



# Fluctuations in abundance of the striped venus clam *Chamelea gallina* in the southern Adriatic Sea (Central Mediterranean Sea): knowledge, gaps and insights for ecosystem-based fishery management

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**Abstract** An assessment on the fluctuations in abundance of the striped venus clam (*Chamelea gallina*) in the southern Adriatic Sea (Central Mediterranean Sea), and the northern Gargano area, has been conducted through both historical information and recent data from monitoring surveys during the period 1997–2019. Production trends, conditions of the commercial stock biomass, and depth distribution pattern of juveniles and commercial sizes were analysed testing temporal differences. Moreover, the exploitation of the clam beds and recruitment events were investigated in 2018–2019. Changes in abundance were analysed using non-parametric tests for

both juvenile (length class,  $LC < 22$  mm) and commercial ( $LC \geq 22$  mm) fractions. Hydrodynamic changes, temperature and salinity variations were explored using a 3D hydrodynamic numerical model (MIKE 3 FM-HD) and statistical analysis, as well as changes in benthic assemblages impacted by hydraulic dredges were investigated through PERMANOVA and other multivariate analysis.

The results showed a temporal decline of production and biomass of *C. gallina* during the 1997–2019 period, and a regression of the depth limit in the clams' distribution towards shallower waters. A significant reduction in juveniles was observed during 2018–2019 with a very limited recruitment. The fishing exploitation showed high impacts on the commercial stock and benthic assemblages in the summer of 2018. Overall, water currents were predominantly directed offshore in 2018, during the *C. gallina* spawning period. This could affect the larval dispersal and settlement on unsuitable bottoms. Anomalies in temperature (high peaks in August 2018,  $> 28$  °C) and salinity (low values in spring 2018,  $< 37$  PSU) could have induced stress and mortality events on the entire clam bed in the study area. This first study highlights the need to integrate environmental information in the assessment of commercial stocks of clams in the Adriatic Sea, to better understand climate change effects on the fluctuations and to support effective ecosystem-based fishery management.

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## Introduction

The management of fishery resources addressed towards sustainability requires a holistic approach such as the ecosystem-based fishery management (EBFM, Pikitch et al. 2004), capable of taking into account all environmental and anthropic drivers affecting the population dynamic of a target species. This is particularly true for species characterized by a life cycle across different ecological domains (e.g. benthic and pelagic), and which are distributed in habitats subject to different environmental and anthropogenic pressures, such as inshore soft bottoms (Román et al. 2023a, b).

The striped venus clam (*Chamelea gallina* Linnaeus, 1758) is one of the most important commercial shellfishes at Mediterranean and global scale (FAO 2020), with the main fishing grounds distributed in Spanish waters (Baeta et al. 2021a), as well as in the Adriatic Sea (Morello et al. 2005). In 2018 and 2019, the commercial value in the Italian fish market was around €51.4 million, representing 6% of all national fishing production (DGPEMAC 2019). The harvesting of the commercial fraction is performed using hydraulic dredgers on the shallowest soft bottoms (Bargione et al. 2023).

This bivalve inhabits the fine well-sorted sand biocenosis (Pérès and Picard 1964), occupying a well-defined ecological niche in the Adriatic Sea, determined by precise chemical-physical conditions of both water and sediment (see Grazioli et al. 2022). The life cycle is characterized by a reproductive period regulated by the rising of temperature in spring, reaching the emission peaking of gametes in June and July, and, in some cases in August and September, as observed in the Adriatic Sea (Trevisan 2011; Bargione et al. 2021a). The planktonic larvae spend a period of 15–30 days before settling on the seabed (Grazioli et al. 2022). Thus, the effects of hydrographic traits and climatic variations are fundamental drivers in the success of recruitment (Baeta et al. 2021b). The striped venus clam is characterized by a filter-feeding habit, and its

growth is affected by seasonal environmental conditions (Gaspar et al. 2004), generally reaching a size of 15–18 mm at the age of 1 year with geographical differences in growth rates (Bargione et al. 2020). In addition, the Minimum Conservation Reference Size (MCRS) established in 2016 (Delegated Regulation (EU) 2016/2376, Regulation (EU) 2020/3, and Delegated Regulation (EU) 2020a/2237) fixed the commercial size for *C. gallina* at 22 mm (age of about 2 years), in derogation to previous one of 25 mm (Annex III to Regulation (EC) 1967/2006). This evolution in European and national regulations followed the need of the clam fishing sector to maintain an effective economic yield from this resource, enhancing the capability of sustainable management of the Mediterranean stocks and the conservation of marine ecosystems in a good health status (Carlucci et al. 2015). In this framework, several studies in the Adriatic Sea have investigated biology aspects linked to the reproductive cycle (Bargione et al. 2021a), and the selectivity of dredge on the target species and the impact associated (Sala et al. 2017; Petetta et al. 2021; Bargione et al. 2021b). Although the life-history traits of this species seem to sustain the adoption of an MCRS of 22 mm, other factors could influence the *C. gallina* health status linked to the fishing impacts and environmental conditions (see Grazioli et al. 2022). Indeed, the hydraulic dredge can cause disturbance of the benthic community (Morello et al. 2006; Constantino et al. 2009; Baeta et al. 2021a), as well as stress and physical damage to bivalve shells (Moschino et al. 2003; Bargione et al. 2023). In general, fishery plays a critical role on the dynamics of adult populations, while environmental factors impact the entire population, thus affecting juvenile recruitment (Bento de Almeida et al. 2021). Some studies concern the effects on growth and stress from salinity solar radiation (Grazioli et al. 2022). Other analyses have investigated the effect of contaminants, such as the aluminium (Guglielmi et al. 2023), or physiological stress which can induce mass mortality events (Milan et al. 2019). However, analysis on the relationships between fluctuations of resources and environmental variables are very scarce in the southern Adriatic Sea. Conversely, attention on these aspects should be as high as possible considering that the species has historically shown declines in different areas of the Mediterranean, included the Adriatic Sea (Romanelli et al. 2009; DGPEMAC 2019). No less

important is the lack of a comprehensive monitoring plan over the past decades, which makes it difficult to understand the evolution of fluctuations in biomass of the resource and the relationships with environmental factors. This condition is more serious when trying to analyse the condition of the resource at the scale of compartments or smaller areas.

In the Adriatic Sea, the species is distributed along the entire Italian coastline up to the north of the Apulia region. In the South Adriatic, large fishing grounds are located in the northern Gargano area (Vaccarella et al. 1996; Marano et al. 1998). Also in this area, fluctuations in biomass of the striped venus clam have been observed since the 1980s with a large reduction in the biomass stock (Vaccarella et al. 1998). However, no temporal comparisons are available between the recent condition of the stocks and that observed in the past. Some information was collected in a report inherent to a monitoring survey performed during 2013 (Carlucci et al. 2013), but more recent information on the status of the stock of *C. gallina* has not been investigated. No less important, the fishing grounds are distributed in an area exposed to local factors (e.g. sediment features, geomorphological and hydrological traits) and global environmental drivers (e.g. climate variables), which affect the condition of the entire coastal ecosystem. This is particularly true for the northern area of the Gargano, where fishing grounds are distributed over 70 km along the coast in a range of 2–10 m depth, affected by fishery and seasonal environmental dynamics (Carlucci et al. 2024). Fishermen report a significant decrease in stock abundance and changes in the location of fishing grounds over time. These events were also detected through the monitoring surveys during the period 2018–2019 (Carlucci et al. 2020). Along with the decrease in the commercial fraction, a reduction in the abundance of juveniles was also observed, even though fishing activities followed the closure provisions of national regulations. Therefore, although the fishing effects are a relevant driver for the stock status and the stability of benthic habitats (Morello et al. 2005, 2011), other environmental factors could affect the juvenile recruitment of *C. gallina* in the area leading to the fluctuations and depletion events.

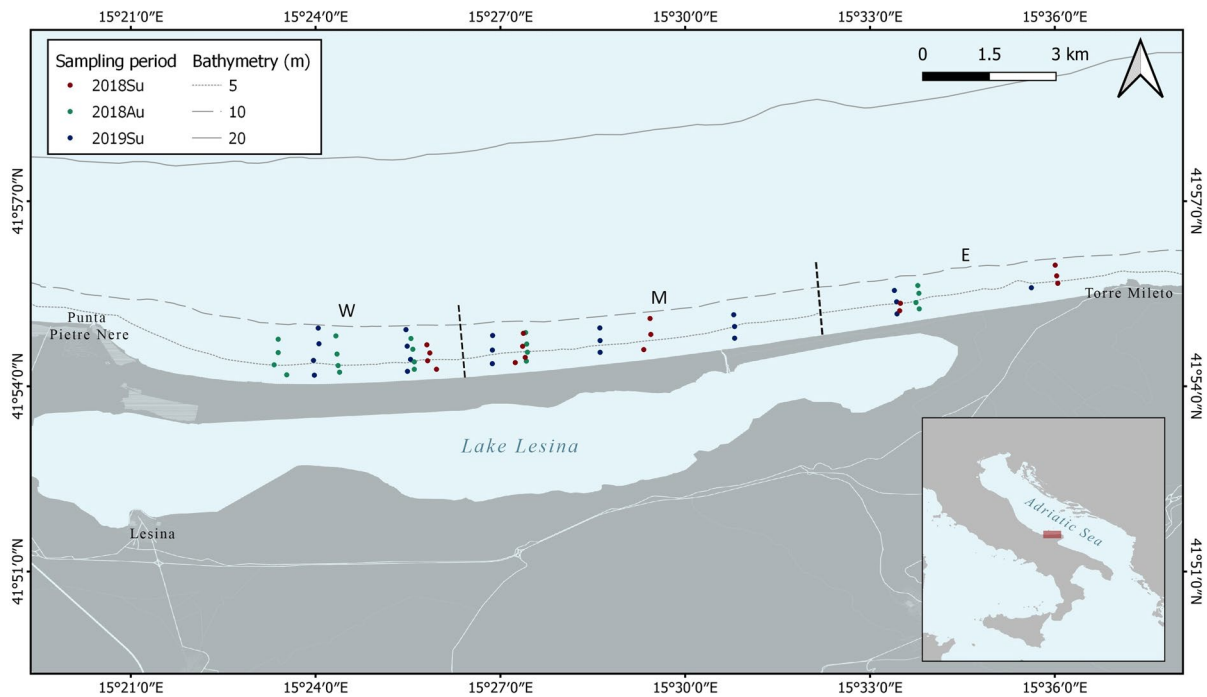
This study provides a baseline on the fluctuations of the *C. gallina* population exploited in the Southern Adriatic Sea, focusing attention on the recent condition of the stock distributed in the northern

Gargano area, considering the potential relationships between the abundance of juveniles and adults and some hydrographic variables. Historical data starting from 1997 were collected and compared with the abundance and biomass of the 2018–2019 period, the depth distribution of commercial and non-commercial fractions was also analysed. In addition, a focus on the period 2018–2019 was carried out investigating (1) changes in the structure of the benthic assemblage and abundances, and (2) trends and potential anomalies of the temperature, salinity, and water currents. The results highlight ecological aspects of the analysis, as well as the importance of the combination of an oceanographic modelling approach and biological survey data to provide information useful to the EBFM approach.

## Material and methods

### Study area

The fishing grounds exploited for harvesting *C. gallina* in the Adriatic Sea (Geographical Sub-Area 18) are primarily located along the shallow and sandy Italian coasts, since this species is strongly linked to the biocoenosis of well-sorted fine sands (WSFS, Pérès and Picard 1964). The clam harvesting activities in the Apulia region are carried out on the soft bottoms distributed from Foce Saccione to Rodi Garganico in the north Gargano and in the Gulf of Manfredonia area down to Barletta in the South. In particular, the area considered for this study is in the north Gargano area, along a stretch of coast of approximately 25 km between Punta Pietre Nere and Torre Mileto, in front of Lake Lesina (Fig. 1). The proximity to Lake Lesina results in peculiar ecological conditions in the area, thus characterised by a transitional nature, with a dynamic interplay between freshwater inflow and the marine environment. The study area covers approximately 2 km along the coast, in a bathymetric range between 0 and 10 m. The area historically represents a fishing ground for local fishermen to harvest the striped venus clam through dredging for commercial purposes. The dredge fleet is distributed between the harbours of Lesina and Capojale, accounting for a total of 44 vessels in 2018.



**Fig. 1** Map of the study area of Lesina (Adriatic Sea), included between Punta Pietre Nere and Torre Mileto. Solid circles indicate the sampling stations monitored for the assess-

ment of *C. gallina* health status during the period 2018–2019, and letters indicate the sub-areas investigated (Western, W; Middle, M; Eastern, E)

### Biological data collection from literature and sampling activities

A first assessment of changes in biomass of the commercial resource in the southern Adriatic Sea was conducted to analyse potential trends in the *C. gallina* fluctuations through data from official reports available in the literature. Therefore, information on the production (as landings) was acquired from several data sources, as well as those inherent to the status of the dredge fleet (Online Resource 1, Table S1).

Further analysis was carried out focusing attention on the study area, collecting biomass data from fishery-independent surveys conducted in the period 1997–2001 and 2018–2019 (more details in Carlucci et al. 2013, 2019, and in Online Resource 1, Table S2).

Finally, a focused analysis to explore the dynamics of the stock and relationships with environmental conditions, was carried out using data acquired from monitoring activities in 2018–2019. Starting from 2018, fishery-independent surveys were carried out on the main fishing bottoms identified with

the fishermen according to the indications of new national regulations (DGPEMAC 2019). Notably, this year represents a restart of the sampling activities required by the new national monitoring plan. Thus, two surveys were carried out during 2018 in the summer (July) and autumn (September), in order to identify the starting condition of the target resource in the fishing area. Moreover, a fishing ban occurred in August 2018, between the two sampling periods. Finally, starting from 2019, the monitoring was conducted with annual frequency. Therefore, the sampling data of the target species, and the associated benthic organisms, were considered for three distinct periods: July 2018 (summer, 2018Su), September 2018 (autumn, 2018Au) and July 2019 (summer, 2019Su). In each period, perpendicular linear transects were placed along the coastline according to information gathered from local fishermen, where the resource was commonly distributed based on their experience. The study area was divided into 5 transects in 2018Su and 2018Au, and 7 transects in 2019Su. Each transect consisted of up to four sampling hauls, spaced approximately 0.25 nautical miles

apart along the transect and carried out in a direction parallel to the coastline. Each following sampling haul was carried out in the case of occurrence of *C. gallina* in the catch of the previous one, otherwise the sampling was relocated to the next transect. A total of 16 sampling hauls were carried out in 2018Su, 20 in 2018Au and 21 in 2019Su, with georeferencing and depth data collected for each of them. The activity was conducted by adopting two sampling tools: the hydraulic dredge to assess the commercial fraction biomass belonging to the length class ( $LC \geq 22$  mm), and a net sampler fixed within the dredge to harvest the juvenile fraction ( $LC < 22$  mm), and the associated benthic organisms. The dredge had a mouth width of 3 m, the spacing between the grid bars set to 19 mm, and it was towed in each haul for a distance detected using GPS (Garmin 600 model). Each haul's catch was conveyed into a vibrating sieve, that served to further select commercial sizes. The net sampler consisted of a stainless-steel frame measuring  $40 \times 20$  cm (length  $\times$  width) with a nylon mesh size of 14 mm. For each haul, samples of about 5 kg for the commercial fraction, and a sample of maximum 2 kg of biomass (fresh weight) collected from the net sampler were taken for laboratory analysis. Striped venus clam individuals were measured with a calliper (1 mm precision) and weighed (0.1 g precision) individually to assess abundances and biomasses of the catches. Individuals of other benthic species were identified to the lowest practical taxonomic level and subsequently measured and weighed, as well.

#### Biological data analysis to assess the striped venus clam condition

Annual production (in tonnes) of GSA 18, obtained for the period 1997–2018, were analysed to detect potential temporal trends, by calculating the Spearman's rank correlation coefficient ( $r_s$ ).

Within the study area, a comparative assessment of the commercial biomass status of the target species with respect to Italian reference points for the clam fishery management (Regulation EU 1967/2006) were carried out, when data from fishery-independent surveys were available. Reference points indicate a good resource status when the biomass (fresh weight) is higher than  $8 \text{ g/m}^2$ ; a warning status for biomasses ranging between  $4\text{--}6 \text{ g/m}^2$ ; and a fishing ban for a biomass lower than  $4 \text{ g/m}^2$ . After a standardization

procedure of data acquired from several sources (Online Resource 1, Table S2), the annual mean values ( $\pm$ SE) of commercial biomass were calculated for the investigated periods (1997–2001 and 2018–2019). Annual means were calculated taking into consideration the modification of the commercial size. Thus, biomasses before 2018 were calculated on individuals of  $LC \geq 25$  mm, while those from 2018 considered individuals with  $LC \geq 22$  mm. Moreover, the distribution of *C. gallina* along a depth gradient (step of 1 m) was analysed considering the commercial biomasses ( $LC \geq 25$  mm), and a juvenile fraction of population included between  $15 < LC < 25$  mm (Online Resource 1, Table S2).

In the study area, a focused analysis was carried out to explore the recruitment dynamics of the striped venus clam during the three sampling periods of 2018–2019. Changes in abundance (expressed as  $N/100 \text{ m}^2$ ) were analysed for both juveniles ( $LC < 22$  mm) and the commercial fraction (or adults,  $LC \geq 22$  mm). In addition, three locations (E=Eastern area, M=Middle area, W=Western area) within the study area were considered to explore potential spatial differences (Fig. 1). The choice was driven by the information provided by the fishermen in 2018 on the displacement of the most productive fishing grounds, which were found in the W, while very low yields characterized both the M and E areas. The median values (min–max, I and III quartiles) were calculated for both sampling periods and sub-areas, and differences were tested using a non-parametric Kruskal–Wallis (KW) test, and a *post-hoc* comparison by Mann–Whitney U test with Bonferroni correction (McDonald 2014), on both population fractions. Finally, the length-frequency distribution (LFD) of *C. gallina* was analysed for the 3 sampling periods considering individuals harvested in the net sampler.

#### Analysis of faunal benthic assemblages associated to the striped venus clam

Taxa collected during the three surveys, were described according to their taxonomic classification, their importance for the commercial fishery (C=commercial, BC=bycatch, D=discard), calculating the mean biomass in all sampling hauls (Online Resource 1, Table S3).

To evaluate the spatio-temporal patterns within the benthic assemblage, a multivariate analysis was

conducted. Taxa were selected according to a frequency occurrence (FO) in more than 5% of the total hauls (Online Resource 1, Table S3). Their abundance was standardized ( $N/100\text{ m}^2$ ) and organized in a taxa/hauls matrix, after a fourth-root transformation of abundance data, to balance the contribution of rare and very abundant species (Legendre and Legendre 2012).

A Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson et al. 2008) based on Bray–Curtis dissimilarities (Bray and Curtis 1957) were performed to test the null hypotheses of no differences between periods, sampling locations, transects, and factor interactions. The experimental design consisted of two fixed and orthogonal factors, Period (Pe, with three levels: 2018 summer, 2018 autumn, 2019 summer), and Location (Lo, with three levels: E, M, W), and the random factor Transect, with 7 levels (1–7) nested in Location. The data collected from each haul were considered independent since the hauls were conducted at random positions within each Location, making the observations exchangeable in order to fulfil the null hypothesis requirements (Anderson 2001a, b). The PERMANOVA test was conducted by applying 9999 unrestricted permutations using the “Permutation of residuals under a reduced model” as the permutation method, and a post-hoc PAIRWISE *t* test was applied to significant differences, calculating Monte Carlo *p* values (*p* value < 0.05; Anderson et al. 2008).

Multivariate distribution patterns of sampling hauls considering the abundance data of the benthic assemblages for the three locations and sampling periods were plotted using the unconstrained ordination method, as Principal Coordinates Analysis (PCo, Gower 1966). To better visualise complex spatio-temporal patterns in the assemblages, the distances between centroids were calculated for significant factor interactions and data were plotted using PCO. Finally, Similarity Percentage (SIMPER) analysis was carried out to determine the species most responsible for the dissimilarities across the locations and sampling periods (Clarke and Warwick 1994).

The univariate tests were performed using the Paleontological Statistics Software Package for Education and Data Analysis (Hammer et al. 2001), while the multivariate analysis was carried out using PRIMER software v.6 with add-on PERMANOVA (Anderson et al. 2008; Clarke et al. 2014).

## Modelling approach and oceanographic data

The 3D hydrodynamic numerical model MIKE 3 FM HD produced by the Danish Hydraulic Institute (DHI 2016), was used to evaluate how hydrodynamic parameters affect the possible spatial distribution of the striped venus clam.

The model is based on the numerical solution of three-dimensional incompressible Reynolds-averaged Navier–Stokes (RANS) equations, subject to the assumptions of Boussinesq and hydrostatic pressure. The turbulent stresses are represented by a two-equation *k*– $\epsilon$  model (Rodi 1987) for the vertical direction and on the Smagorinsky formulation (Galperin and Orszag 1993) for the horizontal direction. According to the sensitivity analysis shown in same area of Adriatic Sea (De Padova et al. 2017, 2020, 2023; Chimienti et al. 2020, 2021), the simulation was performed by adopting the following calibration parameters: a seabed roughness equal to 0.1 m, a wind drag coefficient  $C_d$  equal to 0.02.

The hydrodynamic simulation for 3 years (2017–2019) was carried out in a baroclinic model in order to improve the numerical approach and model more realistic conditions.

At the open boundary of the domain, the model is forced by the temperature, salinity, and *u* and *v* components of sea current vertical profiles extracted by the Mediterranean Sea Physics Reanalysis model characterized by a horizontal grid resolution of  $1/24^\circ$  (ca. 4.6 km in latitude) and by 72 unevenly spaced vertical levels (Simoncelli et al. 2019). At the surface, the atmospheric data (*u* and *v* components of wind, atmosphere pressure, total cloud cover, solar radiation and air temperature), available every 6 h, were used as boundary conditions. These data were taken from the ERA-Interim developed through the Copernicus Climate Change Service (2017). The precipitation data, available every 1-day, was predicted by CPC Merged Analysis of Precipitation (CMAP) (Xie and Arkin 1997).

The data extracted from the model for the subsequent statistical analysis, were derived from a total of 45 measurement points defined for each year, divided into 15 transects perpendicular to the coastline and approximately 1.5 km apart. Five transects were placed in each of the three locations with measuring points 0.25 nautical miles apart along the transect direction.

## Oceanographic data analysis

Salinity, temperature and current speed data were provided by the hydrodynamic numerical model MIKE 3 FM HD for the 45 indicated points at four different depths ( $Z = -1$  m,  $Z = -2$  m,  $Z = -3$  m,  $Z = -5$  m). The raw data provided in hourly form were aggregated by time and depth in order to obtain daily and monthly time series for each of the points. Extensive statistical analyses have been applied to the sampling years (2018 and 2019), considering the oceanographic data as an average of the entire Lesina area or aggregated into the three locations.

For each considered variable and sampling year, the main descriptive statistics were calculated to provide preliminary information on natural marine phenomena in terms of synthesis, range and variability values.

Descriptive statistics are broken down into measures of central tendency and measures of variability. Measures of central tendency include the mean, median and quartiles, while measures of variability include standard deviation, variance, minimum and maximum variables.

The calculated coefficient of variation (CV) is a relative measure of variability that indicates the size of a standard deviation in relation to its mean. It is a standardized, unitless measure that allows different groups and characteristics to be compared (Leti 1983). It is calculated as:

$$CV = \frac{\sigma}{\mu} = \sqrt{\frac{1}{N} \sum_{i=1}^n \left( \frac{X_i - \mu}{\mu} \right)^2} \times 100$$

where the standard deviation is a measure of the dispersion of the data around the mean, and the mean is the central tendency of the data set. The resulting CV value represents the percentage of the mean that the standard deviation encompasses. The interpretation of the coefficient of variation depends on the context and purpose of the analysis. In general, a higher CV indicates greater variability or dispersion of the data relative to the mean, whereas a lower CV indicates lower variability or greater homogeneity of the data.

The following guidelines can be used for interpreting CV values:  $CV < 15\%$ : low variability;  $15\% \leq CV < 30\%$ : moderate variability;  $CV \geq 30\%$ : high variability.

In environmental studies, the CV can be used to analyse the variability or sensitivity of ecological or climatic variables over time or space. A higher CV indicates greater variation and potential impact on the ecosystem or climate, while a lower CV indicates greater stability and potential resilience (Bedeian and Mossholder 2000).

Subsequently, the analysis by the components technique (also known as decomposition analysis) was applied to the time series, to identify its underlying components (typically trend, seasonal, cyclical and irregular components) through the decomposition of the data with an additive model (Dagum 2002). In particular, the irregular component (or "noise") at time  $t$  describes random, irregular influences, it represents the residuals or remainder of the time series after the other components have been removed.

In order to assess the presence of significant residual autocorrelation in the dataset, the Ljung-Box test was applied (Ljung and Box 1978; Box et al. 2013). The test is based on two assumptions:

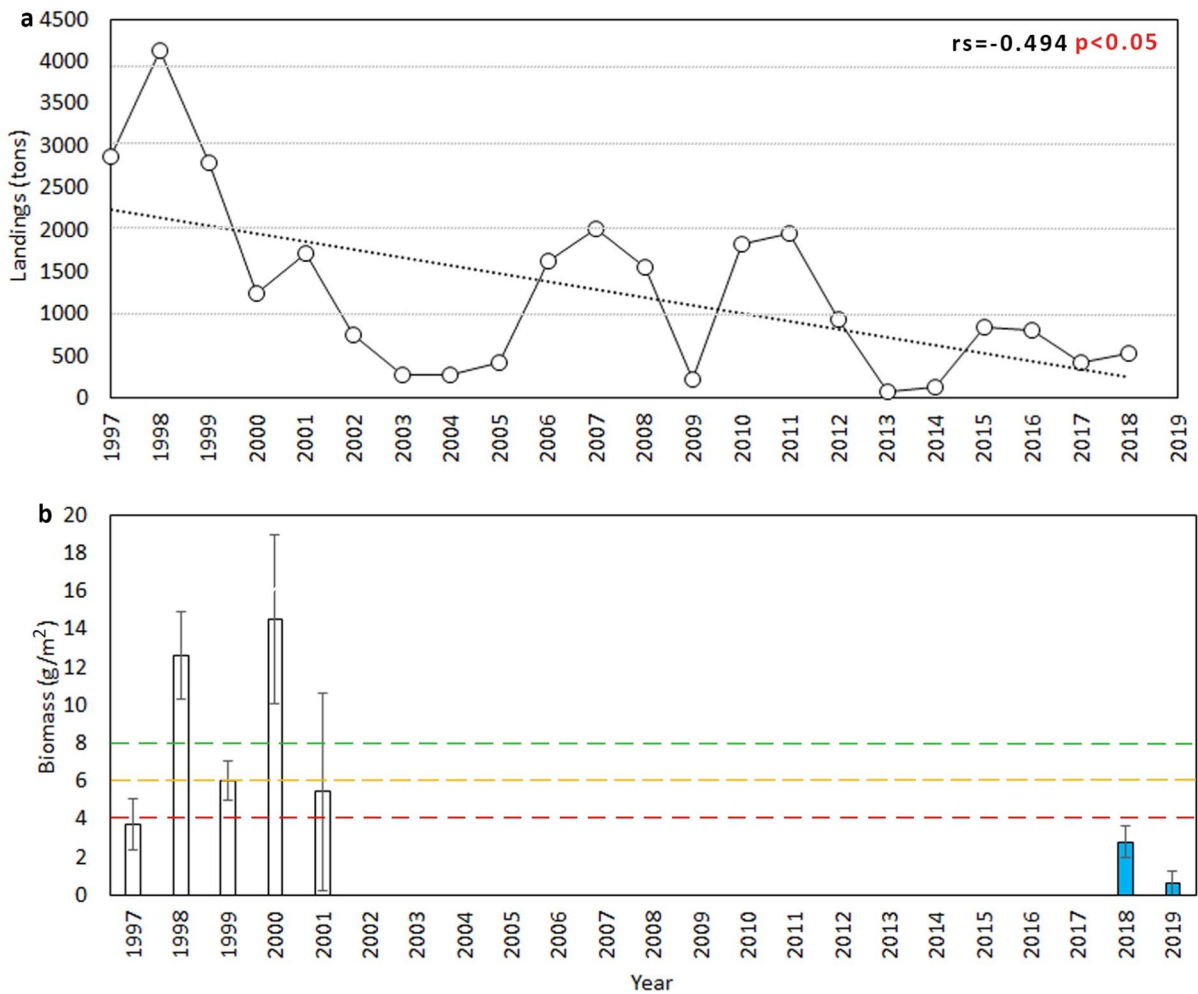
- H0: The residuals are independently distributed;
- HA: The residuals are not independently distributed and therefore, they exhibit serial correlation.

The  $p$  value provided by the test represents the probability of the null hypothesis of no autocorrelation (H0) to be true. If the  $p$  value is smaller than the chosen significance level (e.g., 0.05), it indicates that the observed autocorrelations in the residuals are statistically significant, and the null hypothesis of no autocorrelation can be rejected. On the other hand, a larger  $p$  value suggests that there is insufficient evidence to reject the null hypothesis, implying the independence of the residuals for the considered time series, which is often the assumption when creating a model.

## Results

### Ecological status of commercial resources

During the 1997–2018 period, the production in terms of catches collected from literature and official statistics showed relevant fluctuations in the southern Adriatic Sea (GSA 18) (Fig. 2a). A significant decrease was detected along the investigated period



**Fig. 2** Information on the biomass of *C. gallina* from 1997 to 2019 in terms of **a** Production (landings in tonnes) in the southern Adriatic Sea from 1997 to 2018 (the black dotted line indicates linear correlation expressed by the Spearman correlation coefficient ( $r_s$  and its significant level); **b** Commercial

biomasses sampled in the study area with respect to reference points of the resource status represented by dashed lines (in red fishery ban, in orange warning status, in green good management). Blue bars indicate periods with new MCRS of 22 mm

( $r_s = 0.494$ ,  $p < 0.05$ ), and large reductions in the catches were observed in 2003–2004 (272 tonnes), 2009 (223 tonnes), 2013 (65 tonnes), and 2014 (123 tonnes). Considering the fishing fleet, although the data was fragmented, 44 vessels were registered in the North Gargano area from Foce Saccione to Peschici, starting from 2011.

Fragmentary information on the biomass indices from independent surveys in the study area of Lesina were obtained, with data available for the periods 1997–2001 and 2018–2019 (Fig. 2b). In the former period, the highest mean values were

detected in the years 2000 ( $14.5 \text{ g/m}^2, \pm 4.44$ ) and 1998 ( $12.6 \text{ g/m}^2, \pm 2.28$ ), resulting in the condition of good resource management ( $> 8 \text{ g/m}^2$ ). In the latter years (2018, 2019), the mean biomass indices values were lower than  $4.0 \text{ g/m}^2$ , indicating a status of fishery ban. Notably, the biomass indices in the former period were calculated on the commercial size of 25 mm, while in the latter years the commercial size was lowered at 22 mm, according to the new Italian regulations.

The biomass displacement along the depth gradient showed a general progressive regression towards



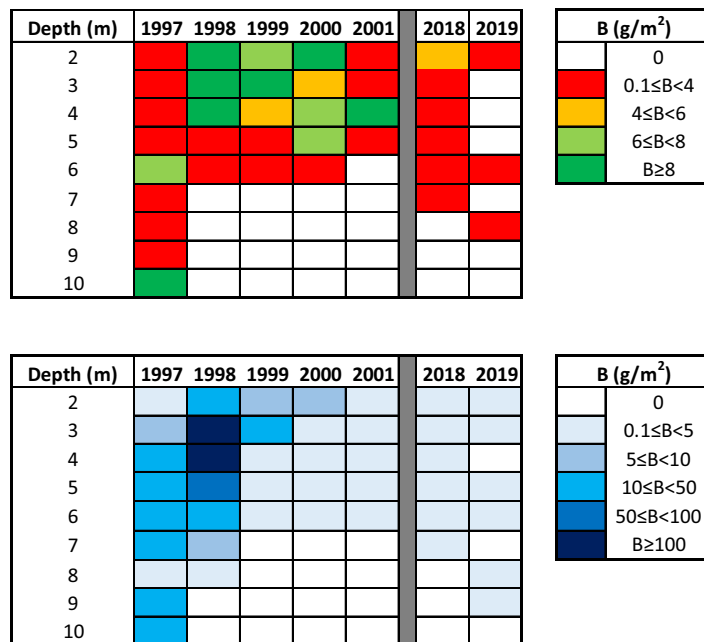
shallowest water over time for both commercial and juvenile fractions (Fig. 3). In the period 1997–2001, the maximum depth of distribution fell from 10 to 5 m in depth, and the commercial biomass showed a yield corresponding to good resource management at a depth of 10 in 1997 and in the range 2–4 m up to 2000. In 2001, the commercial biomass referred to a good level of management was in the depth strata of 4 m, while other strata showed very low biomass under the level of sustainable harvesting. In the same 5-years, the juveniles showed a similar regression with biomass values indicating scarce recruitment in the period 2000–2001 within a maximum depth of 6 m. Considering the period 2018–2019, the commercial biomass of *C. gallina* occurred up to the maximum depth strata of 8 m, but the status of the stock resulted in a warning level for the fishery in the depth stratum of 2 m in 2018, while in 2019 the biomass yield was lower than 4 g/m<sup>2</sup>, indicating an unsustainable fishing condition.

In the study area, the highest median abundance value was found in 2018Su both for juveniles and adults (343 N/100 m<sup>2</sup>, IR = 1219 and 29 N/100 m<sup>2</sup>, IR = 125, respectively) (Fig. 4). On the other hand, the lowest median abundance value was found in 2019 for juveniles (45 N/100 m<sup>2</sup>, IR = 47). Furthermore, in

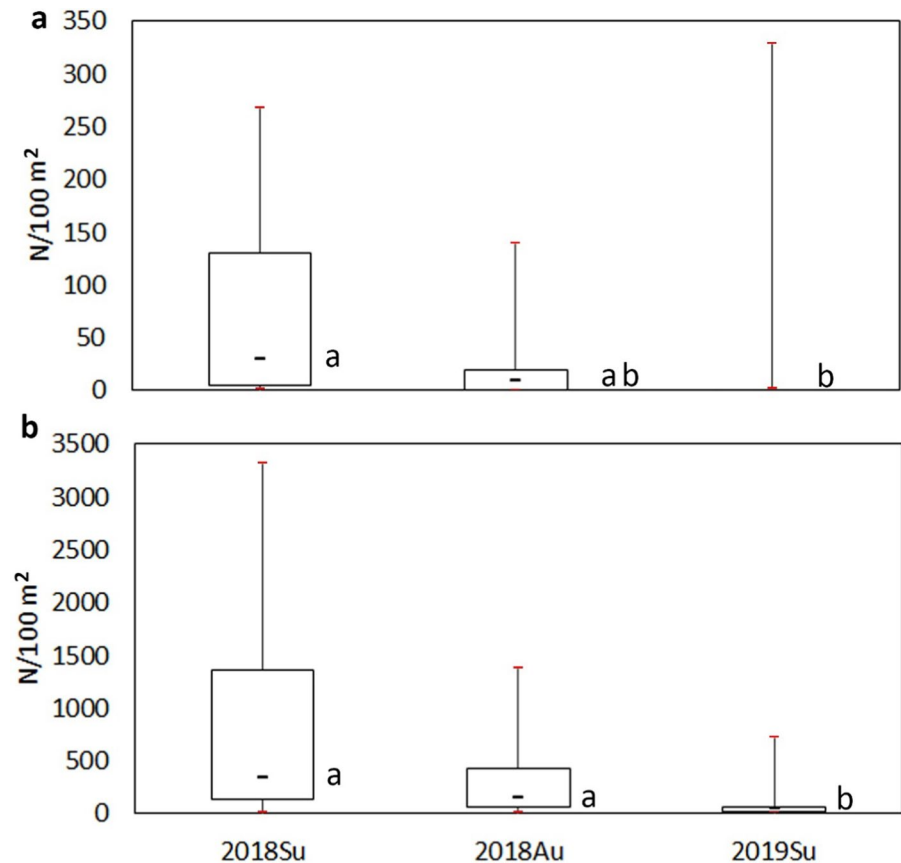
2019, of the 21 stations sampled, only 5 were characterised by the presence of adults. Of these, one haul showed a high abundance of adult clams (328 N/100 m<sup>2</sup>), while the other four hauls showed values below 5 N/100 m<sup>2</sup>. The abundance of juveniles was significantly lower in 2019Su than in 2018Su ( $p < 0.05$ ), while the abundance of the adults in 2019Su was significantly lower than both sampling periods in 2018 ( $p < 0.001$ ) (Online Resource 1, Table S4). On the other hand, considering the three sub-areas, no significant differences were found in the abundances of the two population fractions.

Length-frequency distributions (LFD) showed a sharp reduction for all sizes in a homogenous way during the three sampling periods (Fig. 5a–d). In 2018Su, the population under 22 mm was in a good condition, as shown by a bi-modal LFD having cohorts at modal sizes around 8 mm (> 2000 N/100 m<sup>2</sup>) and 19–20 mm (both length classes around 1000 N/100 m<sup>2</sup>). In 2018Au, LFD was similar to the previous summer, with two cohorts at modal sizes of 11 mm and 19 mm, but the abundance was lower than in 2018Su. Finally, LFD in 2019 was almost flattened, with small peaks at the modal sizes of 7 mm (160 N/100 m<sup>2</sup>), 17–18 mm (around 230 N/100 m<sup>2</sup>) and 21 mm (183 N/100 m<sup>2</sup>). LFDs in the three periods

**Fig. 3** Distribution of biomass (B) along the bathymetric gradient for the commercial (above) and juvenile (below) fractions investigated in annual surveys



**Fig. 4** Boxplots of the adult (a) and juvenile (b) clams' abundance data in the three sampling periods. Different letters indicate significant differences ( $p < 0.05$ ) between periods within each of the population fractions investigated in the analysis. The median value is indicated by the black dash in the box, maximum and minimum values by red dashes at the end of the whiskers



showed a strong decrease in length classes higher than 22 mm without evidence of consistent cohorts. Finally, the reduction in individuals across the three sampling periods showed a decrease in percentage of -37% (summer-autumn 2018), and -18% (autumn 2018- summer 2019) (Fig. 5d).

#### Changes in the structure of the benthic assemblage

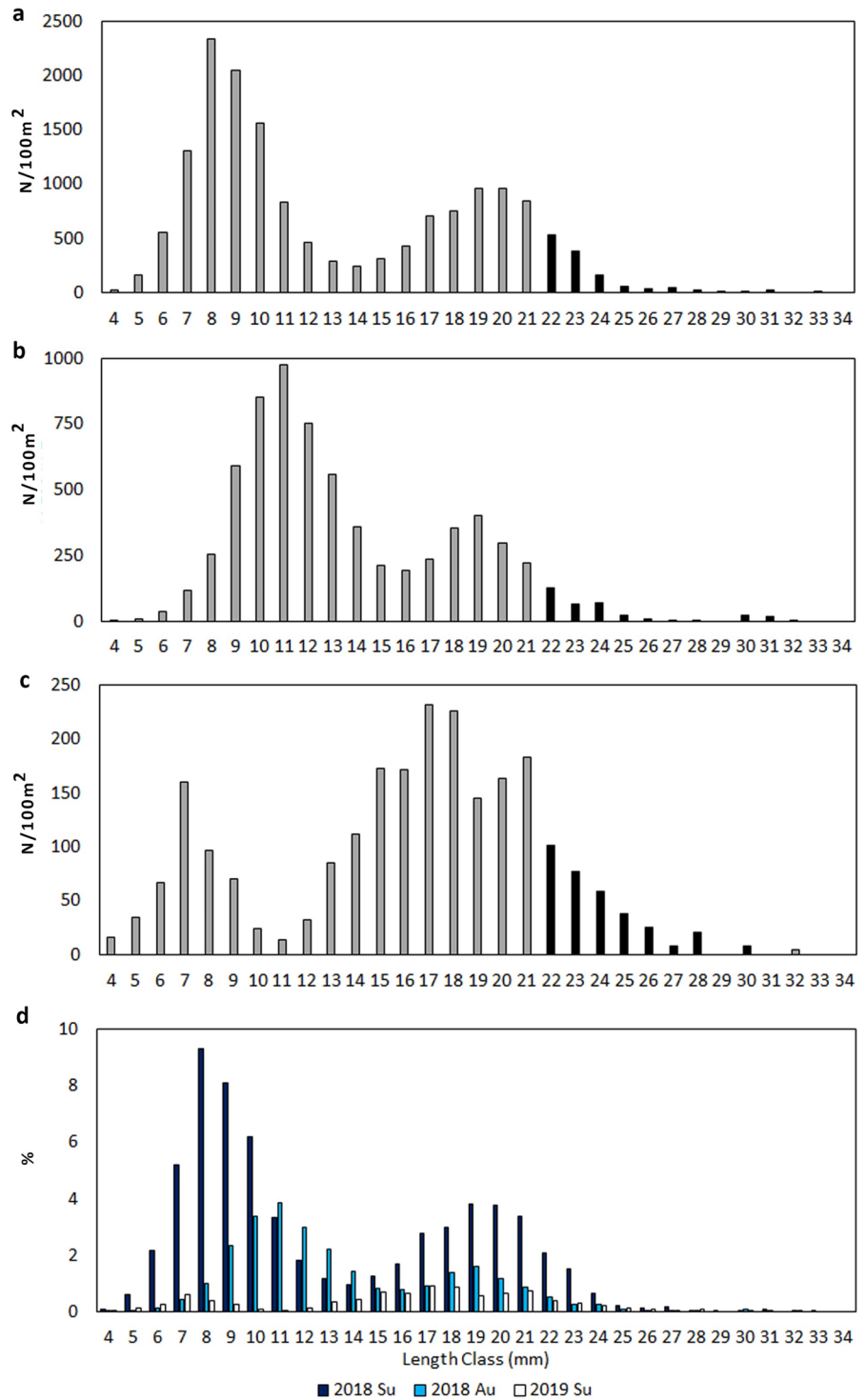
A total of 45 taxa were collected in 57 sampling hauls during the three surveys. Thus, a total of 27 taxa was selected for analysis, including juveniles and adults of *C. gallina*.

The PERMANOVA analysis demonstrated a significant effect of the sampling period (Pe) on the benthic assemblage composition (pseudo-F=9.1654,  $p=0.001$ ; Table 1) while no significant differences were found between the locations (Lo). In particular, all sampling periods resulted significantly different from each other ( $p < 0.01$ ). Moreover, significant differences were detected for the Pe×Lo interaction

(pseudo-F=2.1108,  $p < 0.01$ ). The pairwise test showed significant differences in the W area between 2019Su and both 2018Su ( $p < 0.05$ ) and 2018Au ( $p < 0.01$ ). Significant differences were also found in the M area between 2019Su and both sampling periods in 2018 ( $p < 0.01$ ). Finally, significant differences were also found in the E area, but only between 2018Su and 2018Au ( $p < 0.05$ ).

In the PCO plot, a clear separation was observed among 2019Su hauls and those of 2018Su and Au, while the last two showed some level of overlap in the bi-dimensional space, where the first axis explained 27.7% and the second 20.5% of total variation (the first four axes explain 71.7% of the total variation, Fig. 6a). The species mainly correlated to the first two axes (Pearson correlation  $> 0.4$ ) were: *C. gallina* (adults and juveniles), *Diogenes pugilator*, *Donax semistriatus*, *Dosinia lupinus* and *Liocarcinus depurator* were more associated with 2018Su hauls; *Microchirus* sp., *Polititapes aureus* and *Spisula subtruncata* were related to 2018Au hauls, with a very

**Fig. 5** Length-frequency distribution of *C. gallina* in **a** 2018 Summer, **b** 2018 Autumn, **c** 2019 Summer. Grey and black bars correspond to juvenile (< 22 mm) and commercial (≥ 22 mm) individuals. **d** Frequency occurrence (%) of juveniles and commercial individuals for each length class as a percentage in each sampling period



low overlapping with Su hauls, while *Astropecten* sp., *Bolinus brandaris*, *Callionymus maculatus* and *Macra stultorum* were mainly associated to 2019Su

hauls. In addition, hauls belonging to 2018Su and 2018Au showed a larger dispersion than those of 2019Su.

**Table 1** Summary of PERMANOVA and PAIRWISE *t* test based on Bray–Curtis similarity on four-root transformed abundance data of the macrobenthic assemblages on the basis of a multifactorial model with 3 factors (Period, Pe; Location, Lo; Transect, Tr)

Source	<i>df</i>	SS	MS	Pseudo-F	P(perm)	perms
PERMANOVA test						
Pe	2	15,310.0	7655.0	9.1654	<b>0.0001</b>	9931
Lo	2	4682.9	2341.5	1.8786	0.0912	9931
Tr (Lo)	8	7673.9	959.2	1.3083	0.1021	9864
Pe × Lo	3	4643.0	1547.7	2.1108	<b>0.0062</b>	9893
Residuals	41	30,061.0	733.2			
Total	56	62,371.0				
Groups		t	P(MC)		perms	Av.sim %
Pairwise comparison: period						
2018Su, 2018Au		2.218	<b>0.0018</b>		9947	51.176
2018Su, 2019Su		3.1807	<b>0.0001</b>		9939	51.413
2018Au, 2019Su		3.4285	<b>0.0001</b>		9940	51.677
Pairwise comparison: Pe × Lo interactions within Lo levels (W)						
2018Su, 2018Au		1.4406	0.0992		9950	54.79
2018Su, 2019Su		2.0189	<b>0.0327</b>		7574	51.42
2018Au, 2019Su		2.0951	<b>0.0022</b>		9951	50.56
Pairwise comparison: Pe × Lo interactions within Lo levels (M)						
2018Su, 2018Au		0.92549	0.5648		6655	53.287
2018Su, 2019Su		2.2505	<b>0.0057</b>		9952	52.90 2
2018Au, 2019Su		2.5507	<b>0.0098</b>		9884	53.844
Pairwise comparison: Pe × Lo interactions within Lo levels (E)						
2018Su, 2018Au		2.5256	<b>0.013</b>		1259	48.179
2018Su, 2019Su		2.3204	0.0761		4224	47.486
2018Au, 2019Su		1.9904	0.1458		279	58.486

In PERMANOVA results, the probabilities of each Pseudo-F value were obtained with 9999 permutations (perms) of residuals and degrees of freedom (*df*). Sum of Squares (SS) and mean sum of squares (MS) are reported. In PAIRWISE *t* test, values of *t* test (t), Monte Carlo *p* values (PMC), number of permutations (perms) and Average Similarity (Av. Sim. %) between factor pairs are reported. Significant *p* values in bold

SIMPER results showed an average dissimilarity between 2018Su and 2018Au of 48.8%, between 2018 and 2019Su of 48.6% and between 2018Au and 2019Su of 48.3%. The species that mainly contributed to this dissimilarity are reported in Online Resource 1, Table S5.

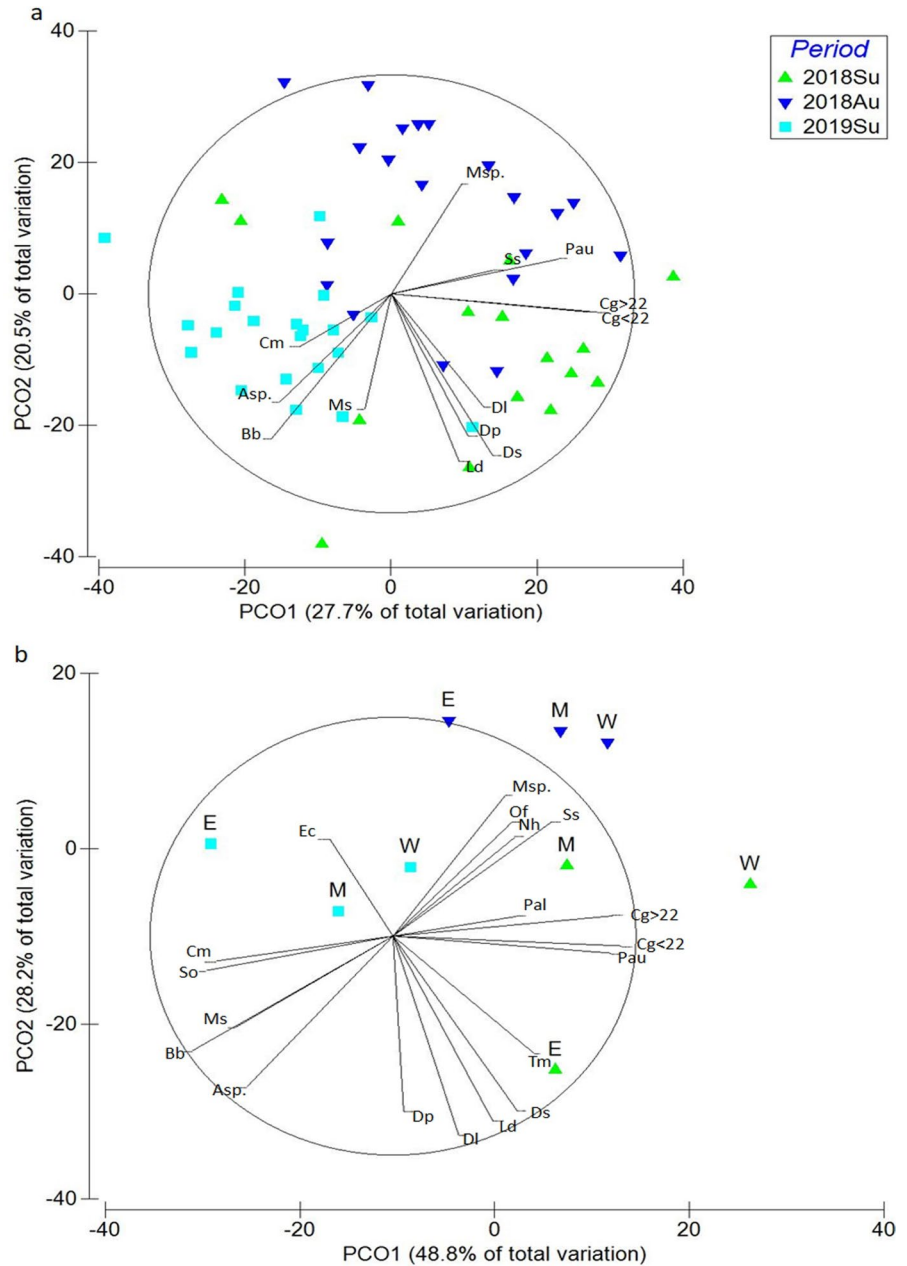
The PCO was also adopted to better visualise the separation of the three locations in the sampling periods, that are well separated, coherently with what shown previously. The first two axes explain 48.8% and 28.2% of total variation (the first four axes explain 91.6% of the total variation, Fig. 6b). The three sub-areas in 2018Au are the least scattered and mostly characterized by *Microchirus* sp., *Nephtys hombergii*, *Owenia fusiformis* and *Spisula subtruncata*, as well

as the M area of 2018Su, which showed the greatest dispersion. The M and W areas in 2018Su are also characterized by *C. gallina*, *Peronidia albicans*, and *P. aureus*. The E area of 2018Su is characterized by *D. pugilator*, *D. semistriatus*, *D. lupinus*, *L. depurator* and *T. mutabilis*. All three locations in 2019Su are characterized by *Astropecten* sp., *B. brandaris*, *C. maculatus*, *Echinocardium cordatum*, *M. stultorum* and *Sepia officinalis*, which are mainly correlated to the first axis.

#### Modelling results for water currents

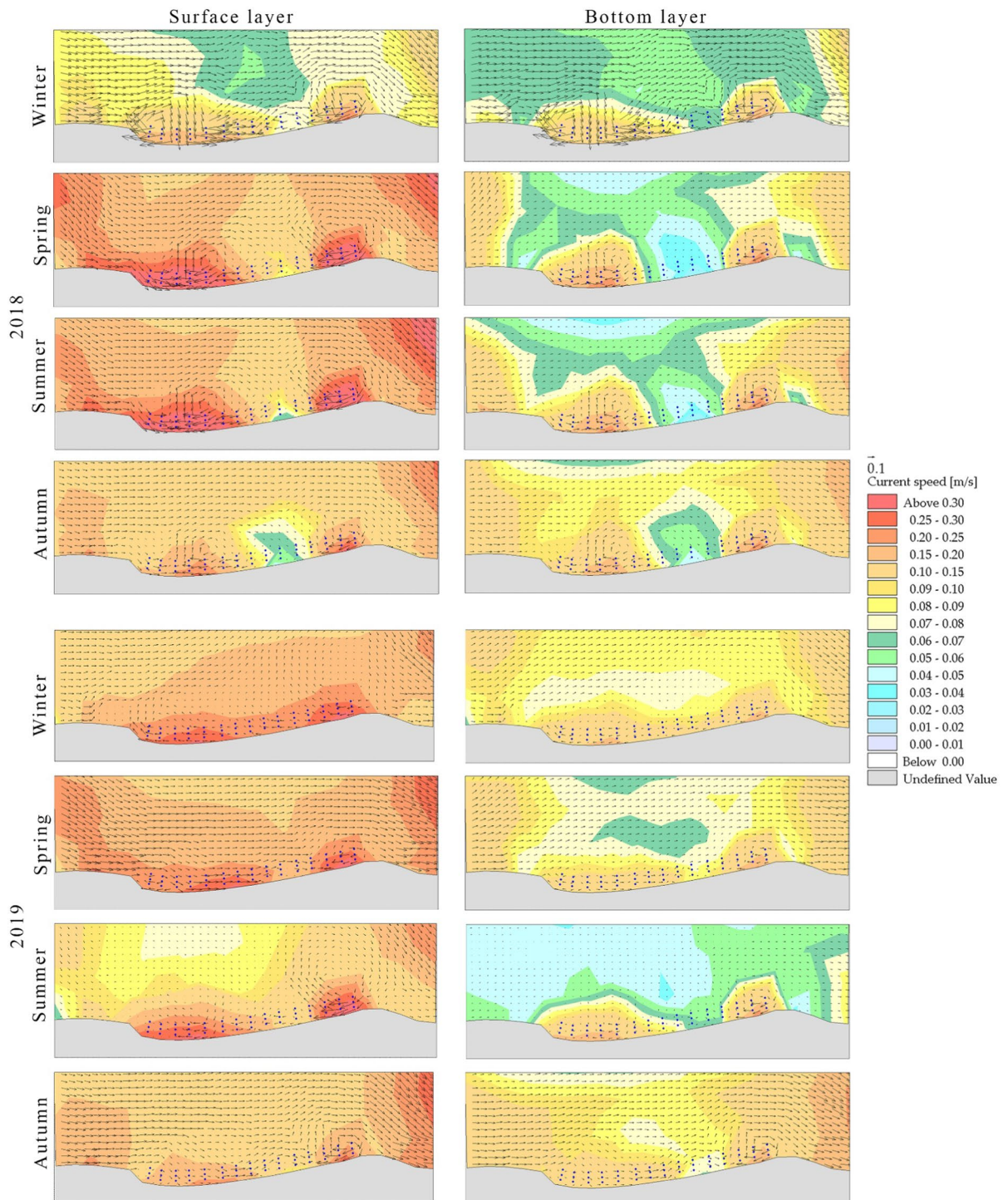
The patterns of the surface and bottom seasonal-averaged currents are here examined for the

**Fig. 6** PCO analysis ordination plot based on Bray–Curtis similarity applied to the species of the benthic assemblages in the three sampling periods (a) and for the Period×Location interactions (b). The taxa that most differentiate the sampling hauls are indicated by black lines (Pearson’s correlation index; cut-off 0.4). Species are coded as: Asp., *Astropecten* spp.; Bb, *Bolinus brandaris*; Dl, *Dosinia lupinus*; Dp, *Diogenes pugilator*; Ds, *Donax semistriatus*; Cm, *Callionymus maculatus*; Cg, *Chamelea gallina*; Ec, *Echinocardium cordatum*; Ld, *Liocarcinus depurator*; Ms, *Mactra stultorum*; Msp., *Microchirus* sp.; Nh, *Nephtys hombergii*; Of, *Owenia fusiformis*; Pal, *Peronidia albicans*; Pau, *Polittapes aureus*; So, *Sepia officinalis*; Ss, *Spisula subtruncata*; Tm, *Tritia mutabilis*



investigated years (2018–2019, Fig. 7) and for the previous year 2017 (Online Resource 2, Fig. S1). The residual circulation shows a change in its structure in the last year. In fact, in 2017 and 2018, currents appear to be stronger in absolute value and describe vortices especially in the two furthest areas (W and E), as if encircling distinct patches, with a central stillness zone in the surface and bottom

layers. In 2019, these patterns appear to be characterised with a greater continuity of flows throughout the area. However, this change in the surface layer, could be observed already from 2018 and was more evident in 2019. Notably, from spring up to autumn during 2018, the main direction of gyres characterising the water circulation was oriented offshore.



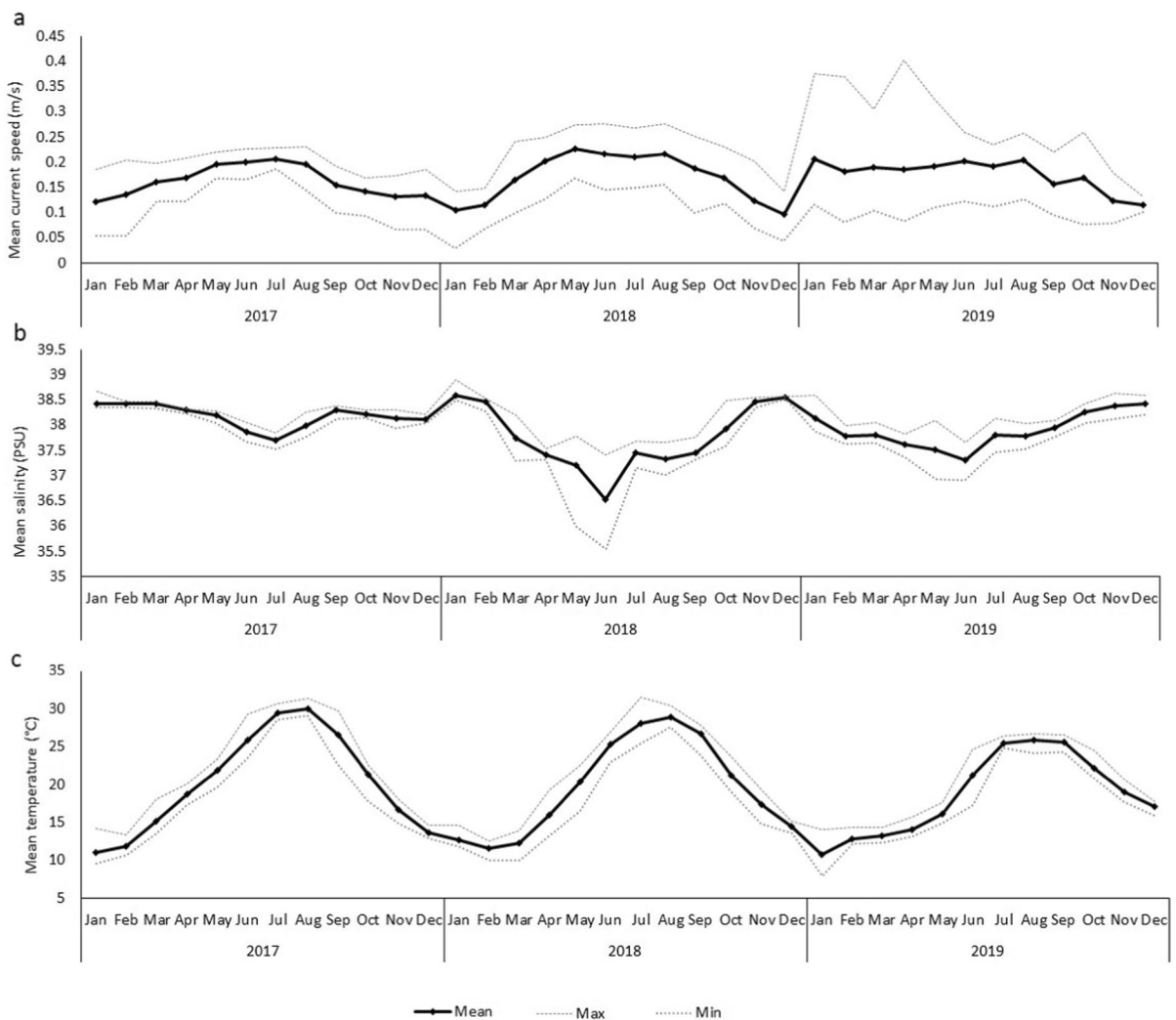
**Fig. 7** Computational maps of the seasons-averaged currents at the surface and at the bottom referred to 2018 and 2019. Sampling hauls are reported in the maps as blue dots

Current speed, water temperature and salinity temporal analysis

The annual trend of the current speed showed a similar regime during the years 2017 and 2018, with the lowest mean values between December and January, and the highest mean values between May and August (Fig. 8a). In particular, the lowest mean values in each year were in January 2017 and December 2018 (0.121 and 0.097 m/s, respectively) while the highest were in July 2017 and May and August 2018 (0.206 and 0.226 m/s, respectively). In contrast, 2019 showed a fairly different trend from

the previous years with an overall decrease from the beginning to the end of the year, displaying the highest mean value in January and the lowest in December (0.205 and 0.116 m/s, respectively).

The salinity mean values time series displayed a similar pattern in all three years, recording higher mean values during the winter (Dec-Feb) and lower mean values during the summer (May-Sep; Fig. 8b). In particular, the lowest mean values were in July 2017 and June 2018 and 2019 (37.69, 36.53, 37.30 PSU, respectively) and the highest in January 2017 and 2018 and December 2019 (38.43, 38.59, 38.42 PSU, respectively). June 2018 also displayed the



**Fig. 8** Annual trends of monthly averages, maximum and minimum values of current speed (a), salinity (b) and temperature (c) in the Lesina area in 2017, 2018 and 2019

lowest minimum value (absolute minimum) of the whole considered period (35.5 PSU).

Finally, water temperature followed a seasonal pattern with the lowest mean values between December and March and the highest between July and August (Fig. 8c). In particular, the lowest mean values were in January 2017, February 2018 and January 2019 (11.0, 11.6, 10.7 °C, respectively) and the highest in August in all three years (30.0, 28.9, 25.9 °C, respectively). In 2019, the temperature time series showed the mean summer values to be about 5 °C lower and the autumn period to be about 2 °C warmer than the same months in previous years.

Considering the three locations, no differences were found in the monthly trend and overall values between the areas for salinity and water temperature (Online Resource 2, Fig. S2 a,b). In addition, the statistical analysis applied to the years 2017, 2018 and 2019 provided information on natural marine phenomena in terms of synthesis, range and variability values reported in Online Resource 1, Table S6. The results highlight a similar annual trend of the current speed for the years 2017 and 2018 in all three sub-areas with increasing values from January to April, higher values from May to August and followed by a decrease until the end of the year (Online Resource 2, Fig. S2c). In both years the W area displayed the highest values, followed by the E and the M areas. On the other hand, 2019 showed a different trend in the current speed compared to previous years in all sub-areas. In the W area the currents were lower and more consistent in speed than in 2017 and 2018 from January to July, then peaking in August and gradually decreasing until the end of the year. In the M area the current speed was higher until August 2019, and then fell back into a range of values similar to the previous years. Finally, in the E area they show a decreasing trend the whole year. In 2019, the minimum values were higher in all three areas compared to the previous years, the maximum values were higher in the M and E areas. The coefficient of variation (CV) used to analyse the variability or sensitivity of environmental variables over time and areas shows different results regarding the considered years. In 2017 the current speed CV value was between 0.237 (W area) and 0.294 (M area) indicating greater current stability and potential resilience to the normal trend. The coefficient of variation values in the years 2018 and 2019 show a not negligible variability with the values

between 0.313 (E area) and 0.382 in the M and W areas which only persisted with the same values in 2019 in the M area. These higher CV values indicate greater current speed variation and potential impact on the sea ecosystem. In all three years observed, sub-area M is the one with the greatest variability (Table S6).

The 2017, 2018 and 2019 residual series show an anomalous trend suggesting the existence of a phenomenon not attributable simply to white noise (Online Resource 2, Fig. S3). The Ljung-Box test  $p$  value calculated for the three areas in 2017, 2018 and 2019 was  $<0.0001$ . Since this value is less than the 0.05 threshold, it obliges rejection of the  $H_0$  hypothesis and affirms that the current speed residual component series are not independent of each other but suggest the existence of a phenomenon not attributable simply to white noise.

## Discussion and conclusions

The management of marine resources sensitive to natural and anthropogenic multiple stressors required the integration of several kinds of environmental information to understand the mechanisms of impacts on the overall population components. This is fundamental for fishery resources, as bivalves are characterized by wide temporal fluctuations influenced by several environmental variables (Bento de Almeida et al. 2021; Delgado et al. 2023).

The case of *C. gallina* fluctuations is widely known in several Mediterranean areas, with a decline in biomass of stocks (Romanelli et al. 2009; Baeta et al. 2021b), stressing the need to expand the monitoring to the collection of environmental information influencing the population dynamics of the striped venus clam (Grazioli et al. 2022). The analysis aimed to provide a summary of the condition of *C. gallina* in very important areas of the southern Adriatic Sea, focusing attention on the potential relationships between changes in hydrographic conditions and the lack of consistent recruitment of juveniles on the fishing grounds. For the first time, these aspects are explored by adopting a 3D hydrodynamic numerical model, which can be a useful tool in the investigation of larval dispersion and spatial connectivity of benthic organisms (Pastor-Rollan et al. 2018).



In the last 20 years, the combination of environmental alteration processes and the exploitation of the clam resource has resulted in the consistent reduction of commercial stocks in the Adriatic, with economic repercussions on the sector (Romanelli et al. 2009). Despite these phenomena of fluctuations, the EU and national regulations have applied several measures addressed at reducing fishing effort and impact on the commercial stocks, such as the reduction of the catchable quota per day to 400 kg, the reduction to 4 fishing days a week, as well as the area of exploitable fishing grounds being reduced with the entry into force of the regulation 1967/2006 (DGPEMAC 2019). In this latter case, the reduction of fishing areas in the southern Adriatic Sea was about 90% of the total area exploited before 2006. However, positive effects on catch yields have been quite poor and not comparable to the levels of the 1980s and the late 1990s period (Vaccarella et al. 1998). The possible cause of the ineffectiveness of these actions should be sought in the lack of information inherent in the environmental conditions that influence the population dynamics of the clam. In fact, the optimal growth conditions of the clam depend on several fluctuating factors (temperature, salinity, dissolved oxygen, hydrology, nature of the substrate, trophism, inter- and intraspecific competition etc.) (Barillari et al. 1979), which must find a positive synergy with the biological recruitment peaks, which occur during the reproductive season of the species extended from spring to early autumn. Therefore, the study of clam stock size along the Italian coastline is the first tool to address the need to collect data on the population structure of the resource and to be able to initiate a general assessment of the indirect effects of fishing exploitation. However, even in light of the results reported in this study, the need to enhance monitoring of the resource by integrating information on other environmental drivers affecting the dynamics of the resource is more urgent than ever.

Our results highlight how the critical condition observed for the *C. gallina* stock in the North Gargano area is affected by the interaction of multiple of anthropogenic and natural pressures. Indeed, commercial biomass estimated during the 2018–2019 period indicates a condition of fishery ban ( $<4.0 \text{ g/m}^2$ ). Notably, the analysis of LFD showed scarce occurrence of adult individuals ( $\text{LC} \geq 22 \text{ mm}$ ), indicating a suffering condition for the spawning component of the population, which is extremely exploited

by the fishery. This population structure was similar to those observed over time in some areas of the central Adriatic Sea during the period 1984–1994, when the disappearance of larger sizes was strictly linked to a high fishing effort (Morello et al. 2011). In the study area, although national guidelines have promoted regulations addressed at reducing the impact of fishing on the resource (DGPEMAC 2019), the local environmental conditions of the exploited areas, as well as the behaviour of fishermen, could affect the conservation of healthy stocks. Indeed, the investigated study area is located between the two main harbours (Lesina and Capojale) hosting the dredge fleets of about 40 vessels in 2018. In addition, the behaviour of fishermen in this area seems to be characterized by the harvesting focused on the low-medium sizes of clams starting from the MCRS, with the lack of a consistent portions of large sizes. Thus, the commercial component, when occurring in high densities, is heavily exploited in an area, and when yields decrease, dredges move towards other zones by searching for new clam beds. Similar behaviour has been described by Morello et al. (2011), explaining the critical condition of these actions, which depend on the success of stochastic recruitment events. Our results show how the combination of these two conditions drives the stocks towards unsustainable status for the fishery, with a severe depletion of the entire clam population. Indeed, the changes in juvenile abundances show the lack of recruitment, so as to support a renewal of the exploitable stock in 2019. This reduction seems to be affected by environmental changes detected through the outputs of the hydrodynamic model. In particular, the water circulation in 2017 and 2018 was characterized by a predominant condition of vortices, where the flow direction was directed offshore. Moreover, the results of the residual component analysis suggest further investigation is necessary to detect any other causes that do not depend on the normal annual regime of the currents or their seasonality, but attributable to ecosystem phenomena probably characteristic of the area under study. Overall, this rapid variation in hydrographic conditions could negatively affect the larval dispersal of striped venus clams, with a distribution of larvae on unsuitable bottoms for the settlement. Indeed, the lifespan of *C. gallina* larval stage ranges between 15–30 days, as reported in a specific study on this species (Cordisco et al. 2003), and in line with the range of days estimated

for the veliger larvae typical of bivalves (Moksnes et al. 2014). During this pelagic stage, several factors linked to the spatial hydrodynamics traits could influence the dispersal and recruitment of the species, such as upwelling currents and wind stress (Baptista et al. 2014). In addition, water current is the only variable that has shown spatial differentiation among the three investigated sub-areas. Although significant differences in abundance were not observed between the three sub-areas, the highest abundance was observed in the western area. Further studies should be carried out to better understand how the spatial articulation of local hydrographic traits acts on the larval dispersal, which represents a fundamental process for the bivalve life cycle (Norkko et al. 2001).

A further critical factor for the entire life cycle of *C. gallina* and its growth is the temperature (Gaspar et al. 2004). Temperature regulates the reproduction periods (Bargione et al. 2021a), but at the same time, high temperature in summer affects the oxygen concentration, inducing risks of hypoxia events in the environment (Nerlovic et al. 2011). This phenomenon impacts both juveniles and adults with mass mortality events (Grazioli et al. 2022). In the study area, the highest temperatures of bottom waters ( $> 30\text{ }^{\circ}\text{C}$ ) were detected in the summer months of 2017 and 2018. Heatwaves were reported in the study area with mortality events of mussels in 2018, where water temperatures reached a maximum of  $29.4\text{ }^{\circ}\text{C}$  in August, with effects also observed on the clams (personal communication). Specifically, large amounts of dead shells were found in the autumn samplings corresponding to about 50% of total biomass, especially for sizes of 18–22 mm. These changes can be connected to the ongoing climate process and atmospheric anomalies, thus altering the thermohaline properties of the northern, central and southern Adriatic and are weakening the exchange of Adriatic water masses (Grbec et al. 2007; Vilibić et al. 2013; Lipizer et al. 2014).

Further environmental pressures on the condition of *C. gallina* in the study area could be due to physiological effects caused by the salinity. It is proven that salinity anomalies have the effect of slowing growth and reduction in the calcification of shell (Mancuso et al. 2019). Other studies on *C. gallina* and other commercial bivalves detected stress responses due to strong salinity variations (Matozzo et al. 2007; Román et al. 2023a, b). In our study, during the spring-early summer period of 2018, salinity showed mean values

( $< 37.5$  PSU) lower than the overall mean value of the investigated period (38.0–38.5 PSU). This variation could be not relevant for the health status of *C. gallina*, since stress responses of the immune system were observed for condition of hyposalinity (28 PSU) and hypersalinity (40 PSU) far from mean value of 34 PSU (Matozzo et al. 2007). However, further studies should be carried out to investigate potential effects of the salinity stress on the shells calcification at different growth stages of the population (Mancuso et al. 2019). The reduction of salinity in 2018 detected in our results could most probably be due to a significant increase in the frequency and intensity of heavy precipitation, of the river flooding and therefore of the river flow due to global warming. These results highlight an increase in the less saline and less dense water outflow along the western Adriatic coast (Western Adriatic Current, WAC) (Hopkins et al. 1999).

During the investigated period, the macrobenthic assemblage showed changes that could be driven by both the effect of fishery and environmental stress. A large reduction in bivalve species was detected between summer and autumn 2018, with a consistent decrease in abundance of *C. gallina*. Species found in summer 2018 indicate a moderate fishing intensity, such as *D. pugilator* as observed in other similar conditions in the Adriatic Sea (Morello et al. 2006). In autumn, the assemblage was characterized by high abundance of more tolerant species that could be favoured by these stress conditions as some polychaete filter feeders (Mikac et al. 2011). In our case, *N. hombergii* and *O. fusiformis* were detected by the PCO analysis, as the main polychaetes correlated to the hauls of autumn 2018. Although at fine-scale the spatial distribution of bivalves could be affected by biological processes (Legendre et al. 1997), the role of the fishing impact seem to be more relevant for the changes observed in the benthic assemblages. Indeed, the time of approximately two months between the sampling periods of 2018 without fishing activities seems to be barely sufficient to the recovery of a benthic community (Morello et al. 2006; Dimitriadis et al. 2014). As observed in the PCO analysis, juveniles and adult of *C. gallina* and other sensible bivalves were not found after the fishing ban period. Notably, the absence of fine-scale spatial differences in the benthic assemblages seems to be confirmed by the PERMANOVA results, which indicates no significant differences for the Location factor. This condition

seems to be consistent with the results reported in Carlucci et al. (2024), in which the assemblages did not show significant differences along the depth gradient in the same area. In the summer of 2019, the benthic assemblage structure highlighted the occurrence of species sensitive to the fishing impacts, such as *E. cordatum* and *M. stultorum* (DGPEMAC 2013; Vasapollo et al. 2020), indicating the low occurrence of dredges activities likely limited to very small western areas as observed in the multivariate analysis. Finally, other drivers could contribute to the spatial variation in the benthic community, such as increase in temperature, salinity and primary production during the summer, as observed in Carlucci et al. (2024). Indeed, heatwaves and hypoxia events occurred in the summer could have reduced the population of many bivalves, as observed in the northern Adriatic Sea (Nerlovic et al. 2011).

Future study should be addressed to improving the investigation of the relationships between the striped venus clam and sediment composition in the area. Our results show a depletion of *C. gallina* abundances along the depth gradient starting from 1999, with a concentration of high densities at the shallowest depth of 2 m in 2018. This regression of both population components could indicate a progressive increase in muddy sediments, which are less suitable for the clams growth (Barillari et al. 1979). This process could be affected by the influence of river sediment transport and coastal erosion which occurs at severe intensity in the Adriatic Sea (Aucelli et al. 2018). Unfortunately, this information on sediments is not detected in situ during the monitoring surveys, requiring the adoption of modelling approaches and integration of data from other monitoring platforms in future analysis.

In conclusion, the extreme variability in catch between the years and sampling stations investigated indicates the need for a very cautious approach. The resource is distributed in circumscribed areas of high clam density that should rather be managed as spawning stocks to fuel a subsequent and more stable renewal of the population and thus sustainable commercial exploitation (DGPEMAC 2019). Therefore, this condition raises the need to consider the adoption of fisheries management plans that take into account the spatial scale of distribution of the resource and the environmental peculiarities of the exploited fishing grounds. Thus, results and methodological approach

used in this study emphasize the urgency of integrating environmental information, also from modelling approaches, in the study of clam stock fluctuations, in order to support the sustainable management of the resource according to the EBFM approach.

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**Data availability** All data supporting the findings of this study are available within the paper and its Supplementary Information.

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