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Population study of non-native bivalves *Mytilaster lineatus* (Mullusca: Mytilidae) and *Mytilopsis leucophaeata* (Mullusca: Dreissenidae) in the Southwestern Caspian Sea

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ABSTRACT
Despite being a closed basin isolated from open marine and oceanic environments, the Caspian Sea has not been spared from alien species, and a large number of invasive species have established themselves. In recent years, man-mediated vectors have further facilitated their introduction and spread, sometimes resulting in destructive ecological impacts. The density and abundance of *Mytilaster lineatus* (Gmelin, 1791) and *Mytilopsis leucophaeata* (Conrad, 1831) were assessed in two Southwestern Caspian Sea ports, revealing habitat segregation and greater environmental tolerance in *M. leucophaeata*. *M. leucophaeata* was primarily distributed at salinities between 0.5 and 3.9 PSU (practical salinity units), although it was observed at levels up to 11.7 PSU. In contrast, *M. lineatus* occurred predominantly at salinities of 10.5 to 12 PSU in the Caspian Sea. The nutrient concentrations were higher in habitats where *M. leucophaeata* was present. During the initial 100 days, *M. lineatus* and *M. leucophaeata* exhibited their peak daily growth rates at approximately 0.12 mm day^{-1} and 0.13 mm day^{-1}, respectively. A year later, their average shell heights reached 15.3 mm and 16.3 mm, with maximum theoretical shell heights (H_∞) estimated at 19.98 mm and 21.49 mm, respectively, based on the von Bertalanffy growth model. Their high growth rate may pose a more severe biofouling threat to maritime and shipping industries than what is typically observed in European brackish waters.

Key words: Bivalve, invasive species, abundance, growth, Caspian Sea.

INTRODUCTION
The endemic Ponto-Caspian mollusc species richness is estimated between 55 and 99 species, but the status of most species point to deterioration (Wesselingh *et al.* 2019). One of the main ecological problems in the Caspian region is the invasion and widespread distribution of alien species. While over two million years (from the Late Pliocene to the Holocene and up to the early 1900s), only 456 invertebrate species colonized the Caspian Basin through natural mechanisms, during the 20^{th} century, 36 non-indigenous invertebrate species were entered via human-mediated vectors (Grigorovich *et al.* 2003).
Mytilaster lineatus, which is identified as part of the Mediterranean biotic complex, was first documented in the Caspian Sea in 1928. It was likely introduced to the Caspian Sea either from Batumi to Baku by ships or via the

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Baltic Sea through the Sea of Azov. Today it dominates the Caspian mollusc community, though it faces intense competition from other Dreissena species (Malinovskaya & Zinchenko 2010).
Studies of Holocene lithology and facies along the Iranian coast confirm the early 20th-century introduction of *M. lineatus* from the Black Sea, a trend further reflected in recent strata (the last few decades to the last century) where the species has become more abundant than the *Cerastoderma–Didacna–Mytilaster* complex (Svitoch *et al.* 2016).
In the Northern Caspian, *M. lineatus* occurs densely on hard, shelly substrates, where its biomass can constitute up to 90% of the total zoobenthos biomass, as its distribution is constrained by salinity and trophic conditions, and it is absent from silty substrates (Malinovskaya & Zinchenko 2010). Research on *M. lineatus* along the various Iranian Caspian shores has examined distribution, abundance, growth, and population dynamics (Zeinalipour 2010; Torabi Jafrodi *et al.* 2017; Sayyadoghly *et al.* 2019; Sharifi & Rahimibashar 2022). This species has been reported from the southern areas of the Northern Caspian Sea, as well as its middle and southern areas down to 35–50 m water depth (Wesselingh *et al.* 2019).
Conrad's false mussel, *Mytilopsis leucophaeata* belongs to the Dreissenidae family, comparable to the freshwater zebra mussel *Dreissena polymorpha*, with notably similar life cycles. In Europe, *M. leucophaeata* spreads more slowly than *D. polymorpha* does in the United States, but it causes more severe fouling and is regarded as the brackish-water counterpart of *D. polymorpha* in Europe (Verween *et al.* 2010). Originally a brackish-water species, *M. leucophaeata* inhabited the subtropical and temperate southern coasts of North America. It has since become invasive across much of North America and Western Europe as a typical estuarine species. The species tolerates a wide range of salinity, mainly oligohaline to mesohaline, and temperature (2–30 °C), reflecting its euryhaline and eurythermal physiology (Laine *et al.* 2006; Kennedy 2011; Van Der Gaag *et al.* 2017; Bat *et al.* 2019; Fernandes *et al.* 2022). The invasion of *M. leucophaeata* is well documented in numerous regions worldwide, including the Ponto-Caspian area (Heiler *et al.* 2010; Mumladze *et al.* 2019; Wesselingh *et al.* 2019; Zhulidov *et al.* 2021).
In the Caspian Sea, *M. leucophaeata* was first detected in the southwestern region in 2009 as a non-native species, though introductions likely occurred earlier, representing the easternmost known occurrence of *M. leucophaeata* whose life history remains unspecified (Heiler *et al.* 2010; Sayyadoghly *et al.* 2019).
The study aimed to investigate the life histories of *M. lineatus* and *M. leucophaeata* from individuals attached to stones in their invaded Southern Caspian Sea habitat. Analyses concentrated on spatial and temporal settlement, bivalve length-frequency distributions, and growth rates.

MATERIAL AND METHODS

Study Area

This study is carried out in two areas: Bandar-e-Anzali (Anzali Port; 37°29'8.30"N, 49°28'31.38"E) and the Anzali Trade-Industrial Free Zone (Caspian Port; 37°27'40.23"N, 49°39'39.46"E; Fig. 1). Anzali Port, Iran's oldest port on the Caspian coast, exhibits distinct environmental conditions on either side of its breakwater, influenced by Anzali Wetland internally and the Caspian Sea externally. Sampling was designed along both sides of the main breakwater, whose western arm extends approximately 1,690 meters. Three sampling stations (S1–S3) were established on the outer wall, directly exposed to sea waves, while three others (S4–S6) were located on the inner wall, affected by freshwater and hyper nutrient discharges from Anzali Wetland. These discharges originate from a watershed of about 374,000 hectares, composed of numerous creeks and rivers flowing through urban and agricultural zones (Naderi *et al.* 2017; Mirzajani *et al.* 2021). The Caspian Port, a coastal facility with consistent environmental conditions on both sides of its breakwater, features a small eastern marina for yachts and small boats, where six sampling stations (F1–F6) were established (Fig. 1, CP).

Methodology

Approximately 2 m² of artificial substrate was cleared of fouling communities at each station during April 2022, with three replicates taken per site. Subsequently, from August 2022 to August 2023, seasonal sampling was performed by scraping a 10 × 10 cm² surface area from each of the three replicates. Quantitative samples were obtained by snorkeling or scuba diving at depths between 0.5 and 1.5 meters using a rectangular scraper. All samples were preserved in 4% formaldehyde on site and transported to the laboratory, where bivalve specimens were sorted and identified (Birshtein *et al.* 1968; Heiler *et al.* 2010). The length, height, and width (mm) of each

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specimen were measured with a Vernier caliper (Leal & Matthews 2013), and their weight (mg) was recorded. The soft tissues were separated from the shells, oven-dried at 70 °C, and weighed.

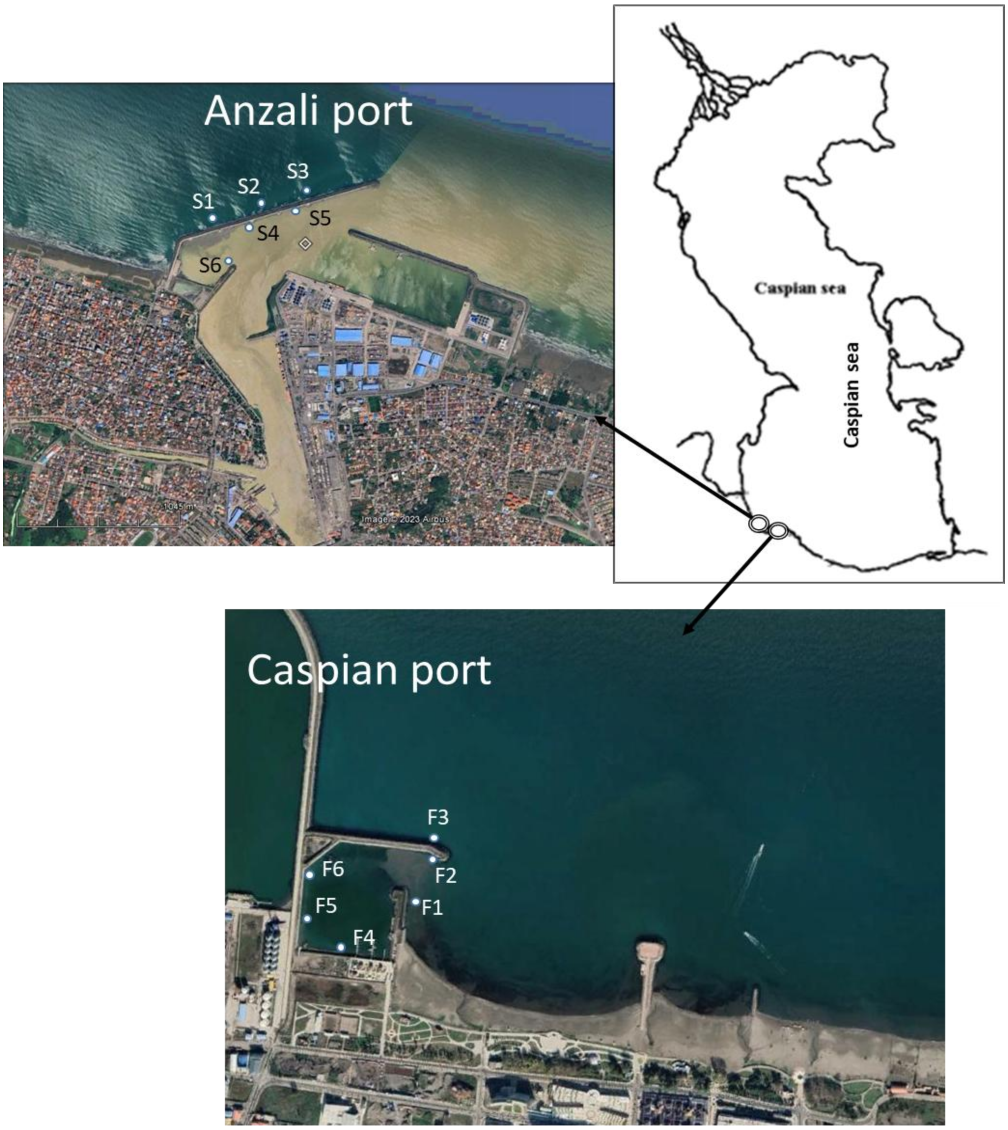

Fig. 1. Sampling locations on both sides of the breakwater construction at Anzali Port (AP) and Caspian Port (CP).

Statistical analysis was performed using One-Way ANOVA to compare shell length and nutrient concentrations across different regions.

During each sampling interval, the 10 to 20 largest specimens were selected for growth rate assessment. The growth rate was calculated using the equation 1, originally described by Neumann & Jenner (1992) based on the mean maximum shell height increment (SHI). In this equation, SH_{t+1} denotes the final shell height (mm), SH_t is the initial shell height (mm), and *dt* is the number of days between the two measurement points (t and t+1).

Equation 1: $SHI\ (mm/day) = (SH_{t+1} - SH_t)/dt$

To estimate the growth parameters of the species, the von Bertalanffy Growth Function (Equation 2) was applied. In this model, Ht represents the shell height at age t, H_∞ denotes the asymptotic shell height, K is the growth coefficient, and t_0 is the theoretical age at which shell height is zero. Growth parameters were obtained using the least-squares optimization approach implemented through the Solver add-in in Microsoft Excel (King 2007).

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$$H_t = H_\infty(1-e^{-k(t-t_0)})$$

Equation 2: $H_t = H_\infty(1-e^{-k(t-t_0)})$

Hydrochemical parameters, including temperature, salinity, total dissolved nitrogen (TN), and phosphorus (TP), were obtained from the archival data of Bagheri *et al.* (2024) and Abedini (2025), who measured these variables simultaneously in areas close to the stations under study. These data, measured by standard methods (APHA 2005), were evaluated for the purposes of this study.

RESULTS

Mytilaster lineatus was absent from the inner section of Anzali Port but was recorded inside the marina of the Caspian Port. During the first sampling, its average (± SE) abundance and biomass in the Caspian Port marina were 1901 ± 1875 ind. m^{-2} and 17.1 ± 14.2 g m^{-2}, respectively (Fig. 3).

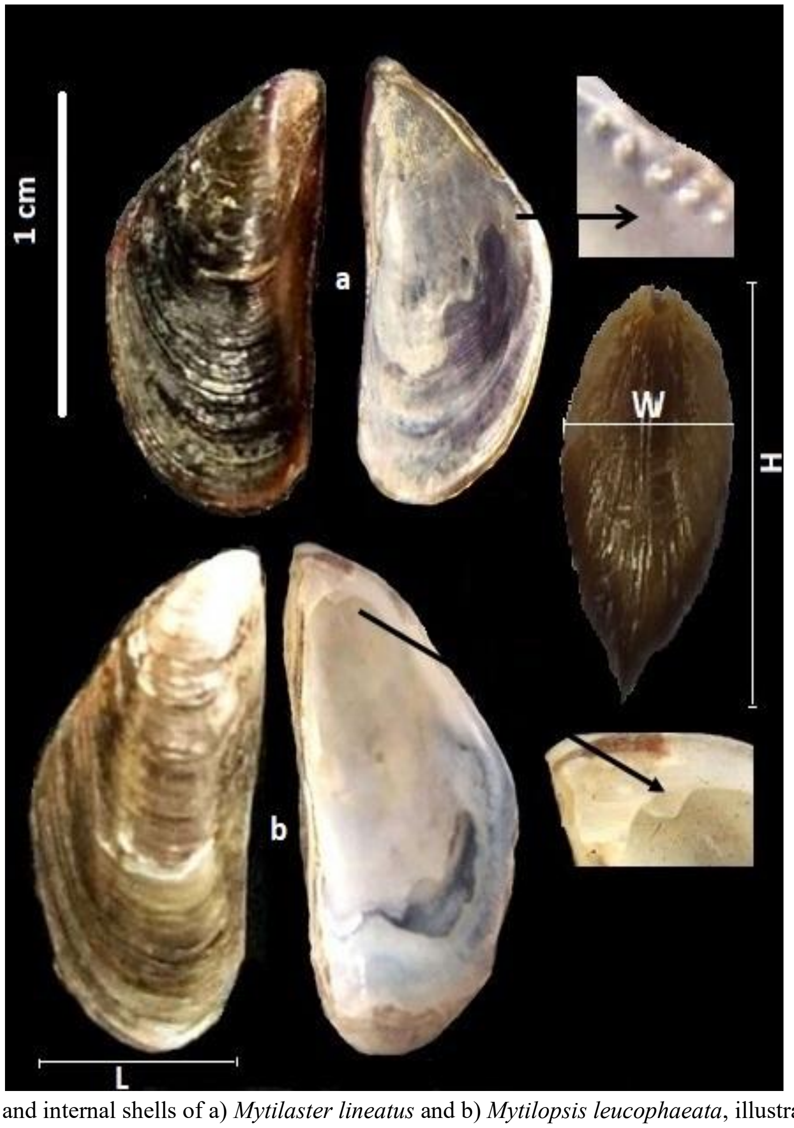

Fig. 2. External and internal shells of a) *Mytilaster lineatus* and b) *Mytilopsis leucophaeata*, illustrating diagnostic characteristics and biometric parameters: height (H), length (L) and width (W).

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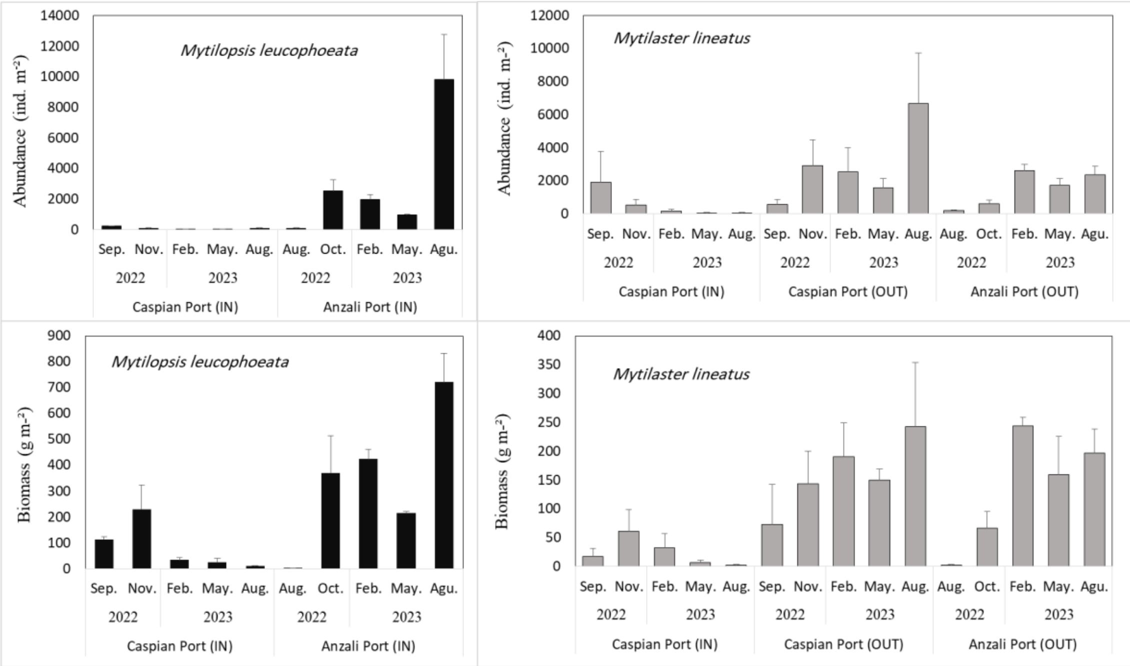

Fig. 3. Spatial and temporal variation in abundance and biomass of the bivalves *Mytilaster lineatus* and *Mytilopsis leucophaeata* in the Southwestern Caspian Sea.

Over time, both abundance and biomass of *M. lineatus* within the marina showed a declining trend, reaching 48.1 ± 28.3 ind. m^{-2} and 2.4 ± 1.3 g m^{-2}, respectively. In contrast, an increasing trend in *M. lineatus* abundance was observed outside the breakwater walls of both ports. By the final sampling, its abundance reached 2365.6 ± 495.6 ind. m^{-2} at the outer wall of Anzali Port and 6679 ± 3055 ind. m^{-2} at the outer wall of the Caspian Port, with corresponding biomass values of 196.8 ± 41.5 g m^{-2} and 242.6 ± 110.5 g m^{-2} respectively. *M. leucophaeata* was the dominant species inside the breakwater wall of Anzali Port but occurred at low densities inside the marina of Caspian Port (Fig. 3). In the final sampling, its mean (± SE) abundance and biomass were 9806.7 ± 2941.6 ind. m^{-2} and 720.5 ± 111.1 g m^{-2}, respectively.

The length-frequency distribution of *M. lineatus* (Fig. 4) indicated that juvenile individuals (<4 mm in height) dominated the population during summer. Throughout the study period, individuals smaller than 8 mm accounted for more than 50% of the population. Larger specimens (>12 mm) were mainly recorded between February and May, reaching a maximum proportion of 17.4%. A comparable pattern was observed for *M. leucophaeata*, with juveniles (<4 mm) dominating in August and an increased proportion of larger individuals (>12 mm) appearing between February and May.

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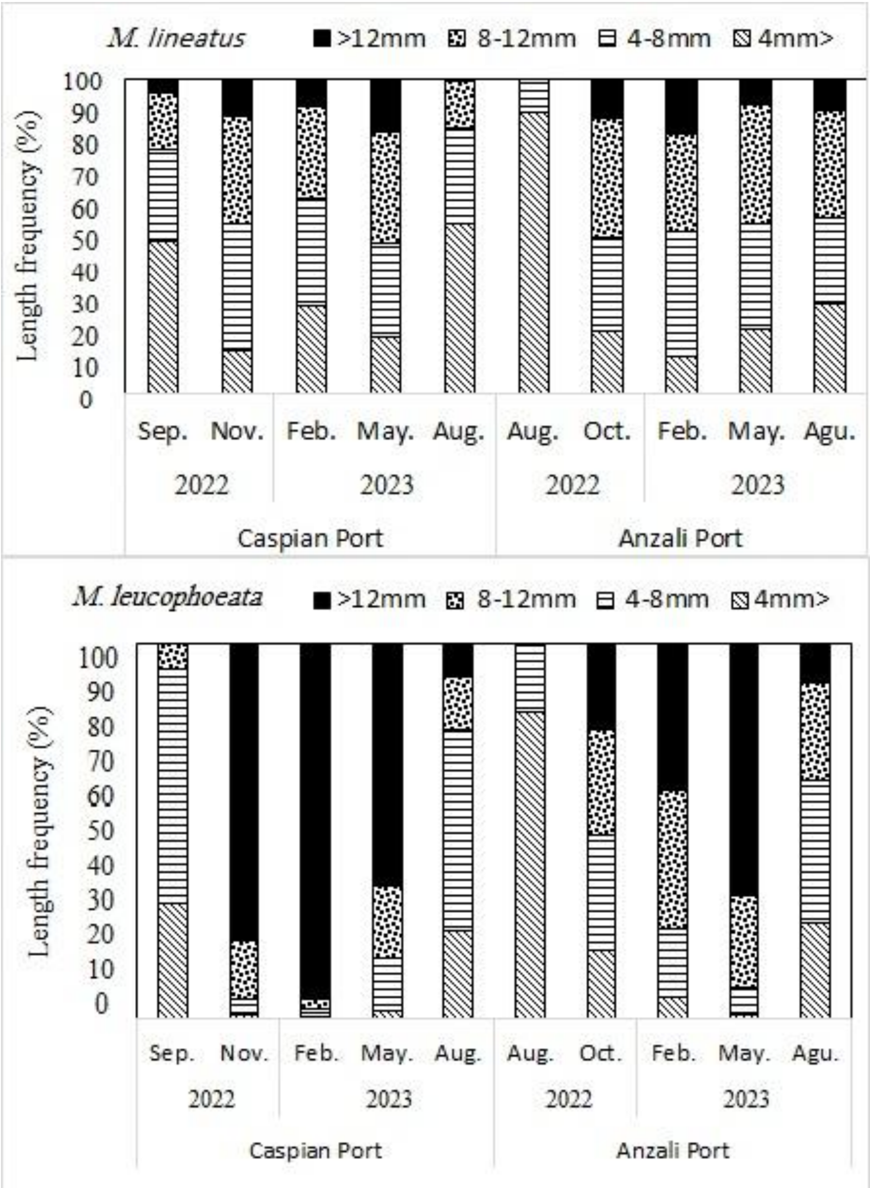

Fig. 4. Length-frequency distributions of *M. lineatus* and *M. leucophaeata* in Anzali and Caspian ports at different sampling periods.

The relationship between shell height and total weight in both bivalve species exhibited a strong allometric pattern (Fig. 5), best described by a power function ($R^2 > 0.95$). The mean (± SD) soft tissue proportion relative to total body weight was 9.6 ± 4.9% in *M. lineatus* and 25.2 ± 15.4% in *M. leucophaeata*.

Fig. 6 shows the growth patterns of the two bivalve species. The highest daily growth rates were recorded during the first 105 days (until August), reaching average (± SD) 0.122 ± 0.0035 mm day^{-1} for *M. lineatus* and 0.126 ± 0.0026 mm day^{-1} for *M. leucophaeata*.

After this initial phase, the daily growth rates of the species converged, declining to 0.053 and 0.056 mm day^{-1}, respectively. Analysis of average shell length at each sampling point revealed that *M. leucophaeata* was consistently larger across all biometric measurements ($p < 0.01$). A year later, maximum shell heights reached 16.7 mm (mean 15.3 ± 1.1 mm SD) for *M. lineatus* and 16.8 mm (mean 16.3 ± 0.3 mm SD) for *M. leucophaeata*. Since the commencement of the study in April 2022, their maximum sizes increased to 18.98 mm and 20.4 mm, respectively. *M. lineatus* had von Bertalanffy growth parameters of K = 0.19 and $H\infty$ = 19.98 mm, while *M. leucophaeata* had K = 0.20 and $H\infty$ = 21.49 mm (Fig. 6).

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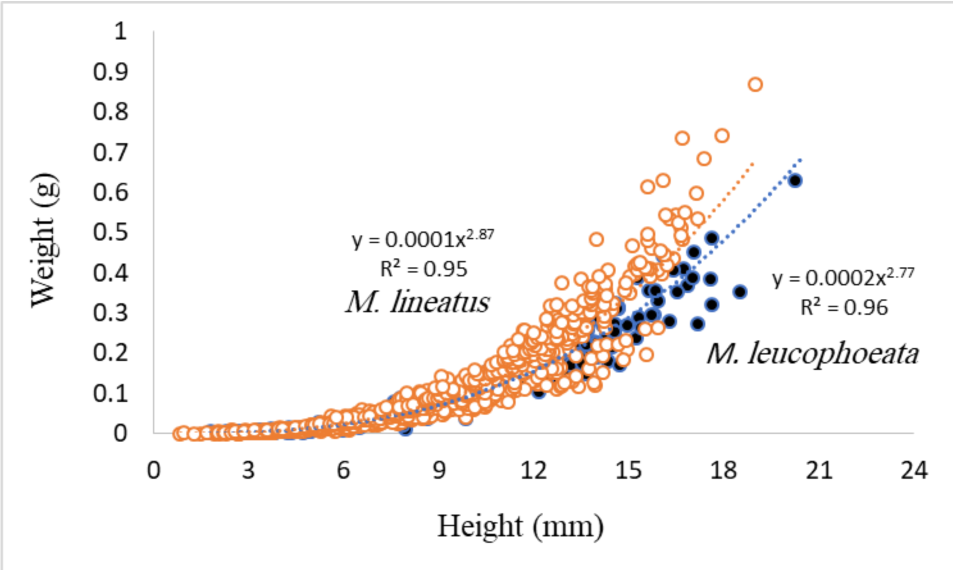

Fig. 5. Relationship between shell Size and weight of the bivalves *Mytilaster lineatus* and *Mytilopsis leucophaeata* in the Southwestern Caspian Sea.

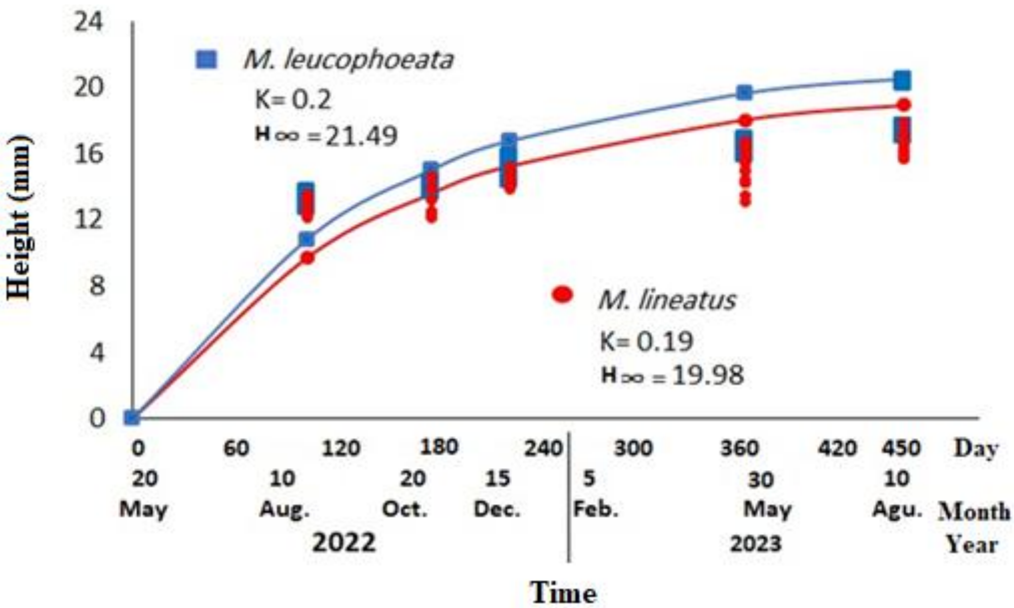

Fig. 6. Growth curves of *Mytilaster lineatus* and *Mytilopsis leucophaeata* from the onset to the conclusion of the experiment in the southwestern Caspian Sea.

Fig. 7 presents the mean values of the hydrochemical parameters across the study sites. Water temperatures across sampling stations ranged from 11.4 to 28.8 °C throughout the study period, with no significant differences observed between regions. Salinity was lowest in the inner section of Anzali port, measuring 2.11 ± 0.96 g L^{-1}, and differed significantly from other three areas, where salinity exceeded 11.32 g L^{-1}. Nutrient concentrations in Anzali port, particularly in its inner section, were significantly ($p < 0.05$) higher than those recorded in the Caspian Port. The mean (± D) of total nitrogen (TN) concentration in the inner part of Anzali Port was 2.142 ± 0.799 mg L^{-1}, which did not differ significantly ($p > 0.05$) from the outer part (1.752 ± 0.630 mg L^{-1}), but was significantly higher compared with the Caspian port (approximately 1.1 mg L^{-1}). Similarly, mean (± SD) of total phosphor (TP) in the inner part of Anzali Port was 0.233 ± 0.110 mg L^{-1}, not significantly different ($p > 0.05$) from the outer part (0.140 ± 0.045 mg L^{-1}), but significantly elevated compared with the Caspian port area, where TP averaged around 0.1 mg L^{-1} (Fig. 7).

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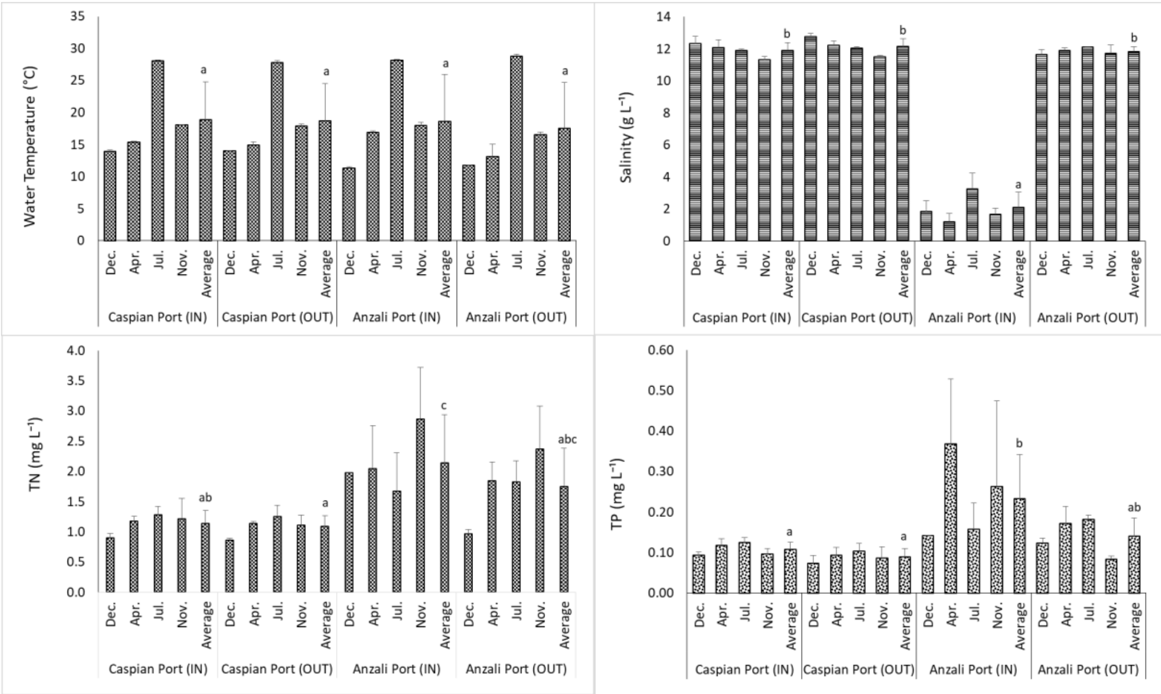

Fig. 7. Hydrochemical parameters in Anzali and Caspian ports across different seasons, using data from Bagheri *et al.* (2024) and Abedini (2025). Statistically similar groups are indicated by identical letters.

DISCUSSION

In this study, the two bivalve species *Mytilaster lineatus* and *Mytilopsis leucophaeata* were found to occupy distinct habitats, occurring outside and inside the Anzali Port breakwater, respectively. Sayyadoghly *et al.* (2019), who observed mean densities of 2,043 ind. m^{-2} for *M. lineatus* and 2,396 ind. m^{-2} for *M. leucophaeata* in 2018, reported a similar pattern.

The inner areas of Anzali Port are strongly influenced by environmental changes resulting from freshwater inflow, sediment accumulation, and pollutant loads from the Anzali Wetland watershed (Mirzajani 2009; Mirzajani *et al.* 2010; Abedini *et al.* 2018), all of which may play a key role in shaping the distribution and population dynamics of the two bivalve species.

M. lineatus is less thoroughly studied regarding its precise salinity tolerance compared to *M. leucophaeata*. Field observations indicate that it generally prefers moderate salinities of approximately 7–13 PSU (practical salinity units; Zaitsev & Oeztuerk 2001) and is usually absent from silty substrates or low-salinity habitats. Available data suggest that it can tolerate salinities ranging from 7 to 30 g L^{-1}, with peak abundance recorded at 11–13 g L^{-1} (Malinovskaya & Zinchenko 2010). However, prolonged exposure to salinities below 7 PSU appears unsuitable for this species (Wesselingh *et al.* 2019).

In contrast, *M. leucophaeata* exhibits a wide salinity tolerance, ranging from near freshwater to moderately brackish conditions. This relatively understudied dreissenid bivalve is native to North American estuaries, where it typically inhabits oligohaline (0.5–5 PSU) to mesohaline (5–18 PSU) waters (Siddall 1980; Kennedy 2011). It can also survive in highly saline water up to 31 PSU, with only true seawater (35 PSU) exceeding its survival limits (Verween *et al.* 2010). However, these high salinity levels are less favorable for reproduction, as reproductive activity declines under elevated salinities, and the larval stage shows high tolerance only at salinities between 0 and 25 PSU (Verween *et al.* 2007). Earlier, Siddall (1980) reported that the larvae and post-larvae are euryhaline and capable of developing to metamorphosis at salinities ranging from 10 to 32 PSU.

In our study area, the annual water salinity in the inner area of Anzali Port fluctuated between 1.2 and 3.9 PSU, while in the outer area it ranged from 11.4 to 12.1 PSU (Fig. 7). Consequently, *M. lineatus* thrives in the higher-salinity zones of the study area, whereas *M. leucophaeata*, with its broader salinity tolerance, is able to persist in the lower-salinity, influenced by freshwater inside the port.

According to Van Der Gaag *et al.* (2017), in areas with suitable salinity, the settlement and shell growth of *M. leucophaeata* were positively correlated with water temperature and day length. In another study (Tkachenko *et*

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al. 2025), water temperature and surf-wave activity were found to have a stronger influence on the abundance of *Mytilaster* species on hard substrates. The optimum temperature range for feeding and growth of *M. lineatus* is 8–26 °C, and it can tolerate temperature fluctuations between 2 and 30 °C (Bat *et al.* 2019). A high temperature tolerance was also observed in *M. lineatus* during long-term periods of abnormal temperature conditions, with individuals enduring temperatures of 29–30 °C for approximately 20 days (Govorin & Shatsillo 2012).

Temperature is also a key environmental factor regulating both gametogenesis and spawning in dreissenid mussels. While *M. leucophaeata* can tolerate temperatures as low as 6.8 °C, allowing it to inhabit temperate waters across Europe, embryonic mortality increases significantly at temperatures below 10 °C or above 30 °C (Verween *et al.* 2007).

In our study area, water temperatures exhibited considerable seasonal variation, ranging from 11.2 to 28.2 °C in the inner part of Anzali Port and from 11.7 to 29 °C in other parts in the Southwestern Caspian Sea (Fig. 7). Therefore, temperature is not currently a limiting factor for the growth and development of these species. However, with ongoing global warming, regional water temperatures are projected to exceed 30 °C (Mahdian *et al.* 2024), which may become a future limiting factor. The high abundance of small individuals (<4 mm) in August indicates a reproductive peak occurring around April–May. Although earlier studies reported small size classes of *M. lineatus* mainly from mid-summer to early autumn (Sharifi & Rahimibashar 2022; Zeinalipour 2010), the year-round presence of juveniles in both our data and previous reports indicates continuous reproduction, with peak activity in late winter and spring.

In this study, an abrupt decline and high mortality of *M. leucophaeata* was observed in the inner region of Anzali Port.

Nutrient inputs from the Anzali Wetland catchment (Mirzajani *et al.* 2008; Mirzajani *et al.* 2010) may have contributed to the high biomass of *M. lineatus*. After one year, its biomass reached 1.97 kg m^{-2} on the breakwater walls of Anzali Port and 2.43 kg m^{-2} on the Caspian Port. Perennial-mass sampling showed an average abundance of approximately 1.14 kg m^{-2} along the southern shores of the Caspian Sea, with higher values reported in Anzali Region (about 4.4 kg m^{-2}; Sharifi & Rahimibashar 2022; Torabi Jafrodi *et al.* 2017). This pattern is complemented by the Northern Caspian Sea data, where *M. lineatus* occurs at depths from 5 to 28 meters; its average biomass at 10 meters depth is 103.2 g m^{-2}, while maximum biomass reaches up to 5 kg m^{-2} at greater depths (Malinovskaya & Zinchenko 2010). The average biomass of *M. lineatus* has been reported as 1.7 kg m^{-2} at the hydraulic structures of Sevastopol Bay, even under conditions of chronic petroleum pollution in the water area (Tkachenko *et al.* 2025).

Nutrient enrichment exerts contrasting effects on these two species. While *M. leucophaeata* is associated with moderate eutrophication, it remains vulnerable to the indirect impacts of severe conditions (Kido *et al.* 2024). *M. lineatus* is also frequently found in organically enriched sediments, suggesting a high tolerance to moderate organic pollution (Tkachenko *et al.* 2025). Both species are likely influenced by the nutrient levels in our study area, where concentrations of total nitrogen (TN) and total phosphorus (TP) inside the Anzali Port breakwater significantly exceeded those recorded outside the breakwater and in the Caspian Port region (Fig. 7). When compared to US EPA nutrient guidelines and other regional studies—where TN $\geq$ 0.15 mg L^{-1} and TP $\geq$ 0.01 mg L^{-1} have been associated with adverse effects on bivalves—our measured levels (TN > 1 mg L^{-1} and TP > 0.1 mg L^{-1}) appear particularly elevated inside Anzali Port. Although conservative protective targets are recommended at TN $\leq$ 0.5–1.0 mg L^{-1} and TP $\leq$ 0.05–0.1 mg L^{-1} (Gibson *et al.* 2000), specific survival thresholds for *M. lineatus* and *M. leucophaeata* remain absent from the literature.

The inner part of Caspian Port is less impacted by external anthropogenic factors than Anzali Port, so mussel density would be expected to be higher. However, their low density in the Caspian Port marina is likely due to the presence of the more aggressive tubeworm *Ficopomatus enigmaticus* (Fauvel 1923), which has rapidly colonized this habitat. During the study period, the biomass of *F. enigmaticus* increased from 335 to 840 g, coinciding with the decline of bivalves (Sayyadoghly *et al.* 2024).

Shell growth also appears closely correlated with water temperature; for instance, the highest growth rates were observed from May to October for *M. lineatus* and from May to December for *M. leucophaeata*, coinciding with a marked decline in growth during the winter. In the harbor of Antwerp, Belgium, an annual growth rate of approximately 3–6 mm was reported, with shell growth ceasing at a minimum threshold temperature of 9.1 °C (Verween *et al.* 2006). On hard substrates, growth rates were very low in winter (less than 1 µm day^{-1}) but increased to about 89 µm day^{-1} during summer (Van Der Gaag *et al.* 2017).

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In our study *M. lineatus* and *M. leucophaeata* exhibited high growth rates (Fig. 6) and achieved significant biomass densities of roughly 2.5 kg m^{-2} and 7.2 kg m^{-2} (Fig. 3). These findings indicate a strong potential for biofouling that could impact the maritime and shipping industries. This is more severe than fouling problems they have caused in European power stations and other brackish-water industries (Verween *et al.* 2006).
Rapidly growing mussels and bivalves possess the capacity to efficiently colonize ship hulls, underwater structures, and aquaculture equipment. Given their status as prey for diverse fish taxa (Malinovskaya & Zinchenko 2010), these biofouling communities may function as a significant, accessible food resource within the Caspian Sea. Our findings, which indicate a soft tissue content at minimum 9.6% of total body mass and a distribution extending to depths of 50 m in the southern basin, support this potential. Consequently, the strategic deployment of artificial habitats at greater offshore depths, aligning with the foraging ranges of *Rutilus kutum* and sturgeon species, could enhance prey availability and fulfill the nutritional requirements of these populations. Nevertheless, further empirical investigation is essential to fully characterize the dietary preferences and trophic capacity of these Caspian fishes in relation to such artificial structures.

CONCLUSION

The study identifies distinct spatial distributions for two bivalves, *Mytilaster lineatus* and *Mytilopsis leucophaeata*, in the Anzali and Caspian Port areas and notes clear differences in how they use habitats and respond to environmental gradients. Both species exhibit rapid growth and increases in biomass with higher nutrient levels, but *M. lineatus* prefers higher salinity, while *M. leucophaeata* tolerates a wider range of salinities. *M. lineatus* is more abundant outside breakwaters in both ports, particularly at the outer walls. Conversely, *M. leucophaeata* is more dominant inside Anzali Port's breakwater but decreases significantly with pollution, especially in the nutrient- and turbidity-rich inner areas. Juveniles predominate in warmer months for both species, suggesting that temperature strongly influence their growth and reproduction. Invasive competition from *Ficopomatus enigmaticus* could reduce mussel densities in exposed areas. Overall, the findings highlight their roles as fouling organisms and as potential prey for the Caspian fishes. Additional research is needed to assess the practicality of cultivating mussels as artificial habitats or fisheries resources in deeper, offshore waters.

Competing interests

No potential conflict of interest relevant to this article was reported.

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Availability of data and materials

Upon reasonable request, the datasets of this study can be available from the corresponding author.

Ethics approval and consent to participate

This study conformed to the guidance of animal ethical treatment for the care and use of experimental animals.

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