter precipitation is predicted to decrease along the Sea of Japan side under the highest emission scenario (i.e., RCP8.5 in IPCC AR5; Kawase et al., 2021). Thus, climate change likely affects the 55 timing and/or volume of winter nutrient supply to coastal phytoplankton in this region. 56 57 Maizuru Bay is an enclosed microtidal bay, located around the middle of the Sea of Japan side of

58 the Japanese archipelago (Fig. 1). The bay is used not only for naval and commercial ports but also 59 for bivalve mariculture and sea cucumber fishing. Although the phytoplankton dynamics of the bay 60 has been studied since the 1950s (e.g., Yamazi, 1953; Furuhashi, 1957), it has attracted less attention in recent years mainly because of the gradual disappearance of serious eutrophication and 61 62 harmful algal blooms. However, sea surface temperature has unnoticeably but significantly increased in the bay during the last four decades, ca. 0.2°C per decade in winter and spring 63 64 (Maizuru Fisheries Research Station, unpublished data). Given the decadal data accumulated since the 1950s, Maizuru Bay will serve as a model field for studying effects of climate change on 65 66 phytoplankton dynamics in this region.

To investigate phytoplankton dynamics in response to variable winter weather conditions, we 67 conducted systematic daily sampling in Maizuru Bay in five winters. Physical parameters were 68 69 measured through the water column using a water quality profiler. Water samples were taken from 70 specific depths for determination of chlorophyll *a* and nutrient concentration, and for observation of 71 phytoplankton taxonomic composition and cell density. Zooplankton was also sampled 72 quantitatively to judge whether bottom-up or top-down control dominates in the phytoplankton 73 dynamics. Based on a brief survey of the results from the five winters, two contrasting winters (i.e., 74 2016/2017 and 2018/2019) were selected for an in-depth analysis of phytoplankton and 75 zooplankton. First, we confirmed whether winter phytoplankton dynamics is controlled mainly by 76 nutrient supply and/or grazing pressure, as suggested by previous sampling programs (Ueda, 1975; 77 Nishioka et al., 1977; Nakahara, 1978). Second, we addressed other potential factors that may 78 trigger the winter-spring phytoplankton bloom in the bay. Variable weather conditions in the five 79 winters gave us a chance not only to assess interannual fluctuations under the present situation but 80 also to gain an empirical insight into effects of climate change.

81

82 MATERIALS AND METHODS

83 Study area

84 Maizuru Bay is an enclosed microtidal bay, connected to the innermost part of Tango Bay, on the 85 Sea of Japan side of the Japanese archipelago (Fig. 1). The winter is characterized by northerly 86 strong winds and recurring heavy precipitation due to the East Asian winter monsoon and the 87 Tsushima Warm Current, while summer weather is usually calm with sporadic rainstorms. The bay 88 is divided into north, west, and east parts according to its topography (average depths of 27, 10 and 89 10 m, and surface areas of 4.2, 8.3 and 10.9 km², respectively; Ikeno and Miwa, 2006). The west 90 and east bays are characterized by its topographic closedness, shallow water depths, and small tidal 91 ranges (usually <0.5 m). Conveying fresh water and nutrients from the catchment area of 178 km², 92 small rivers flow mainly into the innermost parts of the west and east bays (total discharge rates of 93 5.0 and 4.8 m³ s⁻¹, respectively; Ikeno and Miwa, 2006). Two sewage disposal plants operate at 94 each end of the west and east bays (discharge rates of 0.03 and 0.15 m³ s⁻¹, respectively; Ikeno and 95 Miwa, 2006). Located close to the center of the east bay, Maizuru Fisheries Research Station of 96 Kyoto University has been devoted to monitoring the environment since the 1970s. 97 In Maizuru Bay, year-round observations confirmed seasonal diatom blooms of Skeletonema 98 (autumn to early winter) and *Chaetoceros* (winter to early spring) as well as sporadic outbreaks of other diatoms and dinoflagellates mainly in summer (Ueda, 1975; Nishioka et al., 1977; Nakahara, 99 100 1978). Despite eutrophication during the 1960s, nitrogen limitation on phytoplankton growth was 101 suggested based on nutrient stoichiometry in sea water (Nishioka et al., 1977; Nakahara, 1978). 102 Harmful algal blooms of dinoflagellates and raphidophytes have been observed as a potential threat 103 to mariculture since the 1970s (Furuhashi and Ebara, 1976; Tanaka et al., 1977; Nishitani et al., 104 2002; Imai et al., 2013). In addition, dominant phytoplankton species changed in the 1980s possibly 105 due to eutrophication (Riguelme et al., 1987). However, nutrient concentrations have decreased gradually since the 1980s (Fig. S1; Kyoto Prefecture, 1981–2020), although strict comparisons may 106 107 be impeded by inconsistent sampling and measurement methods employed through the monitoring

108	program. The nutrient concentrations of 2000–2019 may be higher than those of the 1950s but
109	comparable with those of the 1960s and 1970s (Nishioka et al., 1977; Nakahara, 1978). Although
110	there is little information about decadal changes in silicate concentrations, nutrient stoichiometry
111	indicated that silicon seldom limits phytoplankton growth in Maizuru Bay (Nakahara, 1978;
112	Maizuru Fisheries Research Station, unpublished data).
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114	Field sampling
115	Daily sampling was conducted at the floating pier of Maizuru Fisheries Research Station (ca. 6.5
116	m deep; Fig. 1) in five winters under variable weather conditions (Table I). Although the sampling
117	location was restricted to one station, the data can at least represent the east bay, where
118	phytoplankton dynamics is approximately synchronous (Nishioka et al., 1977; Maizuru Fisheries
119	Research Station, unpublished data). Temperature, salinity, light quantum and chlorophyll
120	fluorescence were measured at intervals of 0.1 m through the water column, approximately at 10:00
121	AM using a water quality profiler (AAQ177, JFE Advantech, Hyogo, Japan). Two liters of water
122	were taken from the surface using a bucket, as well as 2 and 4 m deep, using a Kitahara-type water
123	sampler (0.2 m in cylinder length, 0.5 L in sampling capacity). Each water sample was poured into
124	a 2-L polypropylene bottle that had been prewashed twice with the identical water sample. To
125	assess herbivorous zooplankton, a conical plankton net (0.3 m in mouth diameter, 1.0 m in length,
126	0.1 mm in mesh aperture) was hauled vertically once from the bottom to the surface and the
127	samples were preserved with formalin (ca. 3% in final concentration). The sequential field sampling
128	was finished within 10 minutes. In the winter 2022/2023, water quality was measured daily, while
129	water and zooplankton were sampled weekly.

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131 Laboratory analysis

132 Immediately after field sampling, each water sample was gently filtered through a Whatman GF/F

133 glass fiber filter using a syringe and a filter holder (25 mm in diameter). For determination of 134 chlorophyll a (Chl a) concentrations, the water volume of filtration was set at 100 mL. In the 135 winters of 2016/2017 and 2018/2019, the filter samples were kept frozen at -20°C and Chl a was 136 extracted in the dark at room temperature for 12 h with 90% acetone within 10 days after filtration. 137 In the winters of 2020/2021, 2021/2022 and 2022/2023, the filter samples were sunk in N, Ndimethylformamide (DMF) and Chl a was extracted in the dark at room temperature for three to six 138 139 hours immediately after filtration. The filtrate samples were poured into 10-mL polymethyl 140 methacrylate tubes and kept frozen at -20°C for determination of nitrite (NO₂-), nitrate (NO₃-) and 141 phosphate (PO₄³⁻) concentrations. In addition, 20 mL of filtrate samples were poured into 60-mL 142 opaque high-density polyethylene bottles for determination of ammonium (NH₄⁺) concentrations. 143 The filtration tools and sample containers had been rinsed with distilled water thrice and prewashed 144 twice with each water sample. 145 The Chl *a* concentrations were measured fluorometrically with a calibrated Trilogy Laboratory Fluorometer (7200-000, Turner Designs, Sunnyvale, CA, USA) according to Japan Meteorological 146 Agency (1970). Concentrations of NO_2^- , NO_3^- and PO_4^{3-} were determined simultaneously with an 147

149 (Bendschneider and Robinson, 1952), the cadmium reduction method (Wood *et al.*, 1967) and the

autoanalyzer (QuAAtro2-HR, BL TEC K. K., Osaka, Japan) using the naphthylenediamine method

150 molybdenum blue colorimetric method (Murphy and Riley, 1962), respectively. NH₄⁺

151 concentrations were measured fluorometrically with the above-mentioned fluorometer using the

152 ortho-phthaldialdehyde method (Holmes *et al.*, 1999).

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Based on a brief survey of results from the five winters, two contrasting winters (i.e., 2016/2017

and 2018/2019; Table I) were selected for an in-depth analysis of phytoplankton and zooplankton.

155 For microscopic examination of phytoplankton taxonomic composition and cell density, one liter of

156 each water sample was preserved with formalin (ca. 1% in final concentration). Phytoplankton was

157 concentrated to 10 mL through a sedimentation method, in which supernatant was removed twice

158 after still standing. Before microscopy, 0.1 mL of each concentrated sample was introduced into an 159 optic plastic plankton counter (MPC-200, Matsunami Glass, Osaka, Japan). Phytoplankton was 160 identified to the lowest taxonomic level possible (usually to genera) and enumerated quantitatively 161 for each taxon under a magnification of 400 in a phase-contrast mode using an inverted microscope 162 (TMS-F13, NIKON, Tokyo, Japan or CKX53, Olympus, Tokyo, Japan). To attach greater importance to spatial than temporal resolution, the taxonomic examination was conducted 163 164separately for the three depths every second day. 165 Under a dissecting microscope (SZX10, Olympus, Tokyo, Japan), zooplankton were identified to

166 the lowest taxonomic level possible (usually to genera) and enumerated quantitatively for each taxon. In copepods, adults and copepodites were identified to genera, while nauplii were pooled. 167 168 Although small copepod nauplii cannot be quantitatively collected using the 0.1-mm mesh, 169 zooplankton samples were usually dominated by developed stages of calanoid nauplii that could 170 feed on phytoplankton including diatoms (cf. White and Roman, 1992; Vogt et al., 2013). To calculate zooplankton density, the volume of water filtered through the net was estimated from the 171 product of the area of the net mouth by the depth of water on the assumption that the filtering 172 efficiency is 100%. The taxonomic identification of phytoplankton and zooplankton followed 173 Chihara and Murano (1997), Omura et al. (2012) and Suemoto (2013). 174

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176 Data processing

- 177 Dissolved inorganic nitrogen (DIN) was defined as the sum of NO_2^- , NO_3^- and NH_4^+ . For
- 178 convenience, the sum of NO_2^- and NO_3^- was expressed as NO_x^- . In the winter 2016/2017, as NH_4^+
- 179 was not measured, DIN concentrations were estimated from concentrations of NO_x using their
- 180 linear relationships with DIN that had been observed at each sampling depth in the winter
- 181 2018/2019 (Fig. S2). The molar ratio of DIN and PO_4^{3-} (N:P ratio) was calculated and compared
- 182 with the Redfield ratio (i.e., 16; Redfield *et al.*, 1963). In the daily data of the winter 2022/2023,

chlorophyll fluorescence was converted into Chl *a* concentration using a linear relationship of the
weekly data of chlorophyll fluorescence and Chl *a* concentration. Allowing for technical
uncertainties of water sampling, the data of temperature, salinity, and light quantum from 0–0.2,
1.8–2.2 and 3.8–4.2 m were averaged and used for 0, 2 and 4 m deep, respectively. To better
describe temporal changes in Chl *a* and environmental parameters through the water column, the
daily means of the three depths were box-averaged (or moving-averaged) with a window of 3 days

189 ($\pm 1 \text{ day}$).

Sea level is monitored at 35° 29'N, 135° 23'E with a tide gauge station by Japan Meteorological
Agency (Fig. 1). Hourly sea level data are available online

192 (https://www.data.jma.go.jp/gmd/kaiyou/db/tide/genbo/index.php). Meteorological parameters

193 including air temperature, wind speed and direction, sunshine duration, precipitation and snow

height are monitored at 2 m in altitude, 35° 27′N and 135° 19′E in latitude and longitude, with

195 Automated Meteorological Data Acquisition System (AMeDAS) by Japan Meteorological Agency

196 (Fig. 1). In Maizuru, sunshine duration has been the only data available for light conditions since

197 2013, when monitoring of global solar radiation terminated. Hourly, daily and monthly

198 meteorological data are available online (https://www.data.jma.go.jp/gmd/risk/obsdl/index.php).

199 For convenience, winter was defined as the period from December to February, in which weather

200 conditions were compared between years (Table I).

To assess the effect of wind mixing through the water column, monitoring data of temperature and salinity were obtained from Kyoto Fishery Cooperative Association. Salinity and temperature were measured hourly at 0.1 m depth intervals with an automatic water quality profiling system (μ profiler DS5X, Hydrolab, Hyogo, Japan), which had been installed on a bivalve mariculture raft in the west bay (ca. 11 m deep; Fig. 1). As the data of < 0.2 m included noises from accidental exposures of the sensors to the air under wavy conditions, the data of 0.2 m deep were used to represent the water surface. Due to technical faults in the system, the monitoring data was available

208 only for the winter 2016/2017.

209 Cross-correlation analysis was performed with R 4.1.1. (R Core Team, 2021) to explore time-210lagged relationships between precipitation, freshwater discharge, nutrient and chlorophyll a concentrations. To remove spurious correlations due to temporal dependencies between adjacent 211 212 values of input time series and to cancel these influences on output time series, prewhitening was conducted before cross-correlation analysis (Probst et al., 2012; Dean and Dunsmuir, 2016). As the 213 214 first step of prewhitening, autoregressive integrated moving average (ARIMA) models were fit to the input time series of each depth in each winter using the function 'auto.arima' of the package 215 216 'forecast'. Within five candidate ARIMA models judged from Akaike Information Criterion (AIC), 217 the best ARIMA model was selected with consideration for the normality and autocorrelation of 218 residuals, which were tested using the function 'jargue.bera.test' of the package 'tseries' and the 219 function 'checkresiduals' of the package 'forecast', respectively. At each depth in each winter, the 220 best ARIMA model was applied to both input and output time series (i.e., prewhitening) and cross 221 correlation between the prewhitened input and output time series was analyzed using the function 222 'pccf' of the package 'tfarima'. As an indicator of freshwater discharge, salinity was always used 223 for the input time series. The significance limits of cross correlation were set at \pm 1.96 n-0.5, where n indicates the number of pairs between the input and output time series ($\alpha = 0.05$; Dean and 224 225 Dunsmuir, 2016).

To compare temporal changes in Chl *a* and environmental parameters at each sampling depth between the two contrasting winters of 2016/2017 and 2018/2019, smoothed values with their 95% confidence intervals were produced using the dynamic linear models (DLMs) with the Kalman filter. The DLMs are a special case of state-space models (i.e., the state and observation time series are modeled with linear equations and normal distributions; Petris, 2010; Auger-Methe *et al.*, 2021). To satisfy the homoscedasticity assumption of the DLMs, Chl *a*, NO_x⁻, PO₄³⁻ and light quantum were log-transformed prior to the DLM application (cf. Lheureux *et al.*, 2022), while water

233 temperature and salinity were used without any transformation. For each parameter at each 234 sampling depth, model selection was conducted based on AIC between the local level and local 235 linear trend models (i.e., the first- and second-order polynomial models). The selected models were validated by examining the homoscedasticity, normality and autocorrelation of the standardized 236 237 one-step-ahead residuals (i.e., standardized prediction error residuals). The validated models, which 238 did not violate the three conditions above, were used for calculations of smoothed values and their 239 95% confidence intervals. All the processes were in accordance with Appendix S1 of Auger-Methe et al. (2021) and performed using the package 'dlm' with R 4.1.1. (R Core Team, 2021). 240 241 Interannual differences in the seasonal average of Chl *a* and environmental parameters at each depth were assessed using two-tailed t-tests. The data were transformed prior to the t-tests in the 242 243 same way as the DLM application. Given that autocorrelation inflates the probability of type I error 244 (i.e., false rejection of the null hypothesis), "equivalent sample size" was calculated when the data 245 were autocorrelated (O'Shaughnessy and Cavanaugh, 2015). The "equivalent sample size" effectively decreased the actual sample size when determining the standard error of the mean and 246 the degree of freedom in t-tests for autocorrelated data. The significance level was set at 0.05. 247

248

249 **RESULTS**

Bloom intensity and weather conditions

Within the five winters, 2016/2017 exhibited the most striking phytoplankton bloom, which lasted at least two months from middle January (Fig. 2A). In contrast, there was no clear phytoplankton bloom in the winters of 2018/2019 and 2020/2021, although Chl *a* concentrations remained lower in the former than in the latter (Fig. 2B, C). When the annual phytoplankton blooms were roughly graded for their duration and Chl *a* concentration, bloom intensity was closely associated with total winter precipitation and snowfall, while there was no close association with average air temperature and daily sunshine duration during winter (Table I). In each winter, although heavy rainfall and/or

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258 snowfall events were not always associated with phytoplankton blooms, they stimulated 259 phytoplankton growth when combined with strong winds (i.e., daily speed > 5 m s⁻¹; Fig. 2A, D, E). 260 Such strong winds usually blew from the north and occurred several times during each winter, otherwise southwesterly mild winds dominated (Fig. 2). Based on these results, the winters of 261 262 2016/2017 and 2018/2019 were selected as typical examples of productive and unproductive winters and further examined for phytoplankton dynamics in relation to weather conditions, 263 264 specifically precipitation, snowfall and wind speed. Compared with the winter 2018/2019, the winter 2016/2017 was characterized by lower air 265 266 temperatures, more variable winds and heavier precipitation including heavy snowfalls (Table I), while interannual differences in sea level and sunshine duration were negligible (Figs. S3, S4). 267 Daily wind speed exceeded 5 m s⁻¹ four and two times during the winters of 2016/2017 and 268 269 2018/2019, respectively (Fig. 2A, B; Table I). Daily precipitation exceeding 10 mm occurred 270 successively in January and February in the winter 2016/2017, while it accumulated to 13 days 271 during the sampling period (i.e., 1 January to 11 March; Fig. 2A). Moreover, heavy snowfalls 272 accounted for three heavy precipitation events, reaching maximum snow height of 34, 50 and 54 cm on 15 and 24 January and 12 February, respectively. In contrast, daily precipitation exceeding 10 273 274mm occurred on 8 days without heavy snowfalls during the sampling period in the winter

275 2018/2019 (Fig. 2B). Total precipitation and snowfall were 594 mm and 165 cm in the winter

276 2016/2017, 381 mm and 15 cm in the winter 2018/2019, respectively (Table I).

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278 Chl *a* and environmental parameters

In the winter 2016/2017, box-averaged concentrations of Chl *a* increased rapidly from ca. 10 to 30

 μ g L⁻¹ in middle January before decreasing gradually to ca. 15 μ g L⁻¹ and fluctuating slowly

afterwards (Fig. 3A). Chl *a* concentrations changed more drastically in the surface (0 m deep) than

in the subsurface (2 and 4 m deep), fluctuating between 1 and 41 μ g L⁻¹, and 5 and 39 μ g L⁻¹,

283 respectively. In contrast, box-averaged concentrations of NO_x⁻ decreased gradually from 9 to 2 µM 284 in early and middle January and remained close to 2 µM in late January, while they fluctuated between 2 and 7 μ M in February and settled down to 1 μ M in early March (Fig. 3B). PO₄³⁻ 285 exhibited spatial and temporal changes similar to those of NO_x, with box-averaged concentrations 286 287 decreasing from 0.7 to 0.1 µM in early and middle January and remaining close to 0.2 µM in late January and early February (Fig. 3C). Thereafter, they fluctuated between 0.1 and 0.3 µM in late 288 February before settling down to 0.1 μ M in early March. In PO₄³⁻ as well as NO_x⁻, sporadic spikes 289 290 were observed in the surface in early January and through February. Water temperature and salinity 291 exhibited approximately identical patterns of spatial and temporal changes, characterized by lower 292 and more variable values in upper waters (Fig. 3D, E). Surface temperature and salinity fluctuated 293 between 7 and 14°C, and 25 and 32 during the sampling period, except for drastic falls observed on 294 1–3 January and 1–4, 11–15 and 22–25 February (minima of 3 and 15°C, respectively). Subsurface 295 temperature decreased from 15 to 9°C in early January and fluctuated between 8 and 13°C 296 afterwards, while the subsurface salinity remained between 27 and 34 through the sampling period. 297 Light quantum fluctuated greatly showing an increasing trend, with means \pm standard deviation during the sampling period being 575 ± 518 , 173 ± 155 and 79 ± 74 µmol m⁻² s⁻¹ at 0, 2 and 4 m 298 299 deep, respectively (Fig. 3F).

300 In the winter 2018/2019, Chl a exhibited consistently low concentrations with small fluctuations at 301 the three depths throughout the sampling period, except for small peaks observed at 2 and 4 m deep in January (up to 19 μ g L⁻¹; Fig. 4A). Box-averaged concentrations of Chl *a* remained at 3 μ g L⁻¹ 302 303 until early February and below 2 μ g L⁻¹ afterwards. Characterized by frequent small peaks in the 304 surface (up to 18 μ M in NO_x⁻ and 14 μ M in NH₄⁺), almost identical patterns of spatial and temporal 305 changes were observed in NO_x^- and NH_4^+ (Fig. 4B, C). NO_x^- was comparable among the three depths except for the small peaks, with box-averaged concentrations being higher than 3 µM only in 306 early January and late February. Although NH₄⁺ was always higher in upper waters, its box-307

308 averaged concentrations were higher than 2 μ M only in early January. In contrast, PO₄³⁻ was 309 slightly higher at 4 m deep, while its box-averaged concentrations remained close to 0.2 µM 310 through the sampling period (Fig. 4D). Both temperature and salinity were characterized by lower and more variable values in upper waters, where minor dips were frequently observed (Fig. 4E, F). 311 312 Through the sampling period, temperature and salinity fluctuated between 8 and 12°C, and 24 and 33 in the surface; between 9 and 14°C, and 30 and 33 at 2 m deep; and between 10 and 15°C, and 30 313 314 and 33 at 4 m deep; respectively. Light quantum fluctuated irregularly without any clear trend through the sampling period, with means \pm standard deviation being 360 ± 299 , 152 ± 140 and $77 \pm$ 315 316 $69 \,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ at 0, 2 and 4 m deep, respectively (Fig. 4G). NO_x⁻ concentrations (X) were correlated linearly with DIN concentrations (Y) at each depth in the 317 winter 2018/2019: Y = 1.07X ($R^2 = 0.95$), Y = 1.26X ($R^2 = 0.98$) and Y = 1.08X ($R^2 = 0.99$) at 0, 2 318 319 and 4 m deep, respectively (Fig. S2). Using these equations, DIN concentrations were estimated 320 from NO_x concentrations at each depth in the winter 2016/2017. At the three depths, the resultant 321 N:P ratio remained above 16 in early January and February 2017, whereas in late January and early March 2017 it fluctuated mainly below 16 (Fig. 5A). In the winter 2018/2019, the N:P ratio 322 wandered up and down across 16 in the surface, while it usually remained below 16 at 2 and 4 m 323 deep throughout the sampling period (Fig. 5B). 324

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326 **Cross correlation and interannual comparison**

Cross correlation was unclear between salinity and Chl *a* irrespective of sampling depth in both winters of 2016/2017 and 2018/2019, although marginally significant values were sporadically observed (Fig. 6A, B). In contrast, cross correlation of salinity with NO_x^- was negative and highly significant without time lag in the surface in both winters, whereas in the subsurface it was significantly negative without time lag only in the winter 2016/2017 (Fig. 6C, D). Between salinity and PO_4^{3-} , a significantly negative cross correlation was found without time lag only in the surface

333 in the winter 2016/2017, whereas in the winter 2018/2019 cross correlation was positive and 334 marginally significant without time lag at 2 and 4 m deep (Fig. 6E, F). As was expected from Figs. 335 3 and 4, cross correlation between salinity and temperature was positive and highly significant without time lag at the three depths in both winters (Fig. 6G, H). Although marginally significant 336 337 values were sporadically observed, there was no clear cross correlation of salinity with precipitation 338 irrespective of time lag or sampling depth in both winters (Fig. 6I, J). 339 In the DLM application, the local level model was always selected because of its smaller AIC. Smoothed values and their 95% confidence intervals were successfully calculated in all cases in Chl 340 341 a, NO_x^{-} , PO_4^{3-} and water temperature (Fig. 7A-D), although they were not determined in a few cases in salinity and light quantum (Fig. 7E, F). As expected from Figs. 3 and 4. Chl a concentrations 342 343 through the water column were always higher in the winter 2016/2017 than in the winter 2018/2019 344 except for the first several days (Fig. 7A). Moreover, the seasonal average of Chl a at each depth 345 was significantly different between the two winters (t-test, P < 0.01). Irrespective of sampling depth, NO_x^{-1} and PO_4^{-3-1} concentrations fluctuated more widely in the winter 2016/2017, whereas in 346 347 the winter 2018/2019 they remained at intermediate values (Fig. 7B, C). For water temperature and 348 salinity, occasional falls were noticeable only in upper waters in the winter 2016/2017 (Fig. 7D, E). 349 The seasonal average of the environmental parameters at each depth was not significantly different 350 between the two winters (t-test, P > 0.05), except that light quantum in the surface was significantly 351 higher in the winter 2016/2017 than in the winter 2018/2019 (Fig. 7F; t-test, P = 0.03).

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353 **Phytoplankton and zooplankton**

In the winter 2016/2017, phytoplankton remained below 200 cells mL⁻¹ in the beginning irrespective of sampling depth, while it increased to >5000 cells mL⁻¹ in middle January before decreasing gradually to <1000 cells mL⁻¹ afterwards (Fig. 8A, B, C). Phytoplankton cell densities were slightly higher and more variable in upper waters and exhibited temporal changes similar to

358 those of Chl a concentrations (Fig. 3A). Through the water column, the diatom Skeletonema usually 359 accounted for >70% of total phytoplankton cells from middle to late January, whereas in February 360 and March another diatom Chaetoceros gradually replaced Skeletonema. As for other diatoms, Dactyliosolen and Thalassionema occurred frequently in February and March, each accounting for 361 362 up to 13% through the water column. Other algae consisting mainly of dinoflagellates and euglenoids dominated when diatoms were scarce, specifically in early January. In zooplankton, 363 364 copepods including nauplii always accounted for >80% in number throughout the sampling period. Copepod densities increased from <10 to >20 inds L⁻¹ during the sampling period with large 365 366 temporal fluctuations (Fig. 8D). Nauplii and Oithona overwhelmingly dominated in the copepod community until early February (range, 72–96%), while Acartia gradually increased dominance 367 afterwards (9–39%). 368 369 During the winter 2018/2019, phytoplankton usually remained below 500 cells mL⁻¹ through the 370 water column, except for a peak of 1800 cells mL⁻¹ observed at 4 m deep on 20 January (Fig. 9A, B, 371 C). Phytoplankton cell densities were slightly lower and less variable in upper waters, with the

average and standard deviation being 152 ± 112 , 201 ± 125 and 323 ± 309 cells mL⁻¹ at 0, 2 and 4 372 m deep, respectively. The higher phytoplankton cell densities in the subsurface were attributable 373 374 mainly to the dominance of the dinoflagellate *Prorocentrum* at 4 m deep in middle and late January (up to 1300 cells mL⁻¹ on 20 January). Other dinoflagellates occasionally increased in dominance 375 376 mainly from late February to early March, when diatoms were scarce. Although the diatom 377 Skeletonema dominated in early January and early to middle February, its contribution usually 378 remained below 70% of total phytoplankton cells through the water column. As the diatoms 379 Chaetoceros and Pseudo-nitzchia occurred continuously during the sampling period, they 380 dominated through the water column (up to 49 and 45%, respectively) from late February to early March when Skeletonema decreased in density. The diatoms Guinardia and Thalassionema were 381 382 characteristic of early and late January, respectively. As observed in the winter 2016/2017,

- 383 copepods including nauplii always accounted for >80% of zooplankton count in the winter
- 384 2018/2019. However, copepod densities always remained below 3 inds L⁻¹ except for at the end of
- the sampling period (6.5 inds L^{-1} ; Fig. 9D). The copepod community was overwhelmingly
- dominated by Oithona and nauplii throughout the sampling period (range, 82–100%), while Acartia
- 387 occurred sporadically mainly in the second half.
- 388

389 Wind mixing in the winter 2016/2017

The water column at least to 8 m deep was completely mixed by strong winds irrespective of sea level and air temperature (Fig. 10). When daily wind speed exceeded 5 m s⁻¹ on 14 and 27 December 2016, and 5 January 2017, temperature and salinity dropped suddenly in lower waters, indicating quick mixing with upper waters. Moreover, vertical mixing was promoted when daily wind speed approached 4 m s⁻¹ on 22 December 2016 and 14 January 2017, as was suggested by approximately homogeneous temperatures and salinities through the water column.

396

397 **DISCUSSION**

398 Weather conditions

Although weather conditions differed markedly between the winters of 2016/2017 and 2018/2019 399 400 excluding their similarly short sunshine duration, it is important to consider them in the historical 401 context. Judging from the statistics during the last six decades (1963/1964-2022/2023; Table I), the 402 winter 2016/2017 can be included among moderate winters except for its heavy precipitation. In 403 contrast, the winter 2018/2019 represents an extremely mild winter, characterized mainly by warm 404 air and light snow. Along the Sea of Japan side of the Japanese archipelago, decadal trends of 405 increasing winter air temperature and decreasing total winter snowfall are statistically significant 406 (Takahashi, 2021) and are predicted to continue in the future (Kawase et al., 2021). Such long-term 407 trends, combined with the highly negative correlation between air temperature and total snowfall in

408 Maizuru Bay (r = -0.83, P < 0.01; Fig. S5), suggest that the warm and snow-free winter 2018/2019 409 will be typical of future winter weather conditions. Although there are no clear relationships 410between the other combinations of meteorological parameters except for the negative correlation of total precipitation and daily sunshine duration (Fig. S5), total precipitation and windy days during 411 412 winter are predicted to decrease gradually under climate change (Suzuki et al., 2011; Kawase et al., 2021). Given that mild winters are likely replacing severe winters in this region, the weather 413 414 conditions and phytoplankton dynamics observed in the winter 2018/2019 may have important implications for the future. 415

416

417 Nutrient supply

Between the winters of 2016/2017 and 2018/2019, the different weather conditions, specifically 418 419 precipitation and snowfall, caused marked differences in nutrient supply and consumption (Fig. 7). 420 In the winter 2016/2017, large freshwater discharge events supplied not only NO_x^{-} through the water column but also PO_4^{3-} at least to the surface (Figs. 3, 6). The N:P ratio remained above or 421 422 close to the Redfield ratio irrespective of sampling depth through the sampling period except in late 423 January and early March (Fig. 5), when freshwater discharge events did not occur. Diatoms rapidly 424 accumulated biomass under such a nutrient-rich condition until the complete depletion of nitrogen 425 in late January and thereafter maintained their biomass by consuming strong nutrient pulses in February (Fig. 3). Diatoms were diluted with fresh water in the surface under large freshwater 426 427 discharge events, whereas during the intervals diatoms consumed available nutrients to depletion. 428 The delayed snowmelt likely contributed not only to the biomass accumulation by creating a stable 429 thermohaline condition in January but also to its maintenance by producing strong nutrient pulses in 430 February.

In terms of taxonomic composition, the winter 2016/2017 was characterized by the overwhelming
dominance of the diatoms *Skeletonema* and *Chaetoceros* through the water column in the early and

433	late phases of the bloom, respectively (Fig. 8). The gradual replacement of Skeletonema by
434	Chaetoceros could be explained by potential advantages of Chaetoceros over Skeletonema under
435	nutrient-limited conditions (Turpin and Harrison, 1979; Yamada et al., 1980; Nishikawa et al.,
436	2010). Although diatoms were not identified to species, Skeletonema dohrnii most likely dominated
437	in the winter 2016/2017, because this species grows well even in cold waters (e.g., specific growth
438	rate, up to 1.0 d ⁻¹ at 10°C; Kaeriyama et al., 2011; Anderson and Rynearson, 2020) and dominates
439	over other Skeletonema species during winter in Japan (Yamada et al., 2014, 2017). As for
440	Chaetoceros, several species occurred in each sample and changed their composition with time
441	during the sampling period.
442	In the winter 2018/2019, large freshwater discharge events scarcely occurred through the sampling
443	period and contributed only to NO_x^- in the surface (Fig. 4). It is notable that PO_4^{3-} was not supplied
444	to the surface through freshwater discharge but supplemented in the subsurface by the emergence of
445	saline water (Figs. 4, 6). Despite the limited nutrient supply, nutrient concentrations were usually
446	maintained above the half-saturation constants of phytoplankton uptake (ca. 1.0 and 0.2 μ M in DIN
447	and PO ₄ ³⁻ , respectively; Fisher <i>et al.</i> , 1988; Dortch and Whiteledge; 1992), mainly because
448	phytoplankton could not accumulate biomass to consume nutrients to depletion. The sudden
449	outbreak of the dinoflagellate Prorocentrum in the subsurface in middle and late January was the
450	only exception (Fig. 9). Based on morphological characteristics confirmed through optical
451	microscopy, the Prorocentrum was identified as P. obtusidens, the senior synonym of P.
452	shikokuense and P. donghaiense (Shin et al., 2019). Although this species has capabilities not only
453	to adapt to wide ranges of temperature and salinity but also to utilize various types of inorganic and
454	organic nitrogen compounds, the specific growth rate is as low as $<0.2 \text{ d}^{-1}$ at 10°C (Xu et al. 2010,
455	Hu et al. 2012). A plausible reason for the sudden outbreak of <i>P. obtusidents</i> may be its advantage
456	over diatoms in nitrogen uptake under the nitrogen-limited condition in the winter 2018/2019. It is,
457	however, uncertain why diatoms failed to accumulate biomass even under a nutrient-rich condition

in early January 2019 (Fig. 4). Although most of phytoplankton dynamics can be explained by
nutrient supply through freshwater discharge in both winters, the trigger of the diatom bloom should
be attributed to other factors.

461

462 **Grazing pressure**

Grazing pressure from zooplankton has often been reported as a major limiting factor in winter 463 464 phytoplankton dynamics in the US Atlantic coast (cf. Martin, 1965; Deason, 1980; Keller et al., 1999; George et al., 2015). As the community structure of zooplankton and resultant grazing 465 466 pressure change with temperature, the diatom bloom generally starts under lower grazing pressure in late winter, while it usually terminates under higher grazing pressure in late spring. In terms of 467 interannual fluctuations, the diatom bloom occurs more extensively under lower grazing pressure in 468 469 colder winters (Keller et al., 1999; George et al., 2015). In accordance with such a top-down 470 scenario, the diatom bloom developed under low grazing pressure in Maizuru Bay in January of the 471 colder winter 2016/2017 (Fig. 8). However, copepod densities were approximately ten times higher 472 in the winter 2016/2017 than in the winter 2018/2019 (Figs. 8D, 9D). This means that grazing pressure was higher in the winter 2016/2017, because such a large difference in density cannot be 473 474 offset by a slight difference in temperature (cf. Deason, 1980). Compared with previous 475 observations conducted in Maizuru Bay (Furuhashi, 1957; Ueda, 1975, 1987a, b), the copepod 476 community observed in the winter 2018/2019 is characterized by exceptionally low densities of calanoids, specifically Acartia adults and copepodites. Contrary to the original idea suggested by 477 478 weekly and monthly sampling programs (Ueda, 1975; Nishioka et al., 1977; Nakahara, 1978), the 479 winter 2018/2019 illustrated that the diatom bloom is not always triggered by the combination of 480 high nutrient concentrations and low grazing pressure in Maizuru Bay.

The observed copepod community dynamics can be explained largely by a bottom-up control scenario. *Acartia* adults and copepodites clearly increased in density in response to the diatom

483 bloom in the winter 2016/2017 (Fig. 8), whereas in the winter 2018/2019 they occurred only 484 sporadically under the extended scarcity of diatoms (Fig. 9). Not only cell density but also 485 taxonomic composition in phytoplankton possibly affected the copepod community, as the dominant copepods Acartia and Oithona have different feeding habits (Uchima, 1988; Zamora-486 487 Terol and Saiz, 2013; Saiz et al., 2014). There is a high possibility that herbivorous Acartia was promoted by abundant diatoms in the winter 2016/2017, while omnivorous Oithona was less 488 489 affected by phytoplankton dynamics in both winters. In Maizuru Bay during winter, the copepod 490 community as well as the phytoplankton community is clearly controlled by bottom-up processes 491 including nutrient supply and diatom growth, although necessary conditions for the development of the diatom bloom remain to be discussed. 492

493

494 Wind mixing

495 Based on the daily observations of the five winters, we hypothesize that wind mixing is the key 496 factor triggering the winter-spring diatom bloom in Maizuru Bay. Within several weeks after strong winds (daily speed > 5 m s⁻¹) and heavy precipitation (> 30 mm d⁻¹), Chl *a* concentrations increased 497 498 noticeably in the productive winters of 2016/2017 and 2021/2022 (Fig. 2A, D). In contrast, Chl a 499 concentrations remained low without experiencing strong winds and/or heavy precipitation in the 500 unproductive winters of 2018/2019 and 2020/2021 (Fig. 2B, C). Strong winds completely mixed the 501 water column at least to 8 m deep in the winter 2016/2017 (Fig. 10), showing the high potential of 502 sediment resuspension in shallow waters. Viable resting stage cells of diatoms might also have been 503 resuspended from the bottom by wind mixing to serve as inocula for the diatom bloom (cf. Ishikawa 504 and Furuya, 2004; McQuoid and Godhe, 2004; Wetz et al., 2004). Although Skeletonema and 505 Chaetoceros, which overwhelmingly dominated in the winter 2016/2017, are known to abundantly produce viable resting stage cells in coastal waters in Japan (Itakura et al., 1997; Ichinomiya and 506 507 Taniguchi, 2003; Ueno and Ishikawa, 2009), their germination and rejuvenation are significantly

delayed under autumn/winter conditions (e.g., 10 days at 15°C under a short photoperiod;

509 Matsubara, 2017). This means that favorable conditions are required to last more than 10 days after

510 wind mixing for the development of the diatom bloom in winter. Although nutrient supply probably

satisfied such a timeline in the winter 2016/2017, light conditions must be addressed in relation to

512 wind mixing.

Light was reported as a limiting factor of winter phytoplankton dynamics in the neighboring bay, 513 514 Tango Bay (Fig. 1; Watanabe et al., 2017). In contrast with enclosed Maizuru Bay, Tango Bay is vulnerable to northerly strong winds of the East Asian winter monsoon and therefore subjected to 515 516 high turbidities incidental to high waves during winter. Phytoplankton likely starts growing in Tango Bay as light conditions gradually improve in late winter (Watanabe et al., 2017). In Maizuru 517 518 Bay, although the data were instantaneous values measured each morning, light quantum fluctuated 519 greatly even within a week (Figs. 3F, 4G). Despite such large fluctuations, light quantum even at 4 520 m deep usually remained above the light levels required for the half saturation of specific growth rate and for the promotion of germination/rejuvenation in the dominant diatom Skeletonema dohrnii 521 (31 and 46 µmol m⁻² s⁻¹, respectively; Kaeriyama *et al.*, 2011; Matsubara, 2017). Moreover, the 522 523 rapid development and gradual recession of the diatom bloom observed in the winter 2016/2017 were related neither with light quantum nor with sunshine duration. If daily light dose is assumed 524 525 simply as the product of light quantum and sunshine duration observed on each sampling day, this 526 rough estimate produces an average of 1.2 mol light quanta m⁻² d⁻¹ at 4 m deep during the sampling 527 period in both winters. In general, the daily light dose necessary for the development of the winterspring phytoplankton bloom ranges between 1.0 and 1.8 mol light quanta m⁻² d⁻¹ (Siegel *et al.*, 528 529 2002; Sommer and Lengfellner, 2008). Although deeper discussion requires closer observations on 530 light conditions, winter phytoplankton dynamics is unlikely controlled by light in Maizuru Bay, 531 possibly because wind mixing makes turbidities high only sporadically and therefore light 532 conditions are usually acceptable to phytoplankton even in the subsurface waters. We argue that

wind mixing preceding nutrient supply during winter likely triggers the diatom bloom in enclosed
Maizuru Bay, as wind mixing would possibly promote the germination/rejuvenation of viable
resting stage cells rather than cause poor light conditions over a long period of time.

536

537 CONCLUSION

The bottom-up effects of weather conditions on winter phytoplankton dynamics were clearly 538 539 illustrated in microtidal Maizuru Bay, thanks to minimal interference by semidaily and fortnightly tidal cycles. The high-frequency systematic sampling enabled the estimation of causative 540 541 relationships between physical, chemical and biological parameters on various timescales. Wind 542 mixing through the water column, combined with nutrient supply through freshwater discharge, 543 likely contributed positively to the development of the diatom bloom. The timing and intensity of 544 these two prerequisites may be prime determinants of the winter-spring dynamics of phytoplankton 545 and zooplankton in Maizuru Bay. Compared with rainfall, snowfall delays nutrient supply until 546 snowmelt and therefore complicates the effects of precipitation on the dynamics. The severe 547 scarcity of phytoplankton and zooplankton observed during extremely mild winter 2018/2019 may 548 give us an advance warning of coastal production including fisheries in the future, as winter is 549 becoming free from coldness and snowfall in this region (Takahashi, 2021). To reveal interactions 550 among key meteorological parameters, such as temperature, precipitation and wind speed, it is necessary to conduct further sampling under various weather conditions. Moreover, laboratory 551 552 experiments are required to test working hypotheses that have been formulated through field 553 sampling.

Ecological responses of phytoplankton to climate change can be generalized globally through macroscopic analyses of extensive data obtained through monthly and/or seasonal monitoring programs (Edwards and Richardson, 2004; Ji *et al.*, 2010; Thomas *et al.*, 2012). Nevertheless, close examinations of phytoplankton dynamics through systematic sampling and practical experiments

558 are still needed to clarify underlying mechanisms and far-reaching effects in local ecosystems 559 (Spilling et al., 2014; George et al., 2015; Makareviciute-Fichtner et al., 2020). These intensive 560 approaches improve our theoretical understanding necessary for the development of process-based models, which can provide more reliable forecasts than the other models in altered environmental 561 562 conditions (Cuddington et al., 2013). In the present study, interannual differences in winter 563 phytoplankton dynamics were untangled through close examinations of temporal changes in 564 physical and chemical parameters, although there was no clear difference in their seasonal averages between the two winters. With the assistance of sophisticated techniques, such as flow cytometry 565 566 and machine learning, new intensive approaches will combine with existing monitoring programs to provide a comprehensive perspective on phytoplankton dynamics under climate change (Thomas et 567 al., 2018; Derot et al., 2020). This is the direction that we should take as a next step toward 568 569 functional harmony between localization and generalization in plankton ecology.

570

571 DATA AVAILABILITY

572 The data used in the present study are available from the correspondence author upon request.

573

574 SUPPLEMENTARY DATA

575 Supplementary data is available at *Journal of Plankton Research* online.

576

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583

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587

588 **REFERENCES**

- Anderson, S.I. and Rynearson, T. A. (2020) Variability approaching the thermal limits can drive
- 590 diatom community dynamics. *Limnol. Oceanogr.*, **65**, 1961–1973.
- 591 Auger-Methe, M., Newman, K., Cole, D., Empacher, F., Grayba, R., King, A. A., Leos-Barajas, V.,
- 592 Flemming, J. M., Nielsen, A., Petris, G., Thomas L. (2021) A guide to state-space modeling of
- 593 ecological time series. *Ecol. Monogr.*, **91**, e01470.
- 594 Bendschneider, K. and Robinson, R. J. (1952) A new spectrophotometric method for the
- determination on nitrate in sea water. J. Mar. Res., 11, 87–96.
- 596 Chihara, M. and Murano, M. (eds) (1997) An Illustrated Guide to Marine Plankton in Japan. Tokai
- 597 University Press, Tokyo (in Japanese).
- 598 Cloern, J. E. and Jassby, A. D. (2008) Complex seasonal patterns of primary producers at the land-
- 599 sea interface. *Ecol. Lett.*, **11**, 1294–1303.
- 600 Cuddington, K., Fortin, M.-J., Gerber, L. R., Hastings, A., Liebhold, A., O'Connor, M., Ray, C.
- 601 (2013) Process-based models are required to manage ecological systems in a changing world.
- 602 *Ecosphere*, **4**, https://doi.org/10.1890/ES12-00178.1.
- 603 Dean, R. T. and Dunsmuir, W. T. M. (2016) Dangers and use of cross-correlation in analyzing time
- series in perception, performance, movement, and neuroscience: The importance of constructing
- transfer function autoregressive models. *Behav. Res. Methods*, **48**, 783–802.
- 606 Deason, E. E. (1980) Grazing of Acartia hudsonica (A. clausi) on Skeletonema costatum in
- Narragansett Bay (USA): Influence of food concentration and temperature. *Mar. Biol.*, **60**,

608 101–113.

- Derot, J., Yajima, H., Schmitt, F. G. (2020) Benefits of machine learning and sampling frequency
 on phytoplankton bloom forecasts in coastal areas. *Ecol. Inform.*, **60**, 101174.
- Dortch, Q. and Whitledge, T. E. (1992) Does nitrogen or silicon limit phytoplankton production in
- the Mississippi River plume and nearby regions? *Cont. Shelf. Res.*, **12**, 1293–1309.
- Edwards, M. and Richardson, A. J. (2004) Impact of climate change on marine pelagic phenology
 and trophic mismatch. *Nature*, 430, 881–884.
- Fisher, T. R., Harding, Jr. L. W., Stanley, D. W., Ward, L. G. (1988) Phytoplankton, nutrients, and
- 616 turbidity in the Chesapeake, Delaware, and Hudson estuaries. *Estuar. Coast. Shelf. Sci.*, 27,
- 617 61**-**93.
- ⁶¹⁸ Furuhashi, K. (1957) On the seasonal distribution of animal plankton at Maizuru Bay, Kyoto Pref.
- 619 *Sea and Sky*, **33**, 14–28 (in Japanese with English abstract).
- Furuhashi, K. and Ebara, S. (1976) Concerning red water found in Maizuru Bay, Kyoto Pref. in
 autumn of 1975. *Sea and Sky*, **51**, 31–37 (in Japanese with English abstract).
- 622 George, J. A., Lonsdale, D. J., Merlo, L. R., Gobler, C. J. (2015) The interactive roles of
- 623 temperature, nutrients, and zooplankton grazing in controlling the winter-spring phytoplankton
- bloom in a temperate, coastal ecosystem, Long Island Sound. *Limnol. Oceanogr.*, **60**, 110–126.
- 625 Goffart, A., Hecq, J. H., Legendre, L. (2002) Changes in the development of the winter-spring
- 626 phytoplankton bloom in the Bay of Calvi (NW Mediterranean) over the last two decades: a
- response to changing climate? *Mar. Ecol. Prog. Ser.*, **236**, 45–60.
- Holmes, R. M., Aminot, A., Kerouel, R., Hooker, B. A., Peterson, B. J. (1999) A simple and precise
- method for measuring ammonium in marine and freshwater ecosystems. *Can. J. Fish. Aquat. Sci.*,
 56, 1801–1808.
- Hu, Z., Mulholland, M. R., Duan, S., Xu, N. (2012) Effects of nitrogen supply and its composition
- on the growth of *Prorocentrum donghaiense*. *Harmful Algae*, **13**, 72–82.

- 633 Ichinomiya, M. and Taniguchi, A. (2003) Seasonal variation in abundance and species composition
- of a planktonic diatom assemblage including viable cells on the bottom in Matsushima Bay,
- northeastern Japan. J. Ocean U. Qingdao, 2, 160–166.
- Ikeno, H. and Miwa, H. (2006) Numerical simulation of tidal current and nutrient distribution in
- 637 Maizuru Bay by multi-level baroclinic model. *Proceedings of the 7th International Conference*
- 638 *on Hydroscience and Engineering*, 1–18.
- Imai, I., Shiraishi, T., Fujii, H., Hiroishi, S. (2013) Seasonal fluctuations 649 of the bivalve-killing
- 640 dinoflagellate *Heterocapsa circularisquama* in Maizuru Bay, Kyoro Prefecture. *Bulletin of*
- *Fisheries Sciences, Hokkaido University*, **63**, 1–5 (in Japanese with English abstract).
- Ishikawa, A. and Furuya, K. (2004) The role of diatom resting stages in the onset of the spring
- bloom in the East China Sea. *Mar. Biol.*, **145**, 633–639.
- Itakura, S., Imai, I., Itoh, K. (1997) "Seed bank" of coastal planktonic diatoms in bottom sediments
 of Hiroshima Bay, Seto Inland Sea, Japan. *Mar. Biol.*, **128**, 497–508.
- ⁶⁴⁶ Japan Meteorological Agency (1970) *Manual of Oceanographic Observation*. The Oceanographic
- 647 Society of Japan, Tokyo (in Japanese).
- Ji, R., Edwards, M., Mackas, D. L., Rouge, J. A., Thomas, A. C. (2010) Marine plankton phenology
- and life history in a changing climate: current research and future directions. *J. Plankton. Res.*,
 32, 1355–1368.
- Kaeriyama, H., Katsuki, E., Otsubo, M., Yamada, M., Ichimi, K., Tada, K., Harrison, P. J. (2011)
- Effects of temperature and irradiance on growth of strains belonging to seven *Skeletonema*
- species isolated from Dokai Bay, southern Japan. *Eur. J. Phycol.*, **46**, 113–124.
- Kawase, H., Murata, A., Yamada, K., Nakaegawa, T., Ito, R., Mizuta, R., Nosaka, M., Watanabe,
- 655 S., Sasaki, H. (2021) Regional characteristics of future changes in snowfall in Japan under
- 656 RCP2.6 and RCP8.5 scenarios. SOLA, 17, 1–7.
- 657 Keller, A. A., Taylor, C., Oviatt, C., Dorrington, T., Holcombe, G., Reed, L. (1999) Phytoplankton

- 658 production patterns in Massachusetts Bay and the absence of the 1998 winter-spring bloom. *Mar*.
- 659 *Biol.*, **138**, 1051–1062.
- 660 Kyoto Prefecture (1981–2020) *Results of Water Quality Monitoring in Public Waters*. Kyoto
- 661 Prefecture, Kyoto (in Japanese).
- 662 Lheureux A., David V., Del Amo Y., Soudant D., Auby I., Ganthy F., Blanchet H., Cordier M-A.,
- 663 Costes L., Ferreira S., Mornet L., Nowaczyk A., Parra M., D'Amico F., Gouriou L., Meteigner
- 664 C., Oger-Jeanneret H., Rigouin L., Rumebe M., Tournaire M-P., Trut F., Trut G., Savoye N.
- 665 (2022) Bi-decadal changes in nutrient concentrations and ratios in marine coastal ecosystems:
- The case of the Arcachon bay, France. *Prog. Oceanogr.*, **201**, 102740.
- 667 Martin, J. H. (1965) Phytoplankton-zooplankton relationships in Narragansett Bay. *Limnol.*
- 668 *Oceanogr.*, **10**, 185–191.
- Makareviciute-Fichtner, K., Matthiessen, B., Lotze, H. K., Sommer, U. (2020) Decrease in diatom
- dominance at lower Si:N ratios alters plankton food web. J. Plankton Res., 42, 411–424.
- 671 Matsubara, K. (2017) Influences of water temperature and photoperiod on germination/rejuvenation
- and growth of marine diatoms. *Bull Plankton Soc Japan*, 64, 45–49 (in Japanese with English
 abstract).
- McQuoid, M. R. and Godhe, A. (2004) Recruitment of coastal planktonic diatoms from benthic
- 675 versus pelagic cells: Variations in bloom development and species composition. *Limnol.*
- 676 *Oceanogr.*, **49**, 1123–1133.
- Murphy, J. and Riley, J. P. (1962) A modified single solution method for the determination of
- 678 phosphate in natural waters. *Anal. Chim. Acta*, **27**, 31–36.
- 679 Nakahara, H. (1978) Studies on phytoplankton in Maizuru Bay. I seasonal variation and vertical
- 680 microdistribution. *Memoirs of the College of Agriculture, Kyoto University*, **112**, 49–82.
- Nishikawa, T., Hori, Y., Nagai, S., Miyahara, K., Nakamura, Y., Harada, K., Tanada, M., Manabe,
- T., et al. (2010) Nutrient and phytoplankton dynamics in Harima-Nada, eastern Seto Inland Sea,

- 683 Japan during a 35-year period from 1973 to 2007. *Estuar. Coast.*, **33**, 417–427.
- Nishioka, J., Nakanishi, M., Sugiyama, M., Tanaka, S. (1977) Studies on water analysis and
- 685 plankton in Maizuru Bay. Bulletin of the Kyoto Institute of Oceanic and Fishery Science, 1,
- 686 74–92 (in Japanese).
- Nishitani, G., Sugioka, H., Imai, I. (2002) Seasonal distribution of species of the toxic
- dinoflagellate genus *Dinophysis* in Maizuru Bay (Japan), with comments on their
- autofluorescence and attachment of picophytoplankton. *Harmful Algae*, 1, 253–264.
- 690 Omura, T., Iwataki, M., Borja, V. M., Takayama, H., Fukuyo, Y. (eds) (2012) Marine

691 *Phytoplankton of the Western Pacific*. Kouseisha Kouseikaku, Tokyo.

- 692 O'Shaughnessy, P. and Cavanaugh, J. E. (2015) Performing t-tests to compare autocorrelated time
- 693 series data collected from direct-reading instruments. J. Occup. Environ. Hyg., **12**, 743–752.
- Petris G. (2010) An R Package for Dynamic Linear Models. J. Stat. Softw., 36, 1–16.
- 695 Probst, W. N., Stelzenmuller, V., Fock, H. O. (2012) Using cross-correlation to assess the
- relationship between time-lagged pressure and state indicators: an exemplary analysis of North
- 697 Sea fish population indicators. *ICES J. Mar. Sci.*, **69**, 670–681.
- 698 R Core Team (2021) R: A language and Environment for Statistical Computing. R Foundation for
- 699 Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
- Redfield, A. C., Ketchum, B. H., Richards, F. A. (1963) The influence of organisms on the
- composition of sea-water. In: Hill, M. N. (ed) The Sea: Ideas and Observations on Progress in
- the Study of the Seas, Vol. 2. Wiley, New York, pp. 26–77.
- Riquelme, C. E., Fukami, K., Ishida, Y. (1987) Annual fluctuations of phytoplankton and bacterial
- communities in Maizuru Bay and their interrelationship. *Bulletin of Japanese Society of*
- 705 *Microbial Ecology*, **2**, 29–37.
- Saiz, E., Griffell, K., Calbet, A., Isari, S. (2014) Feeding rates and prey : predator size ratios of the
- nauplii and adult females of the marine cyclopoid copepod Oithona davisae. Limnol. Oceanogr.,

- 708 **59**, 2077–2088.
- 709 Shin, H. H., Li, Z., Mertens, K. N., Seo, M. H., Gu, H., Lim, W. A., Yoon, Y. H., Soh, H. Y., et al.
- 710 (2019) *Prorocentrum shikokuense* Hada and *P. donghaiense* Lu are junior synonyms of *P.*
- 711 *obtusidens* Schiller, but not of *P. dentatum* Stein (Prorocentrales, Dinophycae). *Harmful Algae*,
- 712 **89**, 101686.
- Siegel, D. A., Doney, S. C., Yoder, J. A. (2002) The North Atlantic spring phytoplankton bloom
- and Sverdrup's critical depth hypothesis. *Science*, **296**, 730–733.
- Sommer, U. and Lengfellner, K. (2008) Climate change and the timing, magnitude, and
- composition of the phytoplankton spring bloom. *Glob. Change. Biol.*, **14**, 1199–1208.
- 717 Spilling, K., Kremp, A., Klais, R., Olli, K., Tamminen, T. (2014) Spring bloom community change
- modifies carbon pathways and C:N:P Chl *a* stoichiometry of coastal material fluxes.
- 719 *Biogeosciences*, **11**, 7275–7289.
- Suemoto, Y. (ed) (2013) A Photographic Guide to Marine Plankton of Japan, the Second Edition.
- 721 Kyoritsu Shuppan, Tokyo (in Japanese).
- Suzuki, Y., Michihiro, Y., Kanohgi, R., Yoshimura, Y. (2011) Long-term variability and future
- projection of wind speed along Japanese coast. *Journal of Japan Society of Civil Engineers, Ser.*
- *B3 (Ocean Engineering)*, **67**, 914–919 (in Japanese with English abstract).
- Takahashi, H. G. (2021) Long-term trends in snowfall characteristics and extremes in Japan from
- 726 1961 to 2012. *Int. J. Climatol.*, **41**, 2316–2329.
- Tanaka, S., Fujita, S., Sugiyama, M., Nishida, J., Nakanishi, M. (1977) On the Hemieutreptia
- *antiqua*, red tide occurred in Maizuru Bay, in October 1975. *Bulletin of the Kyoto Institute of*
- 729 *Oceanic and Fishery Science*, **1**, 94–112 (in Japanese).
- 730 Thomas, M. K., Kremer, C. T., Klausmeier, C. A., Litchman, E. (2012) A global pattern of thermal
- adaptation in marine phytoplankton. *Science*, **338**, 1085–1088.
- Thomas, M. K., Fontana, S., Reyes, M., Kehoe, M., Pomati, F. (2018) The predictability of a lake

- phytoplankton community, over time-scales of hours to years. *Ecol. Lett.*, **21**, 619–628.
- Turpin, D. H. and Harrison, P. (1979) Limiting nutrient patchiness and its role in phytoplankton
- 735 ecology. J. Exp. Mar. Biol. Ecol., **39**, 151–166.
- 736 Uchima, M. (1988) Gut content analysis of neritic copepods Acartia omorii and Oithona davisae by
- a new method. *Mar. Ecol. Prog. Ser.*, 48, 93–97.
- Ueda, H. (1975) *Seasonal Changes of Plankton in Maizuru Bay*. MS dissertation, Kyoto University,
 Kyoto (in Japanese).
- ⁷⁴⁰ Ueda, H. (1987a) Temporal and spatial distribution of the two closely related *Acartia* species *A*.
- 741 *omorii* and *A. hudsonica* (Copepoda, Calanoida) in a small inlet water of Japan. *Estuar. Coast.*
- 742 Shelf. Sci., 24, 691–700.
- 743 Ueda, H. (1987b) Small-scale ontogenetic and diel vertical distributions of neritic copepods in
- 744 Maizuru Bay, Japan. Mar. Ecol. Prog. Ser., 35, 65–73.
- Ueno, R. and Ishikawa, A. (2009) Evaluation of functionality as a seed population of resting stage
- cells of centric diatoms in surface sediments of Ago Bay, central part of Japan. *Bull Plankton Soc*
- 747 *Japan*, **56**, 1–12 (in Japanese with English abstract).
- Vogt, R. A., Ignoffo, T. R., Sullivan, L. J., Herndon, J., Stillman, J. H., Kimmerer, W. J. (2013)
- Feeding capabilities and limitations in the nauplii of two pelagic estuarine copepods,
- 750 *Pseudodiaptomus marinus* and *Oithona davisae*. *Limnor*. *Oceanogr.*, **58**, 2145–2157.
- 751 Watanabe, K., Kasai, A., Fukuzaki, K., Ueno, M., Yamashita, Y. (2017) Estuarine circulation-
- driven entrainment of oceanic nutrients fuels coastal phytoplankton in an open coastal system in
- 753 Japan. Estuar. Coast. Shelf. Sci., 184, 126–137.
- Wetz, M. S., Wheeler, P. A., Letelier, R. M. (2004) Light-induced growth of phytoplankton
- collected during the winter from the benthic boundary layer off Oregon, USA. *Mar. Ecol. Prog. Ser.*, 280, 95–104.
- 757 White, J. R. and Roman, M. R. (1992) Seasonal study of grazing by metazoan zooplankton in the

- mesohaline Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, **86**, 251–261.
- Winder, M. and Sommer, U. (2012) Phytoplankton response to a changing climate. *Hydrobiologia*,
 698, 5–16.
- Wood, E. D., Armstrong, F. A. J., Richards, F. A. (1967) Determination of nitrate in sea water by
- cadmium-copper reduction to nitrite. J. Mar. Biol. Assoc. U. K., 47, 23–31.
- Xu, N., Duan, S., Li, A., Zhang, C., Cai, Z., Hu, Z. (2010) Effects of temperature, salinity and
- irradiance on the growth of the harmful dinoflagellate *Prorocentrum donghaiense* Lu. *Harmful Algae*, 9, 13–17.
- 766 Yamada, M., Tsuruta, A., Yoshida, Y. (1980) A list of phytoplankton as eutrophic level indicator.

767 *Nippon Suisan Gakkaishi*, **46**, 1435–1438 (in Japanese with English abstract).

- 768 Yamada, M., Otsubo, M., Kodama, M., Yamamoto, K., Nishikawa, T., Ichimi, K., Tada, K.,
- Harrison, P. J. (2014) Species composition of *Skeletonema* (Bacillariophyceae) in planktonic and
 resting-stage cells in Osaka and Tokyo Bays. *Plankton and Benthos Research*, 9, 168–175.
- 771 Yamada, M., Otsubo, M., Tada, K., Nakano, Y., Matsubara, T., Iida, N., Endo, Y., Montani, S.
- (2017) Species composition of the genus *Skeletonema* (Bacillariophyceae) in five Japanese
- coastal waters over the subtropics from the subarctic zone. *Nippon Suisan Gakkaishi*, **83**, 25–33
- (in Japanese with English abstract).
- Yamazi, I. (1953) Plankton investigation in inlet waters along the coast of Japan VII. The plankton
- collected during the cruises to the new Yamato bank in the Japan Sea. *Publ. Seto Mar. Biol. Lab.*,
 3, 75–108.
- Zamora-Terol, S., Saiz, E. (2013) Effects of food concentration on egg production and feeding rates
 of the cyclopoid copepod *Oithona davisae*. *Limnol. Oceanogr.*, 58, 376–387.
- Zingone, A., Dubroca, L., Iudicone, D., Margiotta, F., Corato, F., d'Alcala, M. R., Saggiomo, V.,
- Sarno, D. (2010) Coastal phytoplankton do not rest in winter. *Estuar. Coast.*, **33**, 342–361.

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783 LEGENDS FOR FIGURES

- **Fig. 1.** Study area and observation stations in Maizuru Bay. Isobaths are shown with 10 m intervals.
- 785 Daily sampling was conducted at the floating pier of Maizuru Fisheries Research Station
- 786 (MFRS). Japan Meteorological Agency monitors meteorological parameters and sea level with
- Automated Meteorological Data Acquisition System (AMeDAS) and a tide gauge, respectively.
- An automatic water quality profiling system was set at a bivalve mariculture raft (Raft).
- **Fig. 2** Daily changes in wind vector (sixteen directions, m s⁻¹), precipitation (mm d⁻¹), snow height
- (cm) and chlorophyll a concentration (Chl a, $\mu g L^{-1}$) in the winters of 2016/2017 (A), 2018/2019
- 791 (B), 2020/2021 (C), 2021/2022 (D) and 2022/2023 (E).
- Fig. 3. Daily changes in chlorophyll *a* (Chl *a*, μ g L⁻¹; A), nitrite and nitrate (NO_x⁻, μ M; B),
- phosphate concentrations (PO₄³⁻, μ M; C), water temperature (°C; D), salinity (E) and light
- quantum (µmol m⁻² s⁻¹; F) from 1 January to 11 March 2017. The 3-day box-averaged values of
- daily means through the water column are shown using thick curves.
- Fig. 4. Daily changes in chlorophyll *a* (Chl *a*, μ g L⁻¹; A), nitrite and nitrate (NO_x⁻, μ M; B),
- ammonium (NH₄⁺, μ M; C), phosphate concentrations (PO₄³⁻, μ M; D), water temperature (°C; E),
- salinity (F) and light quantum (µmol m⁻² s⁻¹; G) from 1 January to 11 March 2019. See Fig. 3 for
 details.
- **Fig. 5.** Daily changes in the molar ratio of dissolved inorganic nitrogen to phosphate (N:P ratio)
- from 1 January to 11 March in 2017 (A) and 2019 (B). The Redfield ratio (16; Redfield *et al.*,
- 1963) is indicated by broken lines. See Fig. 3 for details.
- **Fig. 6.** Cross-correlation function of salinity in relation to chlorophyll *a* (Chl *a*; A, B), nitrite and
- nitrate (NO_x^{-;} C, D), and phosphate concentrations (PO₄³⁻; E, F), water temperature (G, H) and
- 805 precipitation (I, J). The cross-correlation function was calculated from prewhitened time series
- separately for 0, 2 and 4 m deep in the winters of 2016/2017 and 2018/2019 (see the text for
- details). The 95% significance limits are shown using broken lines.

808	Fig. 7. Comparisons of temporal changes in chlorophyll <i>a</i> (Chl <i>a</i> , µg L ⁻¹ ; A), nitrite and nitrate
809	(NO _x ⁻ , μ M; B), phosphate concentrations (PO ₄ ³⁻ , μ M; C), water temperature (°C; D), salinity (E)
810	and light quantum (μ mol m ⁻² s ⁻¹ ; F) in the winters of 2016/2017 and 2018/2019. Smoothed values
811	and their 95% confidence intervals were shown by bold lines and light shades, respectively. Chl
812	a, NO _x ⁻ , PO ₄ ³⁻ and light quantum were log-transformed prior to the application of the dynamic
813	linear models (see the text for details). P values derived from t-tests are shown on each panel and
814	significant interannual differences in the seasonal average are indicated by underlines (see the
815	text for details).
816	Fig. 8. Temporal changes in phytoplankton cell density (cells mL ⁻¹) and taxonomic composition at
817	0, 2 and 4 m deep (A, B and C, respectively) in relation to temporal changes in copepod density
818	(inds L ⁻¹) and taxonomic composition through the water column (D) during the sampling period
819	in 2017.
820	Fig. 9. Temporal changes in phytoplankton cell density (cells mL ⁻¹) and taxonomic composition at
821	0, 2 and 4 m deep (A, B and C, respectively) in relation to temporal changes in copepod density
822	(inds L ⁻¹) and taxonomic composition through the water column (D) during the sampling period
823	in 2019.
824	Fig. 10. Hourly changes in sea level (cm; A), air temperature (°C; B), wind speed (m s ⁻¹ ; C), water
825	temperature (°C; D) and salinity (E) from 12 December 2016 to 19 January 2017. The shaded
826	areas are periods when daily box-averaged wind speed exceeded 5 m s ⁻¹ . Hourly values and their
827	daily box-averaged values (±12 h) are connected by thin and thick curves, respectively.
828	Fig. S1. Interannual changes in dissolved inorganic nitrogen (DIN, μ M; A), phosphate
829	concentrations (PO ₄ ³⁻ , μ M; B) and their molar ratio (N:P ratio; C) observed in Maizuru Bay from
830	1980 to 2019. Annual means with standard deviations are shown. The Redfield ratio (16;
831	Redfield et al., 1963) is indicated by a broken line.
832	Fig. S2. Relationships of concentrations of nitrite and nitrate (NO _x ⁻ , μ M) with concentrations of

- dissolved inorganic nitrogen (DIN, μ M) observed at 0, 2 and 4 m deep in the winter 2018/2019.
- Equations of linear regression with coefficients of determination (R^2) are shown separately for 0,
- 835 2 and 4 m deep.
- **Fig. S3.** Temporal changes in sea level (cm; A), air temperature (°C; B), wind speed (m s⁻¹; C),
- sunshine duration (h d⁻¹; D), precipitation (mm d⁻¹; E) and snow height (cm; E) from 1 December
- 838 2016 to 11 March 2017. Hourly values and their daily box-averaged values (±12 h) are connected
- by thin and thick curves, respectively.
- Fig. S4. Temporal changes in sea level (cm; A), air temperature (°C; B), wind speed (m s⁻¹; C),
- sunshine duration (h d⁻¹; D), precipitation (mm d⁻¹; E) and snow height (cm; E) from 1 December
- 842 2018 to 11 March 2019. See Fig. S3 for details.
- Fig. S5. Scatter plots between meteorological parameters during winter (December to February)
- observed in Maizuru Bay in the last six decades (1963/1964–2022/2023). Total snowfall (cm; A,
- B, C) and total precipitation (mm; D, E, F) are shown in relation to average air temperature (°C),
- average sunshine duration (h d^{-1}) and number of windy days (>5 m s⁻¹). The Pearson's correlation

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coefficient is indicated by *r*.

Table I. Comparisons of bloom intensity and weather conditions in Maizuru Bay in five winters (December to February). Chlorophyll a (Chl a) was measured daily in the winters of 2016/2017, 2018/2019, 2020/2021 and 2021/2022, whereas in the winter 2022/2023 it was measured weekly. Ranks within the last six decades (1963/1964–2022/2023) are shown in parentheses. Windy days are defined as daily wind speed stronger than 5 m s⁻¹

	Period and frequency of	Bloom intensity	Total precipitation	Total snowfall	Average air temperature	Daily sunshine duration	Windy days
	Chl a measurement	(relative grade)	(mm)	(cm)	(°C)	(h)	(days)
2016/2017	1 Jan to 11 Mar (daily)	++++	594 (5 th)	165 (24 th)	4.9 (20 th)	2.50 (42 nd)	4
2018/2019	1 Jan to 11 Mar (daily)	+	381 (43 rd)	15 (58 th)	5.7 (4 th)	2.24 (56 th)	2
2020/2021	13 Dec to 2 Mar (daily)	++	401 (38 th)	114 (35 th)	5.1 (15 th)	3.73 (4 th)	3
2021/2022	1 Dec to 6 Mar (daily)	+++	516 (18 th)	277 (8 th)	3.8 (43 rd)	2.82 (28 th)	3
2022/2023	1 Dec to 11 Mar (weekly)	++	339 (49 th)	63 (51 st)	4.6 (24 th)	2.72 (34 th)	4



Study area and observation stations in Maizuru Bay. Isobaths are shown with 10 m intervals. Daily sampling was conducted at the floating pier of Maizuru Fisheries Research Station (MFRS). Japan Meteorological Agency monitors meteorological parameters and sea level with Automated Meteorological Data Acquisition System (AMeDAS) and a tide gauge, respectively. An automatic water quality profiling system was set at a bivalve mariculture raft (Raft).



Daily changes in wind vector (sixteen directions, m s-1), precipitation (mm d-1), snow height (cm) and chlorophyll a concentration (Chl a, μ g L-1) in the winters of 2016/2017 (A), 2018/2019 (B), 2020/2021 (C), 2021/2022 (D) and 2022/2023 (E).

Fig. 2 (continued)



Daily changes in wind vector (sixteen directions, m s-1), precipitation (mm d-1), snow height (cm) and chlorophyll a concentration (Chl a, μ g L-1) in the winters of 2016/2017 (A), 2018/2019 (B), 2020/2021 (C), 2021/2022 (D) and 2022/2023 (E).



Fig. 3

Daily changes in chlorophyll a (Chl a, μ g L-1; A), nitrite and nitrate (NOx-, μ M; B), phosphate concentrations (PO43-, μ M; C), water temperature (°C; D), salinity (E) and light quantum (μ mol m-2 s-1; F) from 1 January to 11 March 2017. The 3-day box-averaged values of daily means through the water column are shown using thick curves.



Daily changes in chlorophyll a (Chl a, μ g L-1; A), nitrite and nitrate (NOx-, μ M; B), ammonium (NH4+, μ M; C), phosphate concentrations (PO43-, μ M; D), water temperature (°C; E), salinity (F) and light quantum (μ mol m-2 s-1; G) from 1 January to 11 March 2019. See Fig. 3 for details.



Daily changes in the molar ratio of dissolved inorganic nitrogen to phosphate (N:P ratio) from 1 January to 11 March in 2017 (A) and 2019 (B). The Redfield ratio (16; Redfield et al., 1963) is indicated by broken lines. See Fig. 3 for details.



Cross-correlation function of salinity in relation to chlorophyll a (Chl a; A, B), nitrite and nitrate (NOx-; C, D), and phosphate concentrations (PO43-; E, F), water temperature (G, H) and precipitation (I, J). The cross-correlation function was calculated from prewhitened time series separately for 0, 2 and 4 m deep in the winters of 2016/2017 and 2018/2019 (see the text for details). The 95% significance limits are shown using broken lines.



Fig. 7

Comparisons of temporal changes in chlorophyll a (Chl a, μg L-1; A), nitrite and nitrate (NOx-, μM; B), phosphate concentrations (PO43-, μM; C), water temperature (°C; D), salinity (E) and light quantum (μmol m-2 s-1; F) in the winters of 2016/2017 and 2018/2019. Smoothed values and their 95% confidence intervals were shown by bold lines and light shades, respectively. Chl a, NOx-, PO43- and light quantum were log-transformed prior to the application of the dynamic linear models (see the text for details). P values derived from t-tests are shown on each panel and significant interannual differences in the seasonal average are indicated by underlines (see the text for details).

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Temporal changes in phytoplankton cell density (cells mL-1) and taxonomic composition at 0, 2 and 4 m deep (A, B and C, respectively) in relation to temporal changes in copepod density (inds L-1) and taxonomic composition through the water column (D) during the sampling period in 2017.



Temporal changes in phytoplankton cell density (cells mL-1) and taxonomic composition at 0, 2 and 4 m deep (A, B and C, respectively) in relation to temporal changes in copepod density (inds L-1) and taxonomic composition through the water column (D) during the sampling period in 2019.





Hourly changes in sea level (cm; A), air temperature (°C; B), wind speed (m s-1; C), water temperature (°C; D) and salinity (E) from 12 December 2016 to 19 January 2017. The shaded areas are periods when daily box-averaged wind speed exceeded 5 m s-1. Hourly values and their daily box-averaged values (±12 h) are connected by thin and thick curves, respectively.



Fig. S1

Interannual changes in dissolved inorganic nitrogen (DIN, μM; A), phosphate concentrations (PO43-, μM; B) and their molar ratio (N:P ratio; C) observed in Maizuru Bay from 1980 to 2019. Annual means with standard deviations are shown. The Redfield ratio (16; Redfield et al., 1963) is indicated by a broken line.



Fig. S2

Relationships of concentrations of nitrite and nitrate (NOx-, μ M) with concentrations of dissolved inorganic nitrogen (DIN, μ M) observed at 0, 2 and 4 m deep in the winter 2018/2019. Equations of linear regression with coefficients of determination (R2) are shown separately for 0, 2 and 4 m deep.





Temporal changes in sea level (cm; A), air temperature (°C; B), wind speed (m s-1; C), sunshine duration (h d-1; D), precipitation (mm d-1; E) and snow height (cm; E) from 1 December 2016 to 11 March 2017. Hourly values and their daily box-averaged values (±12 h) are connected by thin and thick curves, respectively.





Temporal changes in sea level (cm; A), air temperature (°C; B), wind speed (m s-1; C), sunshine duration (h d-1; D), precipitation (mm d-1; E) and snow height (cm; E) from 1 December 2018 to 11 March 2019. See Fig. S3 for details.



Fig. S5

Scatter plots between meteorological parameters during winter (December to February) observed in Maizuru Bay in the last six decades (1963/1964–2022/2023). Total snowfall (cm; A, B, C) and total precipitation (mm; D, E, F) are shown in relation to average air temperature (°C), average sunshine duration (h d-1) and number of windy days (>5 m s-1). The Pearson's correlation coefficient is indicated by r.