Species loss and decline in taxonomic diversity of macroalgae in the Gulf of Trieste (Northern Adriatic sea) over the last six decades

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ARTICLE INFO

ABSTRACT

Assessing historical changes in marine biodiversity at regional or local scales is often challenging due to insufficient long-term data for most marine organisms. Yet, these assessments are crucial to understanding potential long-term variation in the species pool in response to complex and interacting local and global environmental changes. Here, we performed a comprehensive review of scientific and grey literature, archival records and floristic data spanning over the last two centuries to reconstruct an updated and revised taxonomic dataset of macroalgae in the Gulf of Trieste (Northern Adriatic Sea), one of the most exposed to human-driven pressures and climatically vulnerable regions in the Mediterranean Sea. The subset of data from 1960 to present, encompassing nearly all available records, was used to assess the contribution of species replacement and gain/loss to temporal β-diversity and to test for changes in the taxonomic distinctness of the species pool over the past six decades.

We identified 68 species that have never been recorded again since 1990, indicating their likely local extinction. The major change, however, was due to species replacement and to a reduction in the taxonomic breadth of macroalgal diversity, as highlighted by a significant decrease in the Average Taxonomic Distinctness of the species pool, especially along the Italian coast. The loss of species has mainly affected habitat-formers (e.g., *Cystoseira sensu lato*) and species with Atlantic/Circumboreal and Mediterranean affinities, which were replaced by turf-formers and species with Pantropical/Cosmopolitan/IndoPacific affinities. While multiple human impacts (e.g., coastal artificialisation, unbalanced N/P ratios) might have contributed to the ongoing change in macroalgal diversity, the observed decline of cold-affinity species in favour of warm-affinity species pointed out a critical role of exacerbating climatic changes. Our study demonstrated that historical reconstructions of species records coupled with effective indicators for the analysis of presence/absence data can help quantify long-term biodiversity changes and provide valuable insights into their possible causes.

1. Introduction

Escalating human pressures on marine ecosystems are driving an unprecedented global loss of marine biodiversity, despite current conservation efforts (Worm et al., 2006; O'Hara et al., 2019; Lotze, 2021). Coastal ecosystems are particularly vulnerable and exposed to multiple threats, such as habitat loss (Duarte et al., 2009), coastal development (2010, Bulleri and Chapman), pollution (Beiras, 2018), overfishing (Baden et al., 2012) and the introduction of alien species (Tsirintanis et al., 2022), which contribute to local extinctions, shifts in species distribution and alterations in population dynamics (McCauley et al.,

2015; Payne et al., 2016; Lotze, 2021). Approximately 30% of fish and invertebrate stocks have been overexploited and 17% have collapsed in recent decades, potentially disrupting the functioning of marine ecosystems (Worm et al., 2006; Trindade-Santos et al., 2020). Moreover, more than 200 marine species are currently at high risk of extinction (i. e., critically endangered), with 13 species already extinct (IUCN, 2023). Yet, most biodiversity assessments have focused on fish and vertebrates, underestimating the full extent of the problem due to data deficiency for many other species (McCauley et al., 2015).

Macroalgae are a prime example of marine organisms that are often overlooked in current assessments of biodiversity changes (Brodie et al.,

2009), despite their critical role in productivity, habitat structuring and nutrient cycling in coastal areas. Alterations in their composition and diversity can lead to far-reaching and often irreversible consequences for marine ecosystems (e.g., Bruno et al., 2005; Bertocci et al., 2010; Matias et al., 2015; Teagle et al., 2017; Krause-Jensen et al., 2018). Globally, local to large-scale decline of long-lived and structurally complex macroalgae (e.g., kelp) caused by cumulative human pressures including ocean acidification, rising sea surface temperatures and the increasing frequency of extreme events has been documented (e.g., Lima et al., 2007; Díez et al., 2012; Strain et al., 2014; Piñeiro-Corbeira et al., 2016; Méndez-Sandín and Consolación, 2016; Yesson et al., 2015). In the Mediterranean Sea, a biodiversity hotspot for macroalgae (Coll et al., 2010), the macroalgal forests of intertidal and subtidal rocky reefs are shrinking, primarily due to the loss of *Cystoseira sensu lato* and *Sargassum* populations (Arévalo et al., 2007; Falace et al., 2010; Thibaut et al., 2005, 2015; Blanfuné et al., 2016; 2019; Catra et al., 2019; Fabbrizzi et al., 2020; Rindi et al., 2020; Tsirintanis et al., 2022). However, trends in overall macroalgal diversity, beyond narrow spatial and temporal scales, remain poorly explored, limiting our understanding of the large-scale impacts of human pressures, including climate change.

Monitoring biodiversity trajectories in response to complex and interacting local and global environmental changes requires long-term studies across large spatial scales to detect meaningful modifications in regional species pools (Lindenmayer and Likens, 2009). Unfortunately, such assessments are often impractical due to limited funding, extensive sampling requirements and the complexities of taxonomic identifications, which is particularly demanding and time-consuming for macroalgae (Ceschia et al., 2007). To overcome the challenge of accurately assessing long-term changes in biodiversity, it is essential to complement and integrate active monitoring programmes by reconstructing species lists from historical data (Gravili et al., 2015). However, a major impediment to this approach is the scarcity or unavailability of comprehensive historical records of marine species, especially of macroalgae.

One notable exception is the northernmost part of the Adriatic Sea, specifically the Gulf of Trieste, where extensive spatial and temporal studies of marine flora have been carried out since the 19th century (e.g., Naccari, 1828; Zanardini, 1841; Agardh, 1842; Hauck, 1885; Schiffner, 1916). Later, Pignatti and Giaccone (1967) made a significant contribution to the to the region's marine flora, by revising existing knowledge and expanding the list of macroalgae. Subsequent contributions often focused on the spring-summer period or on specific locations, which limited a comprehensive assessment of changes in macroalgal diversity (e.g., Franzosini et al., 1983–84; Franzosini and Bressan, 1988; Bressan and Godini, 1990; Vukovic, 1984; Bussani and Vucovič, 1992). More recently, however, extensive sampling campaigns and detailed taxonomic inventories along the Slovenian coast and in protected bioconstructions in the Gulf greatly increased the knowledge of the regional macroalgal flora (Orlando-Bonaca et al., 2008; Curiel et al., 2012; Falace et al., 2015).

The northern Adriatic is a semi-enclosed, shallow basin with significant seasonal spatial and temporal variability in temperature and salinity (Russo and Artegiani, 1996; Artegiani et al., 1997). In winter, strong cold and dry winds drive the formation of intermediate and deep-waters in this area (Cushman-Roisin et al., 2013), which is one of the Mediterranean 'cold engines', along with the Gulf of Lions and the northern Aegean Sea. The northernmost part of the basin is characterized by shallow depths, low salinity due to freshwater inflows from rivers, and relatively low surface water temperatures. These environmental conditions resemble those of cold temperate marine regions rather than the warm temperate or subtropical conditions typical of other Mediterranean sub-basins. As a result, the northern Adriatic serves as a climatic refuge for cold-water and Atlantic species (Bianchi, 2007; Boero et al., 2008) and, therefore, is particularly susceptible to the impacts of climate change, which could promote the spread of warm-water species and elevate the risk of extinction for cold-water species (Boero

and Bonsdorff, 2007; Boero et al., 2008; Orlando-Bonaca et al., 2013).

In this study, we performed a comprehensive review of the literature, combined with an analysis of unpublished floristic data, to compile an updated and revised historical dataset of marine macroalgae in the Gulf of Trieste and to investigate long-term changes in macroalgal diversity over the last six decades. Specifically, we focused on (i) temporal species turnover and nestedness within the macroalgal pool to gain insights into diversity dynamics (ii) potential species loss during the study period, and (iii) changes in macroalgal taxonomic distinctness over time.

2. Material and methods

2.1. Study area

The study area is located in a semi-enclosed basin within the northernmost part of the Adriatic marine ecoregion (Spalding et al., 2007; Giakoumi et al., 2013; El Hourany et al., 2021), encompassing the Italian and Slovenian coasts of the Gulf of Trieste (Fig. 1). Rocky substrates characterize the whole area, except in its northwest portion of the Italian sector, where sandy beaches and coastal lagoons are dominant. The seabed is primarily composed of clay and mud with a maximum depth of −21 m. Far from the coast, the soft bottom is interspersed with thousands of biogenic outcrops formed by calcareous organisms on hard substrates of varied geological origin (Falace et al., 2015; Bandelj et al., 2020) that concentrated in the two offshore protected areas (Fig. 1). The Gulf of Trieste experiences an average tidal range of 0.97 m, the largest in the Mediterranean Sea. The area is characterized by significant seasonal and interannual variations in sea surface temperature, salinity and inorganic nutrient concentrations (Solidoro et al., 2009). Notably, the Gulf records the lowest winter temperatures in the Mediterranean, often below 10 °C, with prevailing winds from the northeast (Boicourt et al., 2021). Freshwater and nutrient input from rivers varies seasonally, with peaks typically occurring in late spring and fall (Burba et al., 1994).

Recent studies have reported a decrease in phosphate and ammonia concentrations, reflected in declining chlorophyll-a levels across the northern Adriatic, indicating a shift towards oligotrophic conditions over the last decade (Solidoro et al., 2009; Mozetič et al., 2010, 2012). The hydrodynamic of the Gulf of Trieste is primarily characterized by a current flowing northward from the coast of Croatia, with a general circulation pattern that is predominantly anticlockwise in the bottom layer and clockwise in the surface layer (Malačič and Petelin, 2009). In recent decades, the coasts of the Gulf of Trieste have undergone significant anthropogenic changes due to socio-economic activities (Giani et al., 2012; Pagano et al., 2023; Russo et al., 2020).

2.2. Literature review and data collection

A comprehensive review of floristic, taxonomic, and ecological studies on macroalgae in the study area dating back to the 19th century was conducted. The literature search included entries from the ISI Web of Knowledge, digital archives and repositories of the University of Trieste and the University of Catania. In total 132 papers documenting macroalgal species in the northern Adriatic were collected. The references, which contain all available floristic information for the Italian and Slovenian coasts, are listed in Table S1 (Supplementary Information). We complemented the dataset analyzing specimens from the TSB Herbarium and unpublished data from sampling campaigns conducted between 2008 and 2023 within various research programmes. The sampling methods documented across the different data records varied, ranging from the herborisation of individual thalli to destructive quantitative sampling protocols. Information on sampling methods is lacking for historical data collected prior to 1960.

The complete list of records, including order, family and chorology, updated with the latest taxonomic nomenclature (www.algaebase.org, accessed February 2024) after expert revision, is provided in Table S2 (Supplementary Information). The entire dataset was divided into three
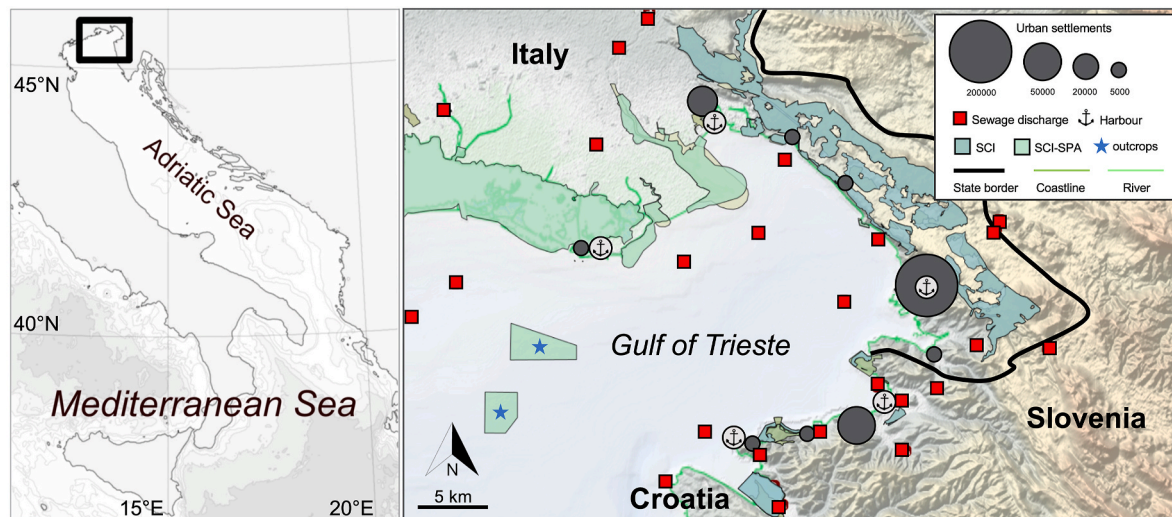
Fig. 1. The study area is located in the northernmost portion of the North Adriatic Sea (Mediterranean Sea) and included two subareas corresponding to the Slovenian coast and the Italian coast in the Gulf of Trieste. Main urban settlements, urban outfalls (coastal and submarine), harbors, rivers, bioconstructions (coralligenous outcrops) and protected areas (SCI: EU Site of Community Importance; SPA: EU Special Protection Areas) were also indicated.

time intervals: records before 1959, between 1960 and 1989 (T1), and between 1990 and 2023 (T2). The pre-1960 records were sparse and fragmented, making it challenging to reliably reconstruct the entire regional species pool, thereby preventing a stringent comparison with more recent data; these records were therefore excluded from the analysis. For the records from 1960 to the present, the categorisation into T1 and T2 was based on significant environmental, climatic and community changes that occurred in the northern Adriatic between the mid-1980s and early 1990s (e.g., Degobbis et al., 2009; Kollmann and Stachowitsch, 2001; Falace et al., 2010; Giani et al., 2012; Skliris et al., 2012; Bevilacqua et al., 2019). We further subdivided the dataset to account for differences in macroalgal species composition between the Italian (ITA) and Slovenian (SLO) coasts, since these two subareas exhibit distinct environmental characteristics, with the Italian coast having undergone substantial modifications and anthropogenic impacts in recent decades (e.g., harbours, marinas, drainage, sewage discharges, and aquaculture), reflecting a higher degree of coastal urbanisation.

Species recorded over the last 30 years (i.e., T2 ITA + SLO), including references and comments on their taxonomy and biogeography, were listed alphabetically by division (Rhodophyta, Phaeophyceae and Chlorophyta) in Table S3 (Supplementary Information).

2.3. Data analysis

The analysis focused on macroalgae recorded in the study area over the last 60 years (i.e., T1 and T2, see Table S2 in Supplementary Information).

We assessed temporal β-diversity in species composition by comparing species pools from the two periods for both the Italian and Slovenian coasts. Temporal β-diversity was calculated based on Jaccard dissimilarity between periods (Jost, 2007; Baselga and Orme, 2012). We followed the approach proposed by Baselga and Orme (2012) to separate the contributions to β-diversity due to species turnover (i.e. species replacement) and nestedness (i.e., gain or loss of species). These analyses were performed using the "*betapart*" package in R (R Development Core Team, 2022; Baselga and Orme, 2012; Baselga et al., 2018).

The species pools from the two periods and sub-areas were further analyzed to identify which main taxonomic group (i.e., Rhodophyta, Phaeophyceae and Chlorophyta) and chorological categories (Atlantic, Circumboreal, Cosmopolitan, Indo-Pacific, Mediterranean, Pantropical) mostly contributed to the overall change in macroalgal diversity. The chorological affinity, which could provide cues on the potential

involvement of climatic factors in the observed changes, was defined following the classification proposed by Cormaci et al. (1982) and was assigned to the species according to Furnari et al. (2003, 2010).

The Average Taxonomic Distinctness index (Clarke and Warwick, 1998) combined with the Variation in Taxonomic Distinctness (Clarke and Warwick, 2001) and the associated randomisation tests were used to assess patterns of change in the taxonomic structure of the macroalgal pool between the two periods for each sub-area. Average Taxonomic Distinctness (Δ^+) measures the average taxonomic path length through the taxonomic hierarchy between two randomly selected species, reflecting the breadth of the taxonomic tree from species to higher taxonomic levels. Variation in Taxonomic Distinctness (Λ^+) measures the heterogeneity of the distribution of species within higher taxa, representing the variance around the average pairwise path length. These indices are independent of the number of species in a sample and virtually unaffected by sample size, sampling effort and methods (Clarke and Warwick, 1998; Leonard et al., 2006; Ceschia et al., 2007; Bevilacqua et al., 2009). They are well-suited for the analysis of incidence-based data in the form of species lists (Price et al., 2006; Ceschia et al., 2007; Bevilacqua et al., 2012).

Δ^+ and Λ^+ have been widely used to investigate patterns of variation in the taxonomic breadth of marine assemblages in relation to natural and anthropogenic disturbances across several geographical and ecological contexts (e.g., Ellingsen et al., 2005; Graham et al., 2006; Tolimieri and Anderson, 2010; Zhao et al., 2024). These indices are particularly valuable for analysing historical trends in the taxonomic structure and diversity of a specific group of organisms (Ceschia et al., 2007; Louzao et al., 2010; Gravili et al., 2015).

The taxonomic reference list, which included all species recorded since 1960, was derived from the full list of records (Table S2, Supplementary Information). This list was used to calculate the two taxonomic distinctness indices, $\Delta+$ and $\Lambda+$, and to test for deviations from random expectations. A histogram of the frequency distribution of Δ^+ values was constructed under the null hypothesis that the *m* species in each sub-area and each period were an equal random subset of macroalgal species from the entire taxonomic pool (Warwick and Clarke, 1998). In this procedure, 1000 random subsets of *m* species were generated from the reference list and the Δ^+ value was calculated for each subset to obtain a random frequency distribution of Δ^+ for *m* species. The index value for the true subset of species was then calculated and tested against the expected frequency distribution. The analysis of the deviations from the random expectation of for Λ^+ values followed a similar procedure. In

this case, randomisations were repeated for a range of *m* values to obtain the 95% 'confidence funnel' for Λ^+, which was used for testing the true values (Clarke and Warwick, 2001). We used the same step length (equal to 1) to calculate the indices when weighting all distances between hierarchical taxonomic levels (i.e., from species, genus, family, order, class, subclass, phylum) (Clarke and Warwick, 1999). Analyses were conducted using PRIMER v6 software package (Clarke and Gorley, 2015).

3. Results

The cumulative species inventory spanning the last two centuries (1795–2023) comprises 487 species, of which 305 were Rhodophyta (62.6%), 101 Phaeophyceae (20.7%) and 81 Chlorophyta (16.7%). (Table S2, Supplementary Information). Only 19 species were documented between 1795 and 1959, highlighting a considerable knowledge gap prior to 1960. In the Italian sector of the Gulf, 471 species were recorded (Rhodophyta 62.8%, Phaeophyceae 21%, Chlorophyta 16.1%), while 269 species (Rhodophyta 59.5%, Phaeophyceae 20.4%, Chlorophyta 20.1%) were documented in the Slovenian sector. Nineteen species disappeared from the records before 1960 (see Table S2, Supplementary Information). These species were primarily turf-forming species (e.g., *Compsonema minutum*, *Polysiphonia flexella*), often occurring as epiphytes on other macroalgae or seagrasses. We also considered species such as *Gloiocladia furcata*, *Liagora distenta,* and *Palmophyllum crassum* to have disappeared from the Gulf of Trieste, as it is very unlikely that these species were overlooked or misidentified in later surveys.

Across the study area, 132 species recorded in T1 were not observed in T2, although 63 new species were recorded in T2 (primarily Rhodophyta and Atlantic/Circumboreal or Mediterranean species, see Table S4 in Supplementary Information), resulting in a net loss of 69 species (Table 1). Many taxa underwent nomenclatural changes or were synonymised, while others disappeared. This subset included species from the genera *Audouinella*, *Polysiphonia s.l.*, *Cladophora* and the families Ectocarpaceae and Ulvaceae, which were previously reported by Giaccone and Pignatti (1967) but no longer found in later works.

The overall β-diversity revealed that 42% of species composition differed between the two time periods, with species replacement (turnover) being the primary driver rather than species gain/loss (nestedness) (Table 1). This pattern was consistent when analysing macroalgae from the Italian and Slovenian coasts separately, although the magnitude of change in the macroalgal pool was more pronounced in the Slovenian sector compared to the Italian one (Table 1).

The decline in species richness was more pronounced in brown algae,

followed by green and red algae, and mostly concerned species with Atlantic/Circumboreal and Mediterranean affinities (see Fig. 2, Table S4 Supplementary Information). This pattern of species loss was consistent across both the Italian and Slovenian sectors, though in the latter the largest declines were observed in Pantropical/IndoPacific species and within Rhodophyta and Phaeophyceae groups. The net species loss in Chlorophyta was also lower in Slovenia than in the Italian sector (0% vs. 29%, respectively), whereas a comparable reduction concerned Rhodophyta (19% vs. 16%, respectively). Conversely, the net change in Phaeophyceae was more pronounced in the Italian sector (35%) compared to Slovenia (28%) (see Fig. 2, Table S4 in Supplementary Information).

The analysis did not highlight significant deviations from expectations ($P = 0.342$) for the Δ^+ values in the Italian species pool during T1 (Fig. 3a), indicating that the macroalgae from 1960 to 1990 could be considered as a random group of species from the regional species pool. In T2, however, there was a marked reduction in the taxonomic breadth of macroalgae in this sub-area, with a significant decrease in Δ^+ ($P = 0.026$) (Fig. 3b), suggesting that the macroalgae were more closely related to each other than would be expected by chance. For both time periods, the Λ^+ values for macroalgae from the Italian coast were within the expected range (Fig. 4).

Macroalgae from the Slovenian coast in T1 had a significantly higher Δ^+ value ($P = 0.022$) (Fig. 3c) coupled with a significantly lower value of Λ^+, indicating that the species pool was taxonomically overdispersed if compared with random expectations. At T2, the Δ^+ remained significantly higher than expected ($P = 0.020$) (Fig. 3d), though the corresponding Λ^+ value was not statistically significant (Fig. 4).

4. Discussion

Multidecadal surveys assessing floristic change across large geographical areas are uncommon, largely due to the considerable sampling effort required and the need for specialized taxonomic expertise (Ceschia et al., 2007; Falace et al., 2010). In the Mediterranean, research has predominantly focused on mapping the distribution and abundance of macroalgae over relatively short-to medium-term period, with only a few studies addressing long-term changes in algal flora (e.g., Cecere et al., 1991; Cormaci and Furnari, 1999; Munda, 2000; Rindi et al., 2020). Furthermore, these assessments often concentrate on updating species inventories by adding new entries without critically evaluating species existing lists or identifying putative locally extinct species (Boero and Gravili, 2013). This narrow approach hampers the ability to fully understand biodiversity changes in response to both natural and anthropogenic environmental pressures.

A key challenge in analysing long-term biodiversity changes lies in the availability and heterogeneity of data, which may stem from varying sampling efforts, fragmented datasets or data limited to species inventories. However, taxonomic distinctness indices are a powerful tool for handling collated species datasets across extensive spatial and temporal scales (e.g., Gravili et al., 2015). When combined with assessments of temporal β-diversity (e.g., Tedesco et al., 2020), these tools provide robust frameworks for testing hypothesis on biodiversity changes, particularly when others statistical frameworks may be inadequate (Bevilacqua et al., 2021).

Our study provides a comprehensive, up-to-date assessment of long-term changes in the marine flora of the Gulf of Trieste, shedding light on the multidecadal shift in taxonomic diversity that have shaped the current floristic composition of the region. This work will serve as a benchmark for future analyses examining changes in marine biodiversity within the northern Adriatic and across the Mediterranean Sea.

Over the past six decades, the regional macroalgal pool underwent substantial changes, with a variation in species composition of mare than 40% between T1 and T2, primarily driven by species replacement. Among the new species recorded in T2, eight (i.e., *Aglaothamnion feldmanniae, Colaconema codicola, Dohrniella neapolitana, Spermothamnion*

Table 1

Total β-diversity and its turnover and nestedness-resultant components between the two periods (T1: 1960–1989, T2: 1990–2023) for the whole study area (Total) and the two sub-areas corresponding to the Italian (ITA) and Slovenian (SLO) coasts. The β-diversity was calculated as Jaccard dissimilarity in species composition between periods and expressed as % change. Species richness for the whole area and the two sub-areas for each period was also given. The columns '-' and '+' indicate the number of species virtually lost and the number of new species added from T1 to T2, respectively.

β-diversity between periods			
	Total	ITA	SLO
Overall	42%	45%	54%
Turnover	32%	32%	47%
Nestedness	10%	13%	7%

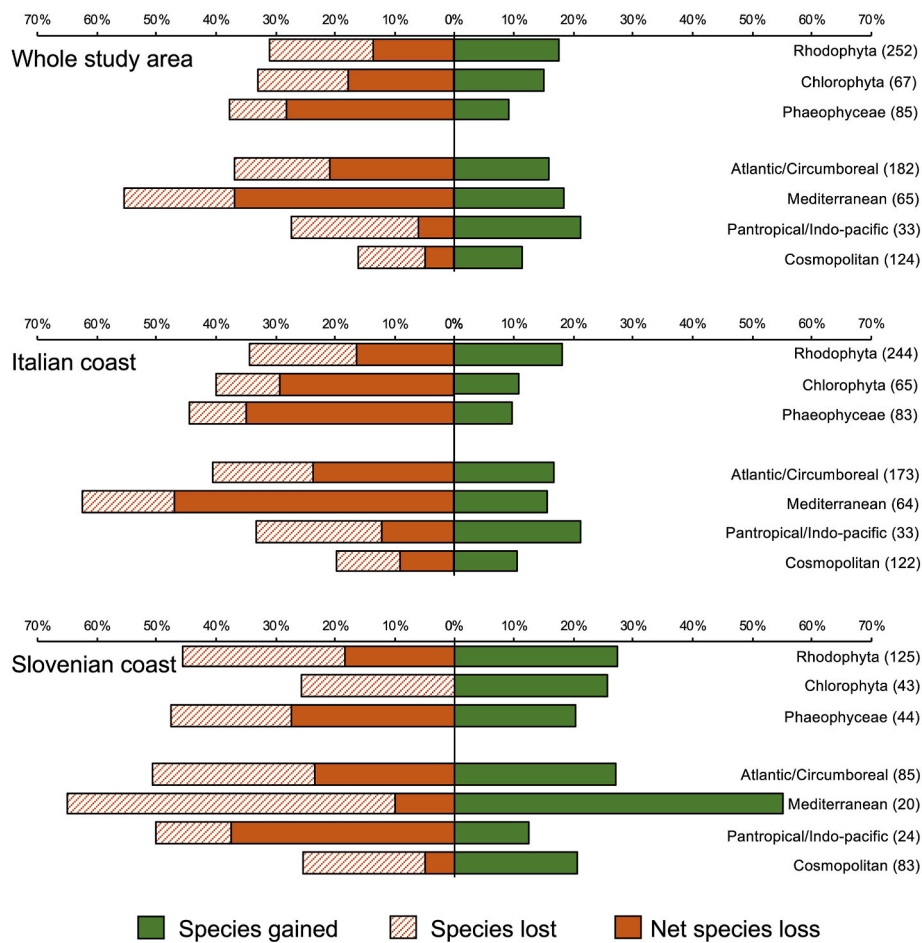| *Number of species*					
	T1	T2	–	+	Net loss
Total	404	336	132	63	69
ITA	393	306	146	59	87
SLO	213	180	89	56	33

Fig. 2. Number of species virtually lost (dashed red bars) and gained (green bars) in T2 (1990–2023) expressed as % on the total number (in brackets) of species in T1 (1960–1989). Solid red bars indicate the net loss. Changes in the number of species were depicted separately for Rhodophyta, Chlorophyta and Pheophyceae, and for main chorological groups. (a) Whole study area, (b) Italian coast, (c) Slovenian coast.

irregulare, Desmarestia viridis, Myriactula stellulata, Osmundea oederi, Ulvella scutata) were previously reported from the Venice Lagoon (Sfriso and Curiel, 2007; Sfriso et al., 2020, 2023) but not yet documented in the Gulf of Trieste. Another species, *Bornetia secundiflora*, is new exclusively for the Gulf of Trieste. In addition to the six alien species already present in the region by the end of 1970s (i.e., *Asparagopsis armata, Bonnemaisonia hamifera, Cladosiphon zosterae, Cutleria multifida, Punctaria tenuissima, Scytosiphon dotyi*), the current species pool also includes five new alien species (Servello et al., 2019), namely *Acrothamnion preissii, Aglaothamnion feldmanniae, Colaconema codicola, Colpomenia peregrina, Codium fragile*. Notably, *C. peregrina* is reported for the first time in the Adriatic, while *A. preissii* and *A. feldmanniae* occurred for the first time in the Gulf of Trieste, although these species were previously found in the lagoons of Grado and Marano (Falace et al., 2009) and Venice (Sfriso and Curiel, 2007).

The species loss primarily affected brown algae, particularly within the *Cystoseira s.l.* complex and the *Sargassum* genus, with a 25% net loss observed between the two periods. For instance, *Cystoseira amentacea* var. *stricta* and *Gongolaria sauvageauana* disappeared from the Italian sector after T1, while *Cystoseira foeniculacea* f. *foeniculacea* and *Sargassum hornschuchii* were no longer found in either the Italian or the Slovenian sectors after T1 (see Table S2 in Supplementary Information for further details). This trend aligns with the widespread decline of fucoid algae observed throughout the Mediterranean since 2000 (e.g., Cormaci and Furnari, 1999; Thibaut et al., 2005, 2015; Falace et al., 2010; Blanfuné et al., 2016, 2019; Iveša et al., 2016; Orlando-Bonaca and Rotter, 2018, 2021a; Rilov et al., 2018; Fabbrizzi et al., 2020;

Nikolau et al., 2023).

In the Italian sector, the decline in species richness between T1 and T2 was accompanied by a reduction in the taxonomic distinctness of macroalgae, indicating a higher level of taxonomic relatedness among species. This reduction in taxonomic distinctness often occurs when changes lead to the loss of higher taxonomic ranks (e.g., orders and families), particularly those with few species, in favour of highly speciose and closely related taxa (e.g., species-rich genera within the same family), resulting in a narrower taxonomic spectrum. Since the 1960s/1990s to present, a total of 38 genera, 14 families, and 3 orders of macroalgae were lost. In contrast, the new species recorded in T2 mainly belonged to historically species-rich taxa of red algae, such as Ceramiales or, to a lesser extent, Corallinaceae. It could be argued that the increase in species richness of these taxa could be partially due to the extensive studies of the coralligenous outcrops carried out in recent years in the Gulf of Trieste (Curiel et al., 2012; Falace et al., 2015; Orlando-Bonaca et al., 2017), which unveiled calcareous species that were already present in T1 but had previously gone unnoticed. Additionally, major taxonomic revisions and rearrangements of some algal genera (e.g., *Audouinella, Polysiphonia sensu lato, Cladophora*) may have affected the estimation of species change. However, only 30% of lost species belonged to these highly-reworked taxa and the observed decrease in taxonomic distinctness was driven by changes in taxonomic composition across several algal groups. This suggests that the changes observed occurred beyond potential biases caused by temporal variations in research efforts and nomenclature revisions. More generally, limited research and sampling efforts along the Slovenian coast might be
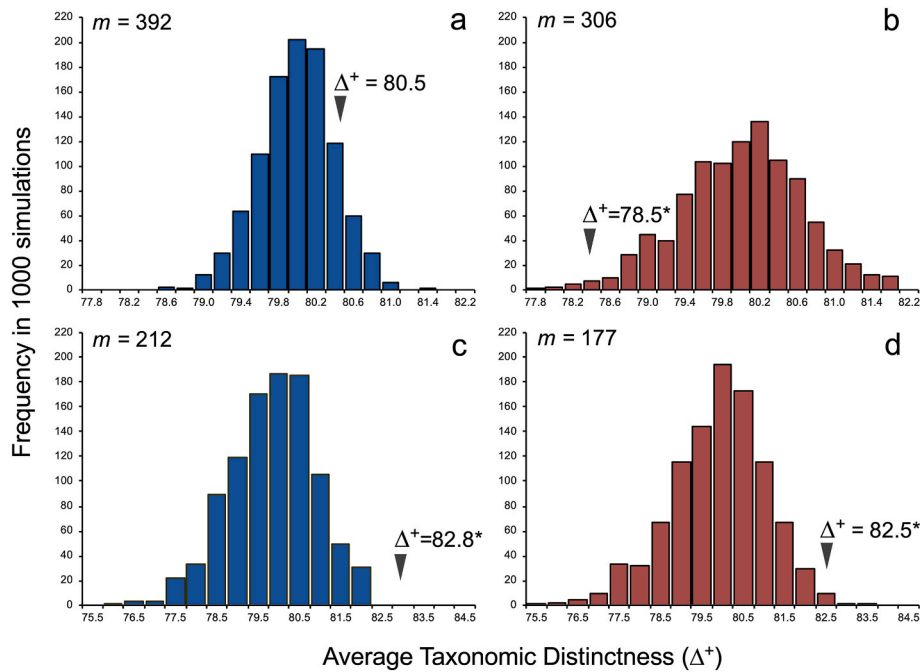
Fig. 3. Frequency distributions of Δ^+ values from 1000 random simulations for different subset of *m* species of drawn on the full list of macroalgae found in the study area. (a) Macroalgae from the Italian coast in T1 (1960–1989), (b) macroalgae from the Italian coast in T2 (1990–2023), (c) macroalgae from the Slovenian coast in T1, (d) macroalgae of the Slovenian coast in T2. Black arrows indicate Δ^+ values of the actual pool of macroalgae in each subarea and period. * = $P < 0.05$.
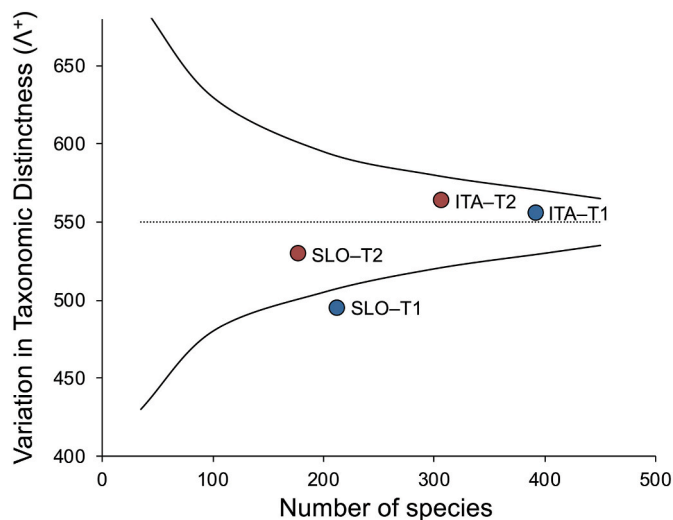

Fig. 4. Variation in taxonomic distinctness (Δ^+) of macroalgae in T1 (1960–1989) and T2 (1990-present) for each subarea (ITA: Italian coast, SLO: Slovenian coast), plotted against the corresponding number of species. The expected mean (dotted line) and the 95% confidence limits (crossed lines) were also plotted. Values exceeding the limits are significantly ($P < 0.05$) different from random expectations.

a possible reason underlying the lower total number of species recorded in this sector compared to the species pool documented for the Italian coast. It should be noted, however, that the Italian sector of the Gulf have a larger spatial extent with respect to the Slovenian sector and is characterised by a greater habitat heterogeneity (including coralligenous outcrops and coastal lagoons, beyond rocky and sandy coasts which are present in both the Italian and Slovenian sectors), which likely supported a higher species richness.

The seascape of the northern Adriatic Sea has undergone a notable structural and functional shift (Falace et al., 2010), with *Cystoseira s.l.*

species being currently limited to reduced stands or patches (Orlando-Bonaca et al., 2021b, 2022). The interaction among abiotic (e.g., warming, nutrient inputs) and biotic (e.g., grazing, invasive species) is contributing to the global flattening of fucoid and kelp forests worldwide (Mineur et al., 2015; Straub et al., 2016; Filbee-Dexter and Wernberg, 2018). This shift is leading to a cascading simplification of the three-dimensional structure of the ecosystems, reducing productivity and carbon sequestration, with profound consequences on the overall species diversity associated to macroalgal canopies and the understorey (Mineur et al., 2015; Filbee-Dexter and Wernberg, 2018). In the Gulf of Trieste, macroalgal assemblages that were once dominated by *Cystoseira s.l.* species have been replaced by communities composed of turf-like mats, such as those formed by Gelidiaceae and *Deltalsia/Xiphosiphonia*. These taxa thrive in environments characterized by frequent environmental disturbances, such as sediment movement and deposition (Perkol-Finkel and Airoldi, 2010; Falace et al., 2010). In some locations, the prevalence of tolerant or ephemeral taxa, such as Ceramiales (which mostly contributed to species replacement between periods), reflected degraded environmental conditions depending on reduced light penetration and high sedimentation rates, commonly associated with highly urbanized areas. These findings confirmed the results of previous studies conducted in the Adriatic Sea that have documented similar patterns of species distribution in response to increased turbidity and pollution (Petrocelli et al., 2019; Rindi et al., 2020).

The trophic changes towards oligotrophic conditions observed in the region over the last decades might also have contributed to the observed shift in macroalgal communities. The Gulf of Trieste, like other areas of the northern Adriatic, was an eutrophic system due to excessive nutrient supply until the 1990s. Since 2000, the system has gradually transitioned toward an oligotrophic state characterized by low phosphorous load, largely due to decreased anthropogenic inputs but also to reduced river flows and runoff as a consequence of altered rainfall regimes (Marini and Grilli, 2023). These changes may have imposed limitations on the growth and persistence of macroalgal populations and contributed to shifts in fisheries productivity (Fortibuoni et al., 2017).

The northern Adriatic Sea is one of the most impacted and exploited marine regions in the Mediterranean Sea (Micheli et al., 2013; Gissi

et al., 2017). The profound modifications of the regional species pool are probably the result of a complex interplay among climate change, pollution, coastal artificialisation, and biological disturbance (e.g., Russo et al., 2002; Falace et al., 2010; Falace et al., 2018; Bevilacqua et al., 2019; Felline et al., 2019; Petrocelli et al., 2019; Savonitto et al., 2021). The alteration of the coastline combined with increased sedimentation rates and nutrient inputs, for instance, may enhance the proliferation of turf-forming species (Falace et al., 2010; Mineur et al., 2015; Bevilacqua et al., 2021) that could outcompete erect and canopy-forming algae. On the other hand, the overfishing of some species of commercial interests (e.g., *Diplodus* spp.), which also play a role in controlling the main herbivores in Mediterranean rocky reefs (e.g., the sea urchins *Paracentrotus lividus* and *Arbacia lixula*), could trigger grazers' outbreaks leading to increased extensions of barren grounds dominated by encrusting algae (Bevilacqua et al., 2021). The overgrazing of macroalgal stands by native herbivores can be exacerbated by invasive alien species, such as the rabbitfish *Siganus* spp., which are drastically impacting rocky reef communities in the eastern basin and the Aegean (Nikolau et al., 2023). Although disentangling the effects of specific drivers and identifying those that mostly contributed to the observed changes is challenging, there are several cues suggesting that intensifying climate-related effects might have played a major role. The northern Adriatic Sea has unique biogeographic features in the Mediterranean Sea, serving as a refuge for cold-water species due to its lower average surface water temperature and salinity (Spalding et al., 2007; Giakoumi et al., 2013; El Hourany et al., 2021). *Fucus virsoides*, for example, is the only species of its genus found in the Mediterranean, where it is endemic to the Adriatic Sea (Linardić, 1949; Giaccone and Pignatti, 1967). Its presence is considered a glacial relict (Munda 1972), with a range extending from northwestern Italy to southern Albania (Linardić, 1949; Kashta, 1992; Mačić, 2006). The presence of *F. virsoides* in the Mediterranean likely results from geographic isolation from Atlantic that occurred during the Pleistocene glaciations, followed by further isolation after the last glacial period (Serrão et al., 1999).

Historical trends indicate a warming of the water masses after 1990, especially during the cold season (Appiotti et al., 2014), with a higher heat flux in the basin, and increased frequency of climatic anomalies (Russo et al., 2005). These changes could have affected the growth rates, distribution and phenology of sensitive algal species (Bevilacqua et al., 2019). The increase in seawater temperature and the occurrence of heatwaves are particularly problematic in the northern Adriatic, where environmental conditions have so far been more typical of cold-temperate regions. This has allowed the survival of cold-affinity species that are particularly sensitive to the current warming trend. The observed decline of *Fucus virsoides* (Descourvières et al., 2024) and other Atlantic-affinity species supports this hypothesis, suggesting an ongoing deborealisation of the region similarly to what is occurring in other parts of the world ocean (McLean et al., 2021; Arriaga et al., 2024), where the shift from cold to warm regimes of seawater temperatures is leading to the decline of cold-affinity species. This loss of typical boreal environmental conditions combines with increased habitat suitability for warm-affinity species and the appearance of species of Pantropical and Indo-Pacific origins (e.g., *Acrothamnion preissii, Tricleocarpa fragilis, Bryopsis pennata, Lophosiphonia cristata*).

Quantifying the cumulative effects of human pressures on marine communities is essential for developing effective management and conservation strategies. While manipulative experiments and targeted impact studies are critical for unravelling the complex dynamics and cause-effect relationships within these ecosystems, they often provide only a narrow view of the broader ecological picture. Within this framework, long-term monitoring and comprehensive assessments of marine biodiversity are indispensable for capturing the magnitude and scale of ecological changes, thereby informing more accurate and effective conservation priorities.

In this context, our research makes a significant contribution by employing historical reconstructions and detailed analyses of regional species pools. This approach enabled us to track biodiversity variations over long-term periods and provided critical insights into the drivers of ecological change. Such findings may contribute to a more informed perspective on ecosystem health, guiding more effective conservation efforts in the face of ongoing and future environmental pressures.

CRediT authorship contribution statement

Annalisa Falace: Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Giuseppina Alongi:** Writing – review & editing, Investigation, Data curation. **Martina Orlando-Bonaca:** Writing – review & editing, Investigation, Data curation. **Stanislao Bevilacqua:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Annalisa Falace reports financial support was provided by University of Trieste. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106828.

Data availability

Data will be made available on request.

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