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Multiscale pH fluctuations on a stable algal reef community (SE Sardinia, Tyrrhenian Sea)

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The Mediterranean Sea is threatened by ocean acidification and warming, in combination with habitat loss, pollution, invasive species, and overexploitation. Assessing local high-frequency pH variability in the context of relevant basin-scale time series data is essential to understand ecosystem vulnerability. We report the results of the Italian national pH monitoring based on the Marine Strategy Framework Directive, and the pH dynamics observed at Capo Carbonara. An experimental station equipped with a pH sensor and CTD probe was deployed at 32 m depth on a sandy bottom bordered by Coralligenous assemblages. Physical and biogeochemical variables were continuously recorded over 345 days and analyzed through additive time series decomposition. The benthic assemblages were surveyed by photographic and destructive sampling in summer and autumn 2016 and spring 2017 on algal reef and sandy bottom, to describe the biological components undergoing and contributing to the pH fluctuations. Seasonal pH variability ranged up to 0.2 units annually and 0.1 units daily, with maxima in January and minima in August, while the range of pH on the basin scale had higher mean values and exceeded local variability. Assemblage changes were driven by algal turf development and the invasive *Caulerpa cylindracea*. Coralligenous taxa appear stable, despite the substantial natural pH variability, shaped by meteo-marine conditions, water mass circulation, Saharan dust inputs, and benthic biological processes, with primary producers and calcifiers exerting a key influence. The ongoing trend of increasing temperatures and decreasing pH may threaten the Coralligenous ability to cope with the shifting future boundaries of such variability.

KEYWORDS

ocean acidification, time-series observations, monitoring, Mediterranean, biogeochemical trends, algal reefs, biological effects

Highlights

- Mean Tyrrhenian surface pH is 8.33, but drops to 8.07 at Capo Carbonara coralligenous.
- High-frequency pH fluctuations are twice the open-sea mean multidecadal pH decrease.
- Intrusion of Atlantic water and Saharan dust outbreaks affect local pH variability.
- Coralligenous assemblage had long-lived, stable components and seasonal turf development.
- Future shifting boundaries of variability by OA may impair Coralligenous tolerance.

1 Introduction

The Mediterranean Sea covers an area an area of 2.5 million km^2 and a volume of 3.7 km^3. Characterized by its own semi-enclosed thermohaline circulation, it acts as a small-scale ocean exhibiting pronounced spatial gradients where salinity, temperature, alkalinity, and stratification increase eastward (Bethoux et al., 1999). Offshore waters are predominantly oligotrophic to ultra-oligotrophic, contrasting sharply with coastal areas impacted by anthropogenic nutrient input and land-based pollution (Danovaro, 2003; Piazzi et al., 2012; Jiménez-Casero et al., 2025). Recognized as a global biodiversity hotspot containing approximately 20% endemic species, the Mediterranean is simultaneously a climate change hotspot warming 20% faster than the global average (Micheli et al., 2013; Fader et al., 2020).

Multiple cumulative stressors threaten this basin, including overexploitation, increase in water temperature and salinity, increasing severity of heatwaves, deoxygenation, invasive species, and ocean acidification (OA) (Marullo et al., 2013; Adloff et al., 2015; Flecha et al., 2015; Iona et al., 2018; Boucher and Billard, 2020; Hassoun et al., 2022; Reale et al., 2022). Despite the basin's high total alkalinity and overturning circulation - which provide a substantial buffering capacity and facilitate anthropogenic CO_2 absorption (Álvarez et al., 2014) - open-sea surface waters exhibit a steady, continuous decline in pH estimated at approximately 0.017 units $decade^{-1}$ (Hassoun et al., 2022; Solidoro et al., 2022). Due to its low volume and heavily populated coastlines, Mediterranean ecosystems are exceptionally vulnerable to these combined pressures (Zeng et al., 2015).

While open-ocean surface waters show predictable, long-term acidification trends, coastal environments display far greater complexity (D'Agostino et al., 2023). In nearshore habitats, pH fluctuates by up to 1 pH unit across hourly, daily, and seasonal scales (Kapsenberg and Hofmann, 2016). This short-term variability is driven by local oceanographic features, freshwater runoff, and metabolic signals—specifically the net balance between community primary production and respiration (Wootton et al., 2008; Carstensen and Duarte, 2019). Day-time photosynthesis by primary producers elevated by nutrient availability uptake dissolved inorganic carbon and elevates pH, whereas night-time community respiration lowers pH and alters local carbonate saturation states (Provoost et al., 2010; Kwiatkowski et al., 2016).

Recent high-frequency monitoring across the Mediterranean demonstrates that these localized biological "excursions" can exceed projected end-of-century anthropogenic OA trends (Kapsenberg et al., 2017b; Carbonne et al., 2022). These natural fluctuations can either temporarily buffer or exacerbate global acidification, creating dynamic mosaics where marine organisms must continuously adapt to rapid chemical shifts (Teixidó et al., 2024). However, interpreting whether these short-term biological signals mask or mitigate long-term anthropogenic trends remains a major challenge for temperate coastal research (Ingrosso et al., 2021). In this context, determining whether coastal ecosystems are entering a state of permanent chemical stress requires datasets that link historical baselines with current trends (Goyet et al., 2016).

The interaction between long-term acidification and short-term fluctuations is particularly critical for biogenic calcareous habitats, such as coralligenous reefs (Gómez-Gras et al., 2021). Coralligenous structures are priority habitats built over centuries to millennia primarily by calcifying red algae (Basso et al., 2022). Their structural integrity relies on mineral phases that are highly sensitive to declining pH and carbonate saturation: members of the Corallinophycidae precipitate high-Mg calcite, while fully calcified Peyssonneliales form aragonitic thalli (Basso, 2012). Because high-Mg calcite and aragonite represent the most soluble biogenic carbonate mineral phases, ongoing ocean acidification threatens coralligenous reefs with accelerated dissolution and structural weakening (Diaz-Pulido et al., 2012; Ragazzola et al., 2012; Teixidó et al., 2024). When night-time community respiration depresses pH levels further within benthic boundary layers, calcifying organisms are pushed toward their physiological limits (Kwiatkowski et al., 2016). Despite these risks, *in situ* studies investigating how biologically induced short-term pH shifts interact with long-term baseline acidification in shallow coralligenous habitats remain sparse (Teixidó et al., 2024).

To establish robust baselines, monitor ecosystem health, and detect early threats to Mediterranean benthic systems, long-term and high-frequency time-series observations are essential (Hofmann et al., 2011). Relying solely on low-density, open-ocean sampling risks overlooking the dynamic micro-environmental conditions that nearshore organisms actually experience. To address these gaps, this study evaluates the range and drivers of present-day pH fluctuations at a pristine shallow coralligenous reef, placing short-term variability within the broader framework of Mediterranean ocean acidification. Specifically, pH time-series records gathered during the initial Marine Strategy Framework Directive (MSFD) assessment (2013) for Italian seas were analyzed to discuss high-frequency localized observations at the study site in the context of regional basin-scale trends. Furthermore, field monitoring was conducted to characterize the local environment and investigate how the temporal dynamics of shallow coralligenous reefs interact with physical and biological drivers under ongoing climate change.

2 Materials and methods

2.1 Study site

The site selected for the deployment of the pH monitoring station is the Marine Protected Area (MPA) "Capo Carbonara"

(Figure 1) located on the south-eastern coast of Sardinia. The criteria that lead to the selection of the study area were the oceanographic regime and dynamics of the Mediterranean (Tyrrhenian) sub-basin in which the MPA is located and the presence of habitats of high conservation interest and protected species such as *Posidonia oceanica* meadows, and coralligenous species of soft corals (order *Alcyonaceae* order). Water circulation in the Tyrrhenian basin is constrained by two main straits: the Sardinia Channel and the Corsica Channel, which connect the Tyrrhenian Sea to the western and eastern Mediterranean (Buffett et al., 2017). This basin contains several water masses with distinct temperature and salinity characteristics, named after their regions of origin. The Tyrrhenian basin is influenced both by the cyclonic circulation of surface Atlantic water (Atlantic Water, AW) a surface water mass characterized by low salinity and variable temperature, located at depths between 0 and 200 meters. The AW surface current enters through the Sardinia Channel, following a broad path along the Sicilian and Italian coasts (Iacono et al., 2021). The oceanographic setting of this area is influenced by the wind-driven flow through the Bonifacio Strait, which affects local circulation. On a regional scale, the Tyrrhenian waters enter the Ligurian Sea primarily through the Corsica Channel, forming the Northern Current as established by Astraldi and Gasparini (1992). Cyclonic features like the 'Cold Tyrrhenian Eddy' are part of a more complex system where the northward transport through the Corsica Channel is the dominant mechanism for water mass and heat exchange between the Tyrrhenian and Ligurian basins. This dynamic setting, characterized by the interaction of different water masses and intense atmospheric forcing, makes Capo Carbonara a key site for monitoring the variability of the carbonate system in the Tyrrhenian/Western Mediterranean. On the other hand, the Levantine Intermediate Water (LIW) or Levantine water, a high-salinity water mass formed in the eastern Mediterranean and typically found at depths of 200–600 meters, mixing with surface and deep water plays an essential role in vertical exchanges within the Tyrrhenian basin. In fact, its entry into the same basin takes place in the deep waters between Sardinia and Sicily. In the southern sector of Sardinia, both Atlantic Water (AW) and Levantine Intermediate Water (LIW) flow eastward to westward along the southern Sardinian coastline (Iacono et al., 2021).

2.2 Biogeochemical-physical and meteorological data

Available surface (depth < 25 m) pH records, collected for the first assessment (2013) of the Marine Strategy Framework Directive (MSFD) within Descriptor 7 (*Permanent alteration of hydrographical conditions does not adversely affect marine ecosystems;* González et al., 2015) by the Italian national programme of marine coastal monitoring and by *ISPRA National Tide Gauge Network* (https://www.mareografico.it) during the years 2006–2009 and 2011-2012 (Finoia, 2013; Babbini et al., 2013) were analyzed as a reference for the Mediterranean sub-basins (Western Mediterranean Sea and Tyrrhenian Sea) (Figure 2). Data were collected by regional environmental agencies (ARPA) SiDiMar campaigns at fixed stations along the Italian coast, and also obtained from the Italian National Tide Gauge Network (Rete Mareografica Nazionale – RMN, https://www.mareografico.it/), managed by the Italian Institute for Environmental Protection and Research (ISPRA). This network provides high-quality monitoring of physical and chemical variables across the Italian coasts. To evaluate the regional context, offshore carbonate system data were obtained from the CNR (National Research Council) ARCo project (Adriatic-Ionian-Regional-Coupled model). The ARCo dataset provides high-resolution

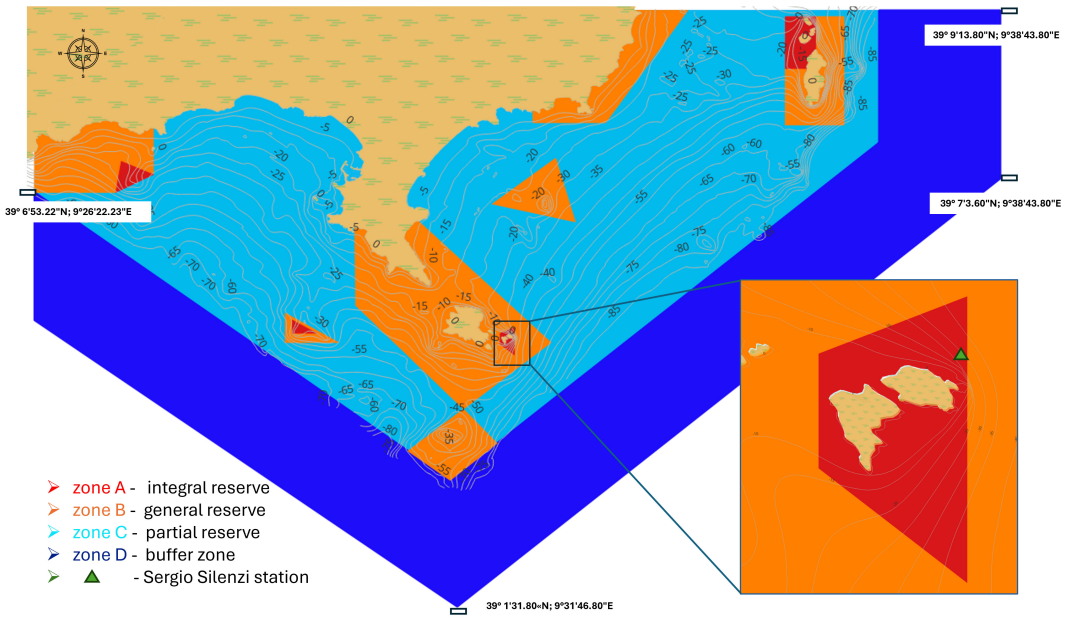

FIGURE 1
Map of the Capo Carbonara Marine Protected Area (southeastern Sardinia, Italy) showing the different protection zones. The inset map shows the Variglioni (rocky islets) of Cavoli island, located in Zone A (no-take reserve); the green triangle marks the exact location of the "Sergio Silenzi" monitoring station.

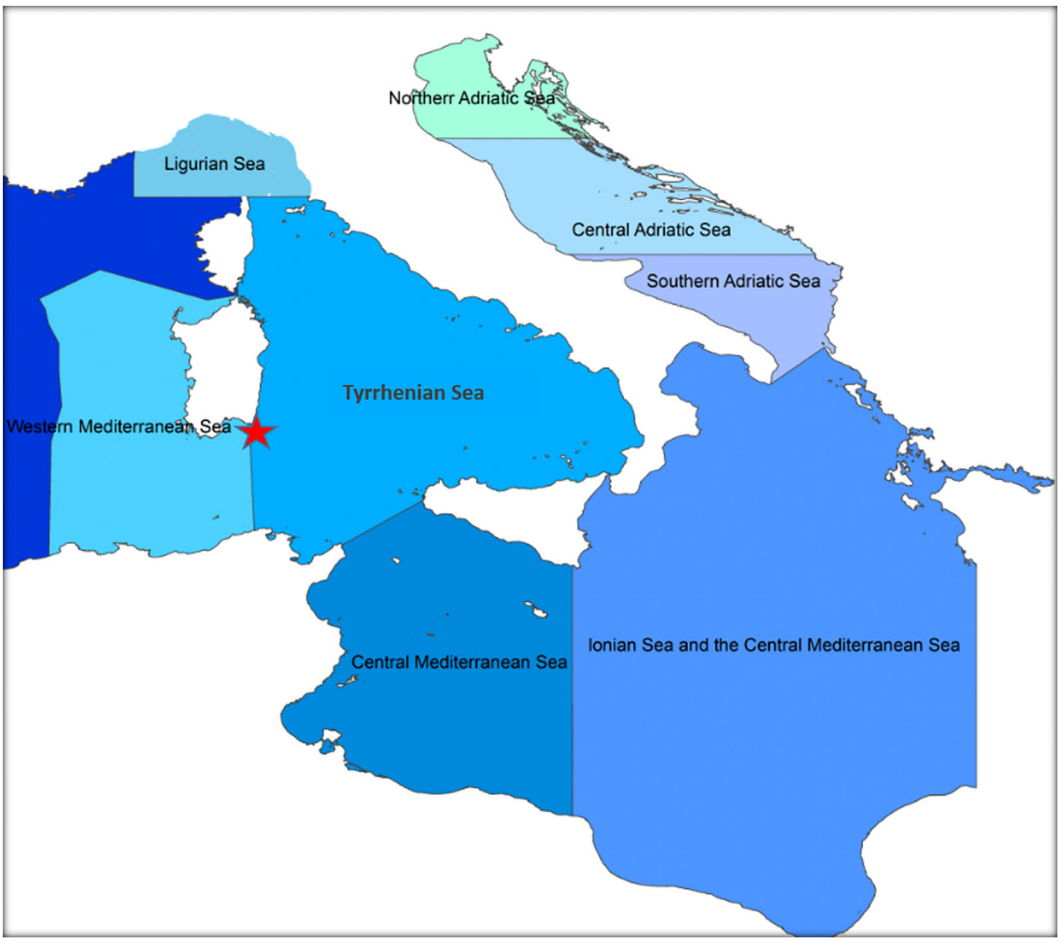

FIGURE 2
Mediterranean sub-basin names and borders defined for the first assessment of the Marine Strategy Framework Directive (MSFD). Red star: location of Cavoli Island, close to the border between the Western Mediterranean Sea and Tyrrhenian Sea sub-basins.

biochemical variables through a combination of periodic oceanographic cruises and numerical reanalysis. The discrete pH measurements used for our regional comparison were collected during dedicated cruises in the Western Mediterranean and Tyrrhenian Sea, where seawater samples were analyzed following strict international protocols (e.g., Dickson et al., 2007). The ARCo system is specifically designed to couple physical oceanographic processes with biogeochemical cycles, providing a reliable baseline for the Mediterranean's chemical state.

Regional background data were also integrated with offshore environmental time-series from the ISPRA-ENI monitoring network, specifically from the platforms located in the Adriatic Sea.

Data were integrated from the ISPRA PR *Ripascimenti* project, carried out in the Adriatic and Tyrrhenian Sea, which monitors the environmental impact of sand extraction for coastal nourishment. The integration of the PR *Ripascimenti* data is particularly relevant as it provides standardized pH measurements from coastal shelf areas (Supplementary Table 1). The national pH time series data are heterogeneous due to being collected with different probes, each characterized by varying levels of accuracy and precision, and expressed on NBS or total scale (Finoia, 2013; Supplementary Table 1). National pH time series data were then compared with those collected by the *in situ* probes of the "Sergio Silenzi" monitoring station, in order to put the high-frequency data from the latter in the context of the background values at the regional scale.

ISPRA "Sergio Silenzi" station was located within a zone A (fully protected) (Figure 1A) called "Variglioni within Cavoli Island" (Figure 1B). The station was placed at a depth of 32 m on a sandy seabed surrounded by rocky walls on three side (1–2 m apart). The rocky walls hosted a coralligenous assemblages characterized by high density of the gorgonians *Eunicella cavolini* (Supplementary Figure 1A) and *Paramuricea clavata* (Supplementary Figure 1B).

The monitoring system of the "Sergio Silenzi" station consisted of a pH sensor and a CTD for measuring conductivity (salinity) and temperature (Figure 3). The pH measurement was performed by the autonomous seawater SeaFET Ocean pH sensor (SeaFET™ V2 Ocean pH Sensor, https://www.seabird.com/products/seafet-v2-ocean-ph-sensor). These sensors for ocean pH measurements use the Ion-Sensitive Field Effect Transistor (ISFET) potentiometric technology of the Honeywell DuraFET (Martz et al., 2010). The commercially available sensor SeaFET (Sea-Bird Scientific) has an excellent accuracy of 0.050 pH units in a pH range between 6.5 and 9.0 units. SeaFET is an electrochemical pH sensor that can provide the high frequency (10 Hz maximum) measurements.

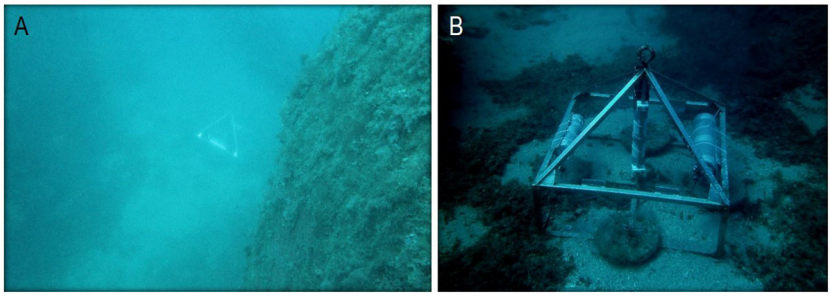

FIGURE 3
The "Sergio Silenzi" station deployed on the sandy bottom at 32 m (Source: ISPRA). **(A)** The station on the sandy seafloor, surrounded by Coralligenous on rocky substrate. **(B)** The station on the sandy seafloor partially covered by algae.

SeaFET sensors include an independent external chloride ion-sensitive electrode (Cl-ISE) reference and the Durafet®'s built-in internal reference electrode (Martz et al., 2010) and dual pH voltage outputs. An embedded thermistor provides a temperature voltage.

Comparisons of the voltage data from the internal (Durafet ®) and external (Cl-ISE) electrodes may be used to identify periods of conditioning, the onset of biofouling, and sensor failure.

This probe is equipped with two potentiometric cells, one internal and one external. The action of the two cells produces a measurement for both, therefore there will be a value measured by the internal cell (internal pH) and one from the external cell (external pH). The measured potential depends on the characteristics of the electrolyte and is sensitive to any change in the ion concentration of the monitored environment. The external reference electrode is more sensitive to changes in salinity than the internal electrode, so the tolerance window may be site-specific. The internal reference electrode (primary source for pH data) may continue to function normally when the external reference electrode fails, and either the internal or external electrode can be used to generate a high-quality pH dataset (Martz et al., 2010).

To ensure data quality and account for potential sensor drift, the SeaFET pH sensor was calibrated following a rigorous protocol. Prior to deployment, a factory-calibration was performed, and the sensor's internal and external electrodes were conditioned in seawater to stabilize the response. Maintenance included the use of anti-fouling copper guards to prevent biological interference with the sensitive membrane, ensuring the long-term stability of the high-frequency dataset.

The *in situ* pH dataset showed here was generated using voltage data from the internal Durafet® pH electrode (internal pH), due to the lack of salinity dependence of the electrode when using the total hydrogen ion scale (pH in total scale; Bresnahan et al., 2014).

The CTD probe installed on the station was an SBE 37 - SMP - MicroCAT C-T (P) Recorder (Sea-Bird Electronics) provided concurrent temperature and salinity measurements necessary for the calculation of *in situ* pH. Conductance range between 0 and 7 Siemens per meter (S/m) and water temperature range between -5 and +45 °C.

The two probes (pH and CTD) acquired data with an interval of 3600 seconds, one every hour. The pH probe records 3 values every hour, one minute apart, one for the internal cell and one for the external cell, for a total of six measurements; then it goes into stand-by until the next hour, when it reactivates to repeat the cycle of measurements.

The "Sergio Silenzi" station was deployed on 3 December 2014 (Figure 3), when the monitoring started, and recovered on 14 November 2015.

Historical data about cloud cover, wind mean and maximum speed and precipitations were retrieved from the archive at https://www.ilmeteo.it/portale/archivio-meteo/, based on the data collected by the meteorological station of the Cagliari-Elmas airport.

Wave data obtained by the Copernicus Monitoring Environment Marine Service (CMEMS) and processed through the mathematical model MEDITERRANEAN SEA WAVES HINDCAST (Korres et al., 2019) were used for estimating the wave regime at the studied site. CMES data have hourly resolution. The wave parameters were acquired in one observation point, within the grid of the model and located in front of the site where the "Sergio Silenzi" station was deployed. Acquired parameters were: Significant Wave Height (SWH m) and direction of wave motion (DIR N). Point location: 39° 07.2' N; 9° 32.3'E.

2.3 Samplings and analyses of benthic communities

With the aim to depict the seasonal change in benthic cover having a potential influence on the local pH (Hofmann et al., 2011; Hurd et al., 2011), the benthic assemblages were monitored three times (July 2016, November 2016 and April 2017) after the termination of the "Sergio Silenzi" station records. Negligible interannual variations in benthic dynamics are expected in this deep habitat characterized by perennial species (Garrabou et al, 2002), thus the probe-based and benthic records were decoupled to avoid any potential disturbance arising from diving and collection activities in close proximity to the probes. Three plots (4 m^2 in size), were selected on vertical bottoms at 32 m of depth, 1–2 m distant from the station and one on the adjacent sandy seafloor. Seven photographic samples of 0.2 m^2 were collected in each plot (Piazzi et al., 2019) (Supplementary Figure 2A).

Photographic samples were analyzed to evaluate the percent cover of the main taxa or morphological groups using ImageJ software (Piazzi et al., 2019). Organisms easily detected by photographic samples were identified to the lowest possible taxonomic level, while those not easily recognizable were identified according to

morphological groups (Piazzi et al., 2019). Moreover, to evaluate the species composition of those algal species that could not be identified on the photoquadrats, three replicate samples of coralligenous algal assemblages and three of algal assemblages developed on the sandy bottom were also collected at each sampling time. Samples consisted of all organisms within 400 cm^2 collected by scraping the hard bottom with hammer and chisel (Boudouresque, 1971) or manually removed on sandy bottom (Supplementary Figure 2B). All the material was preserved at -40 °C. In the laboratory all taxa were identified at the lowest rank and their abundance was expressed as percentage cover of the sample surface.

2.4 Statistical analyses

MSFD pH observations were processed using analytical techniques aimed at summarizing the annual trends of pH and studying the probability distribution of pH values through the application of the Johnson method, in order to determine the range within which the parameter would naturally be expected to vary. The study of the distribution of the variable of interest was conducted independently of the sampling site and time by applying the Johnson method (Johnson, 1949; Hill et al., 1976).

The extensive details of this section's procedures have been reported elsewhere (Conti and Finoia, 2010; Conti et al., 2015, 2019, 2020).

Due to the inherent asymmetry and non-normality of the high-frequency pH time series, data distribution was modeled using the Johnson system of frequency curves (Johnson, 1949). This method generates a family of distributions (including SB for bounded data and SU for unbounded data) by applying a translation to the normal distribution. By fitting our pH observations to a Johnson curve, we were able to characterize the probability density function (PDF), accounting for the observed skewness and kurtosis typically observed in pH time series. This statistical treatment ensures a robust definition of the pH 'natural range' and the regional MSFD datasets.

To compare datasets with different sampling frequencies and environmental characteristics, pH values were standardized using the Johnson translation system (Johnson, 1949). This method transforms the empirical pH distribution into a standardized normal variable, z, which follows a normal distribution N (0,1).

The probability distribution of pH, classified using the Johnson method, falls within the lognormal distribution class (SL). Indeed, the histogram at the top shows a pronounced left skew and a long right tail. The applied method normalizes the data, making the distribution more symmetric.

The analyses were carried out using R version 2.13.0 (R Core Team, 2019) and the SuppDists package (Wheeler, 2013). In brief, Johnson's method (1949) was applied to the pH levels to create a frequency curve system by translation. This method allows, through a translation technique, for the classification of the generic variable distribution in one of the four classes of probability functions defined as follows:

$$z = \gamma + \delta * \log\left(f(u)\right), \quad where \quad u = \frac{(x - \xi)}{\lambda}$$

Where z is a standard normal random variate, γ and δ are shape parameters, Λ is a scale parameter, ξ is a location parameter, x is the observed pH value and f() can have one of the following forms:

SL $f(u)=u$ log-normal distribution

SU $f(u)= u + \sqrt{(1 + u^2)}$ unbounded distribution with two tails

SB $f(u)= \frac{u}{(1-u)}$ bounded distribution with one tail

SN $(u)= e^u$ normal distribution

The normalization procedure was performed with the SuppDists package of R (Wheeler, 2013).

In synthesis, the variables become normally distributed after the aforementioned transformations. Normality in the distribution of a variable is an essential requirement for applying robust statistical inference techniques and defining the limits of the confidence intervals for the studied parameters. This assumption allows us to build the control charts associated with each element, define its range of variation, and highlight the upper tail of the probability distribution. The tail will contain 2.5% of the observations, defining the outliers present in the studied parameter distribution.

Surface pH values (z < 25 m) were indeed analyzed for each of the 8 sub-basins to identify the statistical distributions in order to assign appropriate frequency distributions. Each sample distribution has been analyzed and defined by a probability density function, by means of a powerful method of data analysis that allows for the computation of statistical parameters of a wide variety of non-normal distributions. The Johnson method (Johnson, 1949) allows for the precise estimation of the probability of occurrence of pH values. Once a particular Johnson curve has been fitted, the normal integral can be used to compute the expected percentile point under the respective curve. This methodology has been used to define a baseline range for all available pH data to estimate the lower and the upper bounds corresponding to 95% of the area under the curve of the related probability distribution function (Finoia, 2013; Babbini et al., 2013).

"Sergio Silenzi" *in situ* continuous monitoring station registered 345 days (4 December 2014–14 November 2015) and biogeochemical and physical data collected by the sensors were analyzed by time series decomposition methods. This analysis decomposes the time series by isolating their components, each representing an underlying pattern category. Furthermore, in order to apply the stochastic approach to historical series it was necessary to eliminate the trend and the seasonality in order to obtain a stationary process. The components of a historical series encompass: trend, seasonality, and residuals. Seasonality is poorly significant for historical time series encompassing a single year, therefore it was not shown. Residuals quantify the deviation of observed values from those predicted by the model, providing a measure of model fit. The series components can be related to each other additively or multiplicatively (Hyndman and Athanasopoulos, 2014). Data were analyzed with software R (R version 3.6.2, 2019).

Temporal variability in the structure of assemblages was analyzed by a permutational analysis of variance (Primer 6 + PERMANOVA, Anderson, 2001; 999 permutations) based on Bray-Curtis resemblance matrix of untransformed data, with the crossed factors Time (fixed: July 2016 vs November 2016 vs April 2017) and Plot (random, three levels). The Pair-wise test was used to discriminate between levels of significant factors.

3 Results

3.1 The pH of the Mediterranean Sea

The natural range of seawater pH reported in the literature and the natural range of pH values derived from the analyzed data show mean higher Mediterranean pH values (Figure 4).

The Western Mediterranean sub-basin showed lower pH levels in respect of the Tyrrhenian sub-basin. The mean surface pH in the Western Mediterranean Sea was 8.215 ± 0.164 (N = 20041), whereas in the Tyrrhenian Sea the mean surface pH value was 8.335 ± 0.155 (N = 11580) (Figure 4). The pH probability distribution is represented as an unbounded distribution, following the Johnson *SU* transformation (Figure 4). It is important to note that while the distribution is unbounded, it is non-Gaussian, as it incorporates the specific skewness and kurtosis of the monitored sites. To characterize the distribution tails, we adopted the 2.5th and 97.5th percentiles as the thresholds for the 'natural variability range.' This choice ensures that the extreme values (the outer 5% of the distribution) are clearly identified as the tails, providing a robust statistical threshold to distinguish between standard metabolic fluctuations and anomalous pH events (Figure 4).

In the Tyrrhenian Sea, the mean pH value had a total range of 0.25 (Figure 5).

The mean surface pH monthly values calculated on the Western Mediterranean Sea showed peaks (8.30-8.35) recorded in the winter months (from January to March) whereas in the Tyrrhenian Sea similar values were recorded only in January and February, and peaks (> 8.40) were recorded in autumn (Figure 5). The percentiles 2.5% and 97.5% defined after Johnson transformation and calculated on all

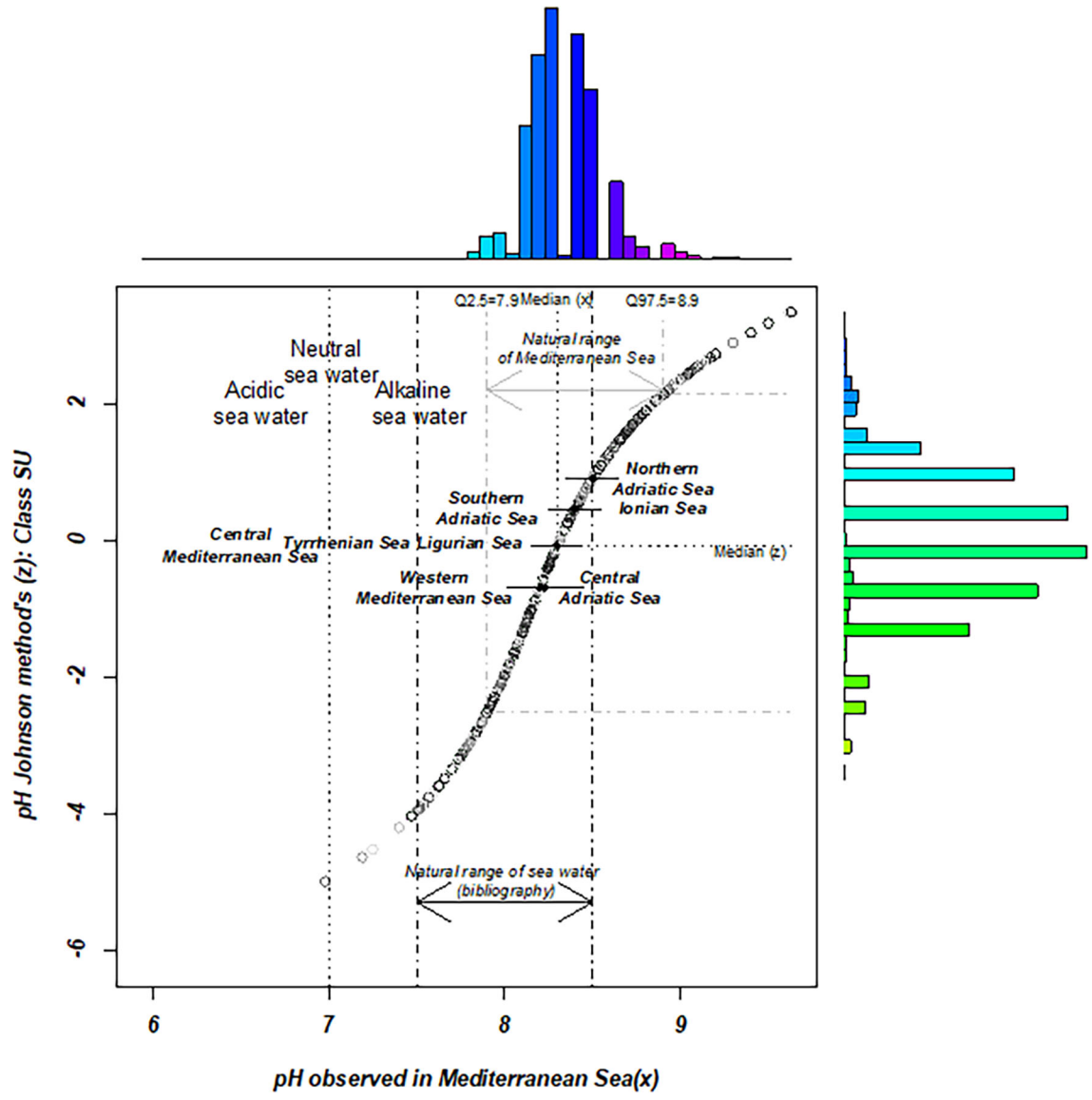

FIGURE 4
Control chart of surface pH values for 8 Mediterranean sub-basins, based on the MSFD first assessment. Names and delimitations of the 8 sub-basins as in Figure 2. Observed values are on x-axes, and values calculated by Johnson's method are on y-axes. Inside the plot are reported: the lower and upper bounds of baseline range (Q2.5 and Q97.5). On top, the frequency histogram shows the observed pH values, while the histogram on the right is based on the normalized values. The medians ± median absolute deviations (m.a.d.) are reported along the curves for each sub-region. The percentiles 2.5% and 97.5% corresponding to pH 7.9 and 8.9 are reported on top.

FIGURE 5
Mean pH values based on the MSFD first assessment for the Western Mediterranean sub-basin (blue line) and the Tyrrhenian sub-basin (orange line) (2006–2009 and 2011-2012). The gray line shows the mean monthly pH values based on the records of the "Sergio Silenzi" station deployed in Villasimius in 2014-2015. Vertical bars indicate the standard deviation.

available pH data collected across the Italian Seas after the MSFD ranged between 7.9 and 8.9 (baseline range) (Figure 4).

3.2 Meteo-marine conditions of Southeast Sardinia

Events with very strong winds were recorded in mid-March (55 km/h) with wind max peaks in mid-April and November (75 km/h) (Figure 6A). Southern warm winds caused an important event of Saharan dust transport over the Mediterranean region and Central Europe on July 1-9, 2015, heavily affecting the southern coasts of Sardinia (Guerzoni et al., 1997; Palacios-Peña et al., 2019).

December and May showed relatively low wind max speed between 20 and 40 km h^{-1}. As expected, marine conditions reflected the wind strength, with significant waves height exceeding 3 m at the end of Dec. 2014, in the first days of Feb. 2015, and several times in Autumn 2015. Waves exceeding 4 m of significant height were recorded in 2015 on March 25, on October 1 and 10, and on November 21 and 26 (Figure 6B).

The average (years 1990-2020) annual precipitation in SE Sardinia is very low, with a total amount of 391 mm. Villasimius had dry conditions in summer, and July was the driest month with 2 mm of precipitation. On average, November was the wettest month with 63 mm of precipitation.

Two continuous rainy intervals were recorded from December 1 to 14, 2014 and from January 19 to February 8, 2015 (Figure 7).

3.3 *In situ* biogeochemical and physical parameters

The analysis of the pH_{Total} measures carried out by the "Sergio Silenzi" station and recorded from 4 December 2014 to 14 November 2015, for a total of 345 days, showed important fluctuations.

The seasonal pattern showed three positive peaks in winter 2015 and specifically in the mid of January, February and in early March (Figure 8). pH_{Total} maximum values were recorded on 20 January 2015 (8.21) whereas minimum values of about 7.97 were recorded several times from late July to early September. The total yearly range in the observed pH values was 0.24, framing a diel, monthly, and seasonal variability (Figure 8). The average pH calculated over the entire sampling period was 8.07 (SD 0.025). Monthly average values fluctuate between 8.05 and 8.11 (Figure 5), while the pH_{Total} values along the 24 h, mediated over the 1-year monitoring, showed a slight but significant increase in the early afternoon (2–3 pm) and minimum values during the early morning (5–6 am) (Figure 8B).

The minimum temperature was recorded in March (13.3 °C) whereas the maximum in August (26 °C) (Figure 9). Large fluctuations in temperature were recorded by the station between May and November.

The record of salinity covered only the first 171 days, due to technical issues. In the observed period the minimum salinity was recorded in December (37.8 ‰) whereas the maximum in mid-March (38.2 ‰) and May (38.1 ‰) (Figure 10A). At the beginning of April, a sharp decrease in salinity of almost 0.2 is recorded, whereas from mid-April to the end of May salinity values increased and stabilized at about 38.15 ‰ (Figure 10).

3.4 Benthic communities

The coralligenous assemblages facing the "Sergio Silenzi" station were characterized by a stratified structure. Encrusting calcareous Rhodophyta constituted a secondary substrate colonized by a basal layer with algal turf, *Peyssonnelia* spp. and encrusting sponges, an intermediate layer characterized by the Chlorophyta *Flabellia petiolata* and erect bryozoans (*Smittina cervicornis*, *Pentapora fascialis*,

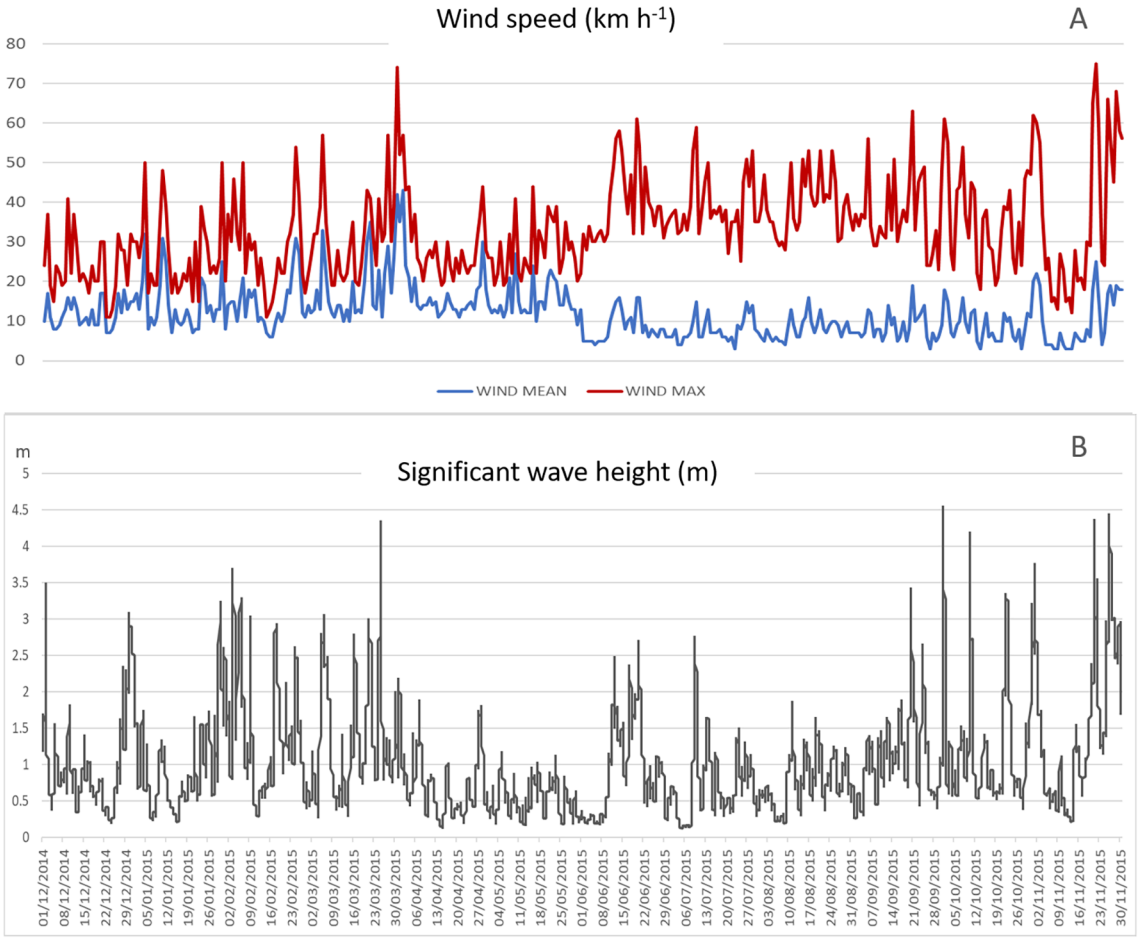

FIGURE 6
(A) Wind speed (km/h). In blue wind mean and in red wind maximum. **(B)** Significant Wave Height (SWH m) obtained by the Copernicus Monitoring Environment Marine Service (CMEMS) Point location: 39° 07.2′ N; 9° 32.3′E.

Myriapora truncata, *Reteporella* spp.) and an erect layer with the gorgonians *Paramuricea clavata* and *Eunicella cavolini* (Table 1). On sand, the assemblage was composed of algal turf and the introduced Cholorophyta *Caulerpa cylindracea* (Figure 11). The percentage cover was always 100 in coralligenous reefs, while on sandy bottom it ranged between 97.0 ± 0.7 in Autumn 2016 and 7.7 ± 2.0 in Spring 2017.

In the algal turf of both habitats a total of 39 taxa (6 Ochrophyta, 5 Chlorophyta and 28 Rhodophyta) were found

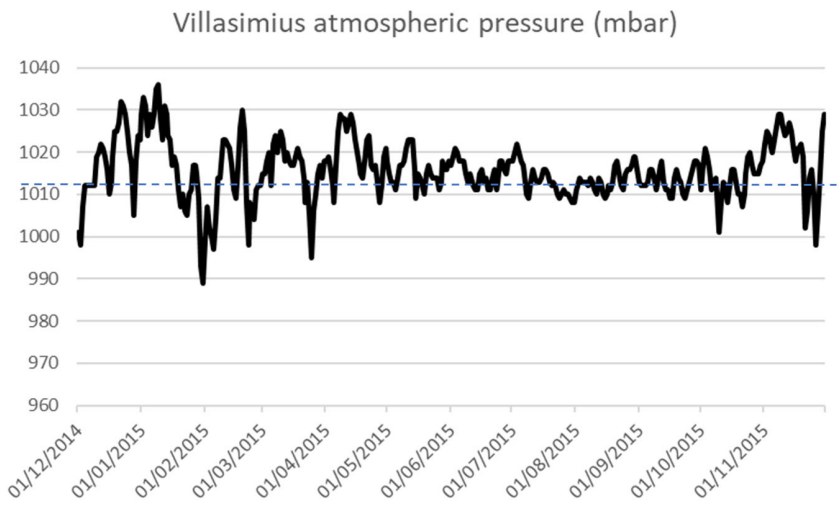

FIGURE 7
Atmospheric pressure at the sea level (mb). 1013 mb is the threshold between low and high pressure. Data below 1013 mb indicate potential rainy days.

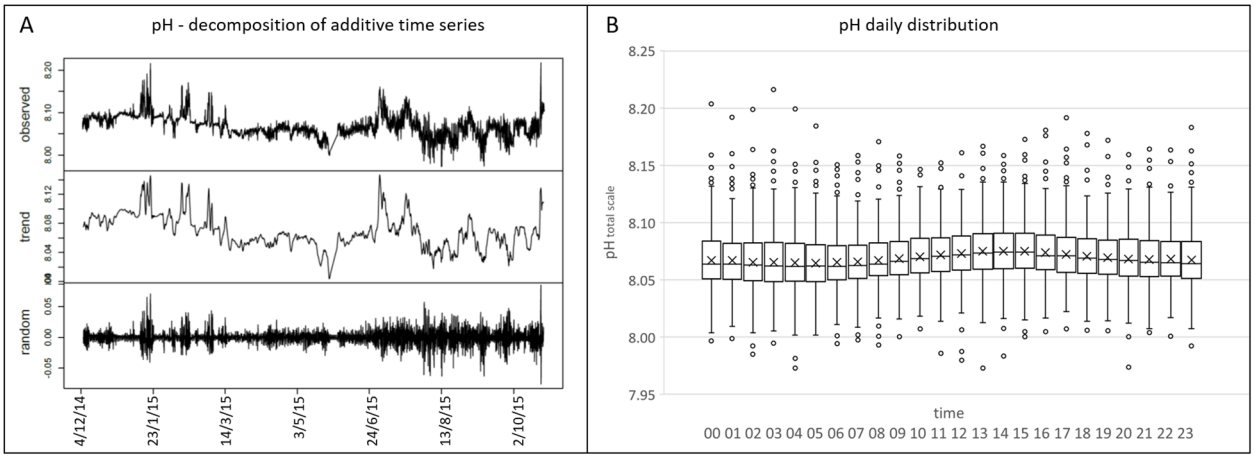

FIGURE 8
Historical series of pH_{Total} records ("Sergio Silenzi" station, 345 days) measured by the internal cell of the probe. **(A)** Upper panel: pH_{Total} observed records; middle panel: trend of the pH_{Total} values; lower panel: residuals. **(B)** Box and whiskers plot showing minimum, mean, and maximum pH_{Total} values over the 24 h. Empty circles are outliers.

(Supplementary Table 2); the most abundant turf species was the non-indigenous Rhodophyta *Womersleyella setacea*.

The coralligenous assemblages display significant temporal variations (Tables 1, 2) mostly due to changes in abundance of algal turf which decreased in April when the cover of encrusting calcareous algae increased (Table 1; Figure 11). On sand, variations are related to both turf and *Caulerpa cylindracea*, that reached its maximum abundance in November (Figure 11).

4 Discussion

4.1 Evaluation of drivers: biological vs. physical processes

In the framework of a comparatively fast-warming Mediterranean, with highly variable rate of surface pH decline (Fader et al., 2020; D'Agostino et al., 2023), our 2014–2015 dataset highlights a system dominated by high-frequency metabolic fluctuations, a condition now recognized as a key feature of Mediterranean 'coastal mosaics' (Ingrosso et al., 2021). However, long-term projections suggest that these natural fluctuations might soon hit critical physiological thresholds for coralligenous frameworks, as extreme pH minima become more frequent (Carbonne et al., 2022; Garrabou et al., 2002).

The Italian Mediterranean Sea is confirmed to have a mean higher pH than the open Atlantic Ocean, north-western Mediterranean, and Strait of Gibraltar waters (Flecha et al., 2015; Yao et al., 2016; Figure 4), while the pH of the monitored Tyrrhenian shallow coralligenous habitat is characterized by a lower mean pH, with values comparable to that of the open ocean (Hofmann et al., 2011; Jiang et al., 2019). The high-frequency pH variability recorded at Capo Carbonara is consistent with a hierarchy of drivers acting at different temporal scales. Given the

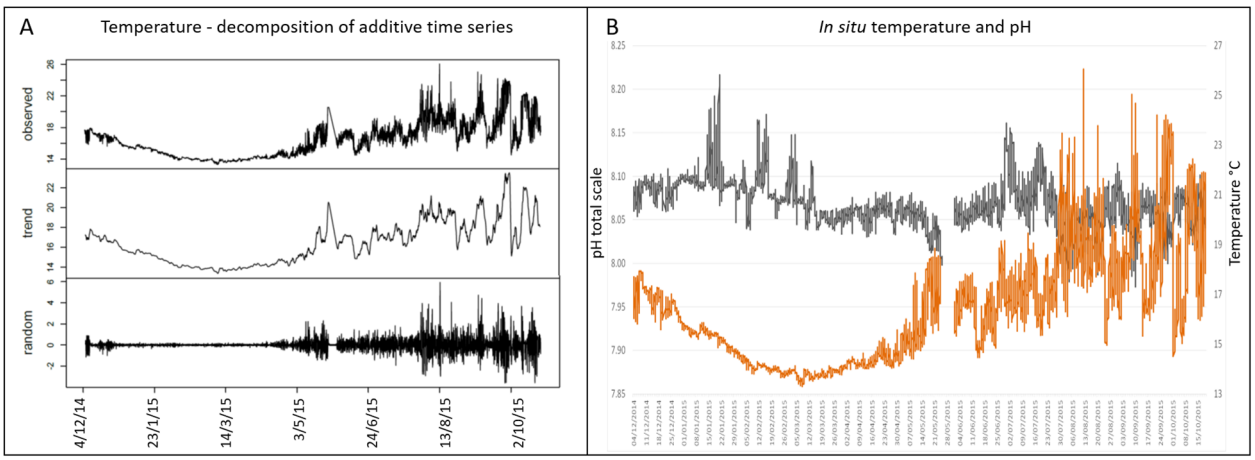

FIGURE 9
Historical series of water temperature (°C) records ("Sergio Silenzi" station, 345 days). **(A)** Upper panel: temperature observed records; middle panel: trend of the temperature values; lower panel: residuals. **(B)** The observed values of temperature (orange line) and pH (black line) show opposite fluctuations and high summer variability.

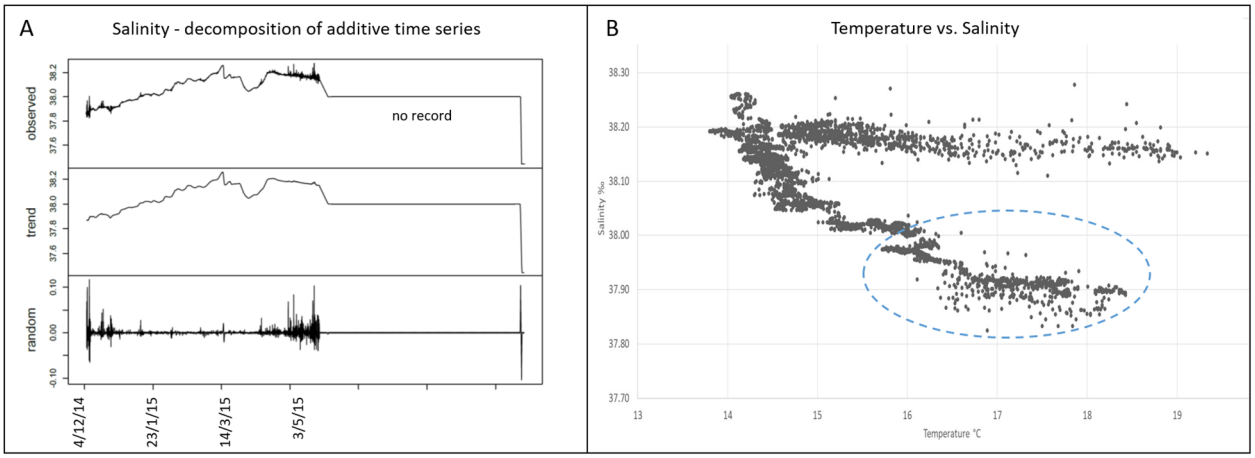

FIGURE 10
Historical series of salinity (psu) records ("Sergio Silenzi" station, 171 days). **(A)** The upper panel shows the observed records of the salinity values, the middle panel shows the trend, the lower panel reports the residuals. **(B)** Plot of salinity (psu) versus temperature (°C) records. The blue dashed line encircles relatively fresher water in respect of most records.

observational and correlative nature of this study, these associations are interpreted as plausible hypotheses rather than definitive proof of causality (Ingrosso et al., 2021).

The strongest evidence for biological forcing is provided by the pronounced diel cycles observed throughout the monitoring period. The systematic increase in pH during daylight hours, reaching its maximum in the afternoon, is highly consistent with intense primary production by the coralligenous and seagrass assemblages. Conversely, the nighttime declines strongly suggest that community respiration becomes the dominant process in the absence of light (Kwiatkowski et al., 2016). These metabolic signals appear to be the primary drivers of short-term fluctuations, a hypothesis further supported by the seasonal intensification of these cycles during the spring and summer growth peaks (Hendriks et al., 2022). On a broader scale, physical and oceanographic factors provide the environmental framework within which these biological signals

TABLE 1 Percent cover (mean ± ES, n=21) of taxa/groups of coralligenous assemblages by photographic samples.

Taxa/groups	July 2016		November 2016		April 2017	
	Mean	SE	Mean	SE	Mean	SE
Algal turf*	24.13	2.82	24.26	2.66	12.13	2.27
Encrusting calcareous algae	14.94	2.28	15.73	3.38	20.33	3.61
Peyssonnelia spp.	20.42	3.34	18.20	2.50	22.66	3.98
Palmophyllum crassum	0.46	0.21	0.20	0.10	0.66	0.12
Caulerpa cylindracea	0.20	0.11	2.40	0.71	0	0
Flabellia petiolata	0.29	0.11	1.33	0.62	0.40	0.12
Erect Rhodophyta*	0	0	0.26	0.11	0	0
Codium bursa	0.80	0.77	1.20	0.64	0.80	0.56
Encrusting bryozoans	0.29	0.15	0.40	0.12	0.20	0.10
Myriapora truncata	0.03	0.03	0	0	0	0
Pentapora fascialis	0.21	0.14	0.13	0.08	0.06	0.06
Smittina cervicornis	0.95	0.46	0.80	0.31	0.86	0.55
Reteporella spp	0.15	0.03	0.20	0.10	0.20	0.10
Encrusting sponges	11.77	3.44	10.20	1.68	14.86	3.69
Massive sponges	0.46	0.33	0.80	0.30	1.46	0.24
Filograna-Salmacina complex	0.46	0.23	0.13	0.08	0.08	0.03
Paramuricea clavata	8.58	3.06	9.93	4.95	11.53	3.06
Eunicella cavolini	15.54	3.59	14.53	2.81	12.46	3.32
Ascidians	0	0	0	0	0.33	0.15

Asterisk for group of algal species that could not be identified on photos (see Supplementary Table 2 for details).

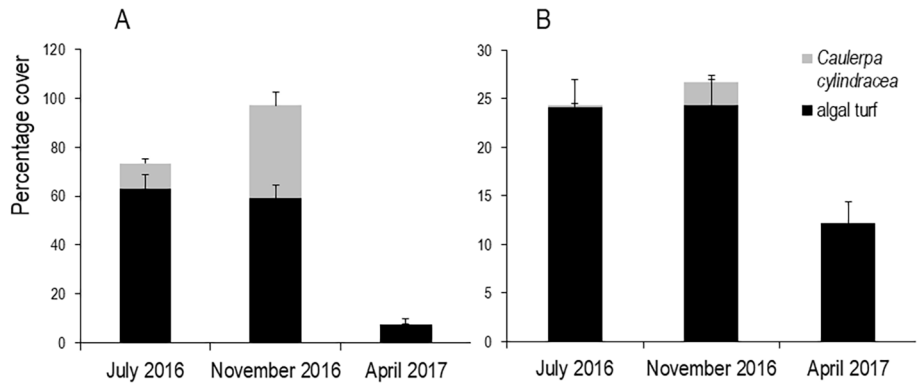

FIGURE 11
Temporal variation in abundance of algal turf and *Caulerpa cylindracea* on sand **(A)** and coralligenous reef **(B)**. Note the different scale in (B), to enhance readability.

operate. While seasonal mean pH declines correlate with increasing temperatures, the magnitude of the observed drop exceeds purely thermodynamic predictions, suggesting that temperature acts alongside other seasonal processes (D'Agostino et al., 2023).

The average pH_{Total} of 8.07 recorded by the *in situ* "Sergio Silenzi" station, at 32 m depth, was lower than surface pH mean values typical for the Tyrrhenian Sea (8.33) and Western Mediterranean Sea (8.20), calculated for the MSFD first assessment (Figures 4, 5, 8). This difference (Figure 5) is partly due to the different depth of measure, because pH decreases rapidly below the ocean surface, and partly to the different method of pH measure, since pH in total scale is typically lower than pH measured on NBS scale (Lopez et al., 2022). However, based on the large number of data, the potential error in MSFD means is negligible at this scale of observation (Carstensen and Duarte, 2019; Lopez et al., 2022). Therefore, our results suggest that pH at the Villasimius shallow coralligenous reef was indeed characterized by lower values, and higher frequency but narrower average fluctuations, in respect of the open sea (Figures 5, 8, 9), supporting a pattern already observed in other non-open ocean sites (Hofmann et al., 2011; Alvarez et al., 2014). The seasonal trend of pH recorded by the "Sergio Silenzi" station broadly fits the trend of the Western Mediterranean Sea, with maximum values recorded in winter and decreasing values in spring (Flecha et al., 2022). The analyzed *in situ* pH data variability (diel, monthly, seasonal) aligns with trends observed in coastal waters on local and global scale (Hofmann et al., 2011).

The three positive pH peaks recorded in mid-January, mid-February and early March could be derived from early favorable light conditions and nutrient availability, fuelling the primary productivity by coastal plankton and benthos, and consequently rising pH, with irregular and very local response (Estrada, 1996). Actually, the 2015 late winter phytoplankton bloom in Sardinia had a particularly early start (around 15 January), a maximum intensity around the middle of March and terminated at the beginning of May (Grossi et al., 2024). The fact that the pH value peaks (8.2) are separated might be due to abiotic factors such as fluctuating irradiance and turbidity, which influence and consequently may affect the photosynthetic rate. In fact, low irradiance by cloud cover and rain occurred at the investigated site after each pH peak (Figures 7, 8), with a likely negative impact on the ongoing bloom. As expected, the *in situ* pH values show winter maxima and late spring to summer minima (Flecha et al., 2022), and in the first 171 days of record (Figure 8) are mostly influenced by marine primary production.

We consider that strong meteorological events might have affected pH on a local scale, such as many consecutive rainy days that affected salinity and likely enhanced turbidity and nutrient availability by increased land-derived runoff (Estrada, 1996). The long rainy periods in December 2014 and January 2015 brought sinking cold and fresher water and generated a decreased salinity. Wind waves generally affect the first 20/25 m of the water column. It could be hypothesized that the strong winds recorded at the end of winter (March), with gusts around 70 km h^{-1} generating extreme hydrodynamics (significant high wave > 4m), cooled the superficial waters and stirred the water column, likely contributing to the abrupt decrease of salinity by approximately 0.2 units at the depth of the monitoring station (Figure 10). An additional or alternative possible explanation for the early April sudden drop in salinity might consider the peculiar pattern of circulation observed on the Sardinia shelf, causing events of subsurface ingression of warm and fresher water of Atlantic origin at depths compatible with our records (Figure 10B; Sorgente et al., 2024). Furthermore, the winter pH peaks may be influenced by regional water mass dynamics, such as the intrusion of Atlantic Water (AW), or by sporadic atmospheric events. For instance, the observed pH increases are consistent with Saharan dust outbreaks, which are known to potentially provide mineral buffering to Mediterranean surface waters (Rodà et al., 1993). Additionally, periods of reduced variability likely reflect increased vertical mixing or shelf-slope exchange, which

TABLE 2 PERMANOVA analysis on coralligenous assemblages.

Source	df	MS	Pseudo-F	P (perm)	N. permutations
Time = T	2	1940	2.40	**0.046**	951
Plot = P	2	11382	14.12	**0.001**	997
TxP	4	692	0.85	0.568	998
Residual	36	805			

Pairwise test: July=November≠April.
Significant values in bold.

homogenize the water column and dampen the local metabolic signals (Kapsenberg and Cyronak, 2019).

During summer and autumn, the general and expected trend in decreasing pH due to high temperatures and community respiration is interrupted by some positive peaks in early July. In coincidence, on 1–9 July 2015, a Saharan dust outbreak, a typical and recurrent desert dust transport episode, affected the entire Mediterranean Basin (Palacios-Peña et al., 2019). The Capo Carbonara area, where our monitoring was conducted, was already considered as a focus point for Saharan dust deposit, inducing an increase of pH from alkaline dust minerals (Guerzoni et al., 1997). We speculate that the deposition of massive quantity of Saharan dust on the sea surface and coastal areas is likely to be followed by at least partial dissolution in rainwater and sedimentation along the water column, inducing a temporary shift toward more positive pH values (Guerzoni et al., 1997), although the positive pH fluctuations started a couple of days before the published starting day of the Saharan dust outbreak (Palacios-Peña et al., 2019), challenging our interpretation.

In late summer and autumn 2015 several negative pH peaks were recorded, corresponding to large temperature fluctuations. This pattern indicates the beginning of the mixing period, with gradual and intense warming repeatedly interrupted by sudden cooling (Figure 9). In those conditions, a second boost to primary production could take place, while the absence of a prolonged warm period would suggest that the conditions for the onset of a summer dormancy of benthic invertebrates (Coma et al., 2000) is unlikely at the monitored site.

In the studied coastal environment, structured by calcareous macroalgae and characterized by a shallow coralligenous community, significant seasonal and diurnal pH fluctuations were observed. The coastal environment and biota, that normally undergo nychthemeral pH fluctuations, are well adapted to the observed variability. The interplay between these daily excursions and broader seasonal trends underscores the role of coastal biogenic habitats as active "biological filters" capable of significantly transforming the local chemical environment relative to larger-scale oceanographic signals (Carbonne et al., 2022).

The results of the estimates of marine acidification (Touratier and Goyet, 2009, 2011) indicate that all water masses of the Mediterranean Sea are already acidified with a range from -0.14 to -0.05 pH units; waters from the eastern basin appear to be less affected than those from the western basin, where the level of acidification always exceeds 0.1 pH units. The recorded basin-scale pH fluctuations (mean range = 0.25 for the Tyrrhenian Sea) and the observed coastal pH fluctuations at our Sardinia monitoring site, with a total range of 0.24, are coherent with previous Western Mediterranean reports (Flecha et al., 2022) and exceed the open-sea mean multidecadal pH decrease of about two times. The annual pH range of 0.24 units observed at Capo Carbonara is consistent with recent high-frequency observations across the Mediterranean basin. Studies conducted between 2015 and 2024 (e.g., Kapsenberg et al., 2017a; Teixidó et al., 2024) have demonstrated that coastal carbonate systems are far more dynamic than previously estimated from open-ocean models. Our findings confirm that local daily fluctuations (up to 0.1 units) are often twice as large as the mean multidecadal pH decrease reported for offshore waters. This highlights that foundational datasets like the one presented here are essential to establish the 'noise' of natural variability against which anthropogenic trends must be measured. The observed fluctuations are attributed to oceanographic patterns, meteorological events, and biological activities predating the ongoing climate change and likely unrelated from anthropogenic impacts, suggesting that the Villasimius coralligenous habitat developed and is adapted to a naturally variable pH seascape. However, the global trend of ocean acidification will lower the observed pH range toward potentially critical levels in the future, with expected detrimental consequences for the habitat formers, although some degree of uncertainty still arises from carbonate chemistry (e.g., Kapsenberg et al., 2009; 2017a), and specific and still poorly known metabolic responses (Hurd et al., 2011; Cornwall et al., 2013; Waldbusser and Salisbury, 2014; Comeau et al., 2017; Cornwall et al., 2022; Gómez-Gras et al., 2021; Teixidó et al., 2024).

Most pH values published in literature do not derive from direct measurements, rather they rely on values calculated from other correlated seawater CO_2 chemistry variables (Jiang et al., 2019). Although our one-year pH record does not allow any modeling nor generalization of the observed short-term patterns, still it contributes to the complex challenge of understanding the amplitude of the pH fluctuations occurring in coastal marine habitats and sketching a context for their potential response to the ongoing OA.

4.2 Benthic communities

The coralligenous assemblages were characterized by a typical stratified structure with a well-developed elevate layer constituted by Alcyonaceae. This structure is considered typical of the studied biogeographical area (Piazzi et al., 2021a, b) and depth range (Pinna et al., 2021).

Interpreting pH variability in shallow habitats remains a major challenge for Mediterranean research, as biological 'noise' can often mask the underlying anthropogenic signal (Ingrosso et al., 2021). Our findings at Capo Carbonara highlight a stable community despite such variability; however, recent experimental evidence suggests that the synergistic effect of acidification and rising temperatures may soon exceed the physiological thresholds of key coralline species (Cornwall et al., 2019; Kelaher et al., 2022). This underscores the necessity of high-frequency datasets to identify short-term extremes that could trigger irreversible shifts in coralligenous frameworks.

A very interesting aspect of the studied area was the presence of a macroalgal assemblage on the sandy bottom. The non-indigenous Chlorophyta *Caulerpa cylindracea* can colonize both hard and mobile bottoms thanks to its stoloniferous structures (Piazzi et al., 2016; Caronni et al., 2023). On the contrary, turf forming algae normally spread on hard substrate (Airoldi, 1998). Most of turf species found in the survey are the same on the two habitats, thus sand assemblages could recruit from thalli detached from the cliffs which then spread and thrive on the mobile substrate, constituting a permanent pleustophytic turf.

Sand assemblages were highly variable temporally as both *C. cylindracea* and turfs deeply changed their abundance through the study period. *C. cylindracea* reached the maximum abundance in

autumn, following the typical seasonal cycle of Mediterranean specimens (Ruitton et al, 2005). Turfs decreased from November to April in relation to the temporal patterns of seasonal filamentous species, such as the dominant non-indigenous Rhodophyta *Womersleyella setacea*, which reaches its highest abundance between the end of summer and autumn (Piazzi and Cinelli, 2001, 2003).

Coralligenous assemblage showed temporal variations mostly related to turf forming macroalgae, while the abundance of sessile animals was stable within the study period, as expected based on their multi-year average lifespan. The results are not surprising as, despite coralligenous assemblages are considered more stable than shallower communities (Garrabou et al., 2002; Abbiati et al., 2009), seasonal temporal variations have been already highlighted and associated to changes in abundance of the macroalgal component (Piazzi et al., 2004; Balata et al., 2005). In fact, some seasonal erect turf algae and filamentous species decrease in cover during the cold season (Piazzi et al., 2004; Balata et al., 2005), which explains their significant decrease in April in respect of the autumn sampling. Interestingly, the long-lived calcareous algae composing the secondary substrate showed an opposite trend, but during the summer-early autumn months they were probably underestimated by the photographic sampling, simply because they were covered by turf. However, based on published experimental data, we can speculate that, in absence of the turf canopy, calcareous algae could have increased their photosynthetic activity and calcification, especially during early spring days with higher light availability and rising temperature. Calcareous algae uptake CO_2 for photosynthesis, but produce CO_2 not only during respiration but also for thallus calcification. This could explain the relatively stable but low pH despite increasing temperature. New turf development is expected to result in a higher uptake of CO_2 during summer. Another process acting at a very slow rate, nevertheless pervasive at the studied site, is carbonate dissolution, enhanced by boring and bioturbation (Schneider and Le Campion-Alsumard, 1999; Tribollet et al., 2022). Our monitoring station was sitting on a biodetritic sediment and encircled by the Coralligenous calcareous buildups. The living algal reef community that we monitored thrives on the older skeletal carbonates encrusting the rocky substrate, produced by the builders community in hundreds or thousands of years (Basso et al., 2022). Carbonate dissolution is a CO_2 sink, thus triggering an increase in alkalinity. Although the absence of alkalinity and pCO_2 data hampers further interpretation of the observed pH fluctuations, we speculate that dissolution could provide a possible explanation for the weak but consistent positive pH fluctuations recorded during the night, when darkness inhibits photosynthesis and dissolution is enhanced (Figure 8B; Reyes-Nivia et al., 2014). The Villasimius shallow Coralligenous reef is composed of long-lived habitat engineers (coralline algae, gorgonians, etc.) appearing stable and adapted to the observed fluctuating environmental variables. The quantification of local pH fluctuations is fundamental for projecting the response of organisms to future scenarios of ocean acidification, and this is particularly important for ecosystem engineers like coralline algae. Local adaptation to fluctuating ambient conditions may represent evidence of tolerance, suggesting that range extremes would provide a good predictor of the tolerance thresholds (Vargas et al., 2017). Different biological response to low pH was observed in constant vs. fluctuating pH conditions (Cornwall et al., 2013; Johnson et al., 2019; Duvane and Dupont, 2024; Shi and Li, 2024), however, large uncertainties still exist about the metabolic trade-off of acclimatization or adaptation to variability (Kelly and Hofmann, 2013; Duvane and Dupont, 2024).

4.3 Limitations and future perspectives

Despite providing high-resolution temporal insights, this study has inherent constraints. First, the reliance on pH as a single carbonate system parameter limits the mechanistic attribution of fluctuations to specific organic (production/respiration) versus inorganic (calcification/dissolution) processes. Future research should incorporate Total Alkalinity (TA) and Dissolved Inorganic Carbon (DIC) to fully disentangle these drivers.

Second, while the 345-day monitoring offers deep seasonal insight, it represents a single annual cycle at one station; thus, spatial and interannual representativeness across broader seascapes remains to be confirmed.

Although biological surveys followed the sensor deployment, the study's conclusions are based on the assumption that the long-lived coralligenous structuring species remained stable during the intervening period. While this assumption is consistent with the slow successional dynamics of these communities, future integrated continuous chemical sensors monitoring programs with real-time biological monitoring should aim to synchronize chemical and biological assessments to eliminate such temporal gaps and assessing the functional resilience of these reefs.

5 Conclusions

The present study provides a critical foundational baseline for understanding the carbonate dynamics of the Central Tyrrhenian Sea by offering a high-resolution, high-frequency characterization of pH behavior and associated environmental variables at a shallow coralligenous reef. The results of this study demonstrate that coastal pH variability is dominated by a strong metabolic signature, where daily and seasonal fluctuations often exceed the long-term anthropogenic acidification trends observed in open waters. The evidence indicates that the observed variability is highly consistent with the *interplay* between community photosynthesis, respiration, and calcification/dissolution, while physical drivers such as temperature and regional water mass patterns provide the broader seasonal context. This highlights the importance of recognizing coastal habitats as dynamic mosaics where local drivers can significantly modulate or even mask global environmental signals.

Ecological surveys revealed a highly structured and stratified coralligenous assemblage dominated by long-lived ecosystem engineers that showed remarkable structural stability, despite the marked chemical instability recorded. This resilience suggests that the structuring species are currently well-adapted to the natural range of pH fluctuations characteristic of this habitat. The single-station annual cycle offers deep temporal insight, although the spatial representativeness and interannual variability across the

broader seascape remain to be confirmed by future long-term studies. Nevertheless, this dataset establishes the necessary reference against which the increasing frequency of extreme events must be measured. As the boundaries of natural variability shift, the structural integrity of coralligenous frameworks may face unprecedented pressure. Therefore, future research must prioritize comprehensive carbonate chemistry monitoring combined with real-time biological assessments to identify potential refugia and predict the long-term viability of these essential Mediterranean ecosystems in an increasingly inconstant environment.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

DB: Conceptualization, Formal analysis, Investigation, Supervision, Visualization, Writing – original draft, Writing – review & editing. MMZ: Conceptualization, Data curation, Investigation, Resources, Supervision, Visualization, Writing – original draft, Writing – review & editing. MF: Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. LB: Resources, Writing – original draft, Writing – review & editing. SG: Data curation, Formal analysis, Resources, Writing – review & editing. SB: Data curation, Resources, Writing – review & editing. FA: Resources, Writing – review & editing. MG: Data curation, Resources, Writing – review & editing. MC: Investigation, Resources, Writing – review & editing. FF: Investigation, Resources, Writing – review & editing. NC: Data curation, Investigation, Resources, Writing – review & editing. LP: Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2026.1782367/full#supplementary-material

References

Abbiati, M., Airoldi, L., Costantini, F., Fava, F., Ponti, M., and Virgilio, M. (2009). "Spatial and temporal variation of assemblages in Mediterranean coralligenous reefs," in *Proceedings of the First Symposium on the Coralligenous and Other Calcareous Bio-Concretions of the Mediterranean Sea, Tabarka, Tunis, 15-16 January 2009*. Eds. C. Pergent-Martini and M. Brichet (UNEP/MAP-RAC/SPA, Tunis, TN), 34–39.

Adloff, F., Somot, S., Sevault, F., Jordà, G., Aznar, R., and Déqué, M. (2015). Mediterranean Sea response to climate change in an ensemble of twenty first century scenarios. *Clim. Dyn.* 45, 2775–2802. doi: 10.1007/s00382-015-2507-3

Airoldi, L. (1998). Roles of disturbance, sediment stress and substratum retention on spatial dominance in algal turf. *Ecology* 79, 2759–22770. doi: 10.1890/0012-9658

Álvarez, M., Sanleón-Bartolomé, H., Tanhua, T., Mintrop, L., Luchetta, A., Cantoni, C., et al. (2014). The CO_2 system in the Mediterranean Sea: a basin wide perspective. *Ocean. Sci.* 10, 69–92. doi: 10.5194/os-10-69-2014

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26, 32–46. doi: 10.1111/j.1442-9993.2001.01070.pp.x

Astraldi, M., and Gasparini, G. P. (1992). The seasonal characteristics of the circulation in the north Mediterranean basin and their relationship with the atmospheric-climatic conditions. *J. Geophys. Res. Oceans.* 97, 9531–9540. doi: 10.1029/92jc00114

Babbini, L., Finoia, M. G., Devoti, S., Bencivenga, M., Bressan, G., and Manca Zeichen, M. (2013). Marine acidification: a new perspective within the framework of the MSFD. *Biol. Mar. Mediterr.* 20, 228–229.

Balata, D., Piazzi, L., Cecchi, E., and Cinelli, F. (2005). Variability of Mediterranean coralligenous assemblages subject to local variation in sediment deposits. *Mar. Environ. Res.* 60, 403–421. doi: 10.1016/j.marenvres.2004.12.005

Basso, D. (2012). "Carbonate production by calcareous red algae and global change," in *Calcareous Algae and Global Change: From Identification to Quantification*. Eds. D. Basso and B. Granier, Geodiversitas, vol. 34. (Paris: Muséum national d'Histoire naturelle), 13–33. doi: 10.5252/g2012n1a2

Basso, D., Bracchi, V. A., Bazzicalupo, P., Martini, M., Maspero, F., and Bavestrello, G. (2022). Living coralligenous as geohistorical structure built by coralline algae. *Front. Earth Sci.* 10, 961632. doi: 10.3389/feart.2022.961632

Bethoux, J. P., Gentili, B., Morin, P., Nicolas, E., Pierre, C., and Ruiz-Pino, D. (1999). The Mediterranean Sea: a miniature ocean for climatic and environmental studies and a key for the climatic functioning of the North Atlantic. *Prog. Oceanogr.* 44, 131–146. doi: 10.1016/S0079-6611(99)00023-3

Boucher, J., and Billard, G. (2020). The mediterranean: mare plasticum (Gland, Switzerland: IUCN). Available online at: https://portals.iucn.org/library (Accessed September 10, 2025).

Boudouresque, C. F. (1971). Méthodes d'étude qualitative et quantitative du benthos (en particulier du phytobenthos). *Tethys* 3, 79–104.

Bresnahan, P. J., Martz, T. R., Takeshita, Y., Johnson, K. S., and LaShomb, M. (2014). Best practices for autonomous measurement of seawater pH with the Honeywell Durafet. *Methods Oceanogr.* 9, 44–60. doi: 10.1016/j.mio.2014.08.003

Buffett, G. G., Krahmann, G., Klaeschen, D., Schroeder, K., Sallarès, V., Papenberg, C., et al. (2017). Seismic oceanography in the Tyrrhenian Sea: thermohaline staircases, eddies, and internal waves. *J. Geophys. Res. Oceans.* 122, 8503–8523. doi: 10.1002/2017jc012726

Carbonne, C., Teixidó, N., Moore, B., Mirasole, A., Gattuso, J. P., and Comeau, S. (2022). Two centuries of ocean acidification show that coastal ecosystems are frontline indicators of global change. *Glob. Change Biol.* 28, 4321–4335. doi: 10.1111/gcb.16202

Caronni, S., Bracchi, V. A., Atzori, F., Citterio, S., Cadoni, N., Gentili, R., et al. (2023). Caulerpa cylindracea spread on deep rhodolith beds can be influenced by the morphostructural composition of the bed. *Diversity* 15, 349. doi: 10.3390/d15030349

Carstensen, J., and Duarte, C. M. (2019). Drivers of pH variability in coastal ecosystems. *Environ. Sci. Technol.* 53, 4020–4029. doi: 10.1021/acs.est.8b03655

Coma, R., Ribes, M., Gili, J. M., and Zabala, M. (2000). Seasonality in coastal benthic ecosystems. *Trends Ecol. Evol.* 15, 448–453. doi: 10.1016/S0169-5347(00)01970-4

Comeau, S., Cornwall, C. E., and McCulloch, M. T. (2017). Decoupling between the response of coral calcifying fluid pH and calcification to ocean acidification. *Sci. Rep.* 7, 7573. doi: 10.1038/s41598-017-08003-z

Conti, M. E., and Finoia, M. G. (2010). Metals in molluscs and algae: a north–south Tyrrhenian Sea baseline. *J. Hazard. Mater.* 181, 388–392. doi: 10.1016/j.jhazmat.2010.05.022

Conti, M. E., Mecozzi, M., and Finoia, M. G. (2015). Determination of trace metal baseline values in Posidonia oceanica, Cystoseira sp. and other marine environmental biomonitors: a quality control method for a study in South Tyrrhenian coastal areas. *Environ. Sci. pollut. Res.* 22, 3640–3651. doi: 10.1007/s11356-014-3603-3

Conti, M. E., Plà, R., Simone, C., Jasan, R., and Finoia, M. G. (2020). Implementing the monitoring breakdown structure: native lichens as biomonitors of element deposition in the southern Patagonian forest connected with the Puyehue volcano event in 2011-a 6-year survey, (2006–2012). *Environ. Sci. pollut. Res.* 27, 38819–38834. doi: 10.1007/s11356-020-10001-0

Conti, M. E., Tudino, M. B., Finoia, M. G., Simone, C., and Stripeikis, J. (2019). Performance of two Patagonian molluscs as trace metal biomonitors: the overlap bioaccumulation index (OBI) as an integrative tool for the management of marine ecosystems. *Ecol. Ind.* 101, 749–758. doi: 10.1016/j.ecolind.2019.01.060

Cornwall, C. E., Diaz-Pulido, G., and Comeau, S. (2019). Impacts of ocean warming on coralline algal calcification: meta-analysis, knowledge gaps, and key recommendations for future research. *Front. Mar. Sci.* 6, 186. doi: 10.3389/fmars.2019.00186

Cornwall, C. E., Harvey, B. P., Comeau, S., Cornwall, D. L., Hall-Spencer, J. M., Peña, V., et al. (2022). Understanding coralline algal responses to ocean acidification: Meta-analysis and synthesis. *Glob. Chang. Biol.* 28, 362–374. doi: 10.1111/gcb.15899

Cornwall, C. E., Hepburn, C. D., McGraw, C. M., Currie, K. I., Pilditch, C. A., Hunter, K. A., et al. (2013). Diurnal fluctuations in seawater pH influence the response of a calcifying macroalga to ocean acidification. *Proc. R. Soc B.* 280, 20132201. doi: 10.1098/rspb.2013.2201

D'Agostino, R., Bellacicco, M., Rivaro, P., and Raicich, F. (2023). Surface ocean pH and carbonate saturation state in the Mediterranean Sea: local and regional trends. *J. Mar. Syst.* 240, 103886. doi: 10.1016/j.jmarsys.2023.103886

Danovaro, R. (2003). Pollution threats in the Mediterranean Sea: An overview. *Chem. Ecol.* 19, 15–32. doi: 10.1080/0275754031000081467

Diaz-Pulido, G., Anthony, K. R., Kline, D. I., Dove, S., and Hoegh-Guldberg, O. (2012). Interactions between ocean acidification and warming on the mortality and dissolution of coralline algae. *J. Phycol.* 48, 32–39. doi: 10.1111/j.1529-8817.2011.01084.x

Dickson, A. G., Sabine, C. L., and Christian, J. R. (2007). Guide to best practices for ocean CO_2 measurements. *PICES. Spec. Publ.* 3, 191.

Duvane, J. A., and Dupont, S. (2024). Drivers of biological response to fluctuating seawater pH conditions in sea urchin Echinus esculentus larvae. *Sci. Total. Environ.* 935, 173383. doi: 10.1016/j.scitotenv.2024.173383

Estrada, M. (1996). Primary production in the northwestern Mediterranean. *Sci. Mar.* 60, 55–64.

Fader, M., Giupponi, C., Burak, S., Dakhlaoui, H., Koutroulis, A., Lange, M. A., et al. (2020). "Water," in *Climate and Environmental Change in the Mediterranean Basin – Current Situation and Risks for the Future. First Mediterranean Assessment Report*. Eds. W. Cramer, J. Guiot and K. Marini (MedECC, Union for the Mediterranean, Plan Bleu, UNEP/MAP, Marseille, France), 57.

Finoia, M. G. (2013). Strategia per l'Ambiente Marino. Acidificazione Marina (Quaderni ISPRA - Rapporti Tecnici Internazionali (Q30/2013 Int. Tech. Rep.), n. 14" in *ISPRA - Istituto Superiore per la Protezione e la Ricerca Ambientale*.

Flecha, S., Giménez-Romero, À., Tintoré, J., Fiz, F., Pérez, F. F., Alou-Font, E., et al. (2022). pH trends and seasonal cycle in the coastal Balearic Sea reconstructed through machine learning. *Sci. Rep.* 12, 12956. doi: 10.1038/s41598-022-17253-5

Flecha, S., Pérez, F. F., García-Lafuente, J., Sammartino, S., Ríos, A. F., and Huertas, I. E. (2015). Trends of pH decrease in the Mediterranean Sea through high frequency observational data: indication of ocean acidification in the basin. *Sci. Rep.* 5, 16770. doi: 10.1038/srep16770

Garrabou, J., Ballesteros, E., and Zabala, M. (2002). Structure and dynamics of north-western Mediterranean rocky benthic communities along a depth gadient. *Estuar. Coast. Shelf. Sci.* 55, 493–508. doi: 10.1006/ecss.2001.0920

Gómez-Gras, D., Linares, C., Dornelas, M., Madin, J. S., Brambilla, V., Ledoux, J. B., et al. (2021). Climate change transforms the functional identity of Mediterranean coralligenous assemblages. *Ecol. Lett.* 24, 1038–1051. doi: 10.1111/ele.13718

González, D., Coughlan, C., Stips, A., Stolk, A., Gonzalez, C., Moreno, I., et al. (2015). "Review of the Commission Decision 2010/477/EU concerning MSFD criteria for assessing Good Environmental Status, Descriptor 7 Permanent alteration of hydrographical conditions does not adversely affect marine ecosystems," in *Joint Research Centre Technical Report* (Publications Office of the European Union, Luxembourg), 32. doi: 10.2788/435059

Goyet, C., Hassoun, A., Gemayel, E., Touratier, F., Abboud-Abi Saab, M., and Guglielmi, V. (2016). Thermodynamic forecasts of the mediterranean sea acidification. *Medit. Mar. Sci.* 17, 508–518. doi: 10.12681/mms.1487

Grossi, F., Lagasio, M., Napoli, A., Provenzale, A., and Tepsich, P. (2024). Phytoplankton spring bloom in the NW Mediterranean Sea under climate change. *Sci. Total. Environ.* 914, 169884. doi: 10.1016/j.scitotenv.2024.169884

Guerzoni, S., Molinaroli, E., and Chester, R. (1997). Saharan dust inputs to the western Mediterranean Sea: depositional patterns, geochemistry and sedimentological implications. *Deep-Sea. Res. II.: Top. Stud. Oceanogr.* 44, 631–654. doi: 10.1016/S0967-0645(96)00096-3

Hassoun, A. E. R., Bantelman, A., Canu, D., Comeau, S., Galdies, C., Gattuso, J. P., et al. (2022). Ocean acidification research in the Mediterranean Sea: Status, trends and next steps. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.892670

Hendriks, I. E., Escolano-Moltó, A., Flecha, S., Vaquer-Sunyer, R., Wesselmann, M., and Marbà, N. (2022). Mediterranean seagrasses as carbon sinks: methodological and regional differences. *Biogeosciences* 19, 4619–4637. doi: 10.5194/bg-19-4619-2022

Hill, I. D., Hill, R., and Holder, R. L. (1976). Fitting Johnson curves by moments. *J. R. Stat. Soc Ser. C. Appl. Stat.* 25, 180–189. doi: 10.2307/2346692

Hofmann, G. E., Smith, J. E., Johnson, K. S., Send, U., Levin, L. A., and Micheli, F. (2011). High-frequency dynamics of ocean pH: a multi-ecosystem comparison. *PloS One* 6, e28983. doi: 10.1371/journal.pone.0028983

Hurd, C. L., Cornwall, C. E., Currie, K. I., Hepburn, C. D., McGraw, C. M., Hunter, K. A., et al. (2011). Metabolically-induced pH fluctuations by some coastal calcifiers exceed projected 22nd century ocean acidification: a mechanism for differential susceptibility? *Glob. Change Biol.* 17, 3254–3262. doi: 10.1111/j.1365-2486.2011.02473.x

Hyndman, R. J., and Athanasopoulos, G. (2014). *Forecasting. Principle and Practice* (Melbourne, Australia: OTexts).

Iacono, R., Napolitano, E., Palma, M., and Sannino, G. (2021). The Tyrrhenian sea circulation: a review of recent work. *Sustainability* 13, 6371. doi: 10.3390/su13116371

Ingrosso, G., Giani, M., Comici, C., Kralj, M., Piacentino, S., De Vittor, C., et al. (2021). Coastal ocean acidification: challenges and opportunities for systems-level research in the Mediterranean Sea. *Front. Mar. Sci.* 8, 663613. doi: 10.3389/fmars.2021.663613

Iona, A., Theodorou, A., Sofianos, S., Watelet, S., Troupin, C., and Beckers, J. (2018). Mediterranean Sea climatic indices: monitoring long-term variability and climate changes. *Earth Syst. Sci. Data* 10, 1829–1842. doi: 10.5194/essd-10-1829-2018

Jiang, L.-Q., Carter, B. R., Feely, R. A., Lauvset, S., and Olsen, A. (2019). Surface ocean pH and buffer capacity: past, present and future. *Sci. Rep.* 9, 18624. doi: 10.1038/s41598-019-55039-4

Jiménez-Casero, J., Ruiz, J. M., Bernardeau-Esteller, J., García-Muñoz, R., Sánchez-Lizaso, J. L., Marin-Guirao, L., et al. (2025). Cascading ecological impacts: from eutrophic coastal lagoon collapse to decline of *Posidonia oceanica* meadows in the Mediterranean. *Mar. pollut. Bull.* 221, 118536. doi: 10.1016/j.marpolbul.2025.118536

Johnson, N. L. (1949). Systems of frequency curves generated by methods of translation. *Biometrika* 36, 149–176. doi: 10.2307/2332539

Johnson, M. D., Rodriguez, L. M., O'Connor, S. E., Varley, N. F., and Altieri, A. H. (2019). pH variability exacerbates effects of ocean acidification on a Caribbean crustose coralline alga. *Front. Mar. Sci.* 6, 150. doi: 10.3389/fmars.2019.00150

Kapsenberg, L., Alliouane, S., Gazeau, F., Mousseau, L., and Gattuso, J. P. (2017a). Coastal ocean acidification and increasing total alkalinity in the northwestern Mediterranean Sea. *Ocean. Sci.* 13, 411–426. doi: 10.5194/os-13-411-2017

Kapsenberg, L., Alliouane, S., Gazeau, F., Mousseau, L., and Gattuso, J. P. (2017b). Coastal ocean acidification and maximum pH of high-frequency variability. *Sci. Rep.* 7, 4580. doi: 10.1038/s41598-017-04245-z

Kapsenberg, L., and Cyronak, T. (2019). Ocean acidification refugia in variable environments. *Glob. Change Biol.* 25, 3201–3214. doi: 10.1111/gcb.14730

Kapsenberg, L., and Hofmann, G. E. (2016). Ocean pH time-series and drivers of variability along the northern Channel Islands, California, USA. *Limnol. Oceanogr.* 61, 953–968. doi: 10.1002/lno.10264

Kelaher, B. P., Mamo, L. T., Provost, E., Litchfield, S. G., Giles, A., and Butcherine, P. (2022). Influence of ocean warming and acidification on habitat-forming coralline algae and their associated molluscan assemblages. *Glob. Ecol. Conserv.* 35, e02081. doi: 10.1016/j.gecco.2022.e02081

Kelly, M. W., and Hofmann, G. E. (2013). Adaptation and the physiology of ocean acidification. *Funct. Ecol.* 27, 980–990. doi: 10.1111/j.1365-2435.2012.02061.x

Korres, G., Ravdas, M., and Zacharioudaki, A. (2019).Mediterranean sea waves hindcast (CMEMS MED-waves) [dataset]. In: *Copernicus Monitoring Environment Marine Service (Cmems)*. doi: 10.25423/CMCC/MEDSEA_HINDCAST_WAV_006_012 (Accessed August 21, 2022).

Kwiatkowski, L., Albright, R., Hosfelt, J., NebuChina, Y., Ninokawa, A., Rivlin, T., et al. (2016). Nighttime enhancement of coral reef calcification by terrestrial alkalinity ocean fertilization. *Sci. Rep.* 6, 21235. doi: 10.1038/srep21235

López, E. P., Bernal, C. A., and Zea, S. (2022). Estimation of pH on total scale in coastal environments for the understanding of the variability of the carbonate system in the context of ocean acidification. *Bol. Cienc. Tierra.* 51, 61–72.

Martz, T. R., Connery, J. G., and Johnson, K. S. (2010). Testing the Honeywell Durafet® for seawater pH applications. *Limnol. Oceanogr-Meth.* 8, 172–184. doi: 10.4319/lom.2010.8.172

Marullo, S., Serva, F., Iacono, R., Napolitano, E., di Sarra, A., Meloni, D., et al. (2013). Cumulative human impacts on Mediterranean and Black Sea marine ecosystems: assessing current pressures and opportunities. *PloS One* 8, e79889. doi: 10.1371/journal.pone.0079889

Micheli, F., Halpern, B. S., Walbridge, S., Ciriaco, S., Ferretti, F., Fraschetti, S., et al. (2013). Cumulative human impacts on Mediterranean and Black Sea marine ecosystems: assessing current pressures and opportunities. *PloS One* 8, e79889. doi: 10.1371/journal.pone.0079889

Palacios-Peña, L., Lorente-Plazas, R., Montávez, J. P., and Jiménez-Guerrero, P. (2019). Saharan dust modeling over the Mediterranean Basin and Central Europe: does the resolution matter? *Front. Earth Sci.* 7, 290. doi: 10.3389/feart.2019.00290

Piazzi, L., Balata, D., Bulleri, F., Gennaro, P., and Ceccherelli, G. (2016). The invasion of *Caulerpa cylindracea* in the Mediterranean: the known, the unknown and the knowable. *Mar. Biol.* 163, 161. doi: 10.1007/s00227-016-2937-4

Piazzi, L., Balata, D., Pertusati, M., and Cinelli, F. (2004). Spatial and temporal variability of Mediterranean macroalgal coralligenous assemblages in relation to habitat and substrate inclination. *Bot. Mar.* 47, 105–115. doi: 10.1515/BOT.2004.010

Piazzi, L., Cecchi, E., Cinti, F., and Ceccherelli, G. (2021a). Extreme events and conservation of subtidal habitats: Effects of a rainfall flood on coralligenous reefs. *Mar. pollut. Bull.* 165, 112106. doi: 10.1016/j.marpolbul.2021.112106

Piazzi, L., and Cinelli, F. (2001). The distribution and dominance of two introduced turf-forming macroalgae in the coast of Tuscany (Italy, northwestern Mediterranean) in relation to different habitats and sedimentation. *Bot. Mar.* 44, 509–520. doi: 10.1515/bot.2001.057

Piazzi, L., and Cinelli, F. (2003). Evaluation of benthic macroalgal invasion in a harbour area of the western Mediterranean Sea. *Eur. J. Phycol.* 38, 223–231. doi: 10.1080/1364253031000136358

Piazzi, L., Cinti, M. F., Guala, I., Grech, D., La Manna, G., Pansini, A., et al. (2021b). Variations in coralligenous assemblages from local to biogeographic spatial scale. *Mar. Environ. Res.* 169, 105375. doi: 10.1016/j.marenvres.2021.105375

Piazzi, L., Gennaro, P., and Balata, D. (2012). Threats to macroalgal coralligenous assemblages in the Mediterranean Sea. *Mar. pollut. Bull.* 64, 2623–2629. doi: 10.1016/j.marpolbul.2012.07.027

Piazzi, L., Gennaro, P., Montefalcone, M., Bianchi, C. N., Cecchi, E., Morri, C., et al. (2019). STAR: an integrated and standardized procedure to evaluate the ecological status of coralligenous reefs. *Aquat. Conserv.* 29, 189–201. doi: 10.1002/aqc.2983

Pinna, F., Piazzi, L., Cinti, M. F., Pansini, A., Stipcich, P., and Ceccherelli, G. (2021). Vertical variation of coralligenous cliff assemblages in marine biogeographic areas. *Estuar. Coast. Shelf. Sci.* 261, 107554. doi: 10.1016/j.ecss.2021.107554

Provoost, P., Van Heuven, S., Soetaert, K., Laane, R. W. P. M., and Middelburg, J. J. (2010). Seasonal and long-term changes in pH in the Dutch coastal zone. *Biogeosciences* 7, 3869–3878. doi: 10.5194/bg-7-3869-2010

Ragazzola, F., Foster, L. C., Form, A., Anderson, P. S. L., Hansteen, T. H., and Fietzke, J. (2012). Ocean acidification weakens the structural integrity of coralline algae. *Glob. Change Biol.* 18, 2804–2812. doi: 10.1111/j.1365-2486.2012.02756.x

R Core Team (2019). R: A Language and Environment for Statistical Computing (Vienna, Austria: R Foundation for Statistical Computing). Available online at: https://www.R-project.org/ (Accessed September 10, 2025).

Reale, M., Cossarini, G., Lazzari, P., Lovato, T., Bolzon, G., Masina, S., et al. (2022). Acidification, deoxygenation, and nutrient and biomass declines in a warming Mediterranean Sea. *Biogeosciences* 19, 4035–4065. doi: 10.5194/bg-19-4035-2022

Reyes-Nivia, C., Diaz-Pulido, G., and Dove, S. (2014). Relative roles of endolithic algae and carbonate chemistry variability in the skeletal dissolution of crustose coralline algae. *Biogeosciences* 11, 4615–4626. doi: 10.5194/bg-11-4615-2014

Rodá, F., Bellot, J., Avila, A., Escarré, A., Piñol, J., and Terradas, J. (1993). Saharan dust and the atmospheric inputs of elements and alkalinity to Mediterranean ecosystems. *Water Air. Soil pollut.* 66, 277–294. doi: 10.1007/BF00479851

Ruitton, S., Verlaque, M., and Boudouresque, C. F. (2005). Seasonal changes of the introduced *Caulerpa racemosa* var. *cylindracea* (Caulerpales, Chlorophyta) at the northwest limit of its Mediterranean range. *Aquat. Bot.* 82, 55–70. doi: 10.1016/j.aquabot.2005.02.008

Schneider, J., and Le Campion-Alsumard, T. (1999). Construction and destruction of carbonates by marine and freshwater cyanobacteria. *Eur. J. Phycol.* 34, 417–426. doi: 10.1017/s0967026299002280

Shi, Y., and Li, Y. (2024). Impacts of ocean acidification on physiology and ecology of marine invertebrates: a comprehensive review. *Aquat. Ecol.* 58, 207–226. doi: 10.1007/s10452-023-10058-2

Solidoro, C., Cossarini, G., Lazzari, P., Galli, G., Bolzon, G., Somot, S., et al. (2022). Modeling carbon budgets and acidification in the mediterranean sea ecosystem under contemporary and future climate. *Front. Mar. Sci.* 8, 781522. doi: 10.3389/fmars.2021.781522

Sorgente, R., Pessini, F., Drago, A. F., Ribotti, A., Genovese, S., Barra, M., et al. (2024). Interannual variability of the hydrology on the Sardinia shelf. *Front. Mar. Sci.* 11, 1411819. doi: 10.3389/fmars.2024.1411819

Teixidó, N., Carlot, J., Alliouane, S., Ballesteros, E., De Vittor, C., Gambi, M. C., et al. (2024). Functional changes across marine habitats due to ocean acidification. *Glob. Change Biol.* 30, e17105. doi: 10.1111/gcb.17105

Touratier, F., and Goyet, C. (2009). Decadal evolution of anthropogenic CO_2 in the northwestern Mediterranean Sea from the mid-1990s to the mid-2000s. *Deep-Sea. Res. I.: Oceanogr. Res. Pap.* 56, 1708–1716. doi: 10.1016/j.dsr.2009.05.015

Touratier, F., and Goyet, C. (2011). Impact of the Eastern Mediterranean Transient on the distribution of anthropogenic CO_2 and first estimate of acidification for the Mediterranean Sea. *Deep. Sea. Res. I.* 58, 1–15. doi: 10.1016/j.dsr.2010.10.002

Tribollet, A., Chauvin, A., and Cuet, P. (2022). Natural photosynthetic microboring communities produce alkalinity in seawater whereas aragonite saturation state rises up to five. *Front. Earth Sci.* 10, 894501. doi: 10.3389/feart.2022.894501

Vargas, C. A., Lagos, N. A., Lardies, M. A., Duarte, C., Manriquez, P. H., Aguilera, V. M., et al. (2017). Species-specific responses to ocean acidification should account for local adaptation and adaptive plasticity. *Nat. Ecol. Evol.* 1, 84. doi: 10.1038/s41559-017-0084

Waldbusser, G. G., and Salisbury, J. E. (2014). Ocean acidification in the coastal zone from an organism's perspective: multiple system parameters, frequency domains, and habitats. *Ann. Rev. Mar. Sci.* 6, 221–247. doi: 10.1146/annurev-marine-121211-172238

Wheeler, B. (2013).SuppDists: supplementary distributions. In: *R Package Version*. Available online at: https://cran.r-project.org/web/packages/SuppDists/ (Accessed September 10, 2025).

Wootton, J. T., Pfister, C. A., and Forester, J. D. (2008). Dynamic patterns and ecological impacts of declining ocean pH in a high resolution multi-year dataset. *P. Natl. A. Sci.* 105, 18848–18853. doi: 10.1073/pnas.0810079105

Yao, K. M., Marcou, O., Goyet, C., Guglielmi, V., Touratier, F., and Savy, J.-P. (2016). Time variability of the north-western Mediterranean Sea pH over 1995–2011. *Mar. Environ. Res.* 116, 51–60. doi: 10.1016/j.marenvres.2016.02.016

Zeng, X., Chen, X., and Zhuang, J. (2015). The positive relationship between ocean acidification and pollution. *Mar. pollut. Bull.* 91, 14–21. doi: 10.1016/j.marpolbul.2014.12.001