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Recent spatial distribution of alien species visually inspected along the Turkish Aegean coast and environment

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Abstract

Biodiversity in the Mediterranean is undergoing rapid restructuring due to climate change and the spread of non-indigenous species (NIS). This study presents the first integrated assessment of alien species distribution along the Turkish Aegean coast, utilizing SCUBA surveys, acoustic seabed mapping, and in situ environmental measurements collected between June and August 2024. Data from 321 dives (5–40 m) and grab samples (40–50 m) were analyzed to characterize NIS assemblages and their habitat associations. A total of 20 alien species were recorded, including eight macroalgae, one seagrass (*Halophila stipulacea*), seven fishes, and four invertebrates. Three macrophytes—*Caulerpa cylindracea*, *Caulerpa taxifolia*, and *Stypopodium schimperi*—were dominant, with *C. cylindracea* increasing toward the north while others remained confined to southern sectors. Invasive fishes, such as *Pterois miles* and *Torquigener flavimaculosus*, showed strong associations with seagrass patches and mixed substrates between 10 and 30 m. Significant regional differences in species composition were observed (PerMANOVA, $p < 0.05$), driven primarily by distinct water masses. Near-bottom temperature and salinity were the strongest environmental drivers, explaining 23.6% and 18.7% of the variance, respectively. Thermophilic and halophilic species were most abundant in southern sites influenced by Levantine water intrusions. These findings provide essential baseline data for monitoring, risk assessment, and the development of targeted management strategies in this highly dynamic marine region.

Keywords: Non-indigenous species; Visual census; Marine bioinvasions; Coastal ecosystems; Environmental gradients; Habitat mapping; Aegean Sea

Introduction

Biodiversity hotspots, despite ongoing debate, remain widely used for guiding conservation priorities and enabling cost-effective strategies to protect biological diversity in both terrestrial and, increasingly, marine ecosystems (Marchese 2015). Understanding biodiversity is essential for maintaining ecosystem sustainability. Earlier work by Médail and Quézel (1997) highlighted two major centers of terrestrial plant diversity within the Mediterranean Basin: a western region encompassing the Iberian Peninsula and Morocco, and an eastern region including Türkiye and Greece.

Marine ecosystems worldwide are under growing pressure from alien species (Wallentinus & Nyberg 2007; Molnar et al. 2008; Katsanevakis et al. 2014b; Perzia et al. 2023). The introduction of alien (non-indigenous) species—defined under EU Regulation 1143/2014 and the Marine Strategy Framework Directive 2008/56/EC—is now considered one of the most significant threats to marine environments (Tsiamis et al.2020). Biological invasions can profoundly affect native biodiversity, ecosystem processes, human health, and economic sectors (Grosholz 2002; Vilà et al. 2010). Global assessments merging species distribution data with human-impact indicators have identified new priority conservation areas, particularly in high-latitude regions and areas beyond national jurisdiction (Selig et al. 2014; Marchese 2015).

In the Mediterranean Sea, more than 500 alien species have long been recognized (Galil 2007). Although the immediate loss of native populations may not always be evident, invasions lead to declines in genetic diversity, ecosystem functions, and habitat complexity, increasing the risk of long-term local extinction and biotic homogenization. These concerns underscore the need for sustained, long-term monitoring across regions (Tsiamis et al.2018). Multiple introduction pathways have been documented—including aquaculture, shipping (ballast water and hull fouling), recreational boating, canals, altered circulation patterns, and climate-driven environmental changes (Boudouresque & Verlaque 2005; Katsanevakis et al. 2013; Zenetos et al. 2012). Proposed mitigation measures include constructing high-salinity locks within the Suez Canal to reduce species transfer, which historically occurred naturally via the hypersaline Bitter Lakes (Hewitt et al. 2006). Introductions can be intentional or accidental, with cascading trophic effects—for example, *Beroe ovata* Bruguière, 1789 controlling *Mnemiopsis leidyi* A. Agassiz, 1865 in the Black Sea (Mutlu 2009), *Pterois miles* (Bennett, 1828) preying on puffer fish larvae and juveniles (non-scientific pers. comm.) fishes, or *Conomurex persicus* (Swainson, 1821) feeding on *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman & Procaccini, 2013 in the eastern Mediterranean (Mutlu et al. 2022a). Conversely, native species such as *Mytilus galloprovincialis* Lamarck, 1819 have been negatively affected by invasive predators like *Rapana venosa* (Valenciennes, 1846) (Mutlu et al. 2022b). Every newly introduced and established species initially colonized shallow waters and subsequently evolved adaptations that allowed expansion to deeper grounds, as later-introduced non-indigenous species were readily accommodated within benthic marine environments (Ketchum, 1983). Regular biodiversity monitoring, therefore remains essential for informed management and regulation (Galil et al. 2014; Zenetos et al. 2017a).

Non-indigenous species (NIS) range from microscopic organisms to large macrofauna. Their population dynamics are shaped by life-history strategies (K- or r-selected), which determine how effectively they exploit available resources after establishment (Coll et al. 2010; Mutlu et al. 2025a). Every newcomer enters an already structured trophic system, often resulting in ecological and economic consequences at local and regional scales (Mutlu et al. 2023). Nevertheless, NIS can disrupt native ecosystems, altering food webs, reducing biodiversity, and causing socio-economic impacts (Galanidi et al.2023; Albano et al.2024).

The Mediterranean Sea—the world's largest semi-enclosed basin—extends from the Strait of Gibraltar to the Suez Canal and harbors exceptional biodiversity (Tsiamis et al.2018). However, it is also one of the most threatened marine regions due to rapid NIS introductions (Katsaros et al. 2022). These species arrive through shipping, aquaculture, escapes from captivity, or natural dispersal via currents (Zenetos et al. 2010; Katsanevakis et al. 2014a). Climate warming further accelerates these processes by facilitating the northward expansion of tropical species (Bianchi 2007; Zenetos et al. 2022). Indeed, the rate of alien species spread now exceeds the pace of temperature increase itself, posing a stark warning for the region's future (Nykjaer, 2009; Raitsos et al. 2010). More than 500 alien macrophytes, invertebrates, and fishes have been documented across Mediterranean coastal habitats (Galil 2008).

Comprehensive inventories show nearly 1000 alien species reported for the Mediterranean, of which approximately 745 are considered valid (Zenetos et al. 2005). Numerous studies have examined the ecological impacts of Lessepsian migrants entering through the Suez Canal (Por 1978; Galil 2000, 2006; Goren & Galil 2005). The Mediterranean has therefore become a global laboratory for studying invasion processes and their ecological implications (Zenetos et al. 2022; Wilcox et al. 2024). Currently, more than 1000 NIS are established in the basin (Galanidi et al. 2023). Introduction patterns vary spatially: approximately 80% of non-indigenous crustaceans in the eastern Mediterranean originate from the Indo-Pacific and arrive via the Suez Canal; while shipping and aquaculture dominate introductions in the western Mediterranean (Zenetos et al. 2010, 2012). Because of its central role as both a filter and a corridor for Lessepsian species, the Suez Canal remains one of the most influential pathways shaping regional biodiversity (Molnar et al. 2008; Essl et al. 2018).

The Aegean Sea, part of the Mediterranean system, is its largest and shallowest subdivision and is connected with surrounding seas and oceans via straits and canals (Coll et al. 2010; Zenetos et al. 2025). Given intensive maritime traffic, warming trends, and the basin's diverse physicochemical conditions, the Aegean is vulnerable to NIS introductions from multiple sources (Katsanevakis et al. 2014a; Ragkousis et al. 2023). Although the highest alien species richness occurs in the southern Aegean (Ragkousis et al. 2023), numerous records have been documented in the north as well. By 2020, 212 NIS had been recorded in Greek Aegean waters—92 in the north and 196 in the south (Zenetos et al. 2020). Historically, the northern Aegean has been considered a biodiversity hotspot due to its high number of endangered species (Coll et al. 2010). Recent assessments report 324 alien species in the Aegean Sea, with Mollusca, fishes, polychaetes, and crustaceans representing the most diverse groups (Zenetos et al. 2025). Peaks in introductions occurred in 2000–2005 and again in 2012–2017, followed by a decline in recent years. Along the Turkish Aegean coast alone, 98 alien species have been documented (Çınar et al. 2005).

Recent SCUBA-based surveys in Greek waters indicate that NIS establishment is most pronounced in the southern and eastern Aegean (Zenetos et al. 2017b; Kampouris et al. 2023). Because many alien species are tropical and most abundant during summer, a comprehensive survey was conducted along the entire Turkish Aegean coastline—from Datça (Muğla) to Enez (Edirne)—in summer 2024. The aim of the present study is to provide updated, quantitative information on both established and newly detected alien species in the region and to contribute to ongoing efforts to refine the regional alien species inventory.

Material and Methods

This study combines SCUBA-based surveys, acoustic mapping, in-situ measurements of physical and optical water properties, and statistical analyses to assess the presence of non-indigenous species (NIS) and their relationship with habitat and environmental conditions along the Aegean coast of Türkiye.

Sampling

SCUBA surveys

Between June and August 2024, a total of 321 SCUBA dives were conducted along shallow coastal zones (5–30 m, occasionally to 40 m) of the Turkish Aegean Sea (Fig. 1). Two buddy divers performed all surveys. Standard dive depths were 5, 10, 15, 20, 25, and 30 m. At deeper sites (40–50 m), a van Veen grab was used where diving was not feasible.

During each dive, macroflora and macrofauna associated with *Posidonia oceanica* (Linnaeus) Delile, 1813 meadows were recorded on underwater plates. Selected immobile or doubtful specimens were collected and brought aboard R/V *Akdeniz Su* for identification. At each station, the bottom depth and station code were documented.

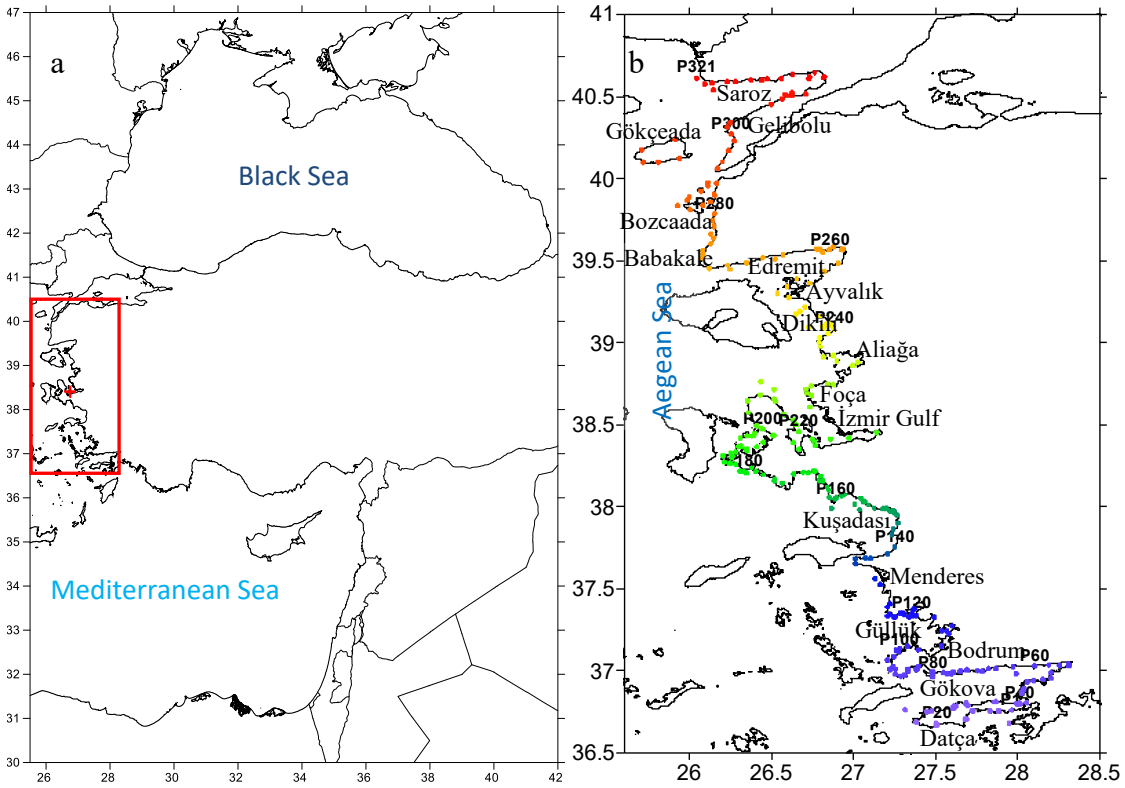


Fig. 1. Study area in red rectangular (a), and SCUBA sampling stations colored with geographical latitude (b)

Acoustic data

Acoustic surveys were performed using a BioSonics DT-X scientific echosounder (206 kHz split-beam), integrated with a differential GPS (GARMIN). The cruise progressed from south to north over three months (June–August 2024) (Fig. 1; tracklines in Fig. 4). Acoustic transects were spaced 100–500 m apart and covered depths from approximately 10–70 m, occasionally extending to 200 m for benthic and plankton-related work, or as shallow as 5 m depending on navigational constraints.

Habitat and bottom classification were processed using PosiBiom (Mutlu, 2023) for *Posidonia* mapping (Mutlu, 2025) and Visual Bottom Typer (VBT ver. 1.10, BioSonics Inc.) for substrate characterization. The first and second echoes of the bottom return were analyzed and calibrated following Mutlu et al. (2022c). Substrate categories included rock (1), sand (slime: 2; rough: 3), and mud (slime: 4; rough: 5). Rock and *Posidonia* substrates could not be acoustically separated and were treated collectively as hard bottom.

The materials and methods included the collection of SCUBA-based data, acoustic data, surface and near-bottom physical water data, and statistical analyses to recognize NIS and NIS-habitat-environment relations in the Aegean Sea.

Environmental measurements

At each of the 321 stations, surface and near-bottom (2–3 m above seabed) water samples were collected using a 5 L Nansen bottle (Fig. 1). Temperature, salinity, conductivity, dissolved oxygen, pH, and total suspended matter were measured using a portable multi-parameter probe (HACH HQ40d).

Optical measurements included Secchi disk depth and vertical profiles of photosynthetically active radiation (PAR) down to 50 m (maximum cable length), recorded using a spherical LI-COR sensor (SPQA-4671) coupled to an LI-1400 data logger. PAR values were converted to mol photons·cm^{-2}·s^{-1}, and the light reaching the seafloor was estimated using depth-attenuation regressions for each station.

Monthly averaged satellite-derived chlorophyll-a (4 × 4 km resolution) for June–August 2024 was provided by Mutlu (2025).

Data analysis

SCUBA and species data

Specimens collected from 0.4 × 0.4 m quadrats and all visual sightings were examined for NIS, and species identifications were verified on board. Presence–absence data were recorded along with depth and station location. Bottom depths obtained acoustically were rounded to the nearest sampling depth for analysis. A histogram of depth distribution across all stations is shown on Fig. 2.

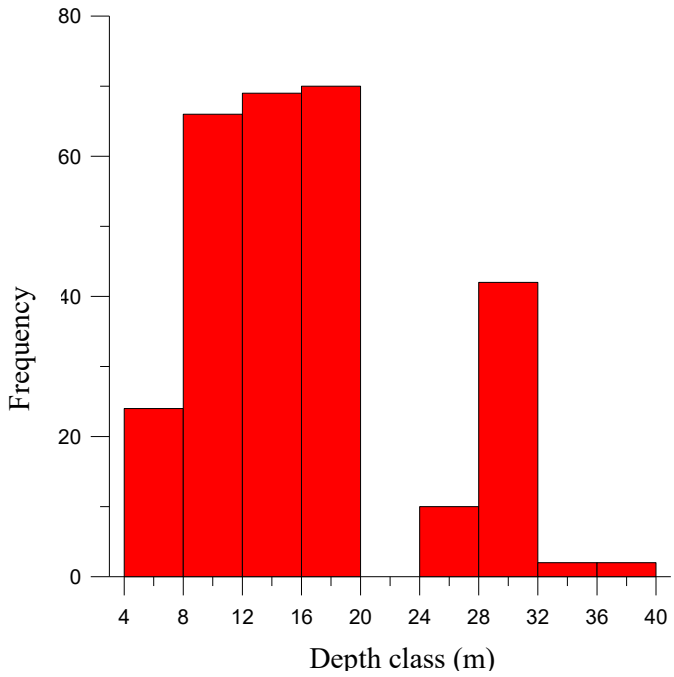


Fig. 2. Frequency-histogram distributions of bottom depth classes of SCUBA sampling stations in the Aegean coast study.

Habitat and environmental mapping

Environmental variables (temperature, salinity, conductivity, dissolved oxygen, pH, and suspended matter) were interpolated using kriging in Surfer 12, based on variogram-optimized models. Water density (σt) was calculated using the formula of Fofonoff and Millard (1983) and used to construct T–S diagrams for water mass identification. Optical parameters (PAR, Secchi depth) and chlorophyll data were processed as described above. Previously

published environmental maps (Mutlu, 2025) are included to support interpretation of NIS–environment relationships.

Statistical analysis

Presence–absence data for NIS and associated environmental variables were analyzed using univariate and multivariate statistical approaches.

Soyer Index (Soyer, 1970) was applied to classify species as constant (DO% ≥ 50), common (25–49%), or rare (DO% < 25). Bray–Curtis similarity based on presence–absence data was used for all multivariate analyses. Non-metric multidimensional scaling (nMDS)** was performed to visualize assemblage patterns. PERMANOVA (one-way: region or water mass; two-way: region × depth) tested differences in NIS composition. SIMPER identified species contributing most to regional similarities and differences. Canonical Correspondence Analysis (CCA) was selected because gradient length exceeded 3, indicating unimodal response patterns. Monte Carlo permutation tests (CANOCO 4.5) evaluated the significance of relationships between NIS assemblages and environmental parameters.

Software used included PRIMER 6 with PERMANOVA+, CANOCO 4.5, and Surfer 12.

Results and Discussion

The comprehensive re-evaluation of established alien species in the Mediterranean by taxonomic specialists led to substantial changes in the list previously compiled by Galil et al. (2016). In total, 73 species were removed—35 reclassified as non-established and 37 deemed not truly alien—while 72 new species were added. As a result, the number of confirmed established alien species in the Mediterranean reached 613 by 2016, representing a 28% rise compared to the previous four years. When casual occurrences are included (208 species), the overall alien fauna in the basin increases to 821 species (Zenetos et al.2017a).

Study Area Environment

The study region includes several national parks and marine protected areas (MPAs). Casual alien species were present only in minimal proportions within these MPAs, indicating that most alien taxa were already well established, with a considerable share recognized as invasive (e.g., Datça–Bozburun, Gökova, Ildır–Karaburun, Foça, Ayvalık, Gökçeada, Saroz) (Bilecenoğlu & Çınar et al.2021). The broader area also includes aquaculture facilities, major metropolitan centers such as İzmir, densely populated summer tourism zones around the İzmir Peninsula, recreational boating and bathing sites, petroleum refineries (e.g., Aliağa), and busy commercial ports (İzmir) (Mutlu, 2025) (Figs. 1b, 3, 4). Recreational pressures intensified notably during summer (June–September). The İzmir Peninsula and Gulf represent one of the most anthropogenically affected coastal sectors (Yelekci et al.2021; Mutlu & Akçalı, 2022). In the last two years, the Gulf experienced severe red-tide events (Fig. 5), leading to mass fish mortality in September (Mutlu, 2025).

Bottom Habitats

The seafloor environment consisted of *Posidonia oceanica* meadows (Fig. 3) and a mosaic of sediment types—including rock, sand, and mud fractions—characterized acoustically for the first time in this region (Mutlu et al.2022c; Yalçın et al.2023) (Fig. 4).

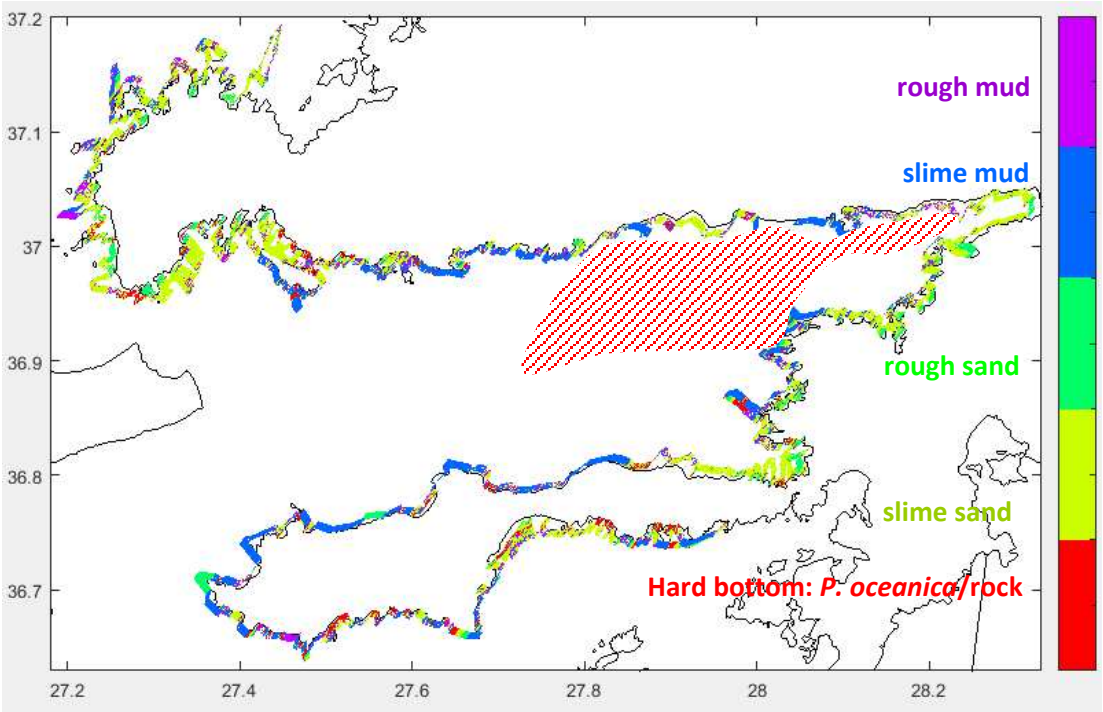
Seagrass coverage is shown in Figure 3. On the southern Aegean coast, *Posidonia* occurred mainly as small, discontinuous patches, whereas in the northern sector it formed larger, more continuous meadows. Areas hosting

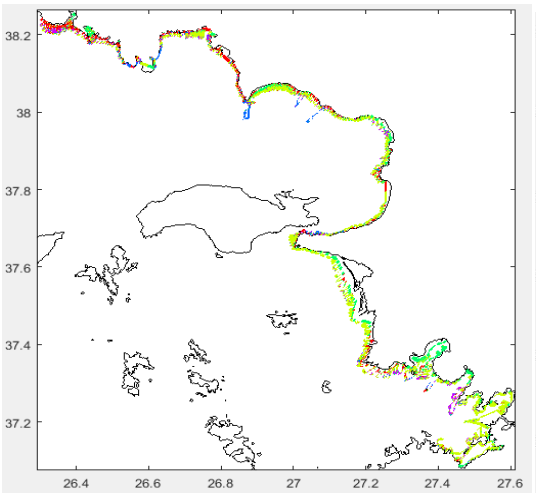
marine fish farms were largely devoid of seagrass. The prevalence of small-fragmented beds in the south contrasted with extensive northern meadows in Dikili, Ayvalık, Bozcaada, Gökçeada, and Enez Bays. Several sites showed evidence of habitat degradation due to anchoring, trawling, aquaculture structures, and pollution (Fig. 3).

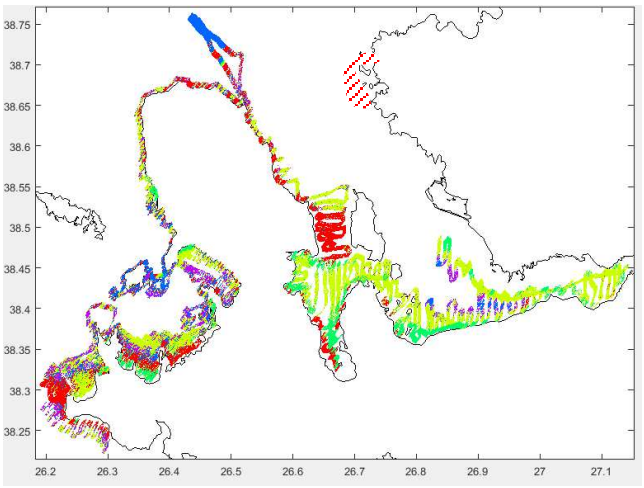
Fig. 3. *Posidonia oceanica* distribution along the Turkish Aegean coast (from Mutlu 2025) and arrival date for the region during the cruise by R/V Akdeniz Su. Circle denotes present location of fish farms and cages, derived from the google map.

Acoustic seabed classification identified two main categories: hard substrates (including seagrass stands and rocky bottoms) and soft substrates (sand and mud). Sediments were further differentiated based on grain size composition, where “slime mud” contained >70% mud and “rough sand” had >70% sand (Mutlu et al.2022c) (Fig. 4).

In most areas, hard bottoms overlapped with *P. oceanica* meadows (Figs. 3, 4). Seagrass also occurred on some soft substrates, especially in the northern section of the study area. Aside from isolated hard-bottom zones, sediment texture generally transitioned from coarse to finer materials with increasing depth, with slime mud dominating the deeper parts of the shelf.







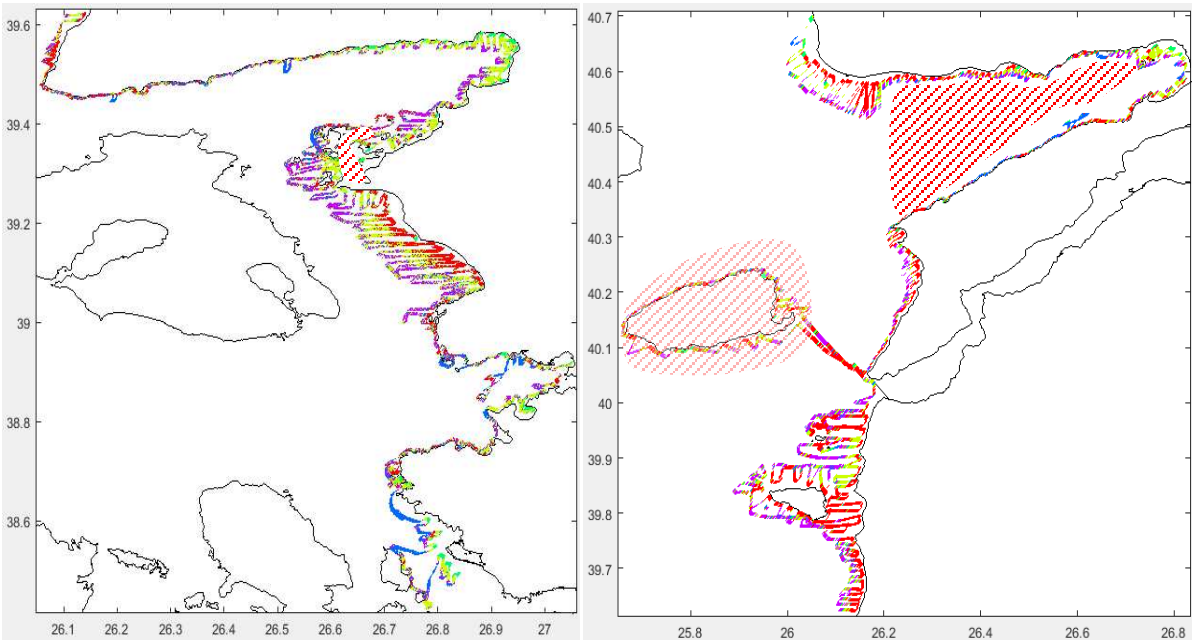


Fig. 4. Regional bottom type distribution classified by VBT along the acoustical tracklines of the Turkish Aegean Sea, in the order of south to north of the study area. Red dashed area shows marine protected area (MPA).

Water Physics

Sea surface temperatures ranged from 20.5 to 28.5 °C, while near-bottom waters varied between 18 and 28 °C (Fig. 5a). Both layers reached their highest temperatures in the Gulf of İzmir. Surface salinity values spanned 30.5–38 PSU, compared with 33–37.5 PSU near the seabed (Fig. 5b). Surface and bottom pH measurements showed similar ranges across stations (Fig. 5c). A general south-to-north decline in salinity was evident, particularly in bottom waters. In contrast, dissolved oxygen and pH increased slightly toward the north, opposite to the pattern observed for total suspended solids (Fig. 5d, e). The Gulf of İzmir displayed the highest pH, lowest oxygen concentrations, and moderate levels of suspended matter in bottom waters.

Cold, low-salinity water entering the Aegean through the Dardanelles—originating from the Black Sea—was detectable near the strait outflow. Farther north, however, surface waters were comparatively warmer. In the northernmost region, the influence of the Meriç River further reduced salinity.

Temperature–salinity (T–S) analyses identified four water masses arranged from south to north (Fig. 5f). This structure was especially clear in near-bottom waters. At the southern stations, warm and saline Mediterranean waters predominated. These transitioned northward into South Aegean waters, characterized by slightly lower salinity and a broader temperature range. Further north, salinity decreased again while temperatures remained relatively comparable. At the northern boundary of the study area, Black Sea inflow contributed to the coldest and least saline bottom waters, while surface waters there were comparatively warm (Fig. 5f).

Because sampling progressed from south in June to north in August (Fig. 1), an overall increase in water temperature from early to late summer was expected and is reflected in the observed south–north thermal structure.

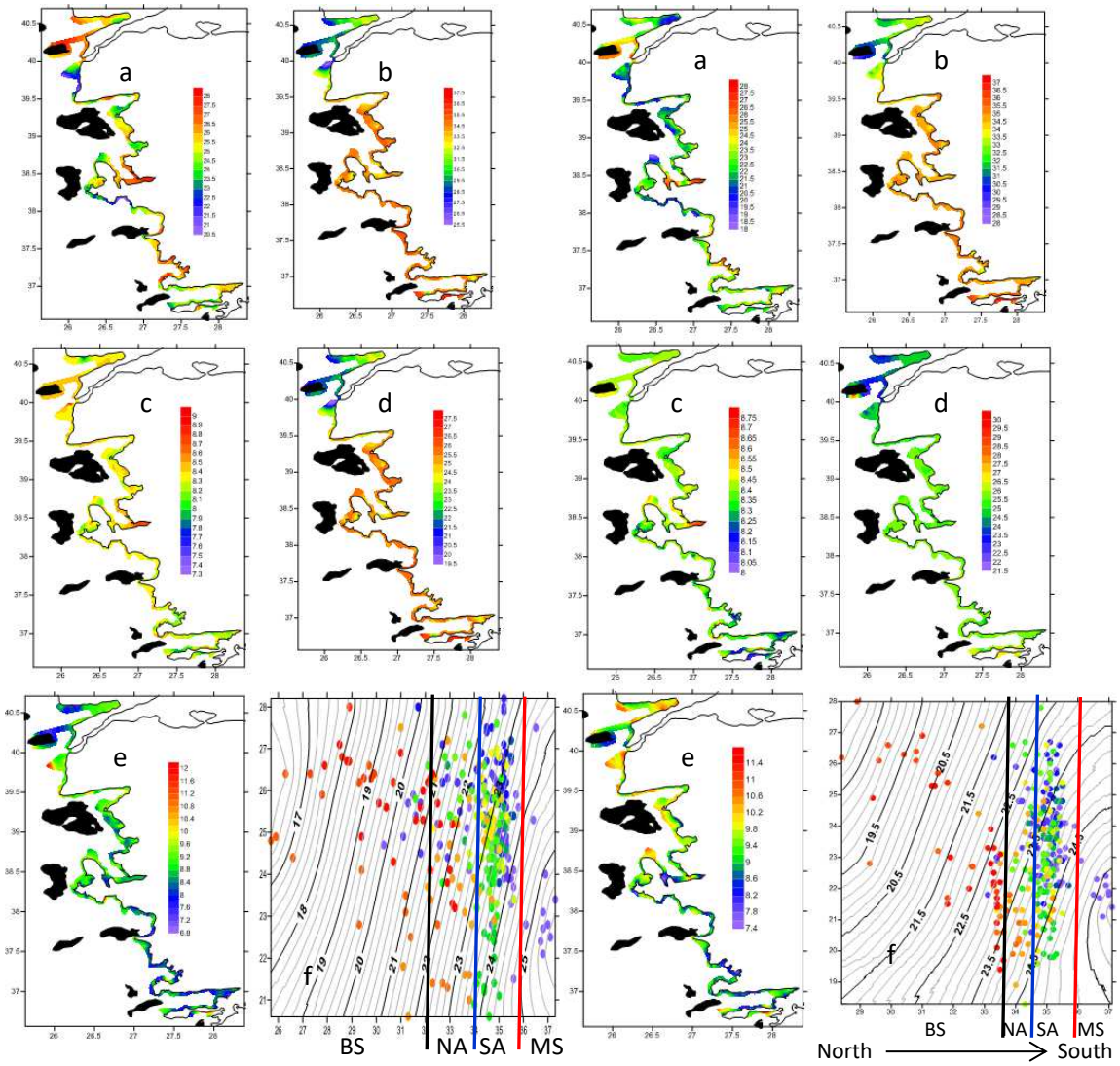


Fig. 5. Sea surface (left panel) and near-bottom (right panel) water temperature in ºC (a), salinity in ppt (b), pH (c), dissolved oxygen in mg/l (d), total suspended matter in mg/l (e) and T-S diagram with isoclines of density, σ_t at the stations colored with geographical latitudes (Water masses: BS: Black Sea, NA: Northern Aegean, SN: Southern Aegean, and MS: Mediterranean Sea) (f) (see Fig. 1 for the station locations) (modified from Mutlu, 2025).

Optics: Secchi Disk Depth and PAR

The greatest Secchi disk depth, 31.5 m, was measured off the Gelibolu Peninsula. Overall, water transparency increased with distance from the coast toward offshore waters. In contrast, notably reduced Secchi depths occurred in areas influenced by fish farming activities (Fig. 6a) and in regions affected by Black Sea inflow, where turbidity was higher. The shallowest Secchi depths were observed at station P93 (3 m) and at station P219 (4 m) (Figs. 1, 6a).

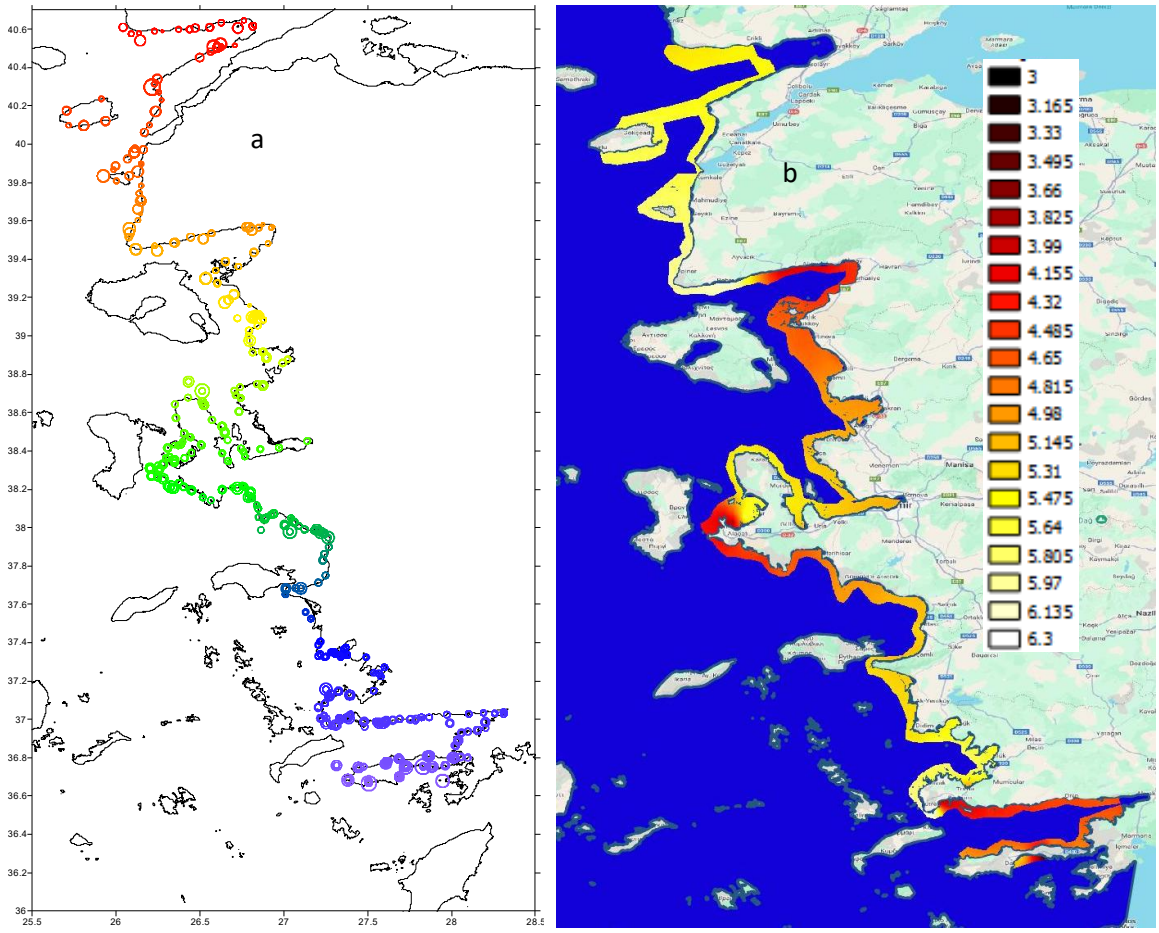


Fig. 6. Secchi disk depth (a) distribution measured in the Aegean Sea study (maximum circle corresponds proportionally to 31.5 m) and the density of the PAR (b) value reaching the bottom measured in the Aegean Sea study (mol photon/cm^2/s) (from Mutlu, 2025).

Because PAR measurements were taken at different times of day and under varying weather conditions, some natural variability is expected; therefore, percent-based comparisons provide a more reliable interpretation of bottom-reaching light. According to the analysis (Fig. 6b), bottom PAR values ranged from 3.243 to 6.261 mol photons cm^{-2} s^{-1} (equivalent to 324.3–626.1 µmol photons m^{-2} s^{-1}). In several regions—Datça, Gökova, the southern İzmir Peninsula, and Edremit Bay including its southern section—bottom irradiance generally fell between 3 and 4 mol photons cm^{-2} s^{-1}. The highest bottom PAR values occurred in the northernmost part of the study area, with Babakale (Edremit) and the cape of the Bodrum Peninsula standing out as the locations receiving the greatest light intensity (Figs. 1, 6b).

Water Chemistry

Chlorophyll (Chl) concentrations generally increased from June to August throughout the coastal zone of the study area. Several locations consistently exhibited elevated Chl levels, most notably the İzmir Gulf—heavily influenced by the metropolitan area—and regions hosting marine fish farms (Figs. 1, 7). These hotspots became increasingly pronounced over time, with the highest values recorded in August. In contrast, Datça and Gökova gulfs showed the lowest Chl concentrations, similar to the typically oligotrophic Turkish Mediterranean coast.

In June, waters adjacent to the Dardanelles Strait displayed moderate Chl levels, reflecting the influence of Black Sea outflow entering the Aegean through the Sea of Marmara. As the season progressed, areas that were persistently high in Chl expanded locally. For example, the İzmir Gulf was entirely covered by very high Chl concentrations in August, during a prolonged brown–reddish discoloration event that coincided with mass fish mortality. Likewise, Chl levels around fish farm zones peaked sharply in August.

These conditions likely promoted intense zooplankton production, as the Aegean Sea—typically cooler than the eastern Mediterranean—is experiencing progressively warmer summers. Elevated zooplankton biomass would, in turn, attract small pelagic fish and contribute to the formation of dense fish school aggregations.

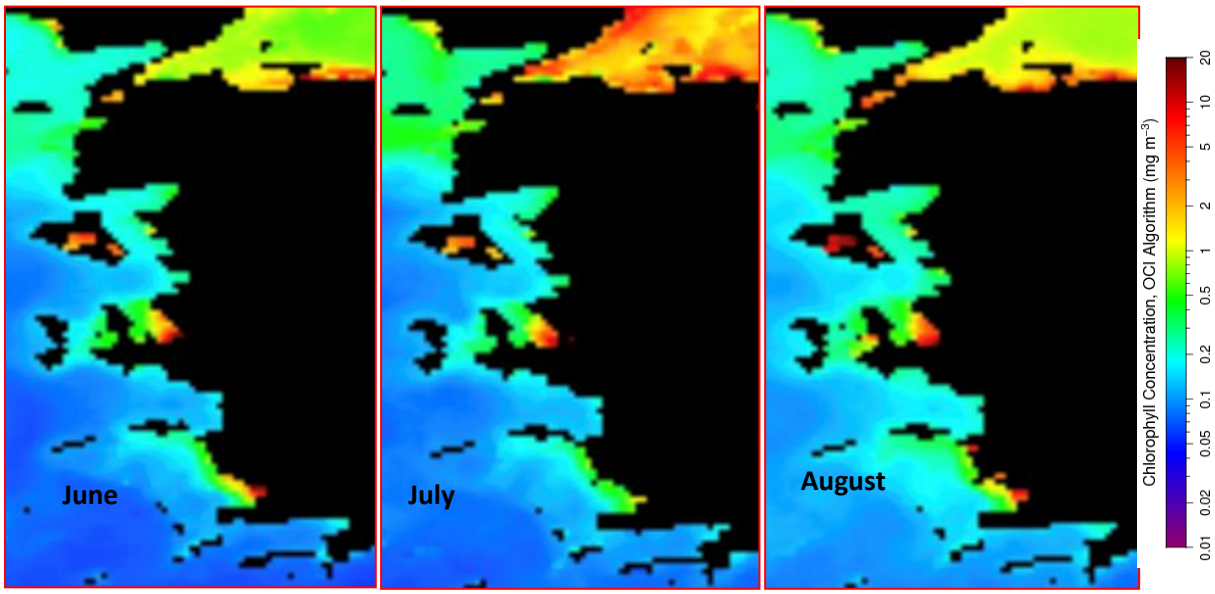


Fig. 7. Monthly averaged surface chlorophyll distribution in a resolution of 4 x 4 km for June, July and August 2024 along the coast of the study area (from Mutlu, 2025).

Alien Species

There is broad global agreement that preventing the arrival and secondary spread of marine alien species requires comprehensive, pathway-based management strategies (Ojaveer et al.2018). Non-indigenous species (NIS) remain a central concern for numerous international and European legislative frameworks (Boon et al.2020). Their distribution varies notably across Mediterranean regions: current records list seven NIS in the Adriatic Sea, 78 in the Ionian, 92 in the North Aegean, 113 in the Levantine Basin, and 196 in the South Aegean. Importantly, transport- and stowaway-related introductions have shown a clear upward trajectory in the Levantine and South Aegean, whereas no comparable increase has been reported for the Ionian or North Aegean sectors (Zenetos et al.2020).

During the present SCUBA surveys, 19 alien species representing six taxonomic groups were recorded (Table 1). These species occurred at 60 sampling stations, with seaweeds and fishes being the most species-rich groups (seven species each). Echinoderms were represented by two species, while the remaining taxa comprised a single species each (Table 1). Across the Mediterranean, a total of 986 alien species has been catalogued, with 775 of them documented in the eastern basin (Zenetos et al.2012). The South Aegean and the Hellenic Levantine Seas remain the most affected subregions, hosting 106 and 84 Lessepsian species respectively, while the North Aegean and Ionian Seas harbour over 40 species each (Zenetos et al.2020).

The influx of non-indigenous organisms has accelerated in recent decades, generating substantial ecological, socioeconomic, and cultural consequences (Zenetos & Galanidi, 2020; Zenetos et al.2012). Recent surveys from the North Aegean reported several newly detected species— *Acanthophora nayadiformis* (Delile) Papenfuss, 1968, *Asparagopsis taxiformis* (Delile) Trevisan de Saint-Léon, 1845, *Caulerpa cylindracea* Sonder, 1845 and *Codium fragile* subsp. *fragile* (Suringar) Hariot, 1889) —despite this region being one of the least impacted areas in the eastern Mediterranean (Katsanevakis et al.2020a; Katsaros et al.2022).

Based on the Soyer constancy index (Soyer, 1970), none of the recorded species exhibited high constancy at the regional scale (DO1% < 25). Among the 60 sites investigated, *Caulerpa cylindracea* was the most prevalent taxon, occurring at 55% of stations and classified as a constant species. *Caulerpa taxifolia* followed, whereas all remaining species were categorized as rare (DO2% < 25). Three species—*Caulerpa taxifolia* var. *distichophylla*, *Caulerpa mexicana* Sonder ex Kützing, 1849, and *Caulerpa taxifolia* (M. Vahl) C. Agardh, 1817 —were reported for the Aegean Sea for the first time in earlier studies (Mutlu et al.2025b, c, d), although their spatial distributions were not previously mapped. *Udotea flabellum* (J. Ellis & Solander) M. Howe, 1904, earlier observed along the Turkish Aegean coast (Fortić et al.2023), is confirmed here again, supporting its ongoing establishment in the region.

Research from other Mediterranean subregions has highlighted similar ecological shifts. For instance, the CIMPAL modelling framework (Cumulative IMPacts of invasive Alien species) has been applied to assess alien species impacts in Maltese waters (Bartolo et al.2021). Studies from the Adriatic Sea documented changes in sediment biogeochemistry beneath *Caulerpa racemosa* var. *cylindracea* canopies—such as elevated surface organic carbon, nitrogen, and phosphorus (Matijević et al.2013)—and reported its lack of sexual reproduction (Žuljević et al.2012) as well as its influence on native sponge communities (Žuljević et al.2011). Additional work has detailed the distribution of the invasive red alga *Womersleyella setacea* (Hollenberg) R.E. Norris, 1992 in the Adriatic (Nikolić et al.2010).

Table 1. Percent dominance of the species in a total number of 321 stations (DO1%), and in number of stations where the alien species occurred. Abb. Species abbreviation used in CCA analysis. Taxa; F: fish, C: Cnidaria, E: Echinodermata, M: Mollusca, S: seagrass, and W: seaweeds.

Taxa	Species	Abb.	DO1%	DO2%	Depth (m)
Fauna					
F	*Pterois miles*	Pvol	1.50	8.33	15-30
F	*Sargocentron rubrum*	Srub	0.30	1.67	15
F	*Lagocephalus sceleratus*	Lsce	0.30	1.67	20
F	*Torquigener flavimaculosus*	Tfla	1.80	10.00	5-30
F	*Apogonichthyoides pharaonis*	Aimp	1.50	8.33	10-30
F	*Siganus rivulatus*	Sriv	0.30	1.67	30
F	*Nemipterus randalli*	Nran	0.30	1.67	15
C	*Rhizostoma pulmo*	Rpul	0.30	1.67	0, 20
E	*Synaptula reciprocans*	Srec	1.80	10.00	5-20
E	*Diadema setosum*	Dset	2.10	11.67	5-30
M	*Pinctata radiata*	Prad	0.30	1.67	10
Flora					
S	*Halophila stipulacea*	Hsti	0.90	5.00	5-20
W	*Caulerpa taxifolia* var. *distichophylla*	Ctvd	0.90	5.00	15-20
W	*Caulerpa cylindracea*	Ccyl	9.88	55.00	5-40
W	*Caulerpa mexicana*	Cmex	0.30	1.67	15

W	*Caulerpa taxifolia*	Ctax	2.40	13.33	15-50
W	*Penicillus capitatus*	Pcap	0.60	3.33	20
W	*Stypopodium schimperi*	Ssch	1.80	10.00	10-25
W	*Udotea flabellum*	Ufla	0.30	1.67	5

Spatial Distribution Patterns

Spatial patterning differed among taxa. Alien fishes and echinoderms were predominantly recorded along the southern Turkish Aegean coast, although *Apogonichthyoides pharaonis* (Bellotti, 1874) showed a northward extension. In contrast, seaweeds were more common along the northern coast, despite also being present in the south. The invasive green alga *Caulerpa cylindracea* was widespread and detected along all northern coastal stations.

Fauna

Fish

Water-column characteristics relevant to alien species distributions are discussed in the ecological section of this study.

Most of the alien fish—particularly the rare species *Lagocephalus sceleratus* (Gmelin, 1789), *Siganus rivulatus* Forsskål & Niebuhr, 1775, *Sargocentron rubrum* (Forsskål, 1775), and *Nemipterus randalli* Russell, 1986—were found near the southern margin of the study area around Gökova Gulf, a designated MPA (Table 1, Fig. 8). Adults of *L. sceleratus* commonly occupy *Posidonia oceanica* meadows, as documented in Saros Gulf (Katsanevakis et al.2014c), whereas juveniles typically settle on sandy bottoms across the Mediterranean (Kalogirou et al.2012). The species' rapid colonization ability has been linked to significant negative effects on local fish and squid populations (Kalogirou, 2013). Its westward expansion has also been confirmed in the Northern Ionian Sea (Ragkousis et al.2020).

In the southeastern Aegean, populations of *S. luridus, S. rivulatus*, and *S. rubrum* have expanded around Karpathos and Chalki Islands (Thessalou-Legaki et al.2012). Rabbitfishes are known to restructure food webs by accelerating algal turnover and serving as abundant prey for coastal predators such as groupers (Goren & Galil, 2005).

Within the present survey, the most frequently observed alien fishes were *Pterois miles* and *Apogonichthyoides pharaonis*, followed by *Torquigener flavimaculosus* Hardy & Randall, 1983 (Fig. 8). A northward expansion of *T. flavimaculosus* has been reported along the southeastern Turkish Aegean coast, and *L. sceleratus* has similarly been recorded around Zakynthos Island in the Ionian Sea (Tsiamis et al.2015).

Alien fish occupied depths between 5 and 30 m (Table 1, Fig. 8). *T. flavimaculosus* was found as shallow as 5 m, whereas *Pterois miles* (Bennett, 1828) was recorded mainly between 15 and 30 m and A. pharaonis between 10 and 30 m. Most pufferfish were found deeper than 5 m, with one exception.

In the present study, *P. miles* was among the taxa with DO_2 >10%. Its presence was primarily associated with small patches of seagrass meadows and rocky substrates, occurring exclusively along the southern Aegean coast—similar to its pattern in the Alboran Sea (Fortič et al.2023). The species was typically recorded in areas with relatively low PAR, but its distribution showed no clear relationship with chlorophyll concentrations (Figs. 3–4, 6–8). Its westward spread in the Mediterranean is believed to occur through natural dispersal processes, consistent with recent assessments of its thermal niche (Dimitriadis et al.2020). Reports compiled from citizen observations in the Aegean Sea (Giovos et al.2018) also support its presence within the depth range surveyed here. *Pterois miles*

is a tropical scorpaenid originating from the Indian Ocean and the Red Sea (Langeneck et al.2023). Although closely related to *Pterois volitans* (Linnaeus, 1758), the two species can be distinguished through genetic markers and specific meristic characters (Wilcox et al.2017). Both are considered among the most successful invasive marine fishes worldwide, exerting strong pressures on native biodiversity wherever they establish (Ulman et al.2022).

Apogonichthyoides pharaonis displayed a different spatial pattern. The species was concentrated around the İzmir Peninsula, likely influenced by prevailing surface currents and the presence of fish-farming facilities. It occurred on rocky bottoms with or without seagrass and was associated with moderate PAR and chlorophyll levels (Figs. 3–4, 6–7).

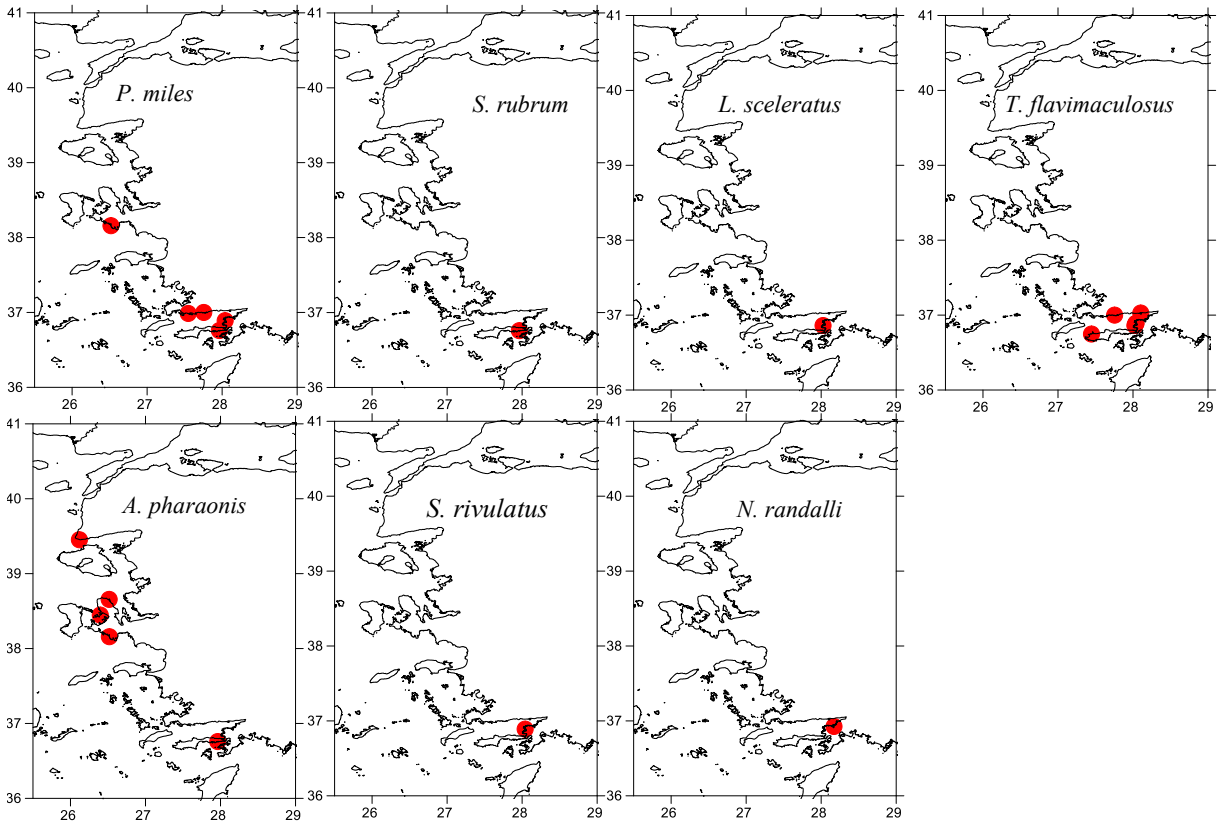


Fig. 8. Spatial distribution for the occurrence of alien fish species.

Cnidaria

A single scyphozoan cnidarian, *Rhizostoma pulmo* (Macri, 1778), was incidentally observed at the surface in front of the Gediz River outflow in the Gulf of Izmir, where an intense red-tide event and pronounced eutrophic conditions were present (Fig. 9). In the Mediterranean, cnidarians include 53 non-indigenous species, ranking seventh among NIS groups and reflecting an increase of seven species (13.2%) compared with the earlier inventory of Zenetos et al. (2010) (Zenetos et al.2012). The western Aegean, along with several islands in the Cyclades, is among the regions most affected by jellyfish proliferations. Recent assessments identified *R. pulmo*—notably due to its capacity to transport bacterial pathogens capable of infecting marine organisms and humans (Stabili et al.2020)—as one of the most impactful species. Other species highlighted for their ecological and socio-economic relevance include *Pelagia noctiluca* (Forsskål, 1775), *Cotylorhiza tuberculata* (Macri, 1778), and *Aurelia aurita* (Linnaeus, 1758) (Chiappi et al.2025).

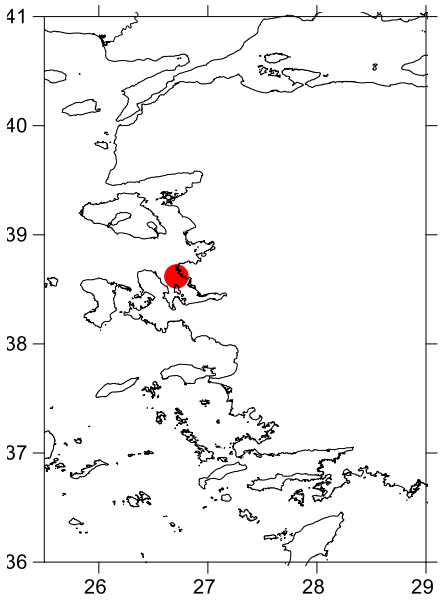


Fig. 9. Spatial distribution for the occurrence of alien cnidarian species *Rhizostoma pulmo.*

Echinodermata

Two echinoderm species were documented: the holothuroid *Synaptula reciprocans* (Forsskål, 1775) and the echinoid *Diadema setosum* (Leske, 1778). Both were recorded at depths of 5–30 m (Table 1), with their distribution confined to the area between Datça and Izmir along the southern Aegean coast (Fig. 10). *D. setosum* was first reported in the Mediterranean in 2006 near the Kaş Peninsula on the southwestern coast of Türkiye (Yokes & Galil, 2006). No further individuals were observed there between 2007 and 2009 (Yokes & Galil, 2006), but subsequent records appeared in Gökova Bay (Katsanevakis et al.2014c; Tsiamis et al.2015).

The two species shared a core distributional area in Gökova Gulf, a marine protected area where extensive proliferation of several non-indigenous species has been noted, including the Indian Ocean seagrass *Halophila stipulacea*, the strombid gastropod *Conomurex persicus*, the Indo-Pacific holothuroid *Synaptula reciprocans*, and the rabbitfishes *Siganus rivulatus* and *S. luridus* (Galil, 2017). Neither echinoderm was detected between the İzmir Peninsula and Gökova. Since its initial detection in Gökova, *D. setosum* has been considered likely to spread further in the Aegean Sea, which is strongly influenced by Lessepsian migration, human-mediated introductions, regional circulation, and ongoing sea warming (Katsanevakis et al.2014c). In the present study, both species (especially *D. setosum*) were observed in association with small seagrass patches and rocky substrates, while no clear relationship was detected with chlorophyll or PAR levels. The first Greek record of *D. setosum* was reported by Tsiamis et al. (2015), adding a new alien echinoderm to Hellenic waters following the earlier documentation of *Synaptula reciprocans* (Zenetos et al.2011). More recently, *D. setosum* has expanded westward into the Ionian Sea (Ragkousis et al.2020).

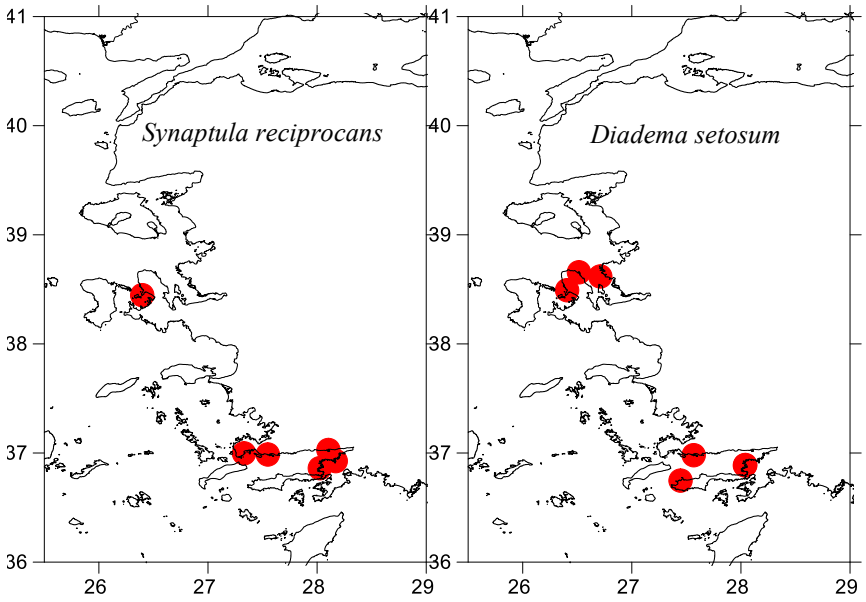


Fig. 10. Spatial distribution for the occurrence of alien echinoderm species

Mollusca

This taxonomic group played only a minor role in the present survey. The bivalve *Pinctada radiata* (Leach, 1814) was detected incidentally, as its larvae had settled on the housing of the acoustic transducer during a 12-day stay in İzmir Harbor. The transducer was cleaned upon retrieval, allowing the specimens to be examined. Given the locations where the species is typically recorded—such as areas near mussel farms, artificial structures including pontoons, marinas, and sheltered bays—aquaculture activities and maritime traffic appear to be the most plausible combined vectors facilitating its introduction to the region (Gozlan et al.2024; Haubrock et al.2025). Citizen-science data further indicate that the most frequently reported molluscs are *Conomurex persicus* (Swainson, 1821) and *Pinctada imbricata radiata*, with 27 and 25 records respectively from Greek waters (Crocetta et al.2017). Among alien molluscs in the Aegean Sea, *P. radiata* shows the widest spatial distribution (Chiappi et al.2025).

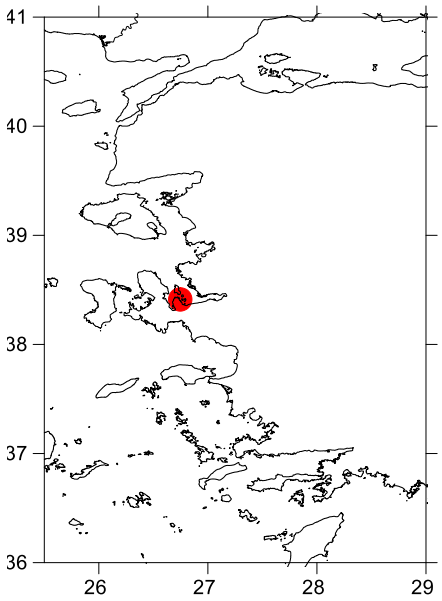


Fig. 11. Spatial distribution for the occurrence of alien molluscan species, *Pinctata radiata*.

Flora

Non-indigenous macrophytes represent a distinct category of human-driven ecological pressure (Coll et al.2012). Over the past two centuries, biodiversity in the Mediterranean Sea has undergone rapid and substantial change, shaped by a combination of historical contingency and contemporary environmental forces. Following the Messinian salinity crisis, most tropical taxa failed to recolonize the Eastern Mediterranean, creating ecological vacancies that later enabled both diversification and biological invasions. In more recent times, multiple anthropogenic stressors—including coastal development, habitat alteration, and pollution—have further reshaped Mediterranean biota, promoted species turnover and facilitated the establishment of newcomers (Orfanidis et al.2021).

Macrophytes, in particular, can profoundly influence ecosystem dynamics by dominating available space and functioning as habitat-forming engineers (Thresher, 2000). Notable invasive examples include *Stypopodium schimperi* (Kützing) Verlaque & Boudouresque, 1991, *Caulerpa taxifolia*, and *C. racemosa* (Bianchi, 2007; Zenetos et al.2012).

Seagrass

A single non-native seagrass, *Halophila stipulacea* (Forsskål) Ascherson, 1867, was recorded exclusively in Gökova Gulf at depths of 5–20 m, with a DO_2% value of 5 (Table 1, Fig. 12). Its occurrences coincided with coarse sandy substrates and small, patchy meadow formations within the gulf (Figs. 3–4, 12). In the southeastern Mediterranean, *H. stipulacea* is considered a recent Lessepsian migrant introduced through the Suez Canal (Sghaier et al.2011). DNA barcoding analyses confirmed that *H. stipulacea* is the only alien seagrass present in the Mediterranean, clarifying that records attributed to *Halophila decipiens* by Gerakaris et al. (2020) were misidentifications (García-Escudero et al.2022). Chemical ecology may contribute to its success of invasion. For example, the establishment of the alien aplysiid *Syphonota geographica* (A. Adams & Reeve, 1850) has been linked to the presence of *H. stipulacea*, suggesting potential facilitative interactions (Mollo et al.2008).

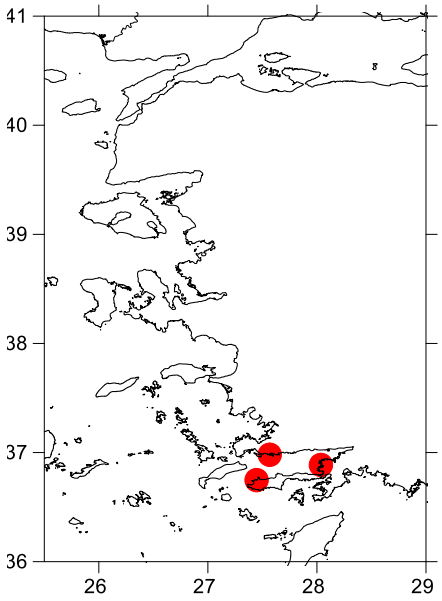


Fig. 12. Spatial distribution for the occurrence of alien seagrass species, *Halophila stipulacea.*

Seaweeds

Eight alien seaweeds were identified in the study area, three of which showed dominance values of $DO_2\% \geq 10\%$: *Caulerpa cylindracea, Caulerpa taxifolia*, and *Stypopodium schimperi* (Kützing) Verlaque & Boudouresque, 1991 (Table 1). Overall, seaweeds occupied a depth range of 5–50 m. In the southeastern Aegean, on Karpathos and Chalki Islands, *Caulerpa racemosa* var. *cylindracea* (accepted name, *Caulerpa cylindracea*) has also been documented (Thessalou-Legaki et al.2012).

The highly invasive form of *C. cylindracea*, native to southwestern Australia, was first detected in the Mediterranean in 1990 and has since expanded from Cyprus to Spain and even to the Canary Islands (Verlaque et al.2003, 2004). In the present study, *C. cylindracea* occurred at only a few sites in the south but was widespread in the northern sector, with increasing abundance toward the north (Fig. 13). This species is capable of dominating even dense, diverse native macroalgal communities (Piazzi et al.2001, 2003). It was typically associated with extensive seagrass meadows, reaching a maximum depth of 41 m, and was recorded across bottoms ranging from 5 to 40 m (Table 1, Figs. 3–4, 13). Its northern distribution also coincided with areas where PAR exceeded 5.5 mol photon/cm²/s (Fig. 5). The proliferation of *C. cylindracea* has been shown to trigger major changes in benthic community structure, including increases in polychaetes, bivalves, and echinoderms, and declines in gastropods and crustaceans. Although total species richness may rise, this is mainly due to increases in polychaete diversity (Galil, 2007).

Caulerpa taxifolia and *C. taxifolia* var. *distichophylla* were recorded expanding northward from the southern Aegean, at depths of 15–50 m and 15–20 m, respectively (Fig. 13). Initial publications (Mutlu et al.2025b, c) did not show full spatial coverage because some samples were analyzed later; the present work now provides both the northernmost and southernmost confirmed occurrences of these taxa in the Aegean Sea. *C. taxifolia* is known to form species-poor assemblages, reducing littoral biodiversity and posing a significant threat to the ecological balance of coastal habitats (Longpierre et al.2005). The variety *C. taxifolia* var. *distichophylla* has been reported from Antalya Bay (Mutlu et al.2022a) and later along the Aegean coast (Mutlu et al.2025b). *C. taxifolia* is also associated with substantial declines (25–55%) in native hard-substrate algal richness and can outcompete *Cymodocea nodosa* (Ucria) Ascherson and *Posidonia oceanica* under certain conditions (Verlaque & Fritayre, 1994; Ville`le & Verlaque, 1995; Ceccherelli & Cinelli, 1999).

Another congeneric species, *Caulerpa mexicana*, was recorded at 10 and 15 m in İzmir Gulf. However, no specimens were confirmed during subsequent laboratory examinations, as reported by Mutlu et al. (2025d), and earlier Mediterranean records remain limited to the easternmost basin.

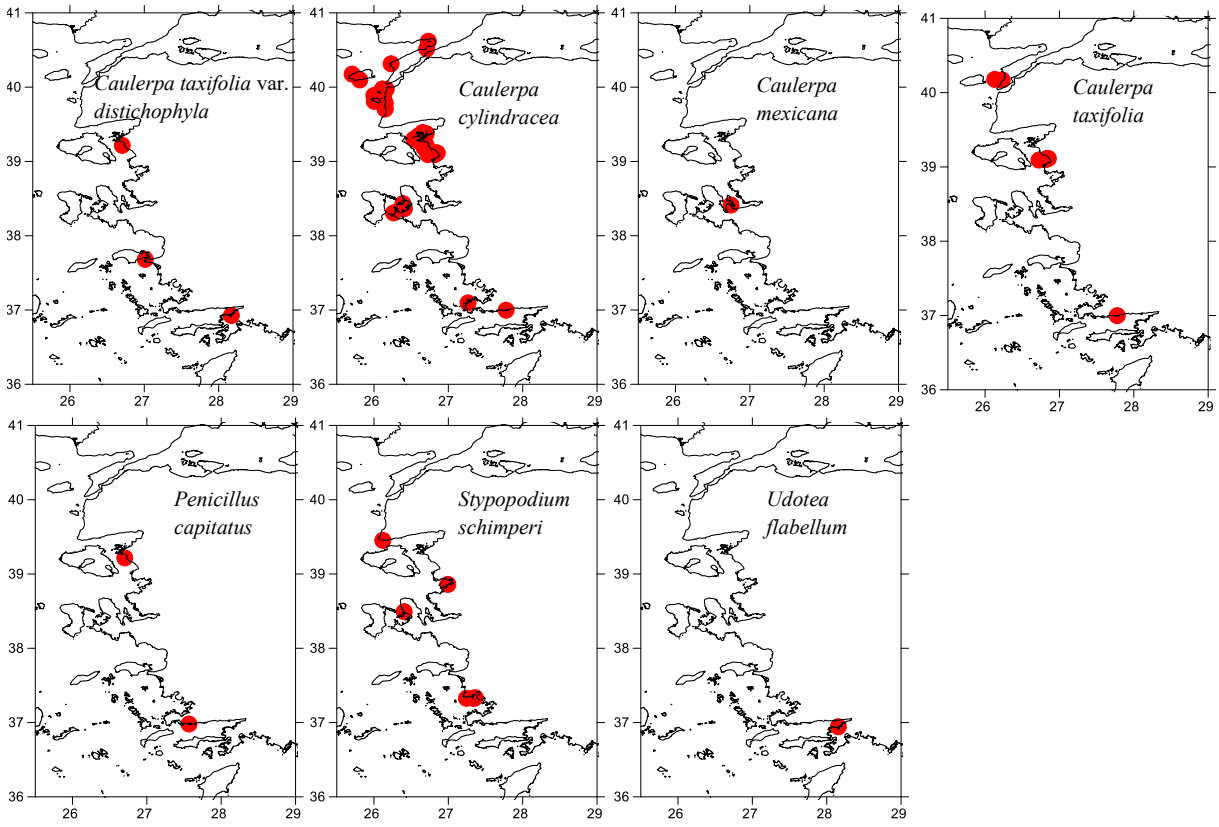


Fig. 13. Spatial distribution for the occurrence of alien seaweeds species.

Stypopodium schimperi was the least dominant of the seven alien seaweeds and was absent from the southernmost part of the study area, outside Gökova Gulf, where the influence of the Mediterranean Sea was strongest (Figs. 5f, 13). The species did not occur at the shallowest or deepest surveyed depths; instead, it was restricted to 10–25 m.

Two additional species, *Penicillus capitatus* Lamarck, 1813 and *Udotea flabellum*, were detected at two and one stations, respectively (Table 1, Fig. 13). *U. flabellum* had been previously reported from Gökova Gulf at 3–11 m, where it exhibited high coverage (70–100%) (Fortić et al.2023).

Çınar et al. (2021) identified six major hot-spot regions for alien species establishment in the Turkish Seas, including the Aegean Sea: İskenderun Bay, Mersin Bay, Antalya Bay, Fethiye Bay, Gökova Bay, and İzmir Bay. These areas are characterized by multiple introduction pathways, such as shipping and the Suez Canal corridor. Several of the species detected in the present study—*Halophila stipulacea, Stypopodium schimperi, Caulerpa cylindracea, Siganus luridus,* and *Pinctada imbricata radiata*—have already been documented in the northern Aegean around Lesvos Island, close to the Turkish coastline (Evagelopoulos et al.2015).

Ecological community of alien species

The alien species assemblage was primarily structured according to regional and water-mass classifications. Some stations overlapped within these classifications, sharing identical species composition with 100% similarity (Figs. 14, A1). Regional separation was statistically significant at $p < 0.05$, and water masses also differed significantly (Table 2). The two-way PerMANOVA confirmed differences among regions ($F = 7.602$, $p = 0.001$; $p(MC) = 0.001$), but no depth-related differences were detected ($F = 0.86516$, $p = 0.656$; $p(MC) = 0.669$) nor an interaction between region and depth ($F = 0.59622$, $p = 0.905$; $p(MC) = 0.912$). Biodiversity tended to be higher in coastal

and shelf environments and decreased with depth. Long-term trends indicate that overexploitation and habitat degradation have historically been major drivers of biodiversity declines (Coll et al.2010).

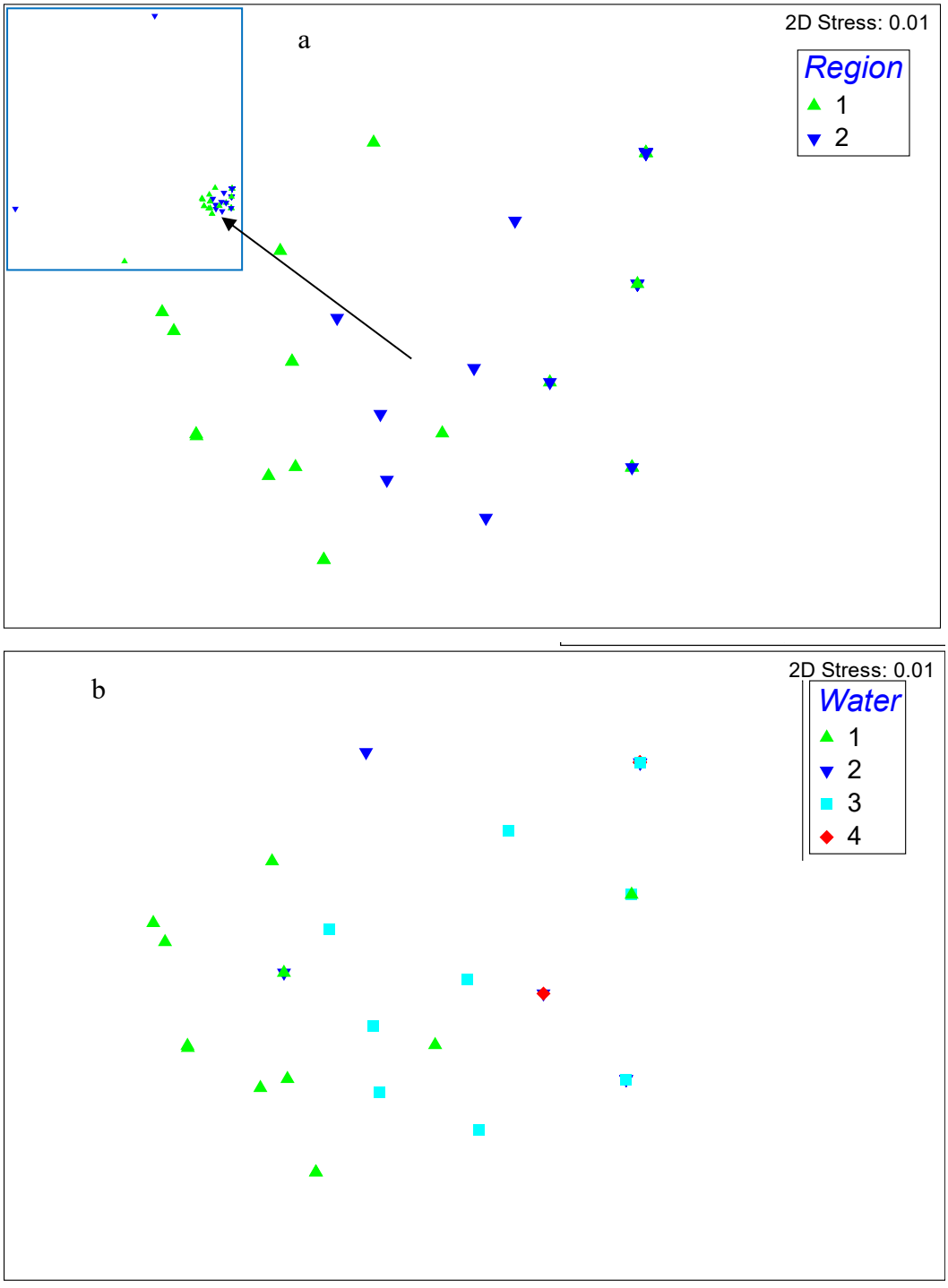


Fig. 14. nMDS plot of alien species analyses based on Bray-Curtis index calculated from presence/absence data of the species: stations classified by regions (1: south and 2: north) (a) and water masses (1: Mediterranean Sea, 2: southern Aegean, 3: northern Aegean and 4: Black Sea waters).

Table 2. PerMANOVA analysis to test difference of alien species among the stations of regions and water masses. p and p(MC) is PerMANOVA and Monte Carlo test significance level, respectively. Bold p denotes significant difference at $p < 0.05$.

Source	df	SS	MS	F	p	p(MC)
Region	1	29871	29871	10.237	**0.001**	**0.001**
Residuals	58	1.6924E5	2917.9			
Total	59	1.9911E5				
Water masses	3	43341	14447	5.1938	**0.001**	**0.001**
Residuals	56	1.5577E5	2781.5			
Total	59	1.9911E5				

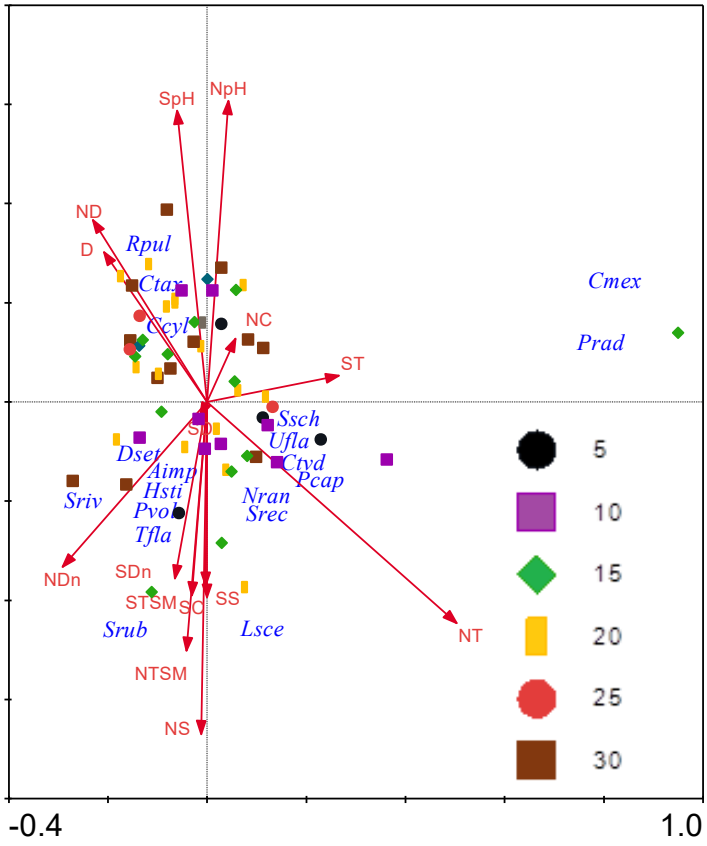
According to FAO (1991) interpretations, the southern region was largely characterized by two dominant contributors—*Torquigener flavimaculosus* and *Synaptula reciprocans*—followed by *Pterois miles*, though mean similarity values remained low (Table 3). In contrast, the northern Aegean was typified by a single key contributor, *Caulerpa cylindracea*, which also acted as the principal discriminator between north and south (85.15% dissimilarity). This species is widely established throughout the Mediterranean (Katsanevakis et al.2020b). No interaction among these dominant species was detected (Fig. A1 in supplementary file). The alien seagrass *Halophila stipulacea* and the invasive ochrophyte *Stypopodium schimperi* occurred mainly in the South Aegean, whereas *C. cylindracea* was abundant in both northern and southern sectors (Ragkousis et al.2023; Tsirintanis et al.2023). In general, faunal aliens appeared predominantly in the south (Coll et al.2010; Katsanevakis et al.2014a), while macrophytes tended to dominate northern areas (Coll et al.2010), although Katsanevakis et al. (2014a) reported high macrophyte diversity extending to the Saroz Gulf under Black Sea influence.

Table 3. Similarity table and contributors of alien species, * is contributor species within each region (R1: south and R2: north) station, determined from an analysis of a similarity of percentages, SIMPER. + is discriminator species between regions (Avg. Sim.: Average similarity at each region, Av. Sim; average similarity, Sim/SD; correction term and Cum.%: cumulative percent contribution of the similarities, and SD; standard deviation of the similarity).

Species R1 Avg. Sim: 11.52	**Av. Sim**	**Sim/SD**	**Cum.%**
**Torquigener flavimaculosus*	2.35	0.26	20.39
Caulerpa cylindracea	2.16	0.16	39.19
**Synaptula reciprocans*	2.06	0.21	57.11
**Pterois miles*	1.73	0.21	72.09
Stypopodium schimperi	1.30	0.11	83.37
Diadema setosum	0.80	0.16	90.35
R2: Avg. Sim: 51.40			
+**Caulerpa cylindracea*	49.53	1.11	96.36

Among the physical variables examined, temperature (especially near-bottom temperature) was the strongest driver of alien species assemblage structure, explaining 23.6% of the variance on CCA1 (Table 4, Fig. 15). Species showed a weak positive relationship with sea-surface temperature and negative relationships with near-bottom dissolved oxygen and density (Table 4, Fig. 15). Near-bottom salinity also structured the assemblage, creating a distinct separation between northern and southern sectors, and pH contributed to this discrimination. Evangelopoulos et al. (2024) reported that the higher establishment success of non-native fishes in the northeastern and southern Aegean is linked to favorable abiotic conditions. The northeastern Aegean receives highly saline (> 38.5 psu) Levantine waters, and coastal SST ranges from mean 19–20°C with winter minima of 12–15°C (Androulidakis & Krestenitis, 2022). In the southeastern Aegean, mean and minimum SSTs are 20–23°C and 14–17°C, respectively (Androulidakis & Krestenitis, 2022). Continued warming and salinity increases may give thermophilic aliens a competitive advantage over native biota. If current hydrographic conditions in the southern Aegean persist, major shifts in biotic composition are expected, with weaker impacts projected for the northern

Aegean (Pancucci-Papadopoulou et al.2012). Species distributions were negatively correlated with total suspended matter in both surface and near-bottom waters. The northern region was characterized by higher pH and density, lower salinity and temperature, and reduced suspended matter, whereas opposite conditions prevailed in the south (Table 4, Fig. 15). This contrast explained 18.7% of the variance. Significant Spearman correlations between species and environmental variables on CCA1 and CCA2 indicated that distribution patterns were strongly associated with specific near-bottom temperature and salinity regimes, consistent with GAM-derived additive co-linear trends (Table 4, Fig. 15b). Total variance explained reached 68% by CCA4. All four canonical axes were validated by Monte Carlo permutation tests (F = 1.784, p = 0.014), although CCA1 alone was not significant (F = 4.271, p = 0.168). Thermophilic species were fewer than species preferring cooler waters; similarly, halophilic species were less numerous than those favoring lower salinity (Fig. 15).



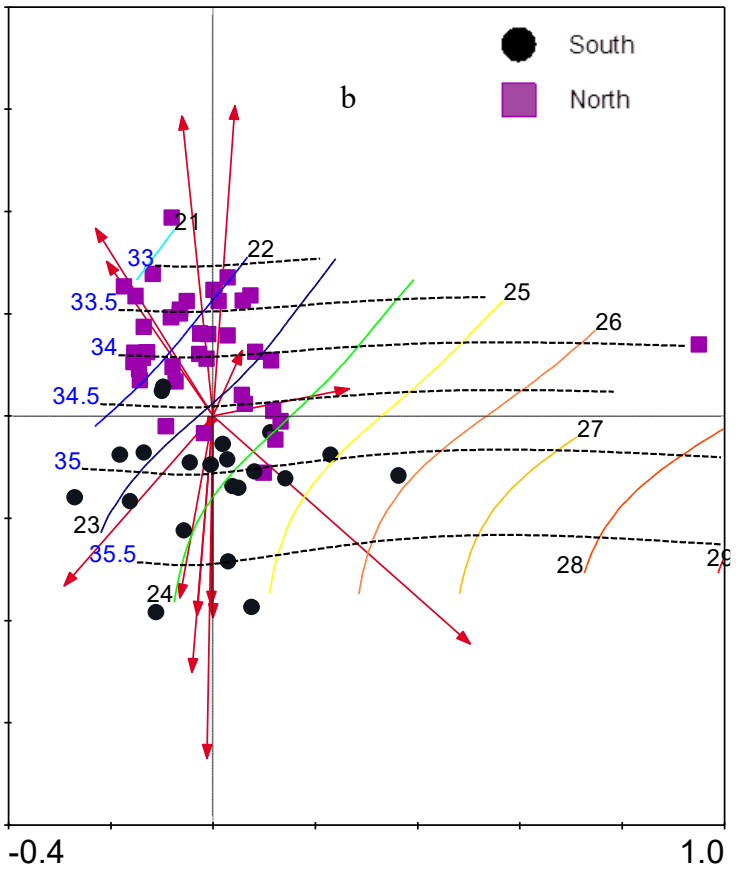


Fig. 15. Triplot (stations, species, and environmental parameters) of CCA analysis based on presence/absence of alien species; species-environment-relation at stations classified by bottom depth (a), and by regions with Generalized Additive Model (GAM) solution of near-bottom temperature in ºC (gradient colors with black label) and salinity in ppt (dashed black line with blue label) (b) (see Table 1 and 4 for abbreviations of species and environmental parameters, respectively).

Table 4. Summary of statistical measures of environmental parameters of CCA correlation (prefix of variables; S: sea surface, and N: Near-bottom water) with NIS.

Variables	**Abb.**	**CCA1**	**CCA2**
Bottom depth	D	-0.1869	0.2515
Sea surface water			
Temperature	ST	**0.2387**	0.0442
Salinity	SS	-0.0031	**-0.3078**
pH	SpH	-0.0546	**0.4880**
Total suspended matter	STSM	-0.0002	**-0.3278**
Dissolved oxygen	SD	-0.0122	-0.0236
Conductivity	SC	-0.0280	**-0.3244**
Density	SDn	-0.0581	-0.2959
Near-bottom water			
Temperature	NT	**0.4509**	**-0.3706**
Salinity	NS	-0.0109	**-0.5567**
pH	NpH	0.0381	**0.5047**
Total suspended matter	NTSM	-0.0373	**-0.4170**
Dissolved oxygen	ND	**-0.2064**	**0.3053**
Conductivity	NC	0.0511	0.1064
Density	NDn	**-0.2613**	-0.2764

Eigen values:	0.768	0.610
Species-environment correlations:	0.896	0.831
Cumulative percentage variance		
of species data :	9.0	16.2
of species-environment relation:	23.6	42.3

The CIMPAL (Cumulative Impacts of Invasive Alien Species) index showed that high-impact scores were four times more common in the South than the North Aegean. Macrophytes were responsible for highest CIMPAL scores (>10), occurring far more frequently in the south (76%) (Tsirintanis et al.2023). Fish contributed 13% of cumulative impacts and were more influential on coastal habitats in the southern Aegean, where high (>10) fish-related CIMPAL scores were also more common (Tsirintanis et al.2023). Caulerpa cylindracea was the only macrophyte among the eight ICAS affecting shallow soft substrates and ranked as the most impactful species in that habitat (Argyrou et al. 1999; Rizzo et al. 2017, 2020). Shallow (0–60 m) hard substrates were the most severely impacted habitat, followed by shallow soft bottoms and seagrass meadows. Several species (C. cylindracea, Siganus luridus, and Siganus rivulatus) were consistently among the most impactful across their distribution, though rankings varied depending on habitat type and the indicator used (Tsirintanis et al.2023). Overall, strong impacts were more frequent in the South Aegean, driven largely by alien fish and macrophytes. Katsanevakis et al. (2014a) demonstrated that alien species composition varies across Mediterranean ecoregions, including within the Aegean Sea, likely due to distinct water-mass characteristics, where NIS/IS ratios are particularly high (Katsanevakis et al.2014a).

Conclusion

This study provides the most comprehensive assessment to date of the spatial distribution, ecological patterns, and environmental drivers of marine alien species along the Turkish Aegean coast. A total of 19 non-indigenous taxa spanning six major groups were documented, with macrophytes and fishes constituting the most species-rich components of the assemblage. Although none of the recorded species exhibited high regional constancy, several—most notably *Caulerpa cylindracea, Caulerpa taxifolia, Pterois miles, Torquigener flavimaculosus*, and *Synaptula reciprocans*—showed clear spatial structuring that reflects both environmental gradients and biogeographic connectivity within the Aegean Sea. Marked north–south contrasts characterized the alien community. The southern Aegean supported a richer assemblage of faunal aliens, influenced by warmer, saltier Levantine-derived waters and multiple introduction pathways, particularly shipping and Lessepsian migration. Conversely, macrophyte invaders such as *C. cylindracea* dominated the northern Aegean, consistent with their broad ecological tolerance and ability to colonize extensive seagrass habitats. Several species recorded here—including *C. taxifolia, C. taxifolia* var. *distichophylla*, and *C. mexicana*—represent the northernmost or most recent occurrences in the basin, underscoring the continuing northward expansion of several thermophilic invaders. Multivariate analyses demonstrated that alien assemblages were structured primarily by region and water-mass characteristics rather than depth. Among environmental variables, near-bottom temperature emerged as the strongest driver, followed by salinity and pH, all of which aligned with known large-scale hydrographic gradients. These findings support previous work, indicating that warming trends and increasing salinity in the eastern Mediterranean enhance the establishment success of Indo-Pacific taxa and may intensify future biotic

homogenization. The presence of invasive macrophytes capable of altering benthic community structure, together with predatory fishes such as *P. miles* and ecosystem-modifying echinoderms like *Diadema setosum*, highlights the potential for substantial ecological consequences in both northern and southern subregions. Moreover, the detection of *Halophila stipulacea* and several caulerpacea species in new localities indicates rapid habitat turnover in coastal and shelf ecosystems. Overall, these results demonstrate that the Turkish Aegean Sea is undergoing an active and spatially heterogeneous phase of biological invasion driven by a combination of environmental change, propagule pressure, and regional circulation processes. Continued monitoring, pathway-based management, and coordinated regional action are essential to mitigate further introductions and to understand the long-term ecological implications of an increasingly alien-dominated seascape.

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Declarations

Conflict of interest The author declares no competing interests.

Ethical approval No animal testing was performed during this study.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the author from the competent authorities and are mentioned in the acknowledgements, if applicable.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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