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Climate-driven shifts in a Mediterranean hydrozoan assemblage over 44 years

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Abstract

Temporal changes in marine assemblages are well documented for large habitat-formers, while data on inconspicuous groups like hydrozoans are scarce. Long-term shifts in hydrozoan communities were assessed by replicating in 2024 an annual survey originally conducted in 1980 and repeated in 2004 along a depth gradient along the rocky cliff of Portofino Promontory (Ligurian Sea). The species richness declined significantly from 83 (1980) to 72 (2004) and 43 (2024), with the greatest losses in cold-affinity species. Several winter-dominant species, such as *Eudendrium glomeratum* Picard, 1952, *Sertularella crassicaulis* (Heller, 1868), and *Ectopleura larynx* (Ellis and Sollander, 1786), have strongly reduced or disappeared. In contrast, summer species like *Eudendrium racemosum* (Cavolini, 1785) are now present year-round. The appearance of southern species like *Corydendrium parasiticum* (Linnaeus, 1767) and *Pennaria disticha* Goldfuss, 1820, along with reduction in sexual reproduction reflect a community-level response to ocean warming, leading to seasonal and bathymetric homogenization. This 44-year dataset provides a rare long-term benchmark and supports the importance of accurate taxonomic analysis for understanding climate-driven transformations in Mediterranean benthic ecosystems.

Keywords: hydroids; historical data; biodiversity loss; Portofino Promontory; Ligurian Sea

Introduction

In recent decades, global climate change has significantly impacted Mediterranean biotas, causing abundance declines, spatial or temporal phenology shifts, and the disappearance of species (Lejeusne et al. 2010, Boero 2015). The Mediterranean Sea is a semi-enclosed basin and therefore a primary 'hot spot' for its vulnerability to global climate change often referred to as a 'miniature ocean' (Lejeusne et al. 2010). Thus, it is an ideal model for extrapolating findings from regional to global-scale climate models (Ulbrich et al. 2006). Under the influence of global warming, species that were once exclusive to the southernmost regions of the Mediterranean Sea have expanded their range northward, a phenomenon known as meridionalization, and numerous non-indigenous species (NIS) of tropical affinity have entered the Mediterranean through the Strait of Gibraltar and the Suez Canal, rapidly advancing northward in a process termed tropicalization (Boudouresque 2004, Coll et al. 2010). Furthermore, in and around port areas, several NIS introduced via ballast water have become dominant (CIESM 2002, Tempesti et al. 2020a, b). The fate of NIS in the Mediterranean is unpredictable, as it depends on a range of factors, including species' specific ecological requirements and the structural characteristics of the community with which they enter into contact (Meinesz et al. 1995, 2001, Santini-Bellan et al. 1996, Piazzi et al. 2005, Ruitton et al. 2005, Montefalcone et al. 2015).

Cnidarians exhibit a variety of responses to increasing temperatures, most of which have been recorded for conspicuous species. Habitat-forming octocorals have been involved in some of the most severe mass mortality events recorded in the Mediterranean Sea (Cerrano et al. 2000). Among scleractinians, some species such as *Cladocora caespitosa* (Linnaeus, 1767) and *Oculina patagonica* de Angelis D'Ossat, 1908 have experienced intense bleaching events (Rubio-Portillo et al. 2016) while other species with warm affinity such as *Astroides calycularis* (Pallas, 1766) have expanded their distribution northward (Musco et al. 2016).

While mass mortality events involving large habitat-formers are well documented, tracking changes in smaller cnidarian populations based on data gathered from recreational divers and citizen science notifications is more challenging (Boero et al. 2003) Mediterranean hydrozoans are a speciose and heterogeneous group able to form small-scale forests which trap sediments, remove seston (Gili and Coma 1998, Cerrano et al. 2015), supply shelter and food for many organisms (Bavestrello et al. 1996), and play an underestimated role in enhancing (Genzano et al. 2003) or limiting (Di Camillo et al. 2012) settlement of larvae of benthic organisms.

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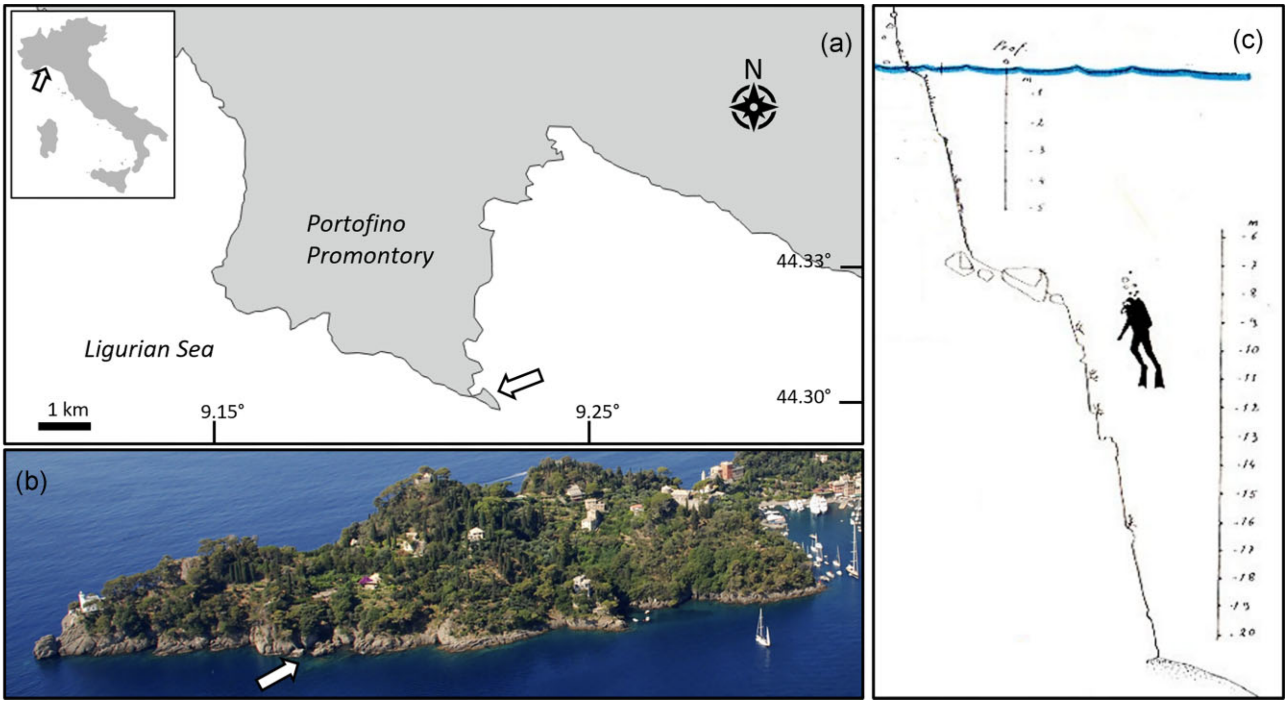

Figure 1. (a) Location of the Portofino Promontory (inset) and close-up indicating the position of the 'Aurora' transect (arrow). (b) Aerial photography of the promontory with an indication of the transect (arrow). (c) The original sketch representation of the bathymetric transect along the vertical cliff.

Hydrozoans' ecological traits make them an exceptional indicator taxon to assess the effects of climate change. First, several species of hydrozoans are abundant and easily detected underwater; moreover, due to their high phenotypic plasticity, seasonal hydrozoans can enter dormancy or spread according to environmental conditions (Bavestrello et al. 2006, Boero et al. 2008, Di Camillo et al. 2017 and references therein). Therefore, their seasonal presence and reproductive periods reflect changes in environmental parameters and food availability (Boero and Fresi 1986, Coma et al. 2000).

In general, the difficulty in obtaining information about hydrozoans' phenology arises from the general lack of baseline data (Boero et al. 2015). However, hydrozoan assemblages have been well-documented at some Mediterranean areas, particularly considering the seasonality of typical species (Boero and Fresi 1986, Bouillon et al. 2004, Fraschetti et al. 2006, Morri et al. 2009, Di Camillo et al.2013; Gravili et al. 2013, González-Duarte et al. 2014, Gravili 2016).

In the period 1976–1983, the most comprehensive study on a Mediterranean hydrozoan assemblage was carried out on the rocky cliff of the Portofino Promontory (Ligurian Sea, Italy) (Boero and Fresi 1986). Specifically, in 1980 hydroids were collected monthly along a vertical transect from 0 to 20 m, subdivided into five depth ranges. A total of 82 species were identified, and their bathymetric and seasonal distribution, their reproductive cycle, and the substrates they were settled on were also reported (Supplementary Material SM1). The population dynamics of one of the most important hydroids in the area, *Eudendrium glomeratum* Picard, 1952 were studied from October 1982 to October 1983, in order to reveal the seasonal patterns of the appearance and disappearance of colonies (Boero et al. 1986).

The hydrozoan assemblage along the Portofino transect was revisited with the same methodology in 2004 (Puce et al. 2009). A slight decrease in species diversity was observed, with a total of 70 species recorded. Some species that were present in 1980 had disappeared by 2004, while other species with southern affinities which were previously unrecorded or had only been recorded very rarely in the area before, became abundant (Puce et al. 2009, Gravili et al. 2017). Additionally, species that were restricted to summer in the first survey were also present in winter. Shallow, summer-affinity species expanded their bathymetric range, reaching deeper zones. These findings strongly suggested that the warming trends observed in the Mediterranean Sea greatly modified the hydrozoan assemblage at Portofino (Puce et al. 2009).

The aim of this study is to further investigate the trajectory of these changes focusing on the species composition, abundance, and reproductive periods of the hydrozoan community. The surveys conducted in Portofino during 2024 were replicated over a full annual cycle, using the same sampling methods as in 1980 and 2004. The new data were compared with previous results and temperature fluctuations. This dataset, encompassing a 44-year span, is a valuable benchmark for future research into the same hydrozoan assemblage, and can be used as a model for similar long-term ecological studies in other regions.

Materials and methods

The sampling techniques were replicated exactly as described by Boero and Fresi (1986) and Puce et al. (2009). Sampling was conducted monthly from January to December 2024, by SCUBA diving on a rocky cliff, on the northern side of the Portofino Promontory (44.300306°N, 9.217804°E) (Ligurian Sea, NW Mediterranean Sea, Italy) (Fig. 1).

The rocky wall is almost vertical to a depth of 10 m and then slopes with several large steps. The transect, which was marked by an iron chain from the surface to a depth of 20 m, was divided into five depth ranges (0–0.5, 0.5–5, 5–10, 10–

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15, and 15–20 m). Along the transect, hydrozoans were visually recognized *in situ* by experienced taxonomists and parts of colonies were collected. Since many species are inconspicuous, substrates that are conducive to the presence of hydroids (e.g. algae, sponges, bryozoans, etc.) were collected and examined in the laboratory. The collected specimens were classified while still alive and their fertility was determined by the presence of gonophores. Finally, the samples were fixed in 70% ethanol for further analysis. The transect was first sampled in November 1976 using scrapings on 20 × 20 cm quadrats (Sarà et al. 1978). Due to identification difficulties, qualitative samples were repeated monthly (Boero and Fresi 1986). The species sampled in November 1976 using the quadrats were 60 whereas the visually oriented seasonal samples yielded 82 species (Boero and Fresi 1986) showing that standard quadrats might not be as informative as visually oriented samples in accounting for biodiversity composition.

For the formal analysis, a pseudo-abundance (0 = absent, 1 = present, and 2 = abundant) and presence/absence matrixes of the recorded species were obtained for the three years of the study (1980, 2004, and 2024).

Statistical analysis

Potential differences in the richness and abundance of the hydroid communities recorded in 2024 were investigated by multivariate methods using PRIMER-e 7 with a PERMutational ANalysis Of VAriance (PERMANOVA) + Add On package (Clarke and Gorley 2015). The differences in bathymetric distribution of the species from 0 to 20 m depth and the seasonal variation were tested by PERMANOVA (Anderson 2001). Moreover, differences across the three survey periods (1980, 2004, and 2024) were tested (factor ‘depth,’ fixed, 5 levels; factor ‘year’ fixed, 3 levels; factor ‘month’ fixed, 12 levels). To assess differences in the multivariate dispersion of hydrozoan assemblages among seasons (winter: January–March; spring: April–June; summer: July–September; and autumn: October–December) across sampling years, a PERmutational analysis of Multivariate DISPersions (PERMDISP) was conducted to test whether variability in community composition differed significantly independently of differences in centroids (Jaccard Index similarity Index measure, permutation = 9999; F: 10 674 df1: 11 df2: 168). Finally, SIMilarity PERcentage (SIMPER) routine was conducted to assess species contribution to the dissimilarity between groups (Bray–Curtis similarity Index measure, permutation = 9999) (Clarke 1993). The non-metric multi-dimensional scaling (nMDS) plots were used to display clustering patterns using the abundance species dataset.

Results

The present situation

The species recorded during the three surveys, together with their seasonal and bathymetric distribution are reported in Supplementary Material (SM1). During the 2024 survey, 47 species were recorded, 17 Anthoathecata and 30 Leptothecata. The most speciose families were Haleciidae (seven species), followed by Eudendriidae and Campanulariidae, both with six species. The distribution in the five analysed depth ranges showed a remarkable homogeneity regarding species number with 28–29 species in the first four ranges and a minimum of 23 species in the deepest depth range 15–20 m. On average, each species was recorded in 2.9 ± 0.2 depth ranges.

When considering species abundance and composition, the PERMANOVA analyses showed significant differences between the two shallower levels (0–0.5 m, 0.5-5 m) and the other ranges deeper than 5 m, while the 10–20 m depths were similar to each other (Supplementary Material SM2). SIMPER test (Supplementary Material SM3) indicated that the shallowest belt (0–0.5 m) was mainly characterized by *Aglaophenia octodonta* (Heller, 1868), *Clytia hemisphaerica* (Linnaeus, 1767), and *Dynamena disticha* (Bosc, 1802); in the 0.5–5 m depth range, *C. hemisphaerica* dominated together with *Eudendrium racemosum* (Cavolini, 1785). From 5 to 15 m depth, the assemblage significantly changed: the main abundant species were *C. hemisphaerica, Scandia gigas* (Pieper, 1884), and *Filellum serpens* (Hassal, 1848), while between 15 and 20 m depth, the community was mainly represented by *Antennella secundaria* (Gmelin, 1791), *C. hemisphaerica*, and *S. gigas*. Overall, 13 species were found at all considered depths while 16 were exclusive to one specific depth range (Supplementary Material SM1 and SM3).

The seasonal distribution showed maximal values in species numbers in winter and spring (21–26 species per month) and a summer reduction (8–16 species per month). On average, each species persisted in the community for 4.7 ± 0.4 months. Significant differences among months were confirmed by PERMANOVA; pair-wise comparisons highlighted differences arising from late spring and summer (Supplementary Material SM2 and SM4).

Overall, 21 species were recorded as fertile. The percentage of fertile species peaked in autumn, with around 50% of the species exhibiting gonophores. On average, there were about 5.1 fertile species per bathymetric level across the transect. (Supplementary Material SM1).

Temporal comparison

The total number of species recorded along the year in the transect progressively decreased from 1980 (83), 2004 (71), and 2024 (47), with a decline of almost 43% (Fig. 2a). A similar trend was observed also excluding rare species (recorded only in one month in each year) which are 69, 54, 38, respectively (Fig. 2a) and analysing the records at the genus level: 49, 36, and 26 (Fig. 2a). In general, Anthoathecata represented about 40% of the records and Leptothecata 60%; this proportion remained constant across the three considered survey periods (Supplementary Material SM1). The species richness in each year showed a strong linear negative correlation with the average sea surface temperature (SST) recorded in the studied area ($r = 0.92$) (Fig. 2b): hydrozoan diversity decreased as temperatures increased.

The hydrozoan communities were significantly different from each other in each survey period, as confirmed by PERMANOVA (Supplementary Material SM5).

During 1980, the annual variation of the species richness showed minimal values in summer with a strong increase in autumn, reaching a peak in November. During 2004, the trend overlapped with the previous one from January to June, while in the summer–autumn period, the species richness showed an evident decrease in comparison with 1980. In 2024, the tendency was towards a general homogeneity along the year with summer minimum (Fig. 2c).

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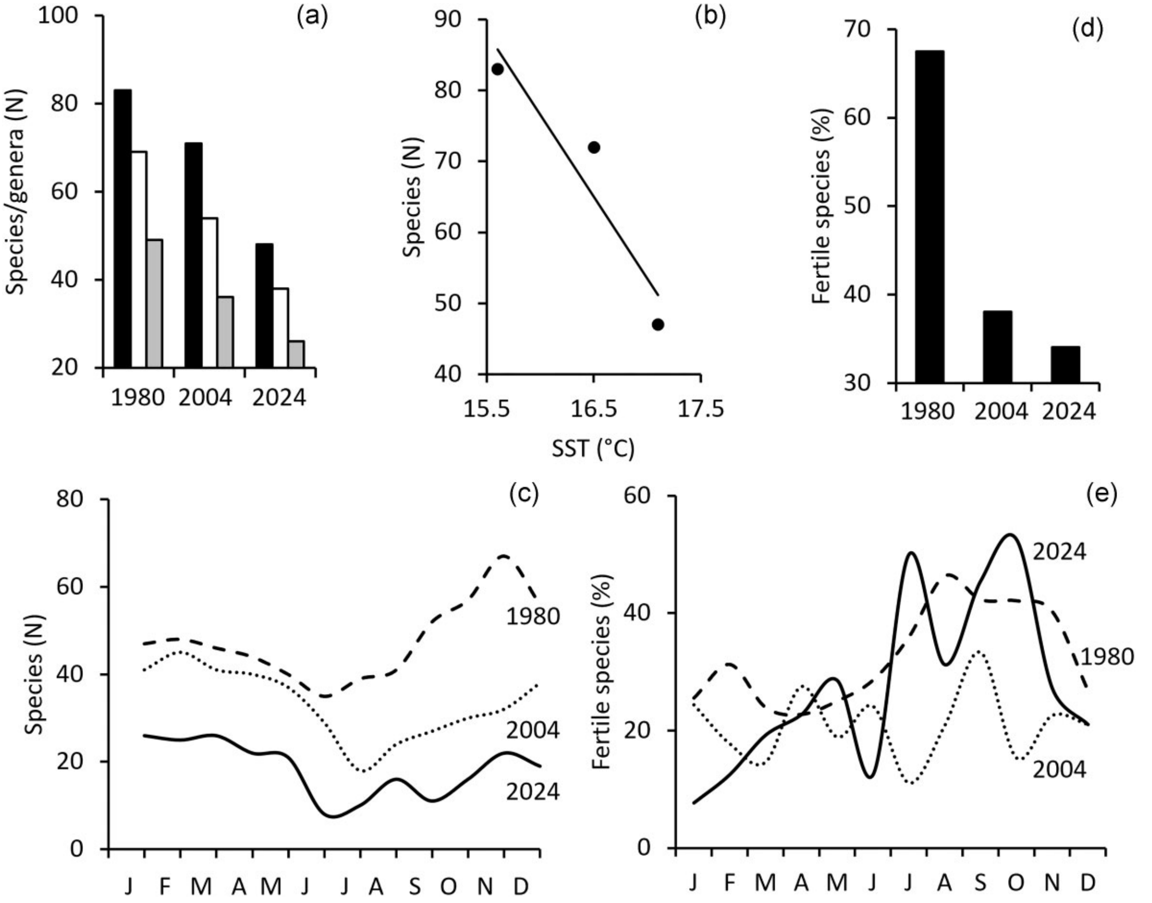

Figure 2. (a) Trend of hydroid richness across the three observation periods obtained considering: all the species (black bars), the species recorded in more than one month per year (white bars), and all the genera (grey bars). (b) Strong linear negative correlation between the average SST and recoded number of species in the three surveyed periods ($r = -0.95$; $R^2 = 0.91$; $P = 0.1$). (c) Annual trend of the species number recorded in each month during the three sampling periods. (d) Percentage of fertile species recorded in the three considered years, showing a marked quantitative decrease. (e) Monthly occurrence of fertile species revealing a consistent peak in late summer across all the 3 years of survey.

The nMDS plot performed on the whole abundance dataset showed that during 1980 all bathymetric ranges were different from the others, particularly the first two depth ranges (0–0.5 and 0.5–5 m) that were clearly cut-separated from those under 5 m. On the contrary, in the following years all the depth ranges were grouped together without evident bathymetric patterns in species occurrence and abundance (Fig. 3a). Based on PERMANOVA, the same depth range across the three years was always statistically different (Supplementary Material SM5). In fact, the percentage of species spread throughout the whole bathymetric range was significantly greater in 2004 (39%) and 2024 (28%) compared to 1980 (10%) (Supplementary Material SM1). Regarding the community's annual trajectory, the situation appeared the opposite. The seasonal differences, already evident in 1980, become wider in the following surveys as confirmed by PERMANOVA (Fig. 3b, Supplementary Material SM5). The PERMDISP analysis detected significant differences in dispersion of hydrozoan assemblages ($P = 0.001$). Between 1980 and 2004 differences arose all around the year while significant difference between 2004 and 2024 occurred only in spring (Supplementary Material SM6).

This pattern was due to a different persistence of each species. In fact, during 1980, 29% of the observed species occurred for at least 10 months, while this value almost reduced in 2004 (24%) and dropped to 11% in 2024 (Supplementary Material SM1).

Finally, the percentage of fertile species dropped from 67% to 34% (Fig. 2d), although the seasonality of sexual reproduction remained similar over time with a higher incidence in late summer (Fig. 2e). Regarding the modalities of sexual reproduction, it was evident an increase of species that reproduce via fixed sporosacs in comparison with those that free medusae or medusoids. In fact, the ratio between the species employing these strategies passed from 1.7 (52 with sporosacs vs. 30 with medusae or medusoids) in 1980, 1.9 (46 vs. 24) in 2004 to 2.5 (34 vs. 13) in 2024.

Variations of conspicuous species

As already stated, numerous species progressively disappeared between 1980 and 2024. Although a large part of these missing species was inconspicuous or rarely recorded, some large, and abundant species whose presence could not go unnoticed showed a drastic reduction. Remarkable differences emerged when the sum of the monthly pseudo-abundances for each year were compared.

For example, *Coryne muscoides* (Linnaeus, 1761) which was one of the main components of the 0-5 m belt in all the months in 1980, progressively became extremely scarce across the year, being recorded only in winter periods (Figs 4a

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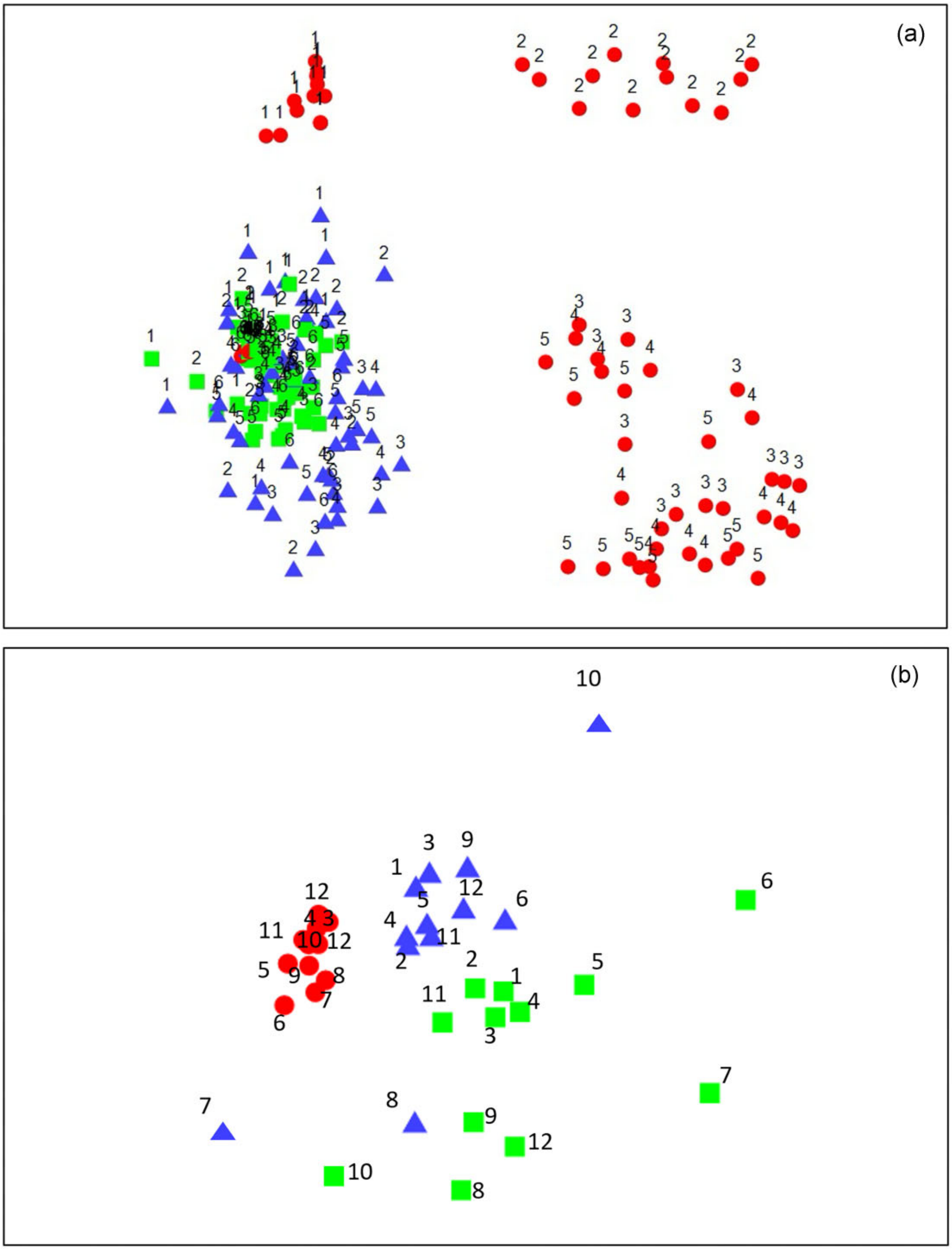

Figure 3. nMDS plots performed using the whole species abundance dataset. (a) The clear bathymetric zonation observed in 1980 (red dots) completely disappeared in 2004 (blue triangles) and 2024 (green squares); numbers referred to the five discrete depth ranges (1: 0–0.5; 2: 0.5–5; 3: 5–10; 4: 10–15; 5: 15–20 m)). (b) Temporal trajectory of the communities, showing greater dispersion in 2004 (triangles) and 2024 (squares) compared to the homogeneity observed in 1980 (dots); number progression indicates month.

and 5a). A similar situation was shown by *Eudendrium capillare* Alder, 1856 that in 1980 was very abundant near the surface, progressively reduced in 2004 and became very rare in 2024. In the same period, the species increased its bathymetric range being present in the entire transect (Fig. 5b). In the shallow depth range, the abundance of *A. octodonta* decreased almost to half between 1980 and 2004 remaining stable in 2024 (Figs 4b and 5c).

In the 0.5–10 m belt, *Ectopleura larynx* (Ellis and Solander, 1786), present with numerous large tufts during winter 1980, after a strong reduction in 2004 completely disappeared in 2024 (Figs 4c; 5d).

In 1980, several eurybathic species like *Halecium* spp. [*H. beanii* (Johnston, 1838), *H. delicatulum* Coughtrey, 1876, *H. halecinum* (Linnaeus, 1758), *H. nanum* Alder, 1859, and *H. pusillum* (Sars, 1857)] were particularly abundant during the autumn months. This group of species has dramatically reduced since 2004 and is now confined in January–March (Figs 4d and 5e). A similar trend was shown by *Sertularella crassicaulis*, a particularly evident species due to its white coloration

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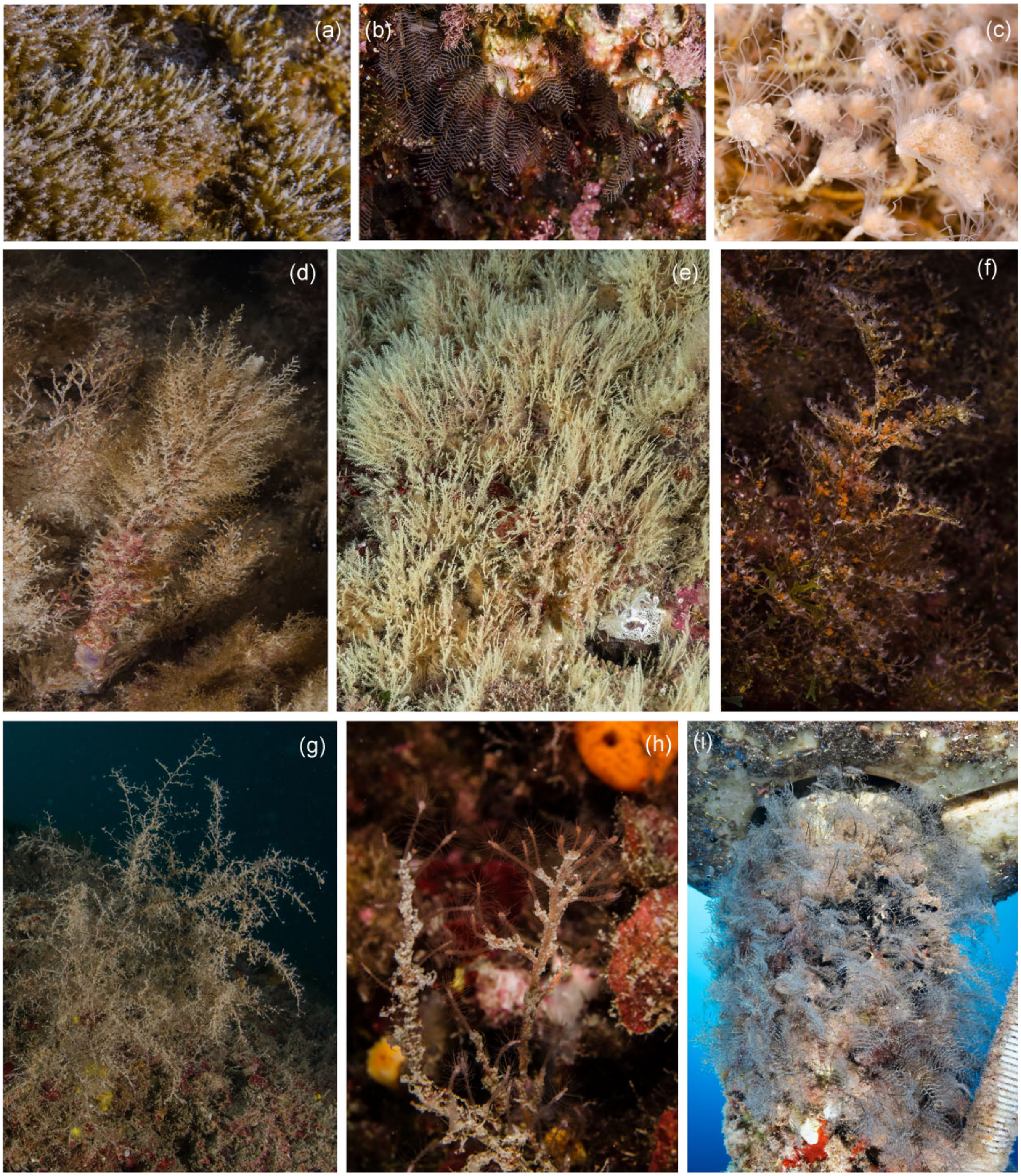

Figure 4. Examples of the main recorded species in the hydroid assemblage of the Portofino Promontory. *Coryne* spp. (a) *Aglaophenia octodonta* (b) and *Ectopleura larynx* (c) in the shallower belt. *Halecium* spp. (d) *Sertularella ellisii* (e), *Eudendrium racemosum* (f), and *E. glomeratum* (g). The two thermophilic species *Corydendrium parasiticum* (h) and *Pennaria disticha* (i), found in high abundance near the Aurora transect.

and its typical epibiotic habitus on the gorgonians *Eunicella cavolini* (Koch, 1887). The species was absent from the transect after 2004 (Fig. 5f). The same situation was recorded for *Sertularella ellisii* (Deshayes and Milne Edwards, 1836) (Figs 4e and 5g).

Some *Eudendrium* species showed different temporal trends. *Eudendrium racemosum* typically recorded during summer in 1980 was strongly reduced in 2004 at all depths but in 2024 showed signals of recovery, especially between 0.5 and 5 m and became perennial (Figs 4f and 5h). The winter species *E. glomeratum* persisted in 2004 with similar abundance to 1980, and was strongly reduced in 2024 (Figs 4g and 5i); *E. ramosum* (Linnaeus, 1758) suffered a sharp, continuous decline since 2004 although it persisted below 10 m depth (Fig. 5j).

Finally, close to the transect, *Corydendrium parasiticum* and *Pennaria disticha*, once absent or scarcely represented, are now very abundant (Fig. 4h, i).

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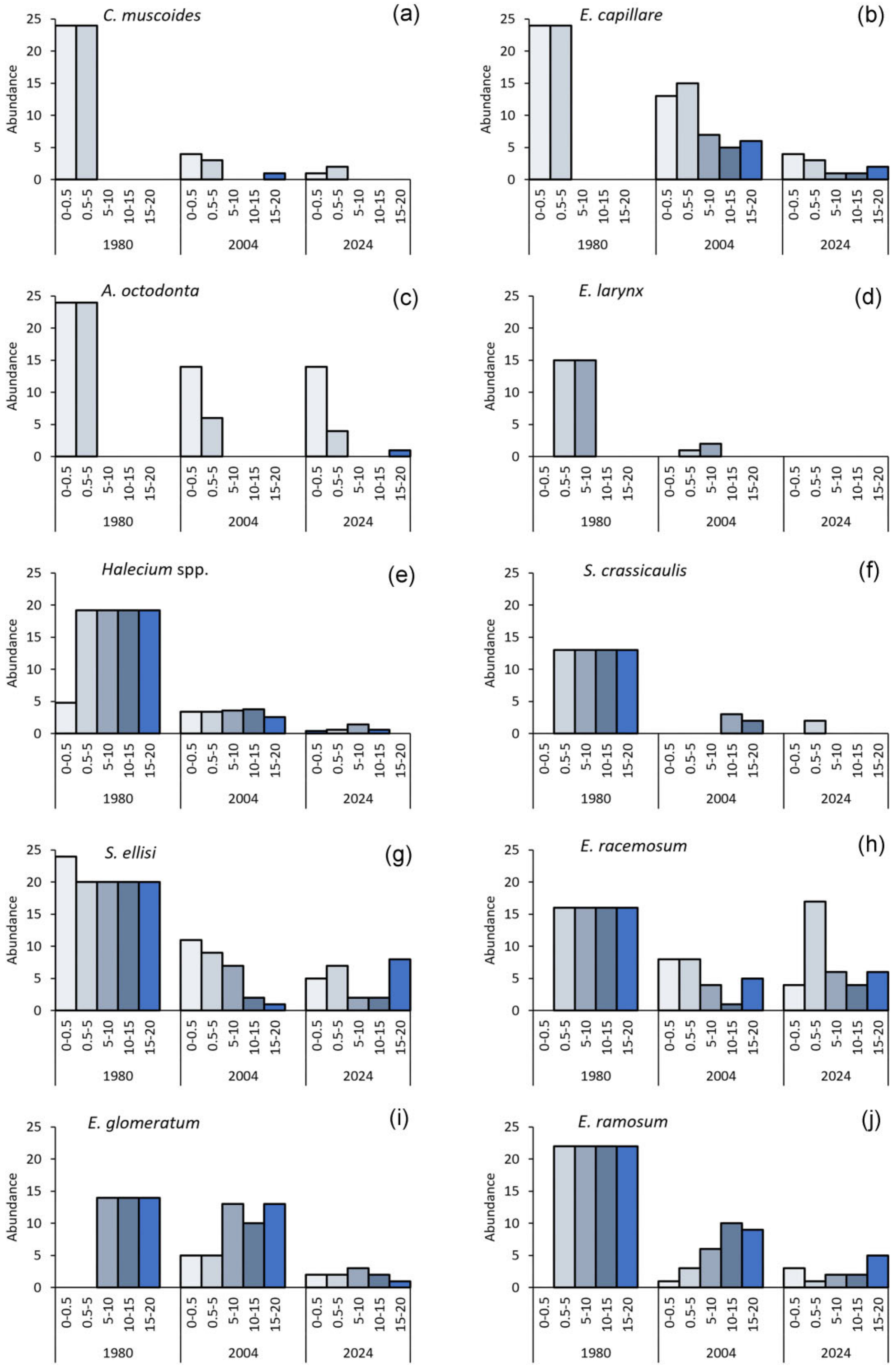

Figure 5. Temporal and bathymetric variation of some conspicuous species obtained by the sum of monthly species pseudo-abundance in each year. In the shallow belt, *Coryne muscoides* (a) and *Eudendrium capillare* (b) progressively disappeared, while *Aglaophenia octodonta* (c) persisted at lower depths. *Ectopleura larynx* (d), which characterized the 0.5–10 m depth range, completely disappeared after 2004. Several eurybathic species, such as *Halecium* spp. (e), *Sertularella crassicaulis* (f), and *S. ellisii* (g), declined across all depths. The typical summer species *E. racemosum* (h) showed a strong reduction at all depths. *E. glomeratum* (i) persisted with similar abundance until 2004, disappearing only in 2024, while *E. ramosum* (j) continuously declined but persisted below 10 m depth.

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Discussion

Thanks to long-term monitoring (Sarà et al. 1978, Boero and Fresi 1986, Puce et al. 2009, present work), and the numerous research projects conducted on single target species or groups of species (Boero et al. 1986, Bavestrello et al. 1992, 2000, 2006), the hydroid assemblage of the Portofino Promontory is probably the best known in the world in terms of its diversity, bathymetric and seasonal distribution, and phenology.

Seasonality is one of the main ecological characteristics of benthic hydrozoans, probably due to competition for substrate with algae and to temperature tolerance. Seasonal cycles allow hydroids to occupy the same substrate by the alternation of different species, each with a definite period of activity, while persisting as resting hydrorhizae (Boero and Fresi 1986, Bavestrello et al. 2006, Bouillon et al. 20066).

The available data suggest that a mosaic of physical factors, biotic interactions, and internal clues triggers the hydroid cyclic occurrence but, particularly for temperate areas, water temperature plays a pivotal role (Brock 1974, Boero and Fresi 1986, Arillo et al. 1989, Bavestrello and Arillo 1992, Bavestrello et al. 2006). Very likely, water temperature is also involved in the bathymetric distribution of different species. For example, *Eudendrium glomeratum*, which in shallow waters makes typical facies during winter months before disappearing in summer, is perennial, with very large colonies under the summer thermocline, at about 50 m depth (Bavestrello and Arillo 1992).

The sensitivity of hydrozoans toward temperature changes makes them an ideal probe to detect the influence of global changes on benthic communities. In a span of time of 44 years, the hydroid communities of Portofino showed dramatic differences in species richness and abundance consistent with the trend observed in 2004 (Puce et al. 2009).

According to PERDISP analysis, the main shift in the assemblage composition occurred between 1980 and 2004. In fact, between 1980 and 2004 differences arose all around the year while significant difference between 2004 and 2024 occurred only in spring. Other studies (e.g. Gatti et al. 2015) indicated that, in the Ligurian Sea, the 1990s were a turning point between two distinct situations. The multivariate analyses at the community level, comparing the three survey periods (1980, 2004, and 2024) revealed opposite patterns in bathymetric and seasonal distribution. In 1980, the vertical zonation showed two distinct biocoenotic units, separated by a sharp discontinuity. Up to 5 m depth, the community consisted of a set of species adapted to high levels of environmental energy, which remained remarkably stable over time. In contrast, deeper communities showed greater variation in timing, with distinct patterns in the warm and cold seasons (Boero and Fresi 1986). By 2004, nearly 30% of the shallow-water species and 60% of deep-water species had disappeared, and the bathymetric distributions of the remaining species became broader. Furthermore, more than 50% of the species shifted to deeper waters, while only a few deep-water species (<10%) moved towards the surface, possibly colonizing substrates freed by disappearing species (Puce et al. 2009). By 2024, this trend had dramatically progressed, with a remarkable loss of species at all depths and a strong homogenisation of the assemblage.

Bathymetric homogenization was primarily due to the loss of characteristic shallow vs. deep species. In 1980, a virtually continuous belt of corynid hydroids and *E. capillare* characterized the shallowest depth. During winter, abundant tufts of *Ectopleura larynx* were also present. However, all these species were either lost or significantly reduced in 2024, with only *Aglaophenia octodonta* remaining.

From a temporal perspective, the significant difference observed at the seasonal level is due to a drastic reduction of the number of species able to face warmer conditions. In 1980, summer species accounted for about 42% of the total, while this value dropped to approximately 25% in 2004 and 21% in 2024.

These patterns align with the temperature variations recorded over the same period. The trend of the SST data from NOAA (www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl), available since 1948, clearly exhibits a warming trend. However, this trend was not linear: it included a cooling phase, particularly evident during the winter and spring, with its relative minimum occurring in the early 1980s. This minimum was followed by a continuously warming phase (Azzola et al. 2024). This scenario indicates that the first sampling of the hydroid community of the Portofino transect was performed during the coolest period of the last century, when cold-affinity species flourished.

This trend fits with the observed decline in species richness within the hydroid assemblage, which was nearly halved by 2024. This datum is unlikely to be influenced by the expertise of collectors and taxonomists, as the reduction remains evident even when rare species are excluded, or diversity is assessed at generic level.

This trend was shared also by some large, easily recongnizable species. For example, large species of the genus *Halecium* have a cold-water affinity (Gravili et al. 2017). During the sampling of 1980, nine species of *Halecium* were recorded, sometimes with impressive abundance. The species number remained the same in 2004, although the abundances were drastically reduced. By 2024, we recorded only seven species with negligible abundance.

In the 1980s, *E. glomeratum* formed a dense facies below 10 m depth during the winter. A study conducted in 1982–1983 indicated a maximal value of 57 col. m^{-2} in December, with a biomass of about 5 g DW m^{-2} (Boero et al. 1986). Today, the species is rarely found also in wintertime.

In the meantime, some hydroids typical of the Southern Mediterranean were first recorded in the studied area starting in 2004. *Pennaria disticha*, common in the southern Tyrrhenian Sea and sporadically recorded in the Ligurian Sea (Rossi 1961, Bianchi and Morri 1994), became extremely abundant at 0–5 m during the summers of 2004 and 2018 (Puce et al. 2009, Bianchi et al. 2019). This thermophilic species, along with *Corydendrium parasiticum*, has been found in abundance near the Portofino transect since 2018, whereas both species were absent from the whole Portofino Promontory forty years ago (Bianchi et al. 2019). A shift from *Ectopleura* to *Pennaria* dominated assemblages was also observed in other localities (Bianchi et al. 2018, Di Camillo et al. 2018). Also, some thermophilic NIS are now abundantly recorded in our transect. One example is *E. moulouyensis* Marques et al. 2000, recorded since 2004 in Portofino (Puce et al. 2009). This species, originally described in Morocco (Marques et al. 2000) and known from Southern Italy (De Vito et al. 2008), is now expanding across the whole Mediterranean basin (González-Duarte et al. 2016). Moreover, also the lessepsian *Clytia linearis* coming from the Indo-Pacific Ocean and recorded in

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1938 in the Suez Canal is now abundantly diffused in the studied area (Boero and Bouillon 1993; Boero et al., 2005).

The percentage of fertile species dramatically decreased in the more recent sampling, with a shift towards a high incidence of asexual reproductive strategies. Nevertheless, the seasonality of sexual reproduction remained consistent over time, with the highest incidence occurring in late summer. Hydrozoans exhibit a wide variety of life cycles and reproductive processes (Boero and Bouillon 1993, Bouillon et al. 20066, Boero et al. 2008). In the considered surveys, the percent of species that reproduce by forming fixed sporosacs increased whereas those with free medusae or medusoids decreased. The production of polyp buds versus planktonic medusae may promote offspring survival and maintenance of the local population rather than enhance dispersal and genetic diversity at the cost of greater survival risk (Boero 1984, Bouillon et al. 2004). Moreover, it is well known that temperature plays a primary role in controlling the shift between reproductive modes, with the incidence of sexual reproduction inversely related to water temperature (Bouillon et al. 20066). From a trophic point of view, it is possible to put in evidence a strong reduction of carnivorous species like *Eudendrium* spp. (Gili and Coma 1998, Di Camillo et al. 2012), Tubulariidae (Gili et al. 1998), Corynidae (Miglietta et al. 2000) and Hydractiniidae (Christensen 1967, Bavestrello 1985) that indicates a trophically downgraded community.

In conclusion, changes in the species composition of hydrozoan assemblages—including shifts in seasonality, bathymetric distribution, and reproductive periods—are crucial indicators for assessing the influence of global change on hard substrate marine benthic communities. As suggested by several authors (e.g. Riedl 1959, Mergner 1977), the species richness, morphologic plasticity, and ecological specialization of this group make it a reliable indicator of environmental quality. In particular, shallow, macroscopic, well-recognizable species reflect climate change and may be effectively considered in monitoring programmes.

Originally the Portofino transect aimed at testing two contrasting models regarding the drivers that determine the vertical distribution of hard bottom benthos, namely light penetration (Pérès and Picard 1964) and water movement (Riedl 1971). The extinction rates of both variables are strongly overlapping at the sampling site, and this cannot single out a prevalence of one over the other (Sarà et al. 1978). The outcome of the present study, together with those on mass mortalities in the Mediterranean Basin (Rivetti et al. 2014) and many papers on benthic mass mortalities due to thermal stratification in the Mediterranean, clearly show that temperature is a major driver of the vertical distribution of species that did not receive proper attention as such.

Besides physical variables (water movement, light penetration, and thermal stratification), also biotic interactions also play a major role in determining the seasonality of species, with a prevalence of algae during the summer months (when light is stronger, temperatures are higher, and water movement is reduced) and hydroids during winter months (when light and temperature are lower, and water movement is higher). Global warming is leading to higher temperatures, with unfavourable conditions for species of cold-water affinity, and favourable conditions for both algae and hydroid species with warm water affinities.

The possibility of performing serious studies on biodiversity requires high taxonomic skills (Boero 2001, 2010). Our results support the claim made by Mammola et al. (2023), who showed that many papers purportedly addressing biodiversity often overlook its fundamental component: species. Over the past four decades, the hydrozoan assemblage of the Portofino Promontory has undergone a dramatic shift, marked by the disappearance of species with temperate affinities, only partially replaced by those adapted to warmer waters. It is likely that this trend is not confined to hydrozoans alone, underscoring the need for more detailed, species-level studies of biodiversity.

Moreover, biodiversity exhibits strong seasonal variation, and single sampling events using standard procedures may not provide an adequate representation. The neglect of taxonomic accuracy in ecological studies likely undermines the reliability of many investigations claiming to address biodiversity.

Given their high diversity and complex life cycles, which are highly sensitive to seasonal changes, hydrozoans serve as particularly effective ‘sensors’ of biodiversity shifts, offering valuable insights into ongoing changes (Yilmaz et al. 2020). Our study reveals a transition from a seasonally dynamic, species-rich assemblage—featuring both warm- and temperate-affinity species—to a less diverse community dominated by warm-affinity species and characterized by altered phenological patterns.

If similar studies are conducted across other locations and taxonomic groups, they may offer a more accurate assessment of biodiversity change than many current approaches to tracking shifts in the diversity of life.

Author contributions

Simona Moglia (Data curation [equal], Formal analysis [equal]), Federico Betti (Visualization [equal], Writing – original draft [equal]), Ferdinando Boero (Conceptualization [equal], Data curation [equal], Writing – original draft [supporting], Writing – review & editing [supporting]), Martina Canessa (Data curation [equal], Formal analysis [equal], Investigation [equal], Writing – original draft [equal]), Cristina Gioia Di Camillo (Data curation [equal], Investigation [equal], Validation [equal], Writing – original draft [equal]), Francesco Enrichetti (Investigation [equal], Validation [equal], Writing – original draft [equal]), Stefania Puce (Data curation [equal], Formal analysis [equal], Writing – original draft [equal]), and Giorgio Bavestrello (Project administration [equal], Supervision [equal], Writing – original draft [equal])

Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

Conflict of interest: None declared.

Data availability

The data supporting the outcomes of this study are included in the article and on Zenodo repository. Citation: Canessa, M. (2025). Moglia et al., 2025_Long-Term Monitoring of Hydrozoan Fauna of the Portofino Promontory [Data set]. Zenodo. https://doi.org/10.5281/zenodo.15242280.

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