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First evidence of the diatom *Hemiaulus* and cyanobacterium *Richelia* endosymbiosis in the Sea of Marmara

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Abstract

The endosymbiotic association between the diatom *Hemiaulus* and the cyanobacterium *Richelia* was first observed in the Sea of Marmara in July 2021. The spatial distribution of the host diatom *Hemiaulus* spp. and the endosymbiont cyanobacterium *Richelia intracellularis* was investigated along with available physicochemical parameters. Three species of the *Hemiaulus* genus (*H. hauckii*, *H. membranaceus*, and *H. sinensis*) were morphologically identified in the study area. *Hemiaulus hauckii* and *H. sinensis* reached up to 128×10^3 cells L⁻¹ and 38×10^3 cells L⁻¹, respectively, while *H. membranaceus* was rarely observed. Each *Hemiaulus* cell contained one *Richelia* trichome, which had heterocysts at both ends. The surface water temperatures and salinity varied between 23.2°C and 28.5°C, 21.4 and 23.5, respectively. Dissolved oxygen levels ranged from 6.2 to 7.6 mg L⁻¹, while chlorophyll-a concentrations were between 0.3 and 6.8 µg L⁻¹. Nutrient concentrations varied between 0.05 and 0.18 µM for NO₃ + NO₂-N, 0.04–0.24 µM for NH₄-N, 0.02–0.39 µM for PO₄-P, and 0.18–1.42 µM for SiO₂-Si. This study reveals that the *Hemiaulus*–*Richelia* symbiosis may promote the proliferation of diatom populations and may play an important role in nutrient dynamics in nitrogen-limiting environments and in the overall functioning of the marine ecosystem.

Introduction

Hemiaulus is a common diatom genus that includes marine plankton species (*H. hauckii*, *H. indicus*, *H. membranaceus*, *H. sinensis*) in warm water regions to temperate zones (Hasle and Syvertsen, 1997) and in warm oligotrophic seas (Guillard and Kilham, 1977). *Richelia intracellularis* Schmidt is a nitrogen-fixing cyanobacterium, cells are shorter than they are wide, 6–8 µm broad and heterocysts develop successively at both ends of trichomes (Guiry and Guiry, 2020). Many studies over the last decades have demonstrated N-fixation and transfer in diatom–cyanobacterial symbiosis (Foster *et al.*, 2011; Inomura *et al.*, 2020; Sundstrom, 1984; Venrick, 1974; Villareal, 1991; Zeev *et al.*, 2008). Nitrogen-fixing organisms (diazotrophs) play a crucial role as an important nitrogen source to phytoplankton nutrient budgets in N-limited marine environments (Pyle *et al.*, 2020). A symbiotic relationship is known between some diatoms and a filamentous cyanobacterium *Richelia intracellularis* (Villareal, 1991; Zeev *et al.*, 2008). *Richelia intracellularis* is usually found as an endosymbiont within diatoms such as *Rhizosolenia* spp. and *Hemiaulus* spp. (Koray, 1988; Pyle *et al.*, 2020; Sundstrom, 1984; Venrick, 1974; Zeev *et al.*, 2008). The presence of a heterocyst indicates that N₂-fixation is likely possible in this symbiosis (Kimor *et al.*, 1978). Diatom–diazotroph associations containing *R. intracellularis* were traditionally considered the dominant nitrogen-fixing plankton in marine tropical oceans (Zeev *et al.*, 2008). Inomura *et al.* (2020) suggested that carbon transfer from the host diatom enables faster growth and N₂ fixation rates by trichomes. *Richelia intracellularis* was also found as an epiphytic cyanobacterium on the diatom *Chaetoceros compressus* Lauder, 1864 (Gomez *et al.*, 2005).

The Sea of Marmara (SoM) is a small, semi-enclosed basin with an area of 11,350 km² and a maximum depth 1,273 m, connected to the Black Sea and the Aegean Sea through the Strait of Istanbul (Bosphorus) and Canakkale (Dardanelles). The SoM has two-layered water masses that the upper layer (0–25 m) is brackish (~22 salinity) originating from the Black Sea, and the lower layer is saline (~38 salinity) originating from the Mediterranean Sea. These two stratified water masses are distinctly separated by an interface layer (Besiktepe *et al.*, 1994; Unluata *et al.*, 1990). The hydrography of the upper layer is strongly associated with the Black Sea (Polat and Tuğrul, 1995). Nutrient concentrations in the upper euphotic zone are relatively low, with

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seasonal variations depending on the photosynthetic activity (Baştürk et al., 1990). Primary production is always higher in the upper layer, while the lower layer has nutrient-rich waters due to the limitation of the euphotic zone by the intermediate layer (Polat et al., 1998). Also, nitrogen is the limiting nutrient (Balkis, 2003; Balkis and Toklu-Alicli, 2014; Tüfekçi et al., 2010). Previous studies have indicated that *Hemiaulus* species were a significant component of the SoM. *Hemiaulus hauckii* was identified by Balkis (2004) with densities ranging from 3900 cells L⁻¹ in September 1998 to 80 cells L⁻¹ in November 1998, and by Tas et al. (2020) in the northeastern SoM in 2004 and 2006 (presence only). Balkis and Toklu-Alicli (2014) reported this species in the Gulf of Bandırma in November 2007 (360 cells L⁻¹) and August 2008 (960 cells L⁻¹), while Balkis-Ozdelice et al. (2020) found it in the Gulf of Erdek in February 2007 (280 cells L⁻¹), November 2007 (120 cells L⁻¹), and August 2008 (100 cells L⁻¹). Kayadelen et al. (2022) reported *H. hauckii* in the coastal waters of Burgazada in November 2013, and Ergul et al. (2021) noted its presence in the Gulf of İzmit and the coastal waters of Fatih (Istanbul) in September 2020 (1400 cells L⁻¹). Additionally, Demir and Turkoglu (2022) recorded an abundance of *H. hauckii* in the Çanakkale Strait (Dardanelles) at 5.4×10^5 cells L⁻¹ in October 2018, constituting 42.86% of the total phytoplankton abundance. *Hemiaulus membranaceus* was reported by Ergul et al. (2021) in the Gulf of İzmit (100 cells L⁻¹), Biga (120 cells L⁻¹), and Fatih (180 cells L⁻¹) coastal waters in September 2020, and by Tas et al. (2020) in the northeastern SoM. *Hemiaulus sinensis* was recorded by Ergul et al. (2021) in the Gulf of İzmit (240 cells L⁻¹), Biga (160 cells L⁻¹), and Fatih (2100 cells L⁻¹) coastal waters in September 2020. However, none of these studies mentioned the *Hemiaulus*–*Richelia* symbiosis, nor was *Richelia* reported.

The present study aimed to reveal the first evidence of the endosymbiotic association between the diatom genus *Hemiaulus* and the diazotrophic cyanobacterium *Richelia* associated with the environmental drivers in the SoM.

Materials and methods

The physicochemical data in the SoM in summer 2021 (July/August) were collected via the TÜBİTAK Marmara Research Vessel as part of “the Integrated Marine Pollution Monitoring 2020–2022 Programme” which was implemented by the Ministry of Environment and Urbanization-CEDIDGM/Laboratory, Measurement and Monitoring Department under the coordination of TÜBİTAK-MAM CTUE. A SeaBird SBE 25Plus/ SBE 27 CTD device was used for temperature and salinity measurements. Inorganic nutrients (NO_x-N, NH₄-N, PO₄-P, and SiO₂) were analysed using an Autoanalyser (QuAatro) available on-board. Dissolved oxygen (DO) concentration was measured using an automatic titrator with the method of the Iodometric Winkler Test. Chlorophyll-a concentration was measured according to the acetone extraction method using a spectrophotometer (Parsons et al., 1984), employing a filter with a mesh size of 0.45 µm and a path length of 5 cm, with 1 L of seawater used for filtration.

The seawater samples for phytoplankton analysis were collected from the surface of 15 sampling stations (Figure 1) using Niskin bottles and transferred into 1-L polyethylene dark containers and immediately fixed with acidic Lugol's iodine solution (Thronsdon, 1978). In the laboratory, samples were left to settle for at least a week, and then the samples were concentrated to 10 mL (Sukhanova, 1978). The phytoplankton cells were counted on

a Sedgewick–Rafter counting cell with 1 mL volume under an “Olympus CK2” model phase-contrast inverted microscope (Semina, 1978).

Prior to epifluorescence microscopy, glutaraldehyde was added to the samples at a final concentration of 2% to preserve cellular structures. The preserved samples were then examined using an Olympus BX51 epifluorescence microscope equipped with a U-MWB2 filter set (blue excitation: excitation filter 460–490 nm, dichroic mirror 500 nm, and emission filter 520 nm). Observations were conducted at magnifications of 200×, 400×, and 1000×, with immersion oil used where applicable. Cells of *Hemiaulus* spp. and their diazotrophic endosymbiont *R. intracellularis* were identified based on their natural autofluorescence. Structural features such as trichomes were distinguished by their linear morphology and characteristic fluorescence signal under blue excitation. No fluorescent dyes or staining procedures were applied during sample preparation or microscopy. For the identification of *Hemiaulus* species, Lebour (1930), Cupp (1943), Hendey (1964), and Hasle and Syvertsen (1997) were used, and *R. intracellularis* was identified according to Foster et al. (2011), Sournia (1986), and Zeev et al. (2008).

Results

Physicochemical parameters

The values of some physicochemical parameters were measured simultaneously with the water samples taken. The water temperature ranged from a minimum of 23.2°C at station 45C to a maximum of 28.48°C at station MD67, with an average of 26.29°C. Salinity values varied from a minimum of 21.35 at station SD3 to a maximum of 32.52 at station GK1, averaging 22.56. The DO levels were recorded with a minimum of 6.22 mg L⁻¹ at station D7MA, a maximum of 7.63 mg L⁻¹ at station SD3, and an average of 7.15 mg L⁻¹. Chlorophyll-a concentrations ranged from a minimum of 0.28 µg L⁻¹ at station D7MA to a maximum of 6.77 µg L⁻¹ at station MD89A, with an average of 1.24 µg L⁻¹.

The concentrations of NO₃ + NO₂-N ranged from 0.05 µM, observed at all stations except MD89A, to 0.18 µM at MD89A. NH₄-N levels varied between 0.04 µM, detected at most stations, and 0.24 µM, which was measured at MD89A. PO₄-P concentrations ranged from 0.02 µM, measured at several stations, to a maximum of 0.39 µM at MD67. SiO₂-Si values spanned from 0.18 µM at MD101 to 1.42 µM at station 45C. The N:P molar ratio ranged between 0.23 at MD67 and 6.29 at MD89A.

An overview to phytoplankton composition

Within the phytoplankton composition observed during the summer period, when *Hemiaulus* species were present, a total of 95 taxa including nano- and microphytoplankton size group were identified (Supplementary Table S1). Thirty-nine taxa of these (41.1%) were diatoms, 39 taxa (41.1%) were dinoflagellates, and 17 taxa (17.8%) belonged to other groups. Also, *R. intracellularis* from Cyanophyceae, *Dactyliosolen fragilissimus* and *H. hauckii* from Bacillariophyceae, and *Gonyaulax fragilis*, *Prorocentrum compressum*, *Prorocentrum micans*, and *Tripes furca* from Dinophyceae were the most frequently encountered species in this period.

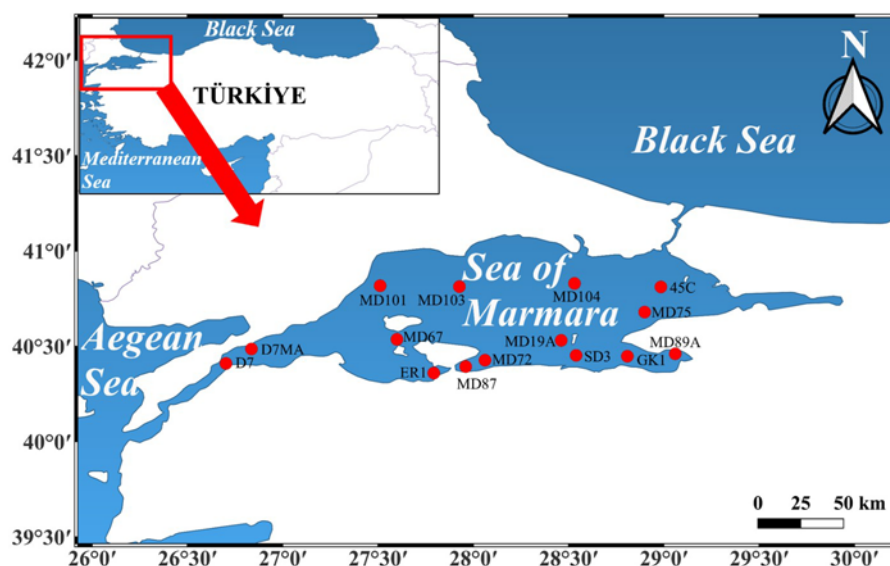


Figure 1. Study area and locations of sampling stations.

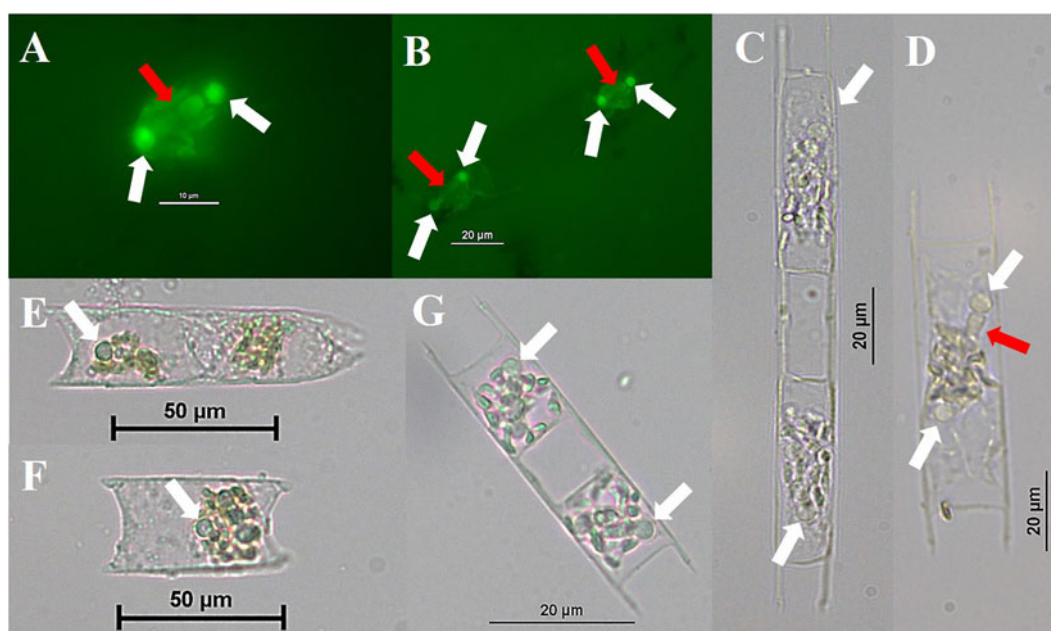


Figure 2. The diatom genus *Hemiaulus* and cyanobacterium *R. intracellularis* symbiosis. (A, B) Epifluorescence microscopy at the two different dimensions of the same cell. (C–G); bright-field microscopy: (C, D) *Hemiaulus hauckii*; (E, F) *Hemiaulus membranaceus*; (G) *Hemiaulus sinensis*. The red arrows indicate the trichomes, while the white arrows point to the terminal heterocysts of *R. intracellularis*.

Identification and characterisation of the diatom genus *Hemiaulus* and endosymbiotic cyanobacterium *Richelia intracellularis*

Three species of the diatom genus *Hemiaulus* – *H. hauckii*, *H. membranaceus*, and *H. sinensis* – were morphologically identified during the light microscopy examination. The genus *Hemiaulus* dominated the phytoplankton community in some sampling stations during this study period.

The presence of the cyanobacterium *Richelia intracellularis* was first detected inside the diatom *Hemiaulus* cells as an endosymbiont using an epifluorescent microscope (Figure 2). This symbiotic association was observed at the stations D7, D7MA, ER1, MD19A, MD67, MD75, MD87, MD89A, and SD3, whereas it was sporadically found at the other stations. Some of the *Hemiaulus*

cells contained one trichome of *R. intracellularis*. The trichome of *R. intracellularis* consisted of two to three vegetative cells and two heterocysts at both ends of each trichome observed in each *Hemiaulus* species (Figure 2).

Hemiaulus hauckii had a large diameter (apical axis) averaged 40–60 µm and a small diameter (transapical axis) averaged 12–22 µm, and their chains could be as long as 180 µm. *Hemiaulus hauckii* was found either as a solitary cell or characterised by chains composed of 2–3 cells. The H-shaped cells had broad girdle view, straight margins, horns long, apertures large and rectangular (Figure 2C, D).

Hemiaulus membranaceus had a large diameter (apical axis) averaging 50–95 µm and a small diameter (transapical axis) averaging 25–35 µm, and it was rarely found as a solitary cell. Its

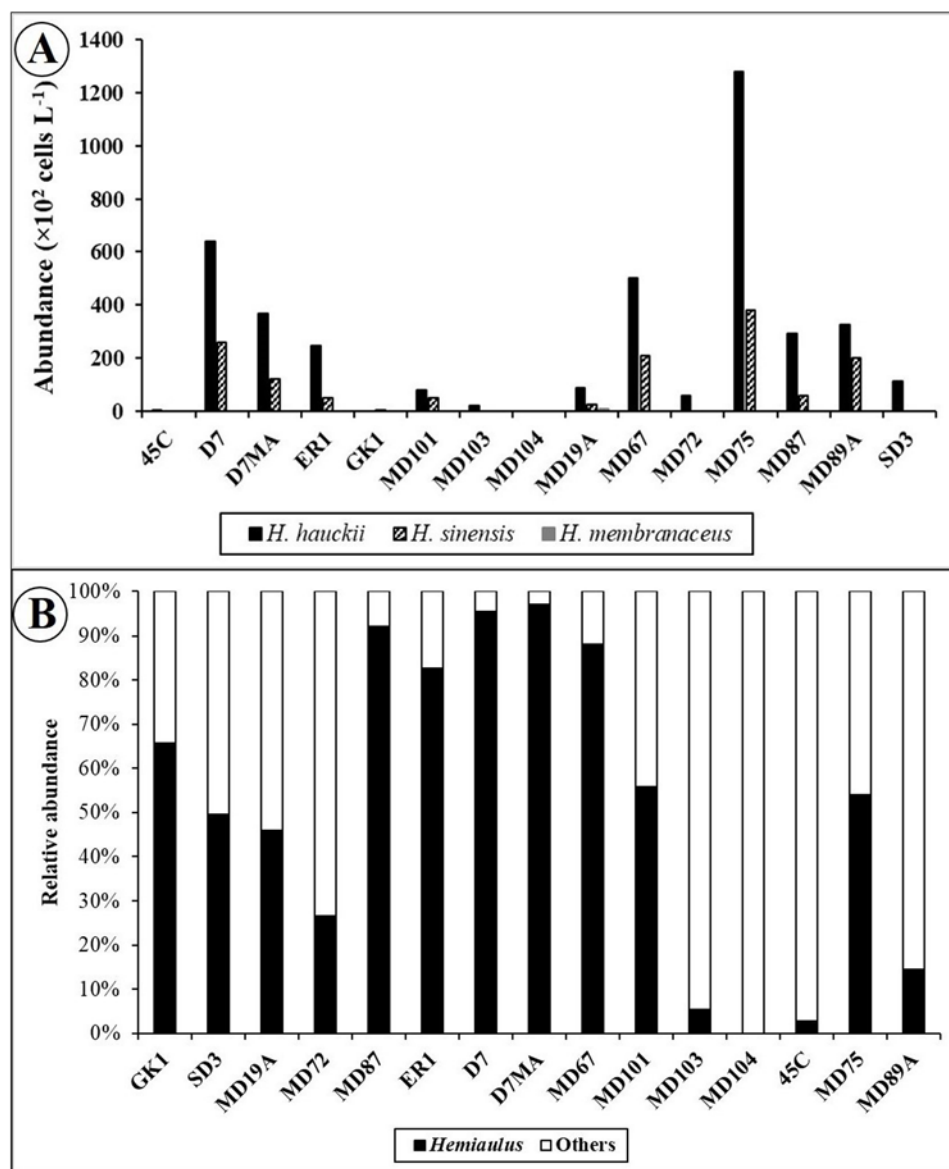


Figure 3. (A) Abundance of *Hemiaulus* species in the study area during summer 2021, (B) The relative abundance of the diatom *Hemiaulus* spp. in the total phytoplankton.

chains were twisted, with short horns and elliptical valves. The *Richelia intracellularis* trichome was found inside the *H. membranaceus* cells (Figure 2E, F).

Hemiaulus sinensis had a large diameter (apical axis) averaging 12–14 μm and a small diameter (transapical axis) averaging 10–12 μm . Its chains were straight and composed of two to three cells, with horns having flattened tips and rectangular valves. The cells were significantly smaller than the other two species. The trichome of *R. intracellularis* inside the *H. sinensis* cells consisted of two to three vegetative cells and two heterocysts at both ends of each trichome (Figure 2G).

Hemiaulus species were clearly distinguished morphologically from each other under a bright-field light microscope (Figure 2C–G). The symbiotic association between *Hemiaulus* and *Richelia* was observed more distinctly under an epifluorescent microscope (Figure 2A, B). However, this symbiosis was also occasionally noticed under a bright-field light microscope (Figure 2D–G). The average diameter of *R. intracellularis* inside *Hemiaulus*

species was approximately 17–18 μm . Two circular heterocysts appeared clearly at both terminal of the vegetative cell (Figure 2A, B).

Abundance of the diatom *Hemiaulus* and cyanobacterium *Richelia*

The diatom *Hemiaulus* species were commonly observed in the study area except for some sampling stations as seen in Figure 3A. *Hemiaulus hauckii* was more abundant than *H. sinensis* and *H. membranaceus*. The highest abundance reached up to 166×10^3 cells L⁻¹ at the station MD75, comprising *H. hauckii* (128×10^3 cells L⁻¹, 77%) and *H. sinensis* (38×10^3 cells L⁻¹, 23%). The other sampling stations with a high abundance of *Hemiaulus* species were the station D7 (90×10^3 cells L⁻¹) and the station MD67 (71×10^3 cells L⁻¹). *Hemiaulus membranaceus* was found in only one station (MD19A) at the low cell density (1×10^3 cells L⁻¹) (Figure 3A). The diatom *Hemiaulus* and endosymbiotic

cyanobacterium *Richelia intracellularis* associations were mostly observed in the stations MD75 and D7. The endosymbiont *R. intracellularis* was often detected in the *H. hauckii* host. No *Richelia* trichomes or *Hemiaulus* species were detected at station MD104 (Figure 3A).

The stations with more than 50% of the relative proportion of *Hemiaulus* species in total phytoplankton were D7MA (96.9%), D7 (95.4%), MD87 (92.2%), MD67 (88%), ER1 (82.6%), GK1 (65.8%), MD101 (55.8%), and MD75 (54.1%) (Figure 3B).

Discussion

Nitrogen has previously been reported to be limited in the SoM (Balkis *et al.*, 2011, 2013; Toklu-Alicli *et al.*, 2020; Tüfekçi *et al.*, 2010). The diatom–diazotrophy associations between *H. hauckii* and *R. intracellularis* have also been reported in other seas around the world (Foster *et al.*, 2007; Zeev *et al.*, 2008). It was detected that there were two terminal heterocysts at each trichome of the *R. intracellularis*.

The symbiotic associations between the diatom genus *Hemiaulus* and the cyanobacterium *Richelia* (diazotrophy), which are nitrogen-fixing organisms via their heterocysts, have a crucial role in N-limited environments. Considering the N-limitation in the SoM, this symbiotic association might have special significance for the functioning of the ecosystem. It is known that after seasonal stratification, *Hemiaulus* can become dominant in the Aegean Sea (Ignatiades, 1969).

Villareal (1991) suggested that *Hemiaulus* obtains fixed-N from the symbionts that serves to sustain the host diatom in oligotrophic environments. This means that new nitrogen inputs via symbiotic N-fixation may increase the host *Hemiaulus* cell abundance in the N-limited environments, as reported by Pyle *et al.* (2020). The role of *Richelia* as a diazotroph (nitrogen-fixing organism) is particularly crucial in such nitrogen-limited settings. Gomes *et al.* (2018) and Cieza *et al.* (2024) have demonstrated that N-fixing organisms proliferate more under increased temperatures, significantly impacting nutrient dynamics. Additionally, Mikaelyan *et al.* (2020) found that decreased silicate levels could limit the photosynthetic capacity of phytoplankton, thereby hindering the growth of *Hemiaulus* species. Zeev *et al.* (2008) highlighted that nitrogen-fixing symbiotic relationships become more pronounced under silicate deficiency. These observations indicate that increases in temperature and decreases in silicate levels contribute to the proliferation of the *Hemiaulus*–*Richelia* symbiosis.

This study revealed the *Hemiaulus*–*Richelia* symbiosis and significant seasonal and abundance changes in the abundance of *Hemiaulus* in the SoM. The highest abundances of *H. hauckii* and *H. sinensis* were observed in summer (July–August 2021), reaching 128×10^3 cells L⁻¹ and 38×10^3 cells L⁻¹, respectively, while *H. membranaceus* was rarely observed. This notable increase in distribution and abundance during the summer, coupled with the symbiotic relationship with *Richelia* demonstrated in our study, highlights a significant shift in the ecosystem dynamics of the SoM. Additionally, Demir and Turkoglu (2022) reported high abundances of *H. hauckii* in the Çanakkale Strait; however, their study did not provide any data on symbiosis. Additionally, *R. intracellularis* has previously been reported as an endosymbiont within *Rhizosolenia styliformis* in the Aegean Sea (Koray, 1988). In that study, Koray (1988) identified 15 distinct symbiotic pairings, including the association between *Rhizosolenia styliformis* + *R. intracellularis*, which was recorded at a density of 1500 cells L⁻¹ in October. Koray (1988) also reported that these taxa were sensitive

to changes in salinity, temperature, and oxygen levels, supporting their potential use as indicators of environmental stress, as previously suggested by Kimor (1985). This study demonstrates for the first time that *R. intracellularis* forms a symbiotic relationship with *Hemiaulus* species in the SoM and Turkish coastal waters.

In conclusion, the identification of the *Hemiaulus*–*Richelia* symbiosis in the SoM, which is the first reported occurrence of the symbiosis between the diatom *Hemiaulus* and cyanobacterium *Richelia* in Turkish seas, adds a significant piece to the marine nutrient dynamics, particularly in nitrogen-limited environments. This symbiotic relationship not only enhances nitrogen availability for *Hemiaulus* but also supports the broader marine ecosystem by contributing to primary production and nutrient cycling. Further research should aim to elucidate the mechanisms behind these associations and their responses to environmental changes, providing valuable insights into marine ecology and the management of coastal ecosystems.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315425100295>.

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Author contributions. Balkis-Ozdelice, N.: Conceptualisation, methodology, identification of species, data curation, writing-original draft. Tas, S.: Conceptualisation, methodology, identification of species, and writing-original draft. Durmus, T.: Conceptualisation, data curation, writing-original draft. Bayram-Partal, F.: Data curation, sampling, and writing-original draft. Balci, M.: Identification of species, data curation, and writing-original draft. Additionally, all the authors read and approved the final manuscript.

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Competing interests. The authors report there are no competing interests to declare.

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