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Protist dynamics in the eastern Tsugaru Strait, Japan from 2010 to 2018: Implications for the relationship between decadal climatology and aquaculture production

Koji Sugie^{a,*}, Masahide Wakita^b, Shoko Tatamisashi^b, Makoto Takada^c, Takashi Yusa^d, Ken-ichi Sasaki^b, Hiroto Abe^{b,e}, Takahiro Tanaka^f

^a Research Institute for Global Change, Japan Agency for Marine-Earth Science and Technology, 2-5, Natsushima-cho, Yokosuka, Kanagawa, 237-0061, Japan

^b Research Institute for Global Change, Japan Agency for Marine-Earth Science and Technology, 690 Kitasekine, Sekine, Mutsu, Aomori, 035-0022, Japan

^c Tohoku Environmental Science Services Corporation, 330-2, Noduki, Obuchi, Rokkasho, Kamikita, Aomori, 039-3212, Japan

^d Fisheries Research Institute, Aomori Prefectural Industrial Technology Research Center, 10 Tsukidomari, Moura, Hiranai, Higasitsugaru, Aomori, 039-3381, Japan

^e Faculty of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido, 041-8611, Japan

^f Fisheries Resources Institute, Japan Fisheries Research and Education Agency, 3-27-5 Shinhama-cho, Shiogama, Miyagi, 985-0001, Japan

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ABSTRACT

Environmental changes such as seasonality, decadal oscillation, and anthropogenic forcing may shape the dynamics of lower trophic-level organisms. In this study, 9-years (2010–2018) of monitoring data on microscopic protists such as diatoms and dinoflagellates, and environmental variables were analyzed to clarify the relationships between plankton and local/synoptic environmental changes. We found that time-series temperature increased in May, whereas it decreased in August and November. Nutrients (e.g., phosphate) decreased in May, remained unchanged in August, and increased in November from 2010 to 2018. The partial pressure of CO₂ increased in May, August, and November over time. It is notable that the change in seawater temperature (−0.54 to 0.32 °C per year) and CO₂ levels (3.6–5.7 μatm CO₂ per year) in the latest decade in the eastern Tsugaru Strait were highly dynamic than the projected anthropogenic climate change. Protist abundance generally increased or stayed unchanged during the examined period. In August and November, when cooling and decreases in pH occurred, diatoms such as *Chaetoceros* subgenus *Hyalochaete* spp. and Rhizosoleniaceae temporally increased from 2010 to 2018. During the study period, we found that locally aquacultured scallops elevated soft tissue mass relative to the total weight as diatom abundance increased, and the relative scallop soft tissue mass was positively related to the Pacific Decadal Oscillation index. These results indicate that decadal climatic forcing in the ocean modifies the local physical and chemical environment, which strongly affects phytoplankton dynamics rather than the effect of anthropogenic climate change in the eastern Tsugaru Strait.

1. Introduction

Phytoplankton form the base of the aquatic ecosystem, and primary production strongly thus affects the production of higher trophic levels including commercially important fish and shellfish (Myers and Worm, 2003; Smetacek and Cloen, 2008). Recent warming has induced changes in the phenology of bloom-forming phytoplankton (Edwards and Richardson, 2004) and has caused the poleward retreat of temperate phytoplankton traits in the Atlantic Ocean (Beaugrand et al., 2009). Because the composition and structure of phytoplankton are the consequence of the abiotic and biotic interactions in an ecosystem,

determining the factors affecting phytoplankton dynamics in the natural environment with long-term monitoring is crucially important.

The coastal environment is highly productive and is often an important spawning ground that helps sustain commercially important fisheries. For this study, we selected a coastal ecosystem in the Tsugaru Strait located between Honshu Island and Hokkaido Island, Japan (Fig. 1). The Tsugaru Strait is an important fishery ground for bluefin tuna (Fujioka et al., 2021) and the Japanese scallop (Aura et al., 2016). The Tsugaru Strait is approximately 100 km in length and 20–40 km in width. It is dominated by the Tsugaru Warm Current (TWC) that flows at a rate of approximately $1.5 \times 10^6 \text{ m}^3/\text{s}$ eastward from the Sea of Japan

* Corresponding author. Japan Agency for Marine-Earth Science and Technology, 2-5, Natsushima-cho, Yokosuka, Kanagawa, 237-0061, Japan.

E-mail address: sugie@jamstec.go.jp (K. Sugie).

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to the Pacific Ocean. The inflow of the Tsushima Warm Current to the Sea of Japan via the Tsushima Strait—located in northern Kyushu and southwest of Honshu Island, Japan—is the origin of the TWC (Isobe, 1999; Kuroda et al., 2020). The current system and the bathymetry of the strait produce turbulent mixing and eddies that enhance nutrient levels in the sunlit surface layer (Ito et al., 2003; Ohta et al., 2015; Tanaka et al., 2021). The TWC is driven by sea-level differences between the Sea of Japan and the western North Pacific. This indicates that the TWC could be affected by the synoptic climatological state such as the position and the strength of the Aleutian low; i.e., Pacific Decadal Oscillation (PDO; Mantua and Hare, 2002). Recent studies reported an increase in the flow of the TWC because of the increasing inflow of the Tsushima Warm Current (Wakita et al., 2021) when the PDO index shifts from negative to positive and the El Niño-Southern Oscillation (ENSO; Trenberth, 1997) phase shifts from La Niña-to El Niño-dominated. Increased TWC flow elevates the dissolved inorganic carbon (DIC) concentration in the surface mixed layer by incorporating deeper seawater from the Sea of Japan, and thus, the rate of pH decrease is faster than that expected solely from the increase in atmospheric CO₂ from 2012 to 2019 (Wakita et al., 2021).

Along with global warming, ocean acidification is potentially one of the most serious environmental problems that modify not only phytoplankton productivity and stoichiometry (Sugie et al., 2013, 2020, 2018) but also the early-stage development of commercially important fish and shellfish (Doney et al., 2009). The combined impacts of higher temperature and lower pH/higher DIC could be beneficial to smaller phytoplankton traits that could reduce the efficiencies of trophic transfer and the biological carbon pump (Schulz et al., 2017; Sugie et al., 2020). Furthermore, archaeological study of the northern Honshu Island (Sannai-Maruyama ruins) suggests that in addition to the terrestrial climate, phytoplankton productivity around the Tsugaru Strait strongly affected civilization and collapsing the colonized community from 5.9 to 4.2 kyr BP (Kawahata et al., 2009). These studies suggest that the recent change in the environmental conditions of the Tsugaru Strait could affect our seafood resources by modifying phytoplankton productivity and community composition. However, the impacts of environmental changes on the biological system have not been investigated in the study area. The effect of ocean acidification on phytoplankton is often species- and trait-specific (Fu et al., 2012; Tatters et al., 2013; Sugie et al., 2018) and is affected by the composition and diversity of protists (Eggers et al.,

2013; Schulz et al., 2017; Riebesell et al., 2018; Sugie et al., 2020). Environmental monitoring is a powerful method to understand the fate of the local ecosystem under future climate change.

In this study, we analyzed monitoring data from 2010 to 2018 for microscopic protists and environmental conditions in the eastern Tsugaru Strait. In addition, we analyzed the relationships among the temporal trends in diatom abundance, decadal climatology, and scallop fertility to better understand the local ecosystem. This study potentially shows the ecological connectivity from the physical and chemical properties of seawater to fisheries production through environmental changes, which could shed light on our understanding of future ecosystem changes under climate change.

2. Materials and methods

2.1. Samplings

Seawater samples at 0, 10, and/or 20 m depth were collected from the stations Sekinehama Port (SP), OS-01, SE-03 and HO-03 during 2010–2018 (Fig. 1; Table 1), where seawater property was characterized as the TWC as reported before (Wakita et al., 2021). A few low salinity seawater samples (<33 in salinity) were excluded from the analysis because that is predominated by modified subarctic coastal water. Because the salinity of surface layer is affected by the meteoric waters, the criteria of <33 salinity is less saline compared to the feature of the TWC (Hanawa and Mitsudera, 1987). Furthermore, we did not apply the criteria of <5 °C at 100 m depth as an indicator of subarctic coastal water (Kuroda et al., 2020), because the composition of seawater mass in the coastal region is not often vertically uniform and the depth at St. SP is shallower than 100 m. Surface seawater samples from the monitoring St. SP, located at the offshore end of the breakwater in Sekinehama Port, were collected using a plastic bucket. Weekly monitoring at St. SP began in February 2014, and the data from 267 samples were used in this study (Table 1). The samples from stations OS-1, SE-03, and HO-03 were collected using the training ships T/S *Ushio-Maru* and T/S *Oshoro-Maru* of Hokkaido University after 2010, and the research vessel R/V *Wakataka-Maru* of the Japan Fisheries Research and Education Agency in the summer of 2018. The plastic bucket (0 m) and Niskin sampling bottles (10 and 20 m) attached to a CTD-CWS system were used on-board sampling. On-board samplings were conducted for

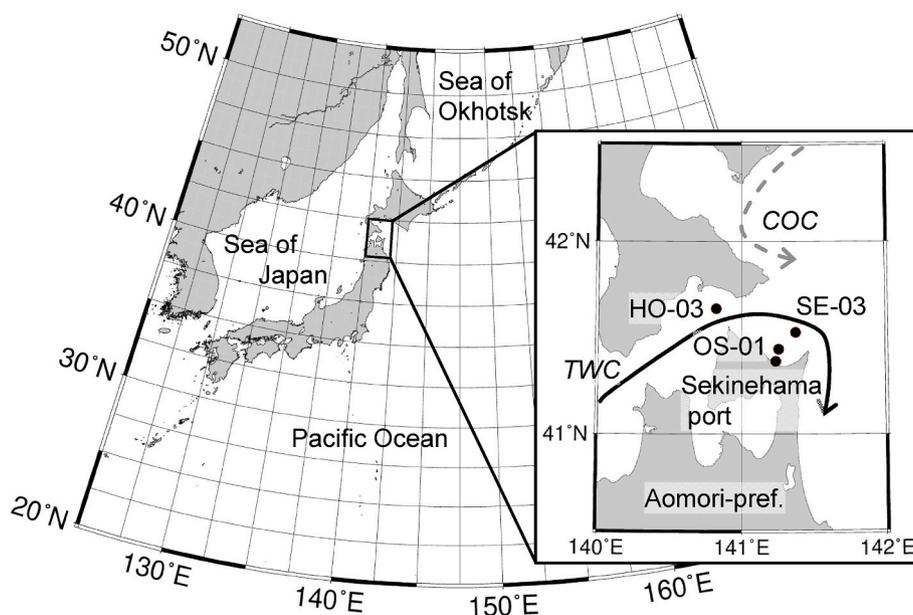


Fig. 1. Map of monitoring stations in the eastern Tsugaru Strait. Solid and dashed lines represent the Tsugaru Warm Current (TWC) and Coastal Oyashio Current (COC), respectively.

Table 1
Properties of samplings at each station that is used in this study.

Station	Latitude (N)	Longitude (E)	Seafloor depth (m)	Sampling method	No. of samples	Period	Frequency
HO-03	41°65'	140°82'	ca. 350	Niskin, bucket	65	2010–2018	2–5 times per year
OS-01	41°44'	141°26'	ca. 80	Niskin, bucket	162	2011–2018	2–4 times per year
SE-03	41°53'	141°37'	ca. 240	Niskin, bucket	119	2011–2018	1–4 times per year
Sekinehama Port	41°38'	141°24'	9	bucket	267	2014–2018	Weekly

covering every season (1–5 times per year), and 162, 119 and 65 samples were used for analysis at stations OS-1, SE-03 and HO-03, respectively (Table 1).

2.2. Chemical and biological analyses

We analyzed temperature, salinity, irradiance, $p\text{CO}_2$, nutrients (NO_3 , NO_2 , PO_4 , $\text{Si}(\text{OH})_4$ and NH_3) and microscopic protists in the present study. The $p\text{CO}_2$ was estimated from DIC and total alkalinity (TA) data. Detailed measurements and calibrations on physical and chemical variables are described in our recent study (Wakita et al., 2021). In brief, temperature and salinity were obtained using CTD sensors (St. SP: RINKO-Profilier; JFE Advantech Co. Ltd.; on-board: SBE911plus; Sea-Bird Sci. Inc.) and water sample for salinity was measured using a salinometer (Model 8400 B AUTOSAL, Guildline Instruments Ltd.) and calibrated using International Association for the Physical Sciences of the Ocean (IAPSO) standard seawater (Ocean Scientific International Ltd.). The DIC and TA were measured with coulometry and titration, respectively, using coulometers (CM5012, UIC Inc. and Model 3000 A, Nippon ANS Inc.) and an alkalinity titration analyzer (ATT-15, Kimoto Electric Co. Ltd.). Accuracies of the DIC and TA measurements were checked using seawater reference material of carbonate chemistry (KANSO Technos Co. Ltd.), which was traceable to certified reference materials distributed by the Scripps Institution of Oceanography (Dickson et al., 2003). The nutrients were measured and calibrated using certified reference materials (KANSO Technos Co. Ltd.) with colorimetry using a spectrophotometer and a QuAatro continuous flow analyzer (see Wakita et al., 2021). The daily irradiance data (MW/m^2) of the Aomori prefecture during the study period was obtained from the Japan Meteorological Agency. Seawater samples for microscopic observation were fixed with formalin (1% in final concentration) and stored in refrigerator (4 °C) until analysis. Samples were concentrated approximately 20–50 times and observed using a Sedgewick-Rafter Counting Chamber under $100\times$, $200\times$ or $400\times$ magnifications (Hasle, 1978). Although identification of protists was performed to the lowest possible levels according to Thomas (1997), data were pooled by genus (diatoms: *Pseudo-nitzschia* spp., *Thalassiosira* spp., *Chaetoceros* subgen. *Hyalochaete*, dinoflagellates: *Heterocapsa* spp., *Prorocentrum* spp.), order (diatom: Rhizosoleniaceae, dinoflagellates: Peridinales, mainly *Prorocentrum* spp.), and class (coccolith-bearing Prymnesiophyceae, coccolithophores) to minimize the bias from several observers during long-term monitoring. The abundances of small flagellates ($<10\ \mu\text{m}$) were pooled and analyzed as flagellates.

2.3. Aquaculture and climatological data

To examine the relationship between the dynamics of protists and the production of higher trophic levels, aquaculture data were examined for the scallop *Mizuhopecten (Patinopecten) yessoensis* in the Aomori prefecture of Japan (Yamauchi et al., 2022), where the TWC is the dominant seawater system. The total catch of scallops is regulated by the local law of the TASC (total allowable scallop culture), so the scallop soft tissue index (STI; $\text{STI} = \text{soft tissue biomass of scallop} \times 100/\text{total weight}$) was used as an indicator of fertility and resource abundance for scallops. Data from the hanging cultures (pearl nets, lantern nets, and ear hanging) of scallops were used because they were normalized by age

of culture, and the depths of the hanging cultures (5–15 m) were similar to the depths of the planktonic protists we analyzed (0–20 m). The scallops are filter feeders and they feed on planktonic protists during the hanging cultures (Jørgensen, 1996). Therefore, the STI of scallop aquaculture data could be a representative indicator of the relationship between the dynamics of protists and local fisheries production. The climatological index of PDO was used from the NOAA website (<https://www.ncei.noaa.gov/access/monitoring/pdo/>) to examine the relationship among protists dynamics, local environmental variability, and climate system.

2.4. Statistics

Seasonal changes in environmental variables and protist abundance were shown as box plots using pooled monthly data during the study period of 2010–2018. The box, vertical bars, and bar in the box represent 25%–75% and 1%–99% of the data range, and the median of the pooled data. The seasonal succession of protists was analyzed by a Gaussian fitting using pooled monthly abundance data. To examine the relationship between protist dynamics and environmental variables, we conducted principal component analysis (PCA) using Canoco 5 software. The Canoco software can compute statistical analysis using multidimensional data with ordination methods to represent ecosystem structure under a gradual environmental change (Šmilauer and Lepš, 2014). To test the long-term trends in environmental variables and protist abundance, we choose February, May, August and November data representing winter, spring, summer and fall data, respectively, partly because of the availability of ample shipboard data. Although there were no significant temporal trends in sampling day in selected months (Supplemental Fig. 1), we offset the sampling time on the middle day of the month using the seasonality of the monthly mean data. The linear change between the neighboring month was applied to offset the environmental variables. Because protist dynamics should be determined by the temporally different non-linear behaviors of growth and grazing, it is difficult to properly offset the sampling day of their abundance data. Linear regression between year and the data of each season was tested with 95% confidence intervals using Origin software (Lightstone Corp., Tokyo, Japan).

3. Results

3.1. Seasonality of the environment

Temperature and irradiance showed unimodal pattern and maxima from August to September and June, respectively (Fig. 2). The $p\text{CO}_2$ showed a bimodal pattern that had peaks in February and September (Fig. 2d). The nutrients, except for NH_3 had maxima in the winter (December to February), and NO_3 depletion was observed from April to September (Fig. 2e and g). The NO_2 , PO_4 and $\text{Si}(\text{OH})_4$ showed minima in August, indicating that regenerated nitrogen plays a role on phytoplankton productivity from the late spring to summer. Salinity (Fig. 2b) and NH_3 (Supplemental Fig. 2) did not show clear seasonal patterns.

3.2. Seasonal dynamics of protists

The unimodal pattern of total diatom abundance showed a broad

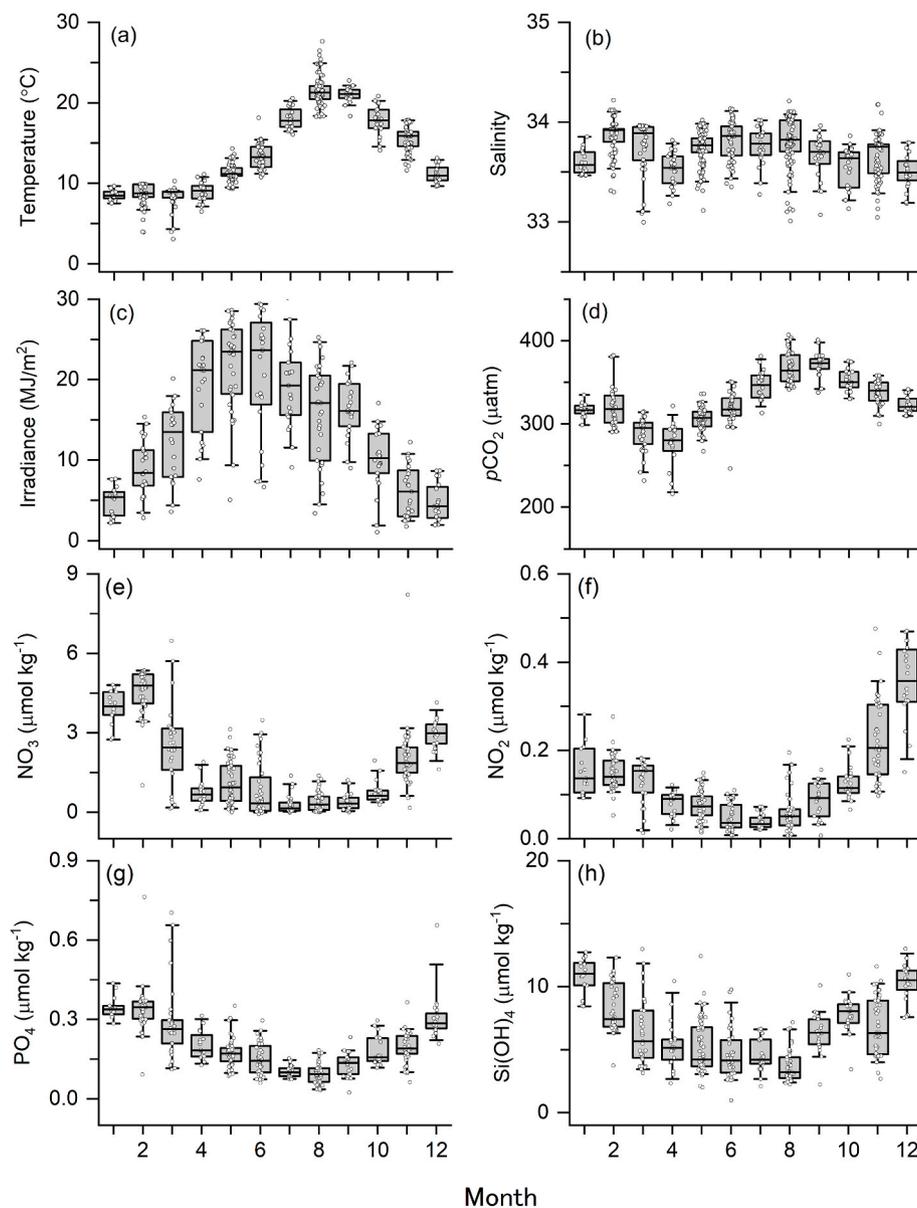


Fig. 2. Seasonal changes in (a) temperature, (b) salinity, (c) irradiance, (d) $p\text{CO}_2$, (e) nitrate, (f) phosphate, (g) silicic acid, and (h) ammonia. Data are pooled for each month from 2010 to 2018. Boxes, bars, and horizontal lines in boxes represent data ranges for 25–75%, data ranges for 1–99%, and medians, respectively.

maximum from April to August (Fig. 3a). The abundance of dinoflagellates peaked in July and was about one order of magnitude lower than that of the total diatoms (Fig. 3b). The seasonal pattern of centric diatoms was similar to that of the total diatoms (Fig. 3c). The pennate diatoms appeared about half in abundance than that of centric diatoms and showed maximum in June (Fig. 3d). The flagellate and coccolithophores did not show clear seasonality but appeared higher abundances from September to November after the maxima of diatoms and dinoflagellates (Fig. 3e and f). Among the diatoms, *Thalassiosira* spp., Rhizosoleniaceae, *Chaetoceros* subgen. *Hyalochaete* spp. and *Pseudo-nitzschia* spp. appeared higher abundances during the months of March–April, May–July, June–August, and June–August, respectively (Fig. 4a–4d). For the dinoflagellates, *Prorocentrum* spp. showed a maximum abundance in July, and *Heterocapsa* spp. and Peridiniales appeared sporadically from June to September (Fig. 4e–4g). According to the Gaussian analysis, the seasonal succession of protists occurred in the following order: *Thalassiosira* spp. (middle March), *Chaetoceros* subgen. *Hyalochaete* spp. (start of June), Rhizosoleniaceae (late June), *Pseudo-nitzschia* spp. (end of June), *Prorocentrum* spp. (start of July),

Peridiniales (early July) and *Heterocapsa* spp. (start of August) (Fig. 4h).

The PCA analysis represents 65.6% of the total variability of protist dynamics in the first two components, with explaining 41.4% and 24.2% in the first (PC1) and second axis (PC2), respectively. The PCA analysis indicates that the abundance of *Thalassiosira* spp., which appeared mainly in the spring, is negatively correlated with temperature and positively correlated with nutrients (Fig. 5). In contrast, the abundances of Rhizosoleniaceae, *Chaetoceros* subgen. *Hyalochaete* spp., and flagellates, which appeared from early summer to autumn, are positively correlated with temperature and negatively correlated with nutrients. The summer to autumn dominated traits (*Pseudo-nitzschia* spp. and dinoflagellates) positively correlated with irradiance and negatively correlated with NO_2 and salinity, and showed intermediate between high nutrient-related and high temperature-related traits. Coccolithophores showed a unique position among the dominant protist traits in the TWC region that they appeared under higher temperature and lower salinity conditions (Fig. 5).

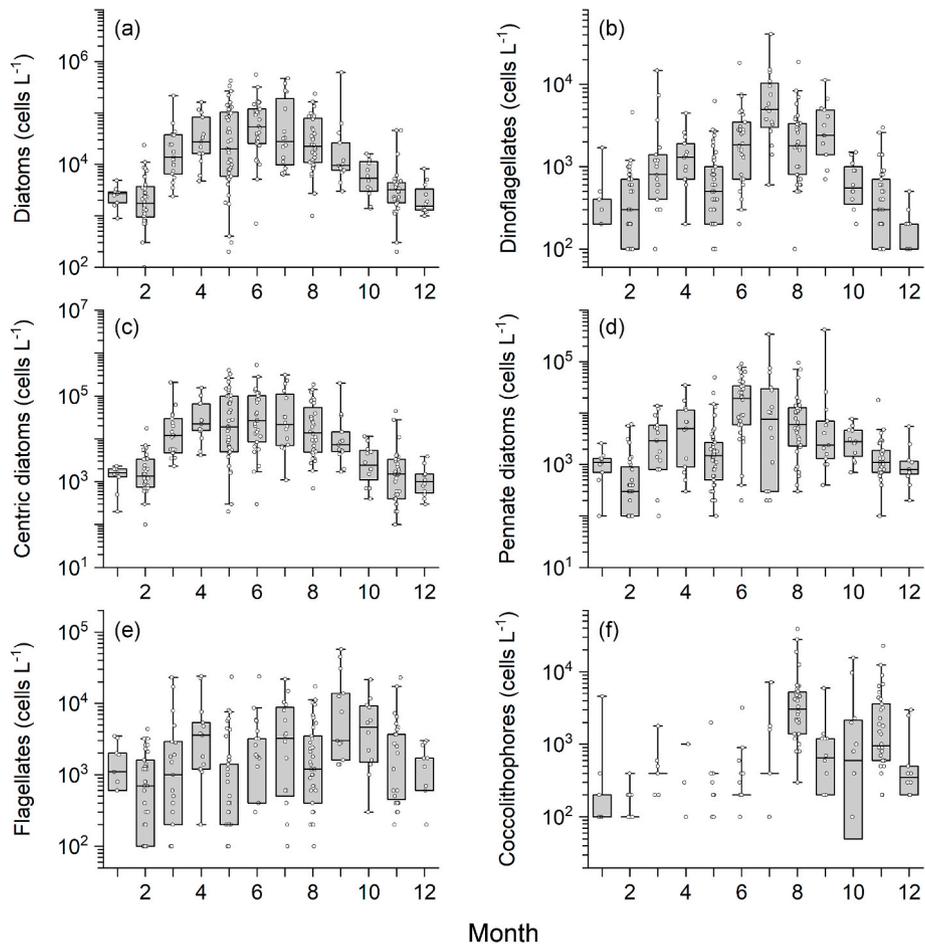


Fig. 3. Seasonal changes in the abundance of (a) diatoms, (b) dinoflagellates, (c) centric diatoms, (d) pennate diatoms, (e) small flagellates, and (f) coccolithophores. Styles of the box diagram are the same as Fig. 2.

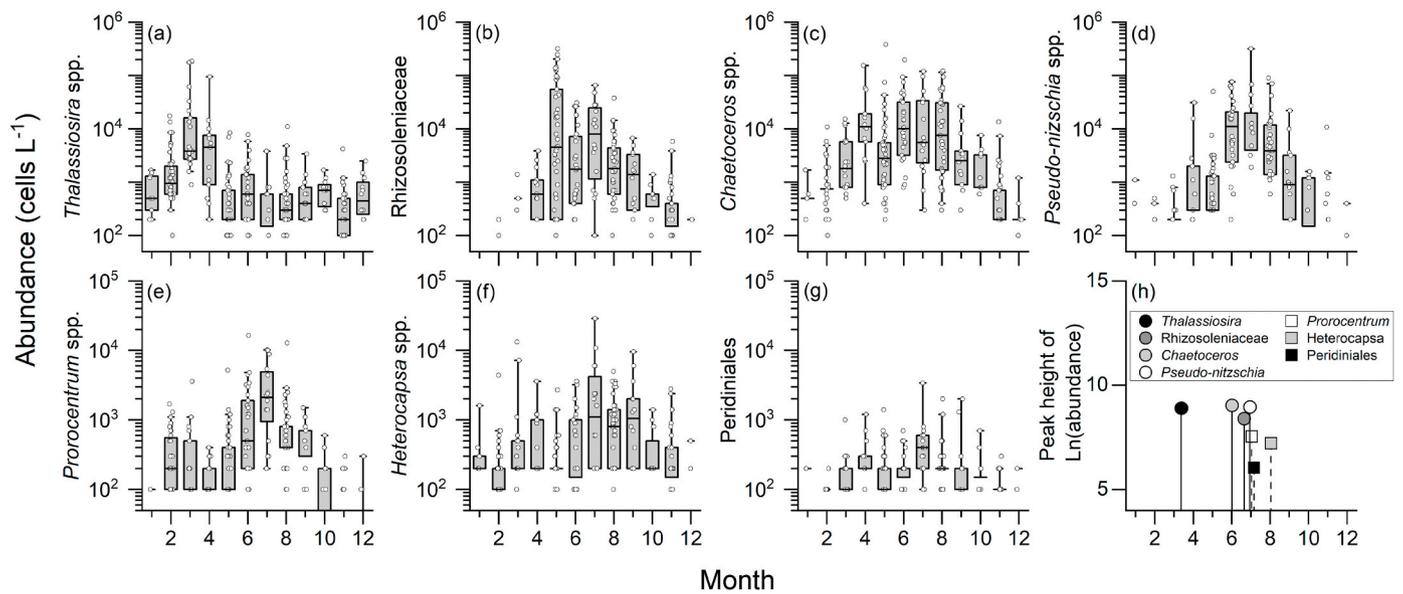


Fig. 4. Seasonal changes in the abundance of (a) *Thalassiosira* spp., (b) Rhizosoleniaceae, (c) *Chaetoceros* subgen. *Hyalochaete* spp., (d) *Pseudo-nitzschia* spp., (e) *Prorocentrum* spp., (f) *Heterocapsa* spp., and (g) Peridinales. (h) The timing of maximum abundance of each planktonic protists as estimated from the Gaussian distribution.

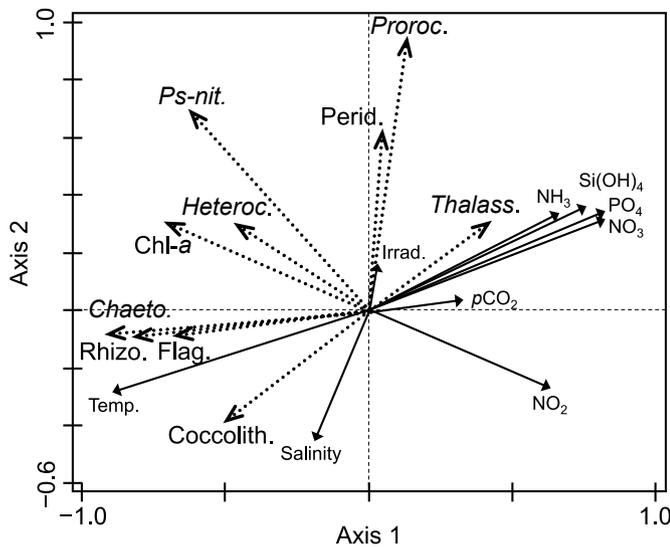


Fig. 5. Principal Component Analysis of environmental variables and microplankton abundance. Axes 1 and 2 represent 41.4% and 24.2% of microplankton dynamics, respectively. Abbreviations: *Chaeto.*: *Chaetoceros* spp.; *Rhizo.*: Rhizosoleniaceae; *Flag.*: small flagellates; *Cocolith.*: cocolithophores; *Thalass.*: *Thalassiosira* spp.; *Proroc.*: *Prorocentrum* spp.; *Perid.*: Peridinales; *Ps-nit.*: *Pseudo-nitzschia* spp.; *Heteroc.*: *Heterocapsa* spp.; *Chl-a*: chlorophyll-*a*; *Temp.*: temperature.

3.3. Long-term trends in the environment

In February, pCO_2 (pH) showed a negative (positive) trend with time, but a few high pCO_2 (low pH) values in 2014 may have been affected by subarctic coastal waters: lower temperature and salinity with higher nutrient levels (Fig. 6a-1, 6b-1, 6c-1 and 6d-1, Table 2). Some data in winter 2014 were excluded according to the criteria of salinity >33, which is probably because of the intrusion of the Coastal Oyashio water in the eastern Tsugaru Strait. More data are required to determine the long-term trends in carbonate chemistry during the winter. Nitrate concentration decreased during the course of the study in February (Table 2). In May, there were significant positive trends in temperature and pCO_2 and negative trends in salinity, nitrate, phosphate, and pH (Fig. 6a-2, 6b-2, 6c-2, and 6d-2, Table 2). In August and November, temperature significantly decreased, whereas salinity and pCO_2 levels increased with time (Fig. 6, Table 2). The phosphate concentration in November significantly increased during the study period (Fig. 6c-4, Table 2).

3.4. Long-term trends in protists

The temporal abundance of dinoflagellates did not change during the study period except in November when Peridinales decreased significantly with time (Fig. 7a, Table 3). *Chaetoceros* subgen. *Hyalochaete* spp. abundance increased during the study period in all examined months (Fig. 7b, Table 3). The abundance of Rhizosoleniaceae and *Thalassiosira* spp. increased with time in May and August, and November, respectively (Fig. 7c, Table 3). The temporal abundance of cocolithophores increased in August (Fig. 7d-3) and that of flagellates increased in November (Fig. 7d-4, Table 3).

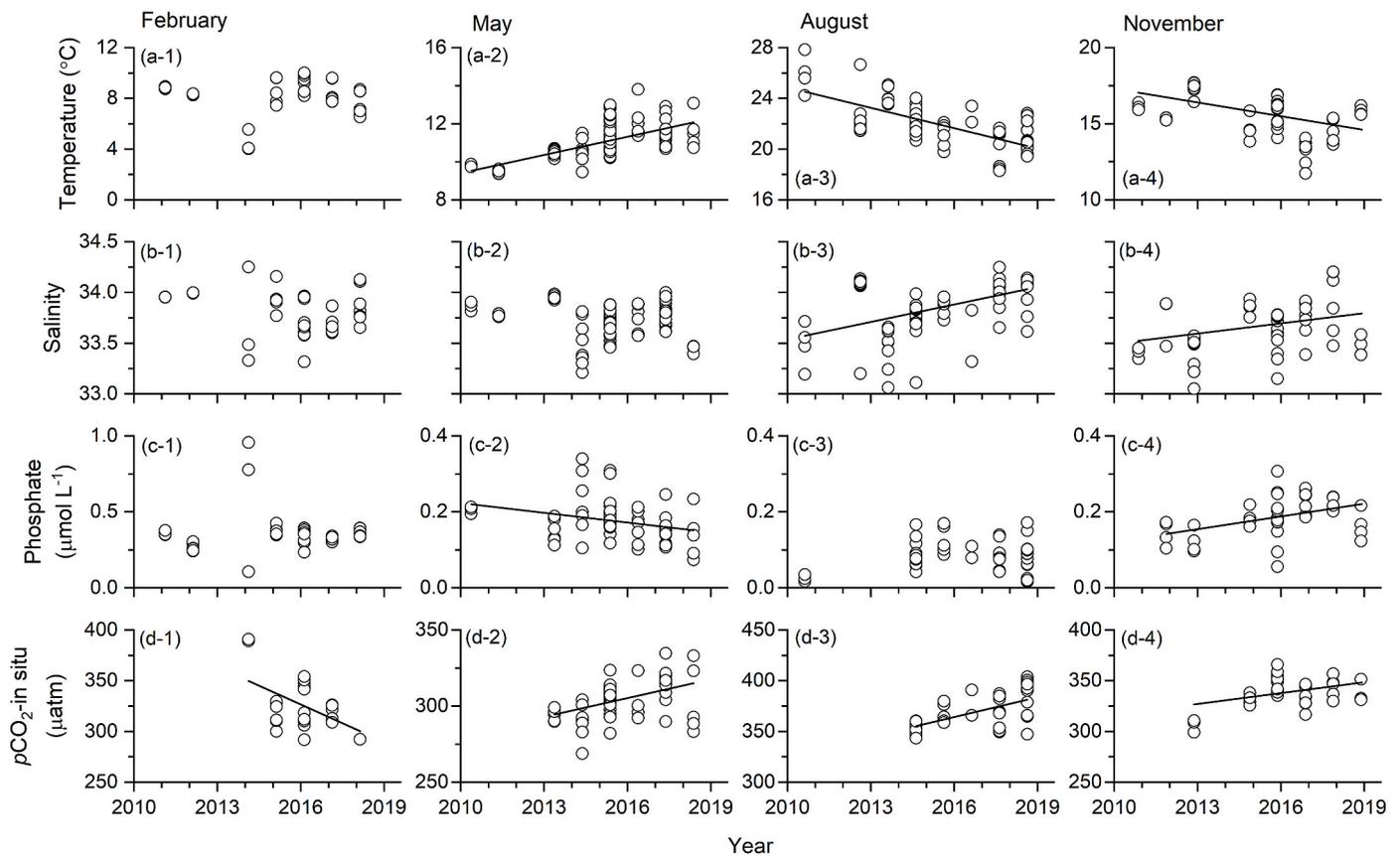


Fig. 6. Long-term changes in (a) temperature, (b) salinity, (c) phosphate, and (d) pCO_2 in situ in (-1) February, (-2) May, (-3) August, and (-4) November. Lines represent the results of significant linear regressions. Statistical results are shown in Table 2. (*) in Fig. 6d-1 indicates that the linear trend disappears by excluding low temperature and salinity data.

Table 2

Long term linear trends (per year \pm 1SE) in temperature, salinity, nitrate, phosphate, $p\text{CO}_2$, and pH, \log_{10} (abundance) of planktonic protists in February, May, August, and November. n.s.: not significant. *: trends disappeared by excluding the data of low temperature and salinity water (see discussion).

	February	May	August	November
Temperature	n.s.	0.32 \pm 0.034 ($R^2 = 0.45$, $F_{1,104} = 89.0$, $p < 0.001$)	-0.54 \pm 0.057 ($R^2 = 0.45$, $F_{1,104} = 86.8$, $p < 0.001$)	-0.30 \pm 0.063 ($R^2 = 0.23$, $F_{1,73} = 22.7$, $p < 0.001$)
Salinity	n.s.	-0.021 \pm 0.0077 ($R^2 = 0.06$, $F_{1,104} = 7.3$, $p = 0.008$)	0.057 \pm 0.0094 ($R^2 = 0.26$, $F_{1,104} = 37.6$, $p < 0.001$)	0.033 \pm 0.012 ($R^2 = 0.09$, $F_{1,73} = 8.0$, $p = 0.006$)
Nitrate	-0.187 \pm 0.089 ($R^2 = 0.06$, $F_{1,55} = 4.4$, $p = 0.040$)	-0.15 \pm 0.051 ($R^2 = 0.11$, $F_{1,63} = 9.1$, $p = 0.004$)	n.s.	n.s.
Phosphate	n.s.	-0.0085 \pm 0.0035 ($R^2 = 0.07$, $F_{1,63} = 6.1$, $p = 0.016$)	n.s.	0.011 \pm 0.0038 ($R^2 = 0.16$, $F_{1,42} = 8.8$, $p = 0.005$)
$p\text{CO}_2$	-12.3 \pm 4.5 (*) ($R^2 = 0.20$, $F_{1,25} = 7.5$, $p = 0.011$)	4.11 \pm 1.07 ($R^2 = 0.19$, $F_{1,57} = 14.8$, $p < 0.001$)	5.69 \pm 1.65 ($R^2 = 0.21$, $F_{1,40} = 12.0$, $p = 0.001$)	3.57 \pm 1.45 ($R^2 = 0.12$, $F_{1,36} = 6.05$, $p = 0.019$)
pH	1.49 $\times 10^{-2}$ \pm 5.28 $\times 10^{-3}$ (*) ($R^2 = 0.21$, $F_{1,25} = 7.9$, $p = 0.009$)	-4.88 $\times 10^{-3}$ \pm 1.28 $\times 10^{-3}$ ($R^2 = 0.19$, $F_{1,57} = 14.6$, $p < 0.001$)	-5.98 $\times 10^{-3}$ \pm 1.78 $\times 10^{-3}$ ($R^2 = 0.20$, $F_{1,40} = 11.2$, $p = 0.002$)	-3.66 $\times 10^{-3}$ \pm 1.53 $\times 10^{-3}$ ($R^2 = 0.11$, $F_{1,36} = 5.7$, $p = 0.022$)
<i>Thalassiosira</i> spp.	n.s.	n.s.	n.s.	0.15 \pm 0.074 ($R^2 = 0.09$, $F_{1,32} = 4.2$, $p = 0.048$)
Rhizosoleniaceae	n.s.	0.38 \pm 0.11 ($R^2 = 0.19$, $F_{1,43} = 11.0$, $p = 0.002$)	0.24 \pm 0.080 ($R^2 = 0.18$, $F_{1,34} = 8.9$, $p = 0.005$)	n.s.
<i>Chaetoceros</i> spp.	0.36 \pm 0.10 ($R^2 = 0.25$, $F_{1,37} = 13.5$, $p < 0.001$)	0.13 \pm 0.064 ($R^2 = 0.07$, $F_{1,43} = 4.2$, $p = 0.046$)	0.21 \pm 0.056 ($R^2 = 0.32$, $F_{1,34} = 17.4$, $p < 0.001$)	0.26 \pm 0.10 ($R^2 = 0.14$, $F_{1,32} = 6.4$, $p = 0.017$)
<i>Pseudo-nitzschia</i> spp.	n.s.	n.s.	n.s.	n.s.
<i>Prorocentrum</i> spp.	n.s.	n.s.	n.s.	n.s.
<i>Heterocapsa</i> spp.	n.s.	n.s.	n.s.	n.s.
Peridiniaceae	n.s.	n.s.	n.s.	-0.22 \pm 0.068 ($R^2 = 0.22$, $F_{1,32} = 10.4$, $p = 0.003$)
Coccolithophores	n.s.	n.s.	0.12 \pm 0.056 ($R^2 = 0.10$, $F_{1,34} = 4.9$, $p = 0.034$)	n.s.
Fragellates	n.s.	n.s.	n.s.	0.26 \pm 0.10 ($R^2 = 0.14$, $F_{1,32} = 6.3$, $p = 0.017$)

4. Discussion

This study clarifies the seasonal dynamics and long-term trends of planktonic protists in the TWC, where rapid pH reduction occurs (Wakita et al., 2021). The decrease in pH or increase in $p\text{CO}_2$ and higher temperature in combination often lead to a decrease in diatoms in phytoplankton communities (Yoshimura et al., 2014; Endo et al., 2015, 2017; Schulz et al., 2017; Sugie et al., 2020). However, diatom abundance in the TWC often increased with time under the progress of increasing $p\text{CO}_2$ levels (Figs. 5 and 6). Sugie et al. (2018) reported that the specific growth rate of the unialgal culture of *Chaetoceros affinis* was enhanced owing to the increase in $p\text{CO}_2$ levels. On the other hand, the specific growth rate of some *Pseudo-nitzschia* strains did not change in response to the increase in $p\text{CO}_2$ levels until approximately 700–1000 μatm (Sugie and Yoshimura, 2013; Ayache et al., 2021; Wingert and Cochlan, 2021). These unialgal culture studies partly support the results of this study under a rapidly acidifying environment (Table 3). Wingert and Cochlan (2021) reported that the increase in the inflow from the subsurface of the Sea of Japan to the TWC results the increase of DIC concentrations in the eastern Tsugaru Strait. This study also supports the results of previous study that the decrease in temperature and the increase in salinity and $p\text{CO}_2$ in August and November probably resulted from the intrusion of subsurface water to the surface (Fig. 6). It is difficult to quantify the increase in nutrient availability in the surface mixed layer of the studied stations because of the uptake of nutrients by the increased phytoplankton (e.g., August of this study, Fig. 6). In November, when phytoplankton abundance was lower with lower irradiance level (Figs. 2 and 3), phosphate concentration increased significantly during the study period. These results indicate that the effect of increased nutrient availability via the increase in turbulent mixing masked the negative impact of acidification on diatoms in the TWC. Previous studies reported that the effect of high CO_2 levels on the coastal phytoplankton assemblage differs among reports, showing positive, negative and neutral effects on specific growth rate. Manipulation experiments of CO_2 , temperature and nutrients using TWC phytoplankton assemblages are indispensable to better understand future ecosystem in the TWC.

We described the seasonality of protists in the TWC using pooled nine-years data that the abundance of *Thalassiosira* spp. increased in early spring, followed by Rhizosoleniaceae, *Chaetoceros* spp., and *Pseudo-nitzschia* spp. during spring to summer (Fig. 4). Dinoflagellates appeared after the peaks of some diatom groups. Seasonal succession from *Thalassiosira* to *Chaetoceros*, centric to pennate diatoms, and diatoms to dinoflagellates are relatively common in temperate coastal waters (e.g., Jeffrey and Carpenter, 1974; Shinada et al., 1999). The broader peak from March to September of *Chaetoceros* spp. may consist of the peaks of many species belonging to *Chaetoceros* subgenus *Hyalochaete* in this region (Tanimura et al., 2017). Highly diverse diatoms in terms of species and size may sustain the production of a variety of herbivores in the TWC system (Tanimura et al., 2017; Sugie and Suzuki, 2017). Possible mechanisms underlying the obscure seasonality of flagellates and coccolithophores (Fig. 3e and f) are heavy grazing on smaller phytoplankton traits by microzooplankton around the study area (Shinada et al., 2001, 2003). The grazing pressure of zooplankton is related to nutrient regeneration that the diurnal pattern of heavy grazing by microzooplankton could modify daily ammonium concentration ranging from <0.5 to $5 \mu\text{mol L}^{-1}$ (Litaker et al., 1998). Interaction with the seafloor in shallow environments can further perturb ammonium concentration up to one to two orders of magnitude at the surface (Litaker et al., 1998; Horner Rosser and Thompson, 2001). Therefore, we cannot detect the seasonal pattern of ammonium concentration in the western TWC system (Supplemental Fig. 2).

The trends of long-term change in protist abundance differed among the examined traits. In August and November, when there were temporal decreases in temperature and increases in salinity (Fig. 6), intensifying turbulent mixing via increasing eastward flow of the TWC would

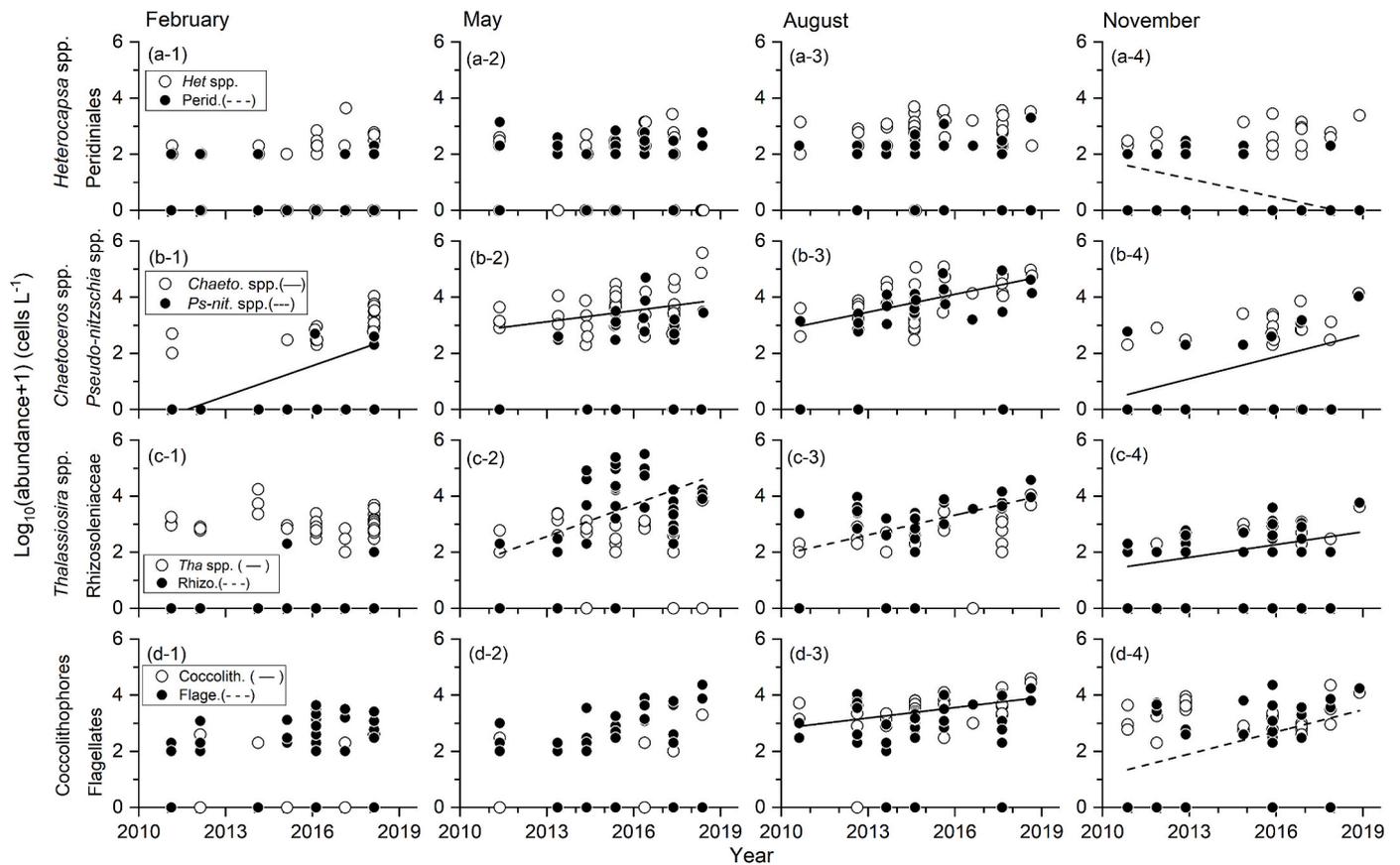


Fig. 7. Long-term changes in (a) *Heterocapsa* spp. and Peridinales, (b) *Thalassiosira* spp., Rhizosoleniaceae, and *Pseudo-nitzschia* spp., and (c) *Chaetoceros* spp. and small flagellates in (–1) February, (–2) May, (–3) August, and (–4) November. Lines represent the results of significant linear regressions. Statistical results are shown in Table 2.

increase nutrient availability. This mechanism may be important for increasing the abundance of larger diatoms such as Rhizosoleniaceae and *Thalassiosira* spp. under seasonally nutrient-limited conditions (Figs. 2 and 7). In addition, it should be adequate that the low temperature and high nutrient preferred *Thalassiosira* spp. (Fig. 5) increased their temporal abundance in November when temperature decreased from 2010 to 2018 (Figs. 6 and 7). In May, *Chaetoceros* subgen. *Hyalochaete* spp., which prefer relatively higher temperatures, increased with time as temporal temperature increased (Figs. 5–7). However, generalizing the dynamics of some traits is rather difficult using the data of this study. For example, *Chaetoceros* subgen. *Hyalochaete* spp. increased in February during the study period when long-term changes in environmental variables were less prominent (Fig. 6). Furthermore, the synchronous increasing trends of *Chaetoceros* subgen. *Hyalochaete* spp., Rhizosoleniaceae, and coccolithophore abundance in August when temporal cooling and acidification occurred were difficult to explain because they would favor higher temperature and $p\text{CO}_2$ conditions (Figs. 5–7). The diatoms in general have a high species diversity in coastal region of Japan (Sugie et al., 2010; Thomas, 1997; Sugie and Suzuki, 2017; Tanimura et al., 2017), detailed studies of functional species/traits that respond environmental changes require more attention.

It is notable that the change in seawater temperature in the latest decade (-0.54 – 0.32 °C per year) is several times faster than the projected anthropogenic global warming (0.015 °C to <0.10 °C per year). Similarly, the change in $p\text{CO}_2$ levels in the eastern Tsugaru Strait was faster than the expected increase in $p\text{CO}_2$ which is estimated from the increase in atmospheric CO_2 levels (Wakita et al., 2021). In the present study, we observed that the abundance of planktonic protists responded to nearly decadal environmental change (Tables 3 and 4).

Kuroda et al. (2020) and Nagano et al. (2022) reported that the temperature regime around Japan from 1982 to 2019 showed decadal shifts that might be affected by synoptic climatic forcings such as PDO and ENSO. Therefore, in addition to the steeper seasonal variability, local planktonic protists have been coping well with a decadal environmental change until the study period. However, it remains largely uncertain that the protist response to the combination of decadal climatic forcing and projected anthropogenic climate change. The threshold temperature and $p\text{CO}_2$ levels of local protists should be tested to better predict the resilience/vulnerability of future ecosystems. Furthermore, the mechanistic relationship between synoptic scale climatic forcing and local ecosystem change is an urgent unresolved issue (Kuroda et al., 2020; Nagano et al., 2022).

Synoptic climatic forcing such as PDO has been known to affect the phenology, biogeography, and production of lower trophic levels in the North Pacific (Chiba et al., 2012, 2015). The change in phytoplankton behavior in response to climate variability could affect the production of higher trophic levels and fisheries catch (Edwards and Richardson, 2004; Koeller et al., 2009). We found significant linear trends between the PDO index and monthly mean temperatures in February and May (warming) and August and November (cooling) (Fig. 8a), similar to the temporal change in seawater temperature (Fig. 6a). In addition, the PDO index and scallop soft tissue index (STI) showed a significant positive linear relationship (Fig. 8b). Possible underlying mechanisms relating PDO and scallop production is the abundance of diatoms such as Rhizosoleniaceae which is positively correlated to the STI and PDO (Fig. 8c and d, Tables 3 and 4). Increasing temperature in spring when nutrients remained could improve food availability for scallop aquaculture by enhancing the growth rate of phytoplankton. In the nutrient-depleted summer, nutrient pulses owing to the increase in turbulent mixing

Table 3

Slope value and statistical results of the relationship between scallop soft tissue index (biomass of scallop \times 100/total weight) and environmental variables and between scallop soft tissue index and \log_{10} (phytoplankton abundance + 1). n.s.: not significant.

	February	May	August	November
Temperature	0.36 \pm 0.072 ($R^2 = 0.22$, $F_{1,80} = 24.3$, $p < 0.001$)	0.50 \pm 0.061 ($R^2 = 0.38$, $F_{1,104} = 66.4$, $p < 0.001$)	-0.34 \pm 0.16 ($R^2 = 0.03$, $F_{1,104} = 4.2$, $p = 0.043$)	-0.52 \pm 0.07 ($R^2 = 0.39$, $F_{1,73} = 48.3$, $p < 0.001$)
Salinity	n.s.	n.s.	n.s.	0.034 \pm 0.016 ($R^2 = 0.05$, $F_{1,73} = 4.5$, $p = 0.037$)
Nitrate	n.s.	n.s.	n.s.	n.s.
Phosphate	n.s.	n.s.	n.s.	0.017 \pm 0.0042 ($R^2 = 0.26$, $F_{1,41} = 15.7$, $p < 0.001$)
pCO ₂	n.s.	n.s.	11.4 \pm 2.3 ($R^2 = 0.36$, $F_{1,40} = 24.1$, $p < 0.001$)	3.4 \pm 1.7 ($R^2 = 0.08$, $F_{1,36} = 4.2$, $p = 0.048$)
pH	n.s.	n.s.	-0.012 \pm 0.0031 ($R^2 = 0.25$, $F_{1,40} = 14.4$, $p < 0.001$)	n.s.
<i>Thalassiosira</i> spp.	n.s.	n.s.	n.s.	n.s.
Rhizosoleniaceae	n.s.	0.64 \pm 0.17 ($R^2 = 0.24$, $F_{1,43} = 15.0$, $p < 0.001$)	n.s.	n.s.
<i>Chaetoceros</i> spp.	n.s.	n.s.	0.33 \pm 0.10 ($R^2 = 0.22$, $F_{1,34} = 10.6$, $p = 0.003$)	1.1 \pm 0.45 ($R^2 = 0.25$, $F_{1,14} = 6.0$, $p = 0.028$)
<i>Pseudo-nitzschia</i> spp.	n.s.	0.76 \pm 0.16 ($R^2 = 0.34$, $F_{1,43} = 23.6$, $p < 0.001$)	n.s.	n.s.
<i>Prorocentrum</i> spp.	-0.29 \pm 0.11 ($R^2 = 0.13$, $F_{1,37} = 6.9$, $p = 0.013$)	n.s.	n.s.	n.s.
<i>Heterocapsa</i> spp.	n.s.	n.s.	n.s.	0.31 \pm 0.12 ($R^2 = 0.15$, $F_{1,32} = 6.7$, $p = 0.014$)
Peridinales	-0.22 \pm 0.085 ($R^2 = 0.14$, $F_{1,37} = 7.0$, $p = 0.012$)	n.s.	n.s.	-0.31 \pm 0.12 ($R^2 = 0.25$, $F_{1,32} = 12.1$, $p = 0.002$)
Coccolithophores	n.s.	n.s.	n.s.	n.s.
Flagellates	0.30 \pm 0.12 ($R^2 = 0.12$, $F_{1,37} = 6.3$, $p = 0.017$)	n.s.	n.s.	n.s.

could elevate the carrying capacity of prey (e.g., *Chaetoceros* subgen. *Hyalochaete* spp.) for scallops (Tables 3 and 4). In general, seawater temperature around Japan decreases during the positive PDO phase (Yamazaki et al., 2016; Nagano et al., 2022), as we observed that cooling trends in August and November were stronger than warming trends in February and May (Fig. 8a). These analyses indicate that the positive phase of PDO is beneficial to scallop aquaculture owing to the increase

Table 4

Slope value and statistical results of the relationship between PDO and environmental variables and between PDO and \log_{10} (plankton abundance + 1). n.s.: not significant.

	February	May	August	November
Temperature	0.29 \pm 0.13 ($R^2 = 0.047$, $F_{1,80} = 5.0$, $p = 0.028$)	0.51 \pm 0.075 ($R^2 = 0.31$, $F_{1,104} = 47.1$, $p < 0.001$)	-0.70 \pm 0.20 ($R^2 = 0.10$, $F_{1,104} = 12.6$, $p < 0.001$)	-0.47 \pm 0.11 ($R^2 = 0.18$, $F_{1,73} = 17.6$, $p < 0.001$)
Salinity	n.s.	-0.057 \pm 0.015 ($R^2 = 0.12$, $F_{1,104} = 15.5$, $p < 0.001$)	n.s.	0.068 \pm 0.020 ($R^2 = 0.12$, $F_{1,73} = 11.5$, $p = 0.001$)
Nitrate	n.s.	n.s.	n.s.	n.s.
Phosphate	n.s.	n.s.	0.028 \pm 0.0091 ($R^2 = 0.14$, $F_{1,49} = 9.3$, $p = 0.004$)	0.022 \pm 0.0069 ($R^2 = 0.18$, $F_{1,41} = 10.1$, $p = 0.003$)
pCO ₂	n.s.	n.s.	-14.9 \pm 5.1 ($R^2 = 0.16$, $F_{1,40} = 8.6$, $p = 0.005$)	11.9 \pm 2.2 ($R^2 = 0.42$, $F_{1,36} = 27.6$, $p < 0.001$)
pH	n.s.	n.s.	n.s.	-0.012 \pm 0.0024 ($R^2 = 0.41$, $F_{1,36} = 26.7$, $p < 0.001$)
<i>Thalassiosira</i> spp.	n.s.	n.s.	n.s.	n.s.
Rhizosoleniaceae	n.s.	1.17 \pm 0.18 ($R^2 = 0.49$, $F_{1,43} = 42.8$, $p < 0.001$)	n.s.	n.s.
<i>Chaetoceros</i> spp.	n.s.	n.s.	n.s.	n.s.
<i>Pseudo-nitzschia</i> spp.	n.s.	n.s.	0.75 \pm 0.23 ($R^2 = 0.22$, $F_{1,34} = 11.1$, $p = 0.002$)	n.s.
<i>Prorocentrum</i> spp.	n.s.	n.s.	0.72 \pm 0.21 ($R^2 = 0.24$, $F_{1,34} = 11.9$, $p = 0.002$)	n.s.
<i>Heterocapsa</i> spp.	n.s.	n.s.	n.s.	n.s.
Peridinales	-0.32 \pm 0.14 ($R^2 = 0.11$, $F_{1,37} = 5.6$, $p = 0.023$)	n.s.	n.s.	-0.44 \pm 0.13 ($R^2 = 0.25$, $F_{1,32} = 11.9$, $p = 0.002$)
Coccolithophores	n.s.	-0.33 \pm 0.14 ($R^2 = 0.09$, $F_{1,43} = 5.4$, $p = 0.024$)	n.s.	n.s.
Flagellates	n.s.	n.s.	n.s.	n.s.

in diatom production driven by climatologically induced physical and chemical perturbations of seawater.

In contrast, the abundance of some dinoflagellates in February and November showed a negative correlation with the STI (Table 4). Increasing such dinoflagellates are an impending threat to fisheries, but we rarely found such trends during the study period in the eastern Tsugaru Strait (Fig. 7). The effect of high CO₂ levels on dinoflagellates can increase toxin production under nutrient-depleted conditions (Fu et al., 2012; Tatters et al., 2013; Riebesell et al., 2018). In addition, episodic warming in 2021 in the coastal region of northern Japan

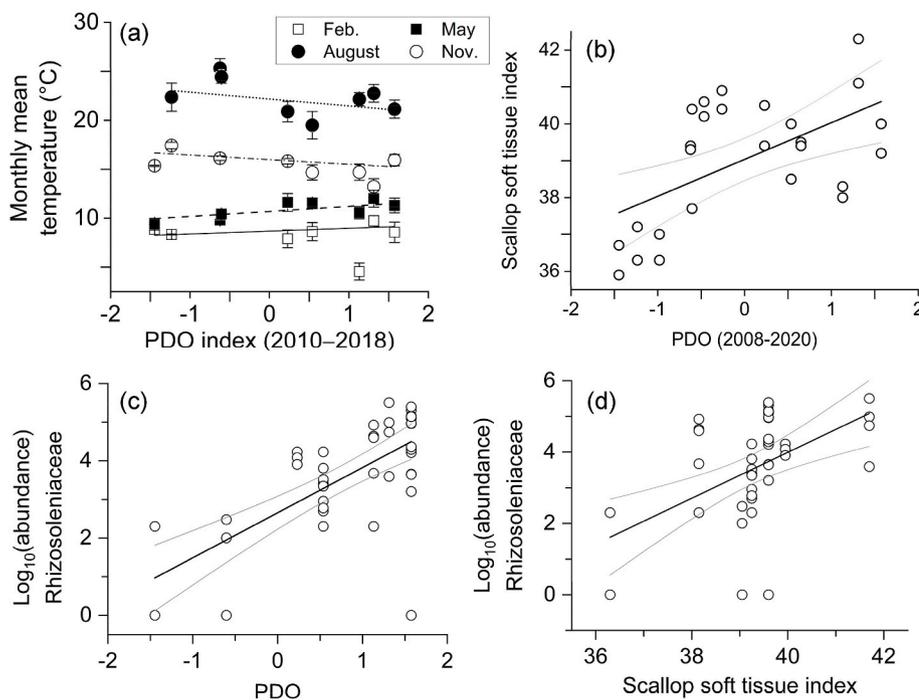


Fig. 8. Relationships (a) between Pacific Decadal Oscillation (PDO) and the monthly mean temperatures in February, May, August, and November, (b) between PDO and scallop soft tissue index (STI), (c) between PDO and Log_{10} (Rhizosoleniaceae) abundance in May, and (d) between STI and Log_{10} (Rhizosoleniaceae) abundance in May. Lines represent significant linear relationships: (a) Temperature (February) = $0.29 \pm 0.13 \times \text{PDO} + 8.7 \pm 0.17$ ($R^2 = 0.05$, $F_{1,80} = 5.0$, $p = 0.028$), Temperature (May) = $0.51 \pm 0.07 \times \text{PDO} + 10.7 \pm 0.09$ ($R^2 = 0.30$, $F_{1,104} = 47.1$, $p < 0.001$), Temperature (August) = $-0.70 \pm 0.20 \times \text{PDO} + 22.2 \pm 0.18$ ($R^2 = 0.10$, $F_{1,104} = 12.6$, $p < 0.001$), Temperature (November) = $-0.47 \pm 0.11 \times \text{PDO} + 16.0 \pm 0.15$ ($R^2 = 0.18$, $F_{1,73} = 17.6$, $p < 0.001$) (b) $\text{STI} = 1.0 \pm 0.29 \times \text{PDO} + 39.0 \pm 0.28$ ($R^2 = 0.30$, $F_{1,24} = 11.7$, $p = 0.002$), (c) $\text{Log}_{10}(\text{Rhizosoleniaceae}) = 1.17 \pm 0.18 \times \text{PDO} - 2.7 \pm 0.21$ ($R^2 = 0.49$, $F_{1,43} = 42.8$, $p < 0.001$), (d) $\text{Log}_{10}(\text{Rhizosoleniaceae}) = 0.64 \pm 0.17 \times \text{STI} - 21.7 \pm 6.5$ ($R^2 = 0.24$, $F_{1,43} = 15.0$, $p < 0.001$).

induced massive blooms of the toxic dinoflagellate (*Karenia selliformis*) that caused severe damage to salmon, octopuses, sea urchins, bivalves, whelks, and other organisms (Kuroda et al., 2021; Iwataki et al., 2022). In addition to the rapid acidification in the TWC system in the last decade (Fig. 6, Wakita et al., 2021), our results and previous studies suggest that the future warming and negative PDO phase may have a negative impact on scallop aquaculture by increasing dinoflagellate abundance and toxicity. Testing the effects of environmental changes on local plankton assemblages using manipulation experiments and feeding experiments of scallops could provide insight into the productivity of local fisheries in the TWC system.

5. Conclusion

This study clarified the seasonal and long-term dynamics of microscopic protists in the TWC ecosystem. Diatoms were the dominant microscopic protists in the TWC, and their seasonality was well explained by environmental variables. Other protists such as dinoflagellates and coccolithophores may fill the open niche of the local ecosystem. The long-term cooling temperature trends in August and November differed from those of global warming, probably due to the change in current volume, which is influenced by synoptic climatic forcing. The change in the TWC current from 2010 to 2018 positively affected the production of diatoms, and higher prey availability is favorable for the aquaculture of scallops in the Aomori prefecture. The impacts of higher temperature and $p\text{CO}_2$ levels, which often reduce diatoms (Endo et al., 2015, 2017; Schulz et al., 2017; Sugie et al., 2020), may be masked by the increase in nutrient availability induced by enhanced turbulent mixing. However, caution is needed because dinoflagellates, which may have a competitive advantage under future high temperature and CO_2 conditions, often negatively influence on scallop fertility. Note that the duration of our protist monitoring covered only one PDO cycle. Because the combination of PDO and ENSO cycles could affect local climatology (Kuroda et al., 2021; Nagano et al., 2022), much longer observation periods are essential for clarifying multi-decadal to centennial ecosystem response. The challenge to identify the individual effects of anthropogenic climate change and climatological variability on the functional protist traits/species could

improve our understanding of sustainable seafood availability and security.

Author contribution statement

K.S., M.W., H.A., K-i.S., H.A., and T.T. designed the research. M.W., S.T., M.T., H.A., and T.T. collected and measured samples. T.U. provided scallop data in the study region. K.S. analyzed and wrote paper, with the support from all co-authors.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envres.2023.115691>.

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