



Population dynamics of a temperate coral along a depth gradient in the Dardanelles

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Abstract

Notwithstanding the importance of analyzing the variations of population dynamic traits along environmental gradients for assessing coral resilience to global climate change, temperate areas are more understudied than tropical regions. In the Mediterranean Sea, some studies are available for its western basin, while there is a lack of information for its eastern basin. This study starts to fill this gap, by determining the demographic characteristics of the solitary zooxanthellate scleractinian *Balanophyllia europaea* in the Dardanelles (Turkey) along a 1–21 m depth transect. The population dynamics of *B. europaea* from this site in the eastern Mediterranean Sea was compared with the populations in the NW Mediterranean Sea. In particular, the sites of Calafuria and Palinuro (Tyrrhenian Sea, Italy) were chosen for the comparison since their temperature and latitude, respectively, were similar to that of the Dardanelles population. The population density in the Dardanelles increased exponentially with depth, possibly due to lower current and wave action, and higher salinity at depth. Age structure in the Dardanelles was relatively overrepresented in younger age classes with increasing depth. Nevertheless, this difference in age structure was not strong enough to cause trends with depth for all derived demographic parameters. In comparison with Italian populations, age structure presented a higher frequency of young individuals and were more stable in the Dardanelles, likely due to the less intense wave action. Hosting different clades of symbiotic algae may also contribute to these differences, but molecular studies are necessary to verify this hypothesis.

Demographic analysis of coral populations may reveal their health status and provide information to assess habitat stability and suitability (Meesters et al. 2001; Caroselli et al. 2016, 2019). Estimating demographic traits of populations (e.g., mortality, lifespan, turnover time, recruitment) helps to assess life strategy, reproductive success, and colonization potential (Goffredo et al. 2008; Caroselli et al. 2019) and to understand the complex relationships between organisms and their environment (Grigg 1984; Meesters et al. 2001; Caroselli et al. 2016).

To apply some population dynamic models, an age–size relationship is needed (Beverton and Holt 1956; Madin et al. 2012), but the life history of scleractinian corals may be complex due to the processes of fragmentation, fusion, partially colony mortality (Babcock 1991), and budding (Hoeksema and Yeemin 2011),

which decouple colony age and size and may even cause taxonomic confusion (Hoeksema and Waheed 2011). Because of this complexity, size-based evaluation of population structure has been performed (Meesters et al. 2001), and new size-structured models for coral growth and population dynamics have been proposed rather than age-based models (Artzy-Randrup et al. 2006). However, in species where the individuals rarely fragment, bud or fuse and partial mortality is detectable by anomalies in the regular growth pattern, it is possible to determine coral age and growth to apply age-based models (Babcock 1991; Madin et al. 2012). In some coral species, age–size relationships can be determined through sclerochronological analyses of annual skeletal growth bands, which can be counted on computerized tomography scans (Grigg 1984; Goffredo et al. 2004, 2008; Caroselli et al. 2016, 2019).

Growth and population dynamics traits of many scleractinian species are sensitive to environmental conditions (Goffredo et al. 2008; Rodolfo-Metalpa et al. 2008; Caroselli et al. 2015) such as temperature (Goffredo et al. 2007), light (Rodolfo-Metalpa et al. 2008), water flow (Purser et al. 2010),

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nutrients (Orejas et al. 2011), waves (Chappel 1980), substrate slope and structure (Vertino et al. 2010), and pH (Caroselli et al. 2019). As a result, depth influences coral growth and phenotype in some scleractinian corals. For example, in some species of the genus *Madracis* from the Caribbean Sea, light availability determines three different life strategies and strongly influences colony morphology (Vermeij and Bak 2002). In addition, their population density decreases at the shallower and deeper margins of species distribution (Vermeij and Bak 2003). In the azooxanthellate coral *Caryophyllia smithii* at the sublittoral cliffs of Lough Hyne, Ireland, population density increases with depth in sites characterized by high sedimentation rates, possibly in relation to the high tolerance to sedimentation of this species in comparison to its competitors (Bell and Turner 2000).

Balanophyllia europaea (Risso, 1826) is a solitary, zooxanthellate scleractinian coral, which lives on rocky substratum and is endemic to the Mediterranean Sea, where it is found at depths from 0 to 50 m (Zibrowius 1980). In the northwestern Mediterranean populations of *B. europaea*, sea surface temperature (SST) negatively influences the photosynthetic efficiency of symbiotic algae, thereby decreasing the available energy for the coral (Caroselli et al. 2015) and resulting in a decrease of population density (Goffredo et al. 2007), stability of population age structure and presence of young individuals (Goffredo et al. 2008), net calcification rate (Goffredo et al. 2009), skeletal density (due to an increase in porosity; Fantazzini et al. 2013), and skeletal mechanical resistance (Goffredo et al. 2015). In contrast, poor information on this species is available for the eastern Mediterranean Sea. Investigations in the Turkish seas have focused on the distribution and ecological differences of scleractinians present in the eastern Mediterranean Sea (Özalp and Alparslan 2011). Among them, *B. europaea* has been observed as one of the most abundant solitary scleractinians, together with *Leptopsammia pruvoti*, *Caryophyllia smithii*, and *Caryophyllia inornata* (Özalp and Alparslan 2011, 2016). In the Dardanelles, polyps of *B. europaea* are shorter in shallow-water populations, possibly due to the stronger flows and wave action and/or as a morphological strategy of photoprotection under high-light conditions (Özalp et al. 2018). Linear extension rate (the increase in one linear dimension of the skeleton over time) and net calcification rate are homogeneous along a 1–21 m depth gradient, possibly due to a compensation between the response of zooxanthellae to temperature and light (Özalp et al. 2018). In fact, the higher temperatures at shallow depths may negatively affect the photosynthetic efficiency of *B. europaea*, thus reducing available energy for calcification. On the other hand, lower light availability with depth is expected to decrease photosynthesis rates and these two effects may compensate each other (Özalp et al. 2018). Related to differences between populations in the Mediterranean Sea, net calcification rate of the Dardanelles population is higher (mean net calcification rate at 6 m depth = 5.5 mg mm⁻² yr⁻¹; Özalp et al. 2018) than populations of *B. europaea* in the western

Mediterranean (mean net calcification rate at similar latitude at 6 m depth = 1.0 mg mm⁻² yr⁻¹, mean net calcification rate at similar temperature at 6 m depth = 2.9 mg mm⁻² yr⁻¹; Goffredo et al. 2009).

The aims of this study were to (1) to characterize the demography of *B. europaea* along a depth gradient in the Dardanelles, and (2) to compare the population dynamics of *B. europaea* from the eastern Mediterranean Sea with the well-characterized populations in the western Mediterranean Sea to better understand the population characteristics of this coral at two opposite sides of the Mediterranean Sea.

Materials and methods

Study area and photoquadrats

The Dardanelles is one of the waterways of the Turkish Straits System, which connects the Sea of Marmara to the Aegean Sea (Fig. 1). A two-layered flow system brings more saline waters (38–39 ppt; Ünlüata et al. 1990) from the Mediterranean Sea to the Marmara Sea between depths of 10 and 100 m (maximum depth: 113 m; Gökaşan et al. 2008), while the brackish surface waters (20–28 ppt; Baba et al. 2007) from the Black Sea to the Mediterranean Sea (Beşiktepe 2003) reach up to 5 m depth on coastal zones in the region (Özalp 2013). The more saline waters at the deeper layer of the strait enable a great biodiversity in some locations and create hotspots for corals, sponges, tunicates, and other invertebrates of the coralligenous (Topçu and Özalp 2017). The substratum at the survey area is characterized by a dense occurrence of seagrass communities such as *Posidonia oceanica* and *Zostera marina* between 4 and 10 m and also by serpulid reefs and the only largest reef habitat of the endangered scleractinian coral *Cladocora caespitosa* in the Turkish Straits System (Özalp and Alparslan 2016). In the Dardanelles, *B. europaea* is recorded up to 23 m depth on rocks (Özalp et al. 2014) and exceptionally on rhizomes of the Mediterranean endemic seagrass *P. oceanica* (Özalp and Alparslan 2016). In this region, *L. pruvoti* and *Caryophyllia smithii* are the dominant species between 41–50 m and 21–30 m, with a percent cover of 43% and 32%, respectively, while most *B. europaea* individuals occur between 11 and 20 m with a percent cover around 15% (maximum reported density is 393 individuals m⁻²; Özalp and Alparslan 2016). The studied population of *B. europaea* was located in the Guzelyali region of the Dardanelles (40°2'4"N; 26°20'2"E; Fig. 1) where this coral is the most common coral species among other scleractinians such as *Cladocora caespitosa* (few sparse colonies) and *Caryophyllia smithii* (6% percent cover; Özalp et al. 2014).

From 17 March 2016 to 31 August 2016, photographs of 10 haphazardly placed 20-m long horizontal transects (parallel to coastline) were taken by scientific divers with SCUBA equipment at 1, 4, 6, 8, 11, 13, 15, 17, 19, and 21 m depth (i.e., one transect per depth up to the maximum depth where the species was found in this site) at a site known for its high coral

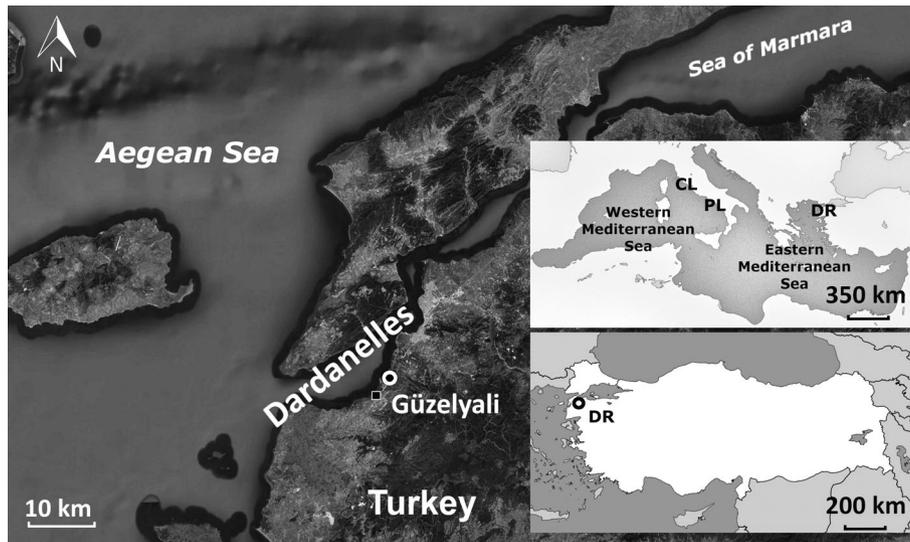


Fig. 1. Map of the Mediterranean Sea (upper small panel) and of Turkey (lower small panel) indicating the site where field surveys were carried out (Güzelyali region, the Dardanelles: 40°2'4"N, 26°20'2"E, large panel) and the two populations previously studied in the NW Mediterranean whose population dynamics data (Goffredo et al. 2008) were compared with the Dardanelles population. CL, Calafuria; DR, Dardanelles; PL, Palinuro.

cover. The total linear distance from the coastline to the 21 m transect was 280 m, and no regular spacing was set between the transects at each depth layer (it was depending on the slope of the substratum). For each meter along each horizontal transect, an aluminum quadrat (1 m²) divided by strings in four square sectors (0.25 m² each), was placed on the seabed and one photograph of each sector was taken (Fig. 2). Photographs of whole quadrats and single photographs of each sector were taken to allow a better resolution of image analysis measurements.

Image analysis, biometry, and age determination

Photographs were analyzed using the software NIKON NIS-Elements D 3.1. Coral species were identified according to Zibrowius (1980). *Balanophyllia europaea* was the only scleractinian coral observed in the photographs, apart from four sparse individuals of *Caryophyllia smithii*. The length (L : maximum axis of the oral disk), width (W : minor axis of the oral disk), and area of the oral disk of each specimen of *B. europaea* were measured. The smallest coral observed had a length of 1–2 mm and no difficulty was found to recognize coral to the species level, as this species has a unique shape. For each sector, the area of substrate suitable for the species (i.e., rocky substratum) was measured and expressed as a percentage of the whole sector area (0.25 m²). The remaining unsuitable area consisted of muddy or sandy substratum (Fig. 2).

The skeletal mass (M) and age of each specimen were calculated using the mass–length relationships and the age–length relationship, respectively, previously recorded for this population along the same depth range (1–21 m; Özalp et al. 2018).

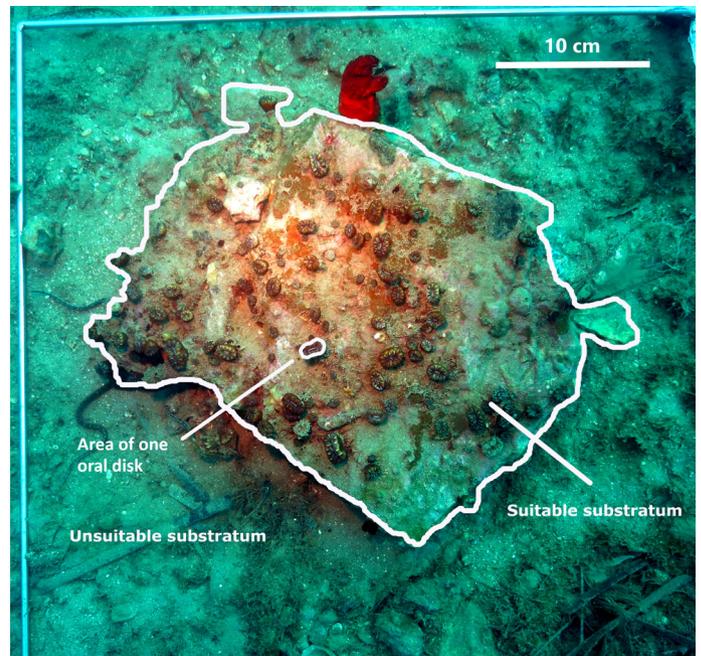


Fig. 2. Picture of quadrat 1, sector A at 21 m depth (0.25 m²). Only the rocky substratum was considered as suitable substratum. All visible corals are *B. europaea* specimens.

Population density and dynamics

Since *B. europaea* occurs on rocky substrata (Zibrowius 1980; Goffredo et al. 2004), only hard substrata were considered as suitable for the species and population density parameters were normalized over this area. The population density of each quadrat was expressed as: (1) NI—number of individuals per m² of suitable substratum; (2) MA—mass per area unit of

suitable substratum; and (3) P —percent coverage of suitable substratum (Goffredo et al. 2007).

The observed population age structure for each quadrat was determined from the image analysis data set described above. The theoretical population age structure and the corresponding population age structure stability were modeled for each depth group (see “Results” section) with a linear regression analysis of the natural logarithm of the number of individuals (frequency) in each age class (N_t) against their corresponding age (t):

$$\ln(N_t) = at + b \quad (1)$$

where a is the slope, indicated also with sign changed as Z (instantaneous rate of mortality), which corresponds to the decrement of the number of individuals with age and is the reciprocal of the turnover time of the population (Goffredo et al. 2008; Caroselli et al. 2016). The intercept b corresponds to the natural logarithm of the number of individuals at age zero (N_0) (Caroselli et al. 2016). In a theoretical steady state population (i.e., no age cohort missing or overrepresented; Grigg 1984), age explains the whole variance in the frequency of age classes and the r^2 of the regression line of Eq. 1 is equal to one. Lower r^2 values correspond to a progressive deviation of the population from the steady state, thus this value is an indicator of the stability of population age structure (Sparre et al. 1989; Goffredo et al. 2004; Caroselli et al. 2016). The Beverton and Holt model described above was used to obtain the theoretical population parameters (Beverton and Holt 1956; Goffredo et al. 2008; Caroselli et al. 2016). Smaller individuals are difficult to observe, so population age structure data are usually underrepresented in the younger age classes. With the Beverton and Holt demographic model, we obtained the “theoretical” population and we reconstructed the youngest age classes, obtaining additional estimations of population demographic traits (Caroselli et al. 2016). Based on the observed and theoretical distribution, we obtained the following demographic parameters for each depth group with standard methods: (1) population age structure stability (r^2 of Eq. 1); (2) observed and (3) theoretical mean age of the individuals; (4) observed and (5) theoretical percentage of individuals below sexual maturity, which is reached at ~ 2 yr (~ 8 mm length; Goffredo et al. 2002); (6) maximum longevity (defined as the age at which $< 0.5\%$ of the initial cohort is still surviving; Sparre et al. 1989); (7) observed and

(8) theoretical age at maximum percentage biomass; (9) observed and (10) theoretical mean age of biomass (Goffredo et al. 2008; Caroselli et al. 2016).

Temperature and wave height data

During 2013 and 2015, divers measured SST and depth temperature (DT) using mercury thermometers ($\pm 0.1^\circ\text{C}$) while taking the photographs at each depth and annotating the data on plastic tables. SST ($^\circ\text{C}$) data for the period 2010–2015 were obtained from NASA Earth Observations (<https://neo.sci.gsfc.nasa.gov>). Mean annual SST values were computed from monthly measurements. A linear regression was obtained between DT and SST data to estimate at-depth temperatures during 2010–2015 (Özalp et al. 2018). More details on the data set are found in the Supporting Information of Özalp et al. 2018. During January 2010–August 2016, daily wave height data for Calafuria and the Dardanelles were obtained from data banks. Data for Calafuria were obtained from the wind-wave forecast system of the LaMMA consortium using the weather research and forecasting model (WRF; National Center for Atmospheric Research [NCAR]; National Oceanic and Atmospheric Administration [NOAA]; Air Force Weather Agency [AFWA]) and WaveWatch III model (WW3; NOAA and National Centers for Environmental Prediction). For the Dardanelles, data were provided by the Çanakkale Provincial Directorate of Meteorological Service.

Statistical analyses

A one-way permutation multivariate analysis of variance (PERMANOVA; Anderson 2001) based on Euclidean distances was performed with 999 permutations, to test differences in age structures among depths. Prior to PERMANOVA, the dimensionality of the problem was reduced by determining the minimum subset of age classes which would generate the same multivariate sample pattern by applying the “global BEST test” (BioEnv + SStepwise; Clarke et al. 2008). An ordination analysis (carried out by principal coordinates [PCO]; Gower 1966) was performed on population age structure data to have a two-dimensional representation of the multi-dimensional differences in population age structure among quadrats at each depth. The above analyses were performed with PRIMER-E version 6.1.18 (PRIMER-E, Ivybridge, UK).

Since assumptions for parametric statistics were met, ANOVA was used to compare mean of number of individuals

Table 1. General PERMANOVA results of age frequency distribution (classes 1–5 yr, following the BEST analysis, number of permutations = 99, $\rho = 0.977$, $p < 0.01$) among depths. SS, sum of squares; MS, mean squares, p (perm), significance; p (MC), significance after Monte-Carlo correction for small sample size.

Source	df	SS	MS	Pseudo-F	p (perm)	p (MC)
de	2	13,914	6957.2	17.224	0.001	0.001
Res	122	49,279	403.93			
Total	124	63,194				

per m², mass per area unit of suitable substratum, percent coverage of suitable substratum, and percentage of suitable substratum among depth groups (Altman 1991). The Kruskal–Wallis test with Monte Carlo correction for small sample size (Potvin and Roff 1993) was instead used to compare mean population densities and percentage of suitable substratum among depths. These analyses were computed using IBM SPSS Statistic 20.

Spearman’s correlation coefficients (Altman 1991) were calculated for the relationships between depth group, population structure stability, observed and theoretical % of individuals below sexual maturity, observed and theoretical mean age, observed and theoretical age at maximum % biomass, and observed and theoretical mean age of biomass.

Table 2. PERMANOVA pairwise test between depth groups 1–13, 15–17, and 19–21 m. *p* (perm), significance; *p* (MC), significance after Monte-Carlo correction for small sample size.

Groups	<i>t</i>	<i>p</i> (perm)	<i>p</i> (MC)
1–13 m vs. 15–17 m	3.1196	0.001	0.001
1–13 m vs. 19–21 m	3.7806	0.001	0.001
15–17 m vs. 19–21 m	6.0267	0.001	0.001

Differences in mean and maximum wave height between Calafuria and the Dardanelles were checked with a paired Student’s *t*-test.

Results

Population age structure and survivorship

Observed age structures were obtained for each depth. Populations at 19–21 m exhibited individuals of all age classes from 0 to 19 yr and presented some sparse plusvariant individuals over 30 yr. Populations at 15–17 m exhibited individuals of all age classes until 11 yr, while populations at 1–13 m exhibited individuals up to 14 yr.

The BEST analysis indicated the age classes of 1–5 yr as the most representative in determining the differences among depths in the multivariate pattern of population age structures (number of permutations = 99, $\rho = 0.977$, $p < 0.01$). Age frequency distributions of these age classes differed among depths (PERMANOVA, $df = 124$, $p < 0.001$, Table 1). Pair-wise tests (PERMANOVA, $p < 0.001$, Table 2) identified three significantly different depth groups: (1) 1–13 m; (2) 15–17 m; and (3) 19–21 m. A two-dimensional representation of the difference in population age structures among depth groups was produced with a PCO (Fig. 3). At 1–13 m depth, the age classes 4–5 yr were more represented relatively to the depth 19–21 m, where age class 1 was relatively overrepresented (Fig. 3). Depth

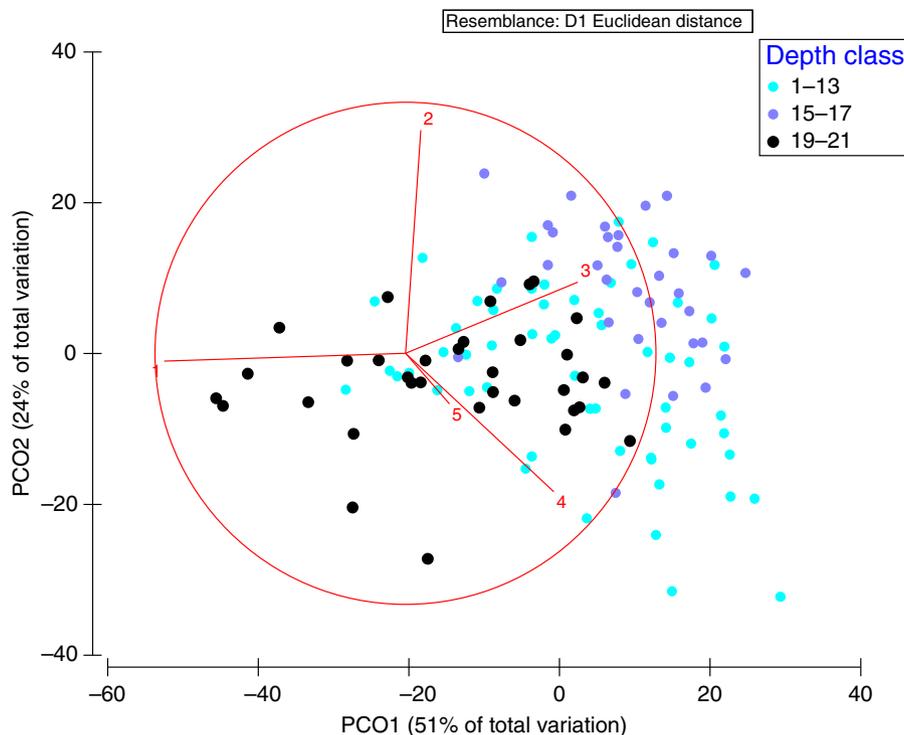


Fig. 3. Principal coordinates plot of age classes 1–5 yr in depth groups (1–13 m, light blue circles; 15–17 m, turquoise circles; 19–21 m, black circles) based on Euclidean distances. Each circle represents a quadrat. Vectors of age classes 1–5 yr (the most representative in determining differences among depth groups; BEST analysis, number of permutations = 99, $\rho = 0.977$, $p < 0.01$) are superimposed on the PCO in red. From each point in the plot, moving in parallel to the direction of each vector indicates an increase in the corresponding age class.

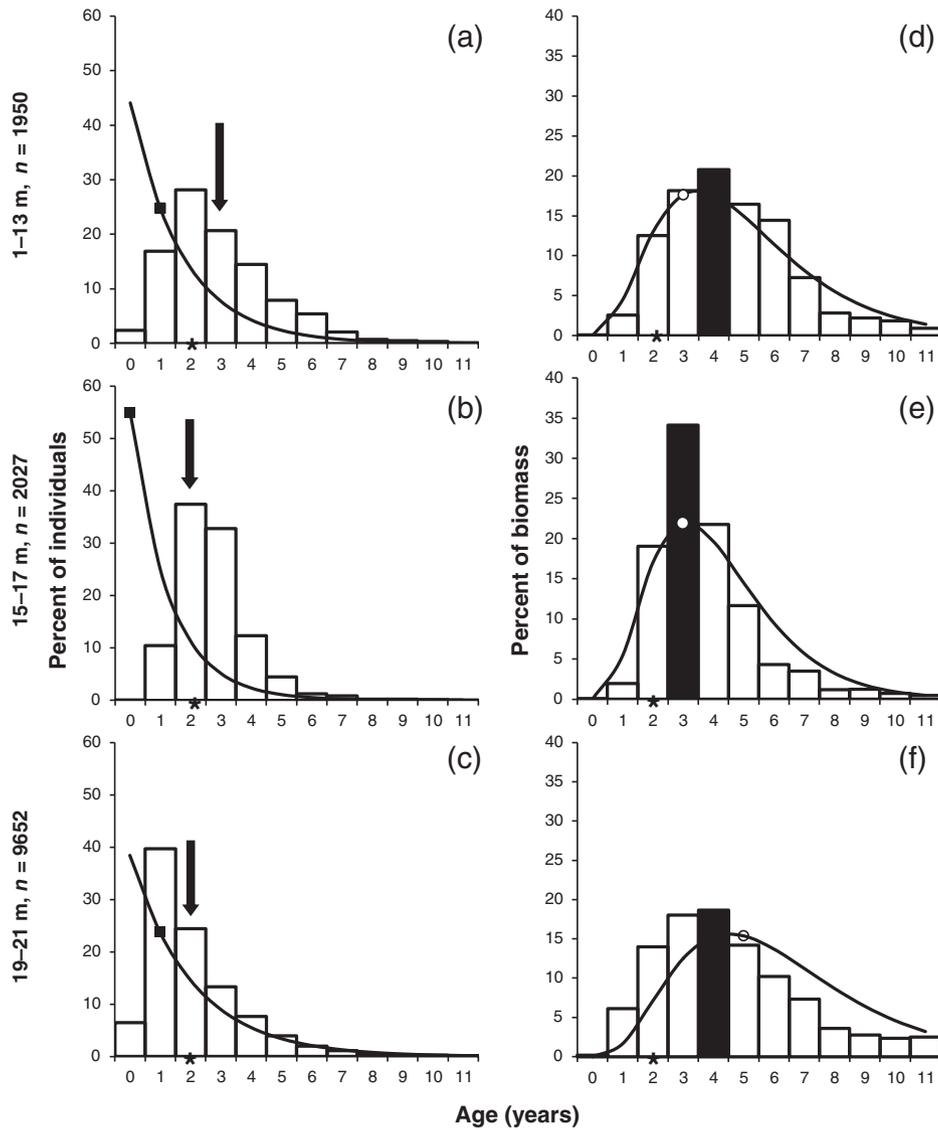


Fig. 4. Age-class structures of each depth group as percent of individuals (a–c) and as percent of biomass (d–f). The lines indicate the theoretical distributions. The observed (arrow) and theoretical (black square) age class containing the mean age of the individuals of sampled population are indicated in (a–c). The observed (black column) and theoretical (black circle) age at maximum percentage biomass are indicated in (e, f). Asterisks indicate the age at sexual maturity. *n* = number of individuals dated by growth curves.

Table 3. Demographic parameters of each depth group.

	1–13 m	15–17 m	19–21 m
Population structure stability (r^2)	0.974	0.978	0.974
Instantaneous rate of mortality (Z)	0.580	0.793	0.484
Observed % of individuals below sexual maturity	19.3	10.5	46.1
Theoretical % of individuals below sexual maturity	68.8	79.6	62.2
Observed mean age (years)	3.0	2.7	2.1
Theoretical mean age (years)	1.3	0.8	1.6
Observed age at maximum % biomass (years)	4	3	4
Theoretical age at maximum % biomass (years)	3	3	5
Observed mean age of biomass (years)	4.6	3.7	4.5
Theoretical mean age of biomass (years)	4.7	4.1	5.6

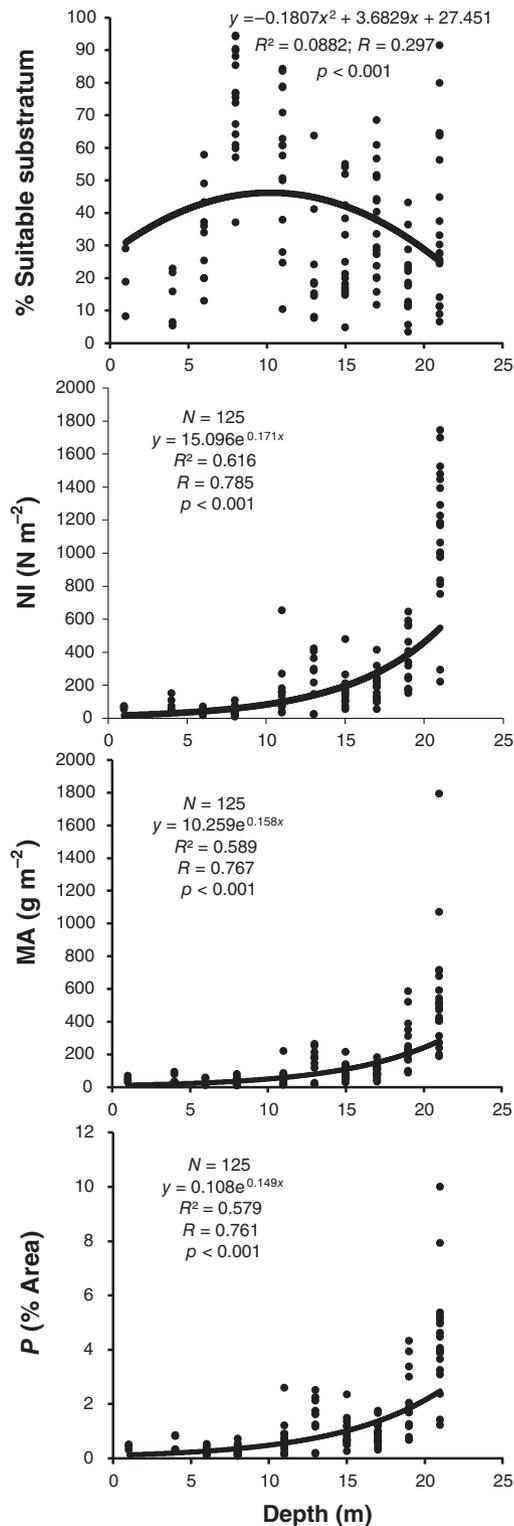


Fig. 5. Regression and correlation analysis between (a) percentage suitable substratum, (b) number of individuals per m^2 (NI), (c) mass per area unit (MA), (d) percentage coverage and depth using a quadratic function model in (a) and an exponential function model in (b–d). R^2 = Pearson's coefficient of determination; R = Pearson's correlation coefficient; N = number of photoquadrats.

group 15–17 represented an intermediate situation with relatively overrepresented age classes 2 and 3 (Fig. 3). Data for each depth group were pooled to obtain age structures (Fig. 4) and derive the corresponding observed and theoretical demographic parameters (Table 3), none of which had a significant trend with depth ($p > 0.05$). The age-frequency distributions revealed a high percentage of individuals under the age of sexual maturity (2 yr old, equivalent to ~ 8 mm; Goffredo et al. 2004; Özalp et al. 2018) in all depth groups, but juveniles contributed only slightly to percentage biomass (Fig. 4; Table 3). The majority of biomass was in age classes 3–6 with peaks at 3 and 4 yr (Fig. 4; Table 3).

Population density parameters and suitable substratum

Along the considered depth range (1–21 m), the mean percentage of suitable substratum varied significantly among depths (Kruskal–Wallis test, $df = 9$, $p < 0.001$) and had a negative parabolic trend with a peak of 46% at around 10 m depth (Fig. 5a).

The number of individuals per m^2 (NI), mass for area unit (MA), and percentage coverage differed significantly (Kruskal–Wallis test, $df = 9$, $p < 0.001$) and were positively and exponentially correlated with depth (Fig. 5b–d). Mean NI varied from 18 individuals m^{-2} at 1 m to 548 individuals m^{-2} at 21 m, mean MA varied from 12 $g m^{-2}$ at 1 m to 283 $g m^{-2}$ at 21 m, and percentage coverage varied from 0.1% at 1 m to 2.5% at 21 m (Fig. 5b–d).

Discussion

This study provided the first assessment of population dynamics traits of a scleractinian coral in the eastern Mediterranean Sea, starting to fill the gap of information regarding coral demography in this relatively understudied part of the Mediterranean basin. Variations in coral abundance and population age structure were observed with depth, while demographic parameters resulted different from populations studied in Italy (NW Mediterranean Sea). Increasing temperature has been considered as the environmental parameter that mainly drives demographic differences in this species (Goffredo et al. 2007, 2008), by decreasing the available energy coming from zooxanthellae photosynthesis (Caroselli et al. 2015) and causing bleaching and tissue necrosis that lead to mass-mortality events (Kružić and Popijač 2014). Nevertheless, SST was similar between the NW Mediterranean population of Calafuria and the Dardanelles population in the eastern Mediterranean Sea, while demographic parameters were different between the two locations. Another environmental parameter (i.e., wave height) seems to be the most likely cause that determines this difference, highlighting the need for analyzing multiple environmental parameters when trying to determine the resilience of coral populations to a changing environment.

Population density parameters and suitable substratum

Since *B. europaea* is a zooxanthellate coral, its bathymetric distribution is limited by light availability to depths of 0–50 m and it usually lives on subtidal rock and rocky reefs exposed to light (Zibrowius 1980). In the Dardanelles, the average higher salinity of 38.67 PSU (Beşiktepe 2003) below 10 m depth, as compared to the brackish characteristic of the most superficial water layer, seems to favor higher coral densities below 10 m depth (Baba et al. 2007; Özalp and Alparslan 2016). Accordingly, in the present study, all estimates of population density of *B. europaea* increased exponentially with depth from 1 to 21 m (Fig. 5).

In symbiotic corals, photosynthesis modulates the population density by supplying energy needed for gametogenesis and larval development (Carlon 2002) and influencing polyp fecundity and larval dispersion capability (Goffredo et al. 2002, 2004). High temperatures affect negatively *B. europaea* photosynthesis, leading to thermal inhibition of symbiont and reducing available energy for the coral (Caroselli et al. 2015). In the NW Mediterranean Sea, demographic characteristics of *B. europaea* have been determined in six populations, on a latitudinal SST gradient along the Italian coast (Goffredo et al. 2008). Among these six sites, the Palinuro site is at the same latitude of the Dardanelles population and it is characterized by mean annual SST of 19.1°C (Table 4). The Calafuria site is at 43°27'N of latitude, further north than the Dardanelles site and it presents temperature range similar to the Dardanelles population (i.e., mean annual SST in the Calafuria 18.0 vs. 18.3 in the Dardanelles; Table 4).

At the Palinuro site (same latitude as the Dardanelles population; Table 4), population density is lower (24 individuals m⁻², derived from Goffredo et al. 2007) than the Dardanelles population (41 individuals m⁻²) and this is consistent with the higher temperatures that characterize Palinuro (Goffredo et al. 2008) and which are proposed as the main environmental factor limiting the abundance of this species in the NW Mediterranean

(Goffredo et al. 2007). At the Calafuria site (same SST mean and variability as the Dardanelles; Table 4), *B. europaea* shows a mean of 113 individuals m⁻² at 6 m depth (Goffredo et al. 2004), much higher than the Dardanelles population at the same depth (41 individuals m⁻²). Consequently, factors other than temperature have to be taken into account to explain these differences. The negative effects of the lower salinity on coral populations reported above 12 m depth in the Dardanelles (Baba et al. 2007; Özalp and Alparslan 2016) may indeed play a role in determining a lower abundance than at Calafuria. Moreover, the Calafuria population occurred from 2 to 12 m with an average density of 16 individuals m⁻² (Goffredo et al. 2004), while in the Dardanelles it increased exponentially from 1 m (18 individuals m⁻²) to 21 m (548 individuals m⁻²). The limited population distribution at Calafuria has been attributed to water turbidity that reduces light penetration (Goffredo et al. 2004) and may be influenced also by the stronger wave action with respect to the Dardanelles, especially in winter (Fig. 6; Özalp et al. 2018). Also temperature varies with depth and the maximum population density at 6 m depth at Calafuria may depend on a balance between the responses to all these environmental factors that allows *B. europaea* to perform better at 6 m depth. In the Dardanelles population, turbidity and temperature effects are likely to be similar to Calafuria, while wave action is lower due to the enclosed nature of the strait (Fig. 6; Özalp et al. 2018). The influence of salinity favoring corals in deeper water is reported in the Dardanelles (Baba et al. 2007; Özalp and Alparslan 2016) while it is not present at Calafuria, possibly causing the different response of population abundance to depth observed in the present study.

Population age structure and survivorship

Observed frequency of age classes < 2 yr was underestimated due to the difficulty in detection of small corals during photoquadrats observation (Fig. 4), a common bias when

Table 4. Sea surface temperatures, latitude, r^2 (coefficient of determination), and demographic parameters of Calafuria (CL) and Palinuro (PL) populations and the 1–13 m group in the Dardanelles (DR). Data for Calafuria and Palinuro come from Goffredo et al. (2004, 2007, 2008, 2009) while data for the Dardanelles come from Özalp et al. (2018).

	CL	PL	DR
SST (°C), annual mean	18.0	19.1	18.3
Latitude	43°27'N	40°02'N	40°02'N
Population structure stability (r^2)	0.872	0.587	0.974
Observed % of individuals below sexual maturity	39.6	19.7	19.3
Theoretical % of individuals below sexual maturity	55.7	41.2	68.8
Observed mean age (years)	5.5	7.3	3.0
Theoretical mean age (years)	3.1	5.3	1.3
Theoretical maximum longevity (years)	20	31	10
Observed age at maximum % biomass (years)	6	9	4
Theoretical age at maximum % biomass (years)	6	12	3
Observed mean age of biomass (years)	7.5	9.9	4.6
Theoretical mean age of biomass (years)	9.0	14.3	4.7

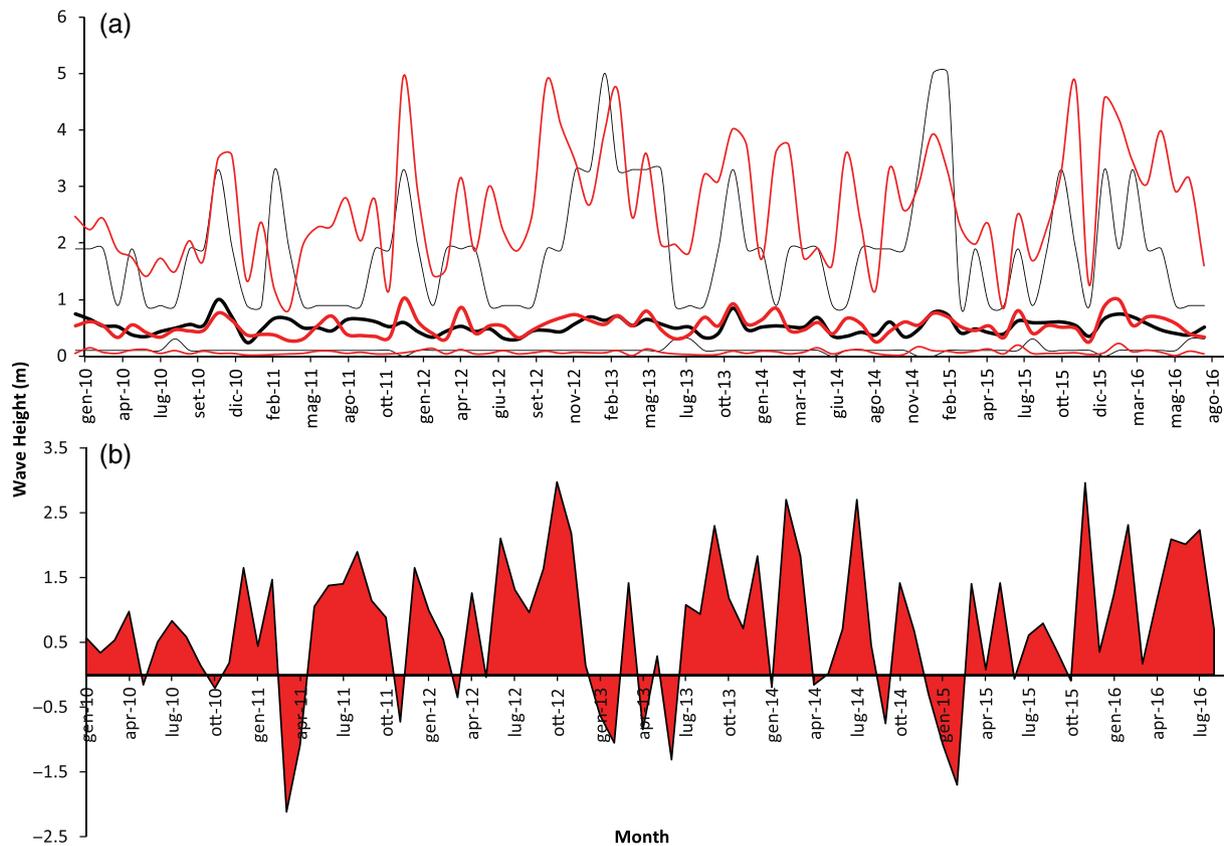


Fig. 6. (a) Time series of wave height data from January 2010 to August 2016 at the Dardanelles (black lines) and at Calafuria (red lines). The bold lines represent the monthly mean height and the thin lines represent the monthly minimum and maximum height. (b) Time series of the difference between Calafuria and the Dardanelles maximum wave height from 2010 to 2016.

analyzing field samples (e.g., Goffredo et al. 2008; Caroselli et al. 2016). Polyps became sexually mature at 2 yr and this class showed high percentage of individuals in all depth groups even if relatively more 1-yr-old polyps were found in the 19–21 m group (Fig. 4). Mean coral age at all depth groups was close to the age at sexual maturity (Table 3). Population age structures were significantly different among depths, but this difference was not strong enough to cause clear differences or trends related with depth for all derived demographic parameters (Table 3).

The stability value for the Dardanelles population of *B. europaea* r^2 was similar in all depth groups and >0.97 (Table 3), indicating stable populations across the whole environmental variation along the depth gradient. Stability in the Dardanelles was higher than at Calafuria ($r^2 = 0.872$) and Palinuro ($r^2 = 0.587$). This difference might depend on the enclosed nature of the strait which makes its shores less subject to the frequent and violent storms that characterize the winter along Italian shores, especially at Calafuria (Fig. 6; Özalp et al. 2018). In fact, while mean wave height is similar between the two sites, the maximum wave height is definitely higher in Calafuria (Fig. 6). Studies on tropical coral species have demonstrated how intense wave action is able to dislodge corals from their

substratum, thus influencing population demography (Madin et al. 2012). In addition, the higher stability in the Dardanelles population might also be influenced by the clade of zooxanthellae in polyp tissues, which could have different environmental tolerances (e.g., light, temperature, sedimentation; Knowlton and Rohwer 2003). For *B. europaea*, high temperatures experienced in summer inhibit photosynthesis and contribute to reduce calcification rate and reproductive efficiency (Goffredo et al. 2007, 2008, 2009; Caroselli et al. 2015). In the NW Mediterranean, *B. europaea* is reported to host zooxanthellae belonging to clade A that showed to be resistant to short-term increases in temperature (Rodolfo-Metalpa et al. 2006), but recently, individuals at Ischia Island (Italy) have been reported to host mixed clade A and phylotype B2 (Meron et al. 2012). Clade B responds differently to temperature than clade A and shows maximum activity only at warm temperature, while it is inactive in the cold season (Casado-Amezúa et al. 2014). Molecular analysis of clades of zooxanthellae in the eastern Mediterranean could clarify if they have a role in determining a higher stability in the Dardanelles. Other possible explanations include a better representativity of sampled population in the Dardanelles than in Italy, where the number of quadrats analyzed is higher (10 per depth in the Dardanelles against 3 in

Italian populations; Goffredo et al. 2008) and may have resulted in a better shape of age class frequencies without any over/underrepresented age classes, except for very small ones.

The solitary coral *B. europaea* reaches sexual maturity at the size of 6–9 mm (Goffredo et al. 2002), which corresponds to and age of 2 yr in the Dardanelles and an age of 3–4 yr at Calafuria and Palinuro (Goffredo et al. 2008), due to the different linear extension rate (Özalp et al. 2018). The Dardanelles population also presented lower mean ages than all Italian populations. In particular, all depth groups had mean age ≤ 3 yr (Table 3). Consistently, observed and theoretical age at maximum percentage of biomass and observed and theoretical mean age of biomass in the Dardanelles were similar along the depth gradient (Table 3) and all Italian populations presented higher values (Table 4). The Dardanelles population was younger and had more biomass gathered in young age classes than Italian populations. Moreover, maximum estimated longevity in the Dardanelles (10 yr) was very low in comparison with Calafuria and Palinuro (20 and 31, respectively), strongly contributing to the observed younger age of the Dardanelles population. The older mean age caused by a deficiency of young individuals with increasing temperature has been considered a negative response of this species along Italian coasts (Goffredo et al. 2008). Accordingly, Dardanelles populations seem to thrive in their environment, consistently with the higher stability discussed above. Nevertheless, the observed decrease in maximum longevity, the higher instantaneous mortality rate, and the younger population age seems to indicate that the Dardanelles population has a more rapid turnover and thus behaves more like an *r*-strategist species than in the Calafuria population (sensu Pianka 1970). In the context of climate change scenarios, this may indicate that populations of this species in the eastern Mediterranean Sea may have more chances to face the ongoing increase in seawater temperature and acidification than their counterparts in the NW Mediterranean Sea, as *r*-strategists are generally more resilient to a rapidly changing environment than *K*-strategists (Pianka 1970).

Conclusions

This is the first investigation on the population dynamics of a scleractinian coral across a depth gradient in the eastern Mediterranean Sea and represents the first approximation to unravel different stabilities between populations along this environmental gradient. This study showed that: (1) Population density of *B. europaea* in the Dardanelles increased exponentially with depth, possibly due to lower current and wave action, and higher salinity under 12 m depth; (2) Age structures of *B. europaea* in the Dardanelles differ among depths but there are no clear differences or trends with depth for all derived demographic parameters; and (3) Populations of *B. europaea* in the Dardanelles are younger, more stable, and more oriented toward an *r*-strategy than Italian populations, in spite of similar temperature and latitudinal conditions.

References

- Altman, D. G. 1991. Practical statistics for medical research. Chapman & Hall.
- 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](https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x)
- Artzy-Randrup, Y., R. Olinky, and L. Stone. 2006. Size-structured demographic models of coral populations. *J. Theor. Biol.* **245**: 482–497. doi:[10.1016/j.jtbi.2006.10.019](https://doi.org/10.1016/j.jtbi.2006.10.019)
- Baba, A., O. Deniz, M. Turkoglu, and H. Ozcan. 2007. Investigation of discharge of fresh water in the Çanakkale Strait (Dardanelles-Turkey). In I. Linkov, G. A. Kiker, and R. J. Wenning [eds.], *Environmental security in harbors and coastal areas. NATO security through science series (Series C: Environmental security)*. Springer. pp. 421–427.
- Babcock, R. C. 1991. Comparative demography of three species of scleractinian corals using age- and size-dependent classifications. *Ecol. Monogr.* **6**: 225–244. doi:[10.2307/2937107](https://doi.org/10.2307/2937107)
- Bell, J. J., and J. R. Turner. 2000. Factors influencing the density and morphometrics of the cup coral *Caryophyllia smithii* in Lough Hyne. *J. Mar. Biol. Assoc. U. K.* **80**: 437–441. doi:[10.1017/S0025315400002137](https://doi.org/10.1017/S0025315400002137)
- Beşiktepe, Ş. T. 2003. Density currents in the two-layer flow: An example of Dardanelles outflow [Courants de densité dans un flux à deux couches: l'exemple du courant de sortie des Dardanelles]. *Oceanol. Acta* **26**: 243–253. doi:[10.1016/S0399-1784\(03\)00015-X](https://doi.org/10.1016/S0399-1784(03)00015-X)
- Beverton, R. J. H., and S. V. Holt. 1956. A review of methods for estimating mortality rates in fish populations, with special reference to sources of bias in catch sampling. *Rapports et Proces-Verbaux des reunions - Conseil International pour l'Exploration de la Mer* **140**: 67–83.
- Carlson, D. B. 2002. Production and supply of larvae as determinants of zonation in a brooding tropical coral. *J. Exp. Mar. Biol. Ecol.* **268**: 33–46. doi:[10.1016/S0022-0981\(01\)00369-0](https://doi.org/10.1016/S0022-0981(01)00369-0)
- Caroselli, E., G. Falini, S. Goffredo, Z. Dubinsky, and O. Levy. 2015. Negative response of photosynthesis to natural and projected high seawater temperatures estimated by pulse amplitude modulation fluorometry in a temperate coral. *Front. Physiol.* **6**: 317. doi:[10.3389/fphys.2015.00317](https://doi.org/10.3389/fphys.2015.00317)
- Caroselli, E., F. Ricci, V. Brambilla, G. Mattioli, O. Levy, G. Falini, Z. Dubinsky, and S. Goffredo. 2016. Relationships between growth, population dynamics, and environmental parameters in the solitary non-zooxanthellate scleractinian coral *Caryophyllia inornata* along a latitudinal gradient in the Mediterranean Sea. *Coral Reefs* **35**: 507–519. doi:[10.1007/s00338-015-1393-9](https://doi.org/10.1007/s00338-015-1393-9)
- Caroselli, E., and others. 2019. Low and variable pH decreases recruitment efficiency in populations of a temperate coral naturally present at a CO₂ vent. *Limnol. Oceanogr.* **64**: 1059–1069. doi:[10.1002/lno11097](https://doi.org/10.1002/lno11097)

- Casado-Amezúa, P., A. Machordom, J. Bernardo, and M. Gozález-Wangüemert. 2014. New insights into the genetic diversity of zooxanthellae in Mediterranean anthozoans. *Symbiosis* **63**: 41–46. doi:10.1007/s13199-014-0286-y
- Chappel, J. 1980. Coral morphology, diversity and reef growth. *Nature* **286**: 249–252. doi:10.1038/286249a0
- Clarke, K. R., P. J. Somerfield, and R. N. Gorley. 2008. Testing of null hypotheses in exploratory community analyses: Similarity profiles and biota-environment linkage. *J. Exp. Mar. Biol. Ecol.* **366**: 56–69. doi:10.1016/j.jembe.2008.07.009
- Fantazzini, P., and others. 2013. A time-domain nuclear magnetic resonance study of Mediterranean scleractinian corals reveals skeletal-porosity sensitivity to environmental changes. *Environ. Sci. Technol.* **47**: 12679–12686. doi:10.1021/es402521b
- Goffredo, S., S. Arnone, and F. Zaccanti. 2002. Sexual reproduction in the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). *Mar. Ecol. Prog. Ser.* **229**: 83–94. doi:10.3354/meps229083
- Goffredo, S., G. Mattioli, and F. Zaccanti. 2004. Growth and population dynamics model of the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). *Coral Reefs* **23**: 433–443. doi:10.1007/s00338-004-0395-9
- Goffredo, S., E. Caroselli, E. Pignotti, G. Mattioli, and F. Zaccanti. 2007. Variation in biometry and population density of solitary corals with environmental factors in the Mediterranean Sea. *Mar. Biol.* **152**: 351–361. doi:10.1007/s00227-007-0695-z
- Goffredo, S., E. Caroselli, G. Mattioli, E. Pignotti, and F. Zaccanti. 2008. Relationships between growth, population structure and sea surface temperature in the temperate solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). *Coral Reefs* **27**: 623–632. doi:10.1007/s00338-008-0362-y
- Goffredo, S., E. Caroselli, G. Mattioli, E. Pignotti, Z. Dubinsky, and F. Zaccanti. 2009. Inferred level of calcification decreases along an increasing temperature gradient in a Mediterranean endemic coral. *Limnol. Oceanogr.* **54**: 930–937. doi:10.4319/lo.2009.54.3.0930
- Goffredo, S., and others. 2015. Skeletal mechanical properties of Mediterranean corals along a wide latitudinal gradient. *Coral Reefs* **34**: 121–132. doi:10.1007/s00338-014-1222-6
- Gökaşan, E., and others. 2008. Factors controlling the morphological evolution of the Çanakkale Strait (Dardanelles, Turkey). *Geo-Mar. Lett.* **28**: 107–129. doi:10.1007/s00367-007-0094-y
- Gower, J. C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika* **53**: 325–338. doi:10.1093/biomet/53.3-4.325
- Grigg, R. W. 1984. Resource management of precious corals: A review and application to shallow water reef building corals. *Mar. Ecol.* **5**: 57–74. doi:10.1111/j.1439-0485.1984.tb00307.x
- Hoeksema, B. W., and Z. Waheed. 2011. Initial phase of autotomy in fragmenting *Cycloseris* corals at Semporna, eastern Sabah, Malaysia. *Coral Reefs* **30**: 1087. doi:10.1007/s00338-011-0807-6
- Hoeksema, B. W., and T. Yeemin. 2011. Late detachment conceals serial budding by the free-living coral *Fungia fungites* in the Inner Gulf of Thailand. *Coral Reefs* **30**: 975. doi:10.1007/s00338-011-0784-9
- Knowlton, N., and F. Rohwer. 2003. Multispecies microbial mutualism on coral reefs: The host as a habitat. *Am. Nat.* **162**: S51–S62. doi:10.1086/378684
- Kružić, P., and A. Popijač. 2014. Mass mortality events of the coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae) in the Mljet National Park (eastern Adriatic Sea) caused by sea temperature anomalies. *Coral Reefs* **34**: 109–118. doi:10.1007/s00338-014-1231-5
- Madin, J. S., T. P. Hughes, and S. R. Connolly. 2012. Calcification, storm damage and population resilience of tabular corals under climate change. *PLoS One* **7**: e46637. doi:10.1371/journal.pone.0046637
- Meesters, E. H., M. Hilterman, E. Kardinaal, M. Keetman, M. DeVries, and R. P. M. Bak. 2001. Colony size-frequency distributions of scleractinian coral populations: Spatial and interspecific variation. *Mar. Ecol. Prog. Ser.* **209**: 43–54. doi:10.3354/meps209043
- Meron, D., R. Rodolfo-Metalpa, R. Cunning, A. C. Baker, F. Maoz, and E. Banin. 2012. Changes in microbial communities in response to a natural pH gradient. *ISME J.* **6**: 1775–1785. doi:10.1038/ismej.2012.19
- Orejas, C., and others. 2011. Long-term growth rates of four Mediterranean cold-water coral species maintained in aquaria. *Mar. Ecol. Prog. Ser.* **429**: 57–65. doi:10.3354/meps09104
- Özalp, H. B. 2013. Taxonomic and ecological characteristics of hard coral species (Cnidaria, Anthozoa, Scleractinia) distributed in Çanakkale Strait [in Turkish]. Ph.D. thesis. Univ. of Çanakkale Onsekiz Mart.
- Özalp, H. B., and M. Alparslan. 2011. In situ studies on scleractinian corals around Çanakkale Strait (Marmara Sea), p. 4–9. *In* Proceedings of the 5th International Underwater Research Symposium, Famagusta. KKTC.
- Özalp, H. B., F. Sengun, Z. Karaca, and O. Hisar. 2014. A preliminary study on habitat characteristics and substrate preference of coral species distributed in the Dardanelles. *Mar. Sci. Tech. Bull.* **3**: 5–10.
- Özalp, H. B., and M. Alparslan. 2016. Scleractinian diversity in the Dardanelles and Marmara Sea (Turkey): Morphology, ecology and distributional patterns. *Oceanol. Hydrobiol. Stud.* **45**: 259–285. doi:10.1515/ohs-2016-0023
- Özalp, H. B., E. Caroselli, F. Raimondi, and S. Goffredo. 2018. Skeletal growth, morphology and skeletal parameters of a temperate, solitary and zooxanthellate coral along a depth gradient in the Dardanelles (Turkey). *Coral Reefs* **37**: 633–646. doi:10.1007/s00338-018-1687-9

- Pianka, E. R. 1970. On $-r$ and $-K$ selection. *Am. Nat.* **104**: 592–597. doi:10.1086/282697
- Potvin, C., and D. A. Roff. 1993. Distribution-free and robust statistical methods: Viable alternatives to parametric statistics. *Ecology* **74**: 1617–1628. doi:10.2307/1939920
- Purser, A., A. I. Larsson, L. Thomsen, and D. Van Oevelen. 2010. The influence of flow velocity and food concentration on *Lophelia pertusa* (Scleractinia) zooplankton capture rates. *J. Exp. Mar. Biol. Ecol.* **395**: 55–62. doi:10.1016/j.jembe.2010.08.013
- Rodolfo-Metalpa, R., C. Richard, D. Allemand, C. N. Bianchi, C. Morri, and C. Ferrier-Pagès. 2006. Response of zooxanthellae in symbiosis with the Mediterranean corals *Cladocora caespitosa* and *Oculina patagonica* to elevated temperatures. *Mar. Biol.* **150**: 45–55. doi:10.1007/s00227-006-0329-x
- Rodolfo-Metalpa, R., A. Peirano, F. Houlbrèque, M. Abbate, and C. Ferrier-Pagès. 2008. Effect of temperature, light and heterotrophy on the growth rate and budding of the temperate coral *Cladocora caespitosa*. *Coral Reefs* **21**: 17–25. doi:10.1007/s00338-007-0283-1
- Sparre, P., E. Ursin, and S. C. Venema. 1989. Introduction to tropical fish stock assessment. FAO Fisheries Technical Paper no. 306. FAO.
- Topçu, N. E., and H. B. Özalp. 2017. Anthozoans of the Sea of Marmara, p. 428–448. In E. Özsoy, M. N. Çağatay, N. Balkis, N. Balkis, and B. Öztürk [eds.], *The Sea of Marmara: Marine biodiversity, fisheries, conservation and governance*. Turkish Marine Research Foundation.
- Ünlüata, Ü., T. Oğuz, M. A. Latif, and E. Özsoy. 1990. On the physical oceanography of the Turkish straits, p. 25–60. In L. J. Pratt [ed.], *The physical oceanography of sea straits*. Springer.
- Vermeij, M. J. A., and R. P. M. Bak. 2002. How are coral populations structured by light? Marine light regimes and the distribution of *Madracis*. *Mar. Ecol. Prog. Ser.* **233**: 105–116. doi:10.3354/meps233105
- Vermeij, M. J. A., and R. P. M. Bak. 2003. Species-specific population structure of closely related coral morphospecies along a depth gradient (5–60 m) over a Caribbean reef slope. *Bull. Mar. Sci.* **73**: 725–744.
- Vertino, A., A. Savini, A. Rosso, S. I. Di Geronimo, F. Mastrototaro, and R. Sanfilippo. 2010. Benthic habitat characterization and distribution from two representative sites of the deep-water SML Coral Province (Mediterranean). *Deep-Sea Res. Part II Top. Stud. Oceanogr.* **57**: 380–396. doi:10.1016/j.dsr2.2009.08.023
- Zibrowius, H. 1980. Les scléactiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Mém. Inst. Océanogr.* **11**: 1–284.

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Conflict of Interest

None declared.

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