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Seasonal and bathymetric effects on macrofouling invertebrates' primary succession in a mediterranean non-indigenous species hotspot area

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Abstract

The present study investigates macrofouling development in the Mar Grande of Taranto (Central Mediterranean Sea), a wide confined area that has attracted considerable attention in recent years due to the establishment of numerous non-indigenous species (NIS). Different starting times of a yearly primary succession on artificial substrates were tracked so as to investigate the matching of the development pattern with contingency and/or convergence models, identifying NIS's structural role in the community endpoint. Our results show that during the experiment all assemblages tended to converge towards multiple contingent communities according to starting times and depths. The differences are due to propagule availability which influence further species interactions. Thus the endpoint patterns are defined by a contingent community development determined by the seasonal species pool, their phenologies, pre- and post-settlement events, and species interactions. The most important structuring species was *Mytilus galloprovincialis*, which was present in almost all the endpoint assemblages, in particular when it recruits at early stages of the community development. Another abundant species at the endpoint was the alien *Branchiomma boholense*; which was a persistent structural component contributing to an alternative state in which *Mytilus galloprovincialis* loses its structural importance and where *B. boholense* becomes dominant, leading to an increase in fouling biodiversity of the endpoint assemblage.

Keywords: Biological succession; end points; alien species; Mediterranean sea.

Introduction

Although succession was first defined as a linear sequence towards a climax community (Clements 1916), experimental works on marine hard substrata from the late 1970s onwards have shown succession as a continuous process with changing trajectories depending on different physical and biological features. In particular, emphasis has been placed on biological factors, taking into consideration that variation in community structure can be explained by mechanistic models which incorporate strong interactions among species (e.g. Greene & Schoener, 1982; McCook, 1994). Moreover, in recent decades, growing importance has been given to the recruitment limitation hypothesis (Fraschetti *et al.*, 2002; Palardy & Witman, 2014), incorporating recruitment rate and supply larval ecology into community developmental theories (Menge & Sutherland, 1987; Underwood & Fairweather 1989).

Connell & Slatyer (1977) first described alternative models of community succession according to different mechanisms driving species replacements. Early arrival can facilitate, inhibit or tolerate the colonization of 'late

successional' species. These models have had a great influence on subsequent studies, and are still useful in community successional pattern description (Laure *et al.*, 2009), albeit Benedetti-Checchi (2000) underlined their limited predictive powers. Connell & Slatyer's hypothesis has been tested in many experimental studies that show the importance of biological interaction in enabling succession to proceed by interrupting the inhibitory process (see review of Sousa & Connel, 1992). The inhibition model is the most widespread model in hard bottom systems where competition for space can drive the process and where succession proceeds only when first colonizers are damaged or die. However, the role of facilitation has also been adopted as a term to define positive interaction involved in structuring assemblages (Bertness & Callaway, 1994).

More recently Berlow (1997) has redirected attention to the historical effects in community development defining succession as "canalized" when trajectories are predictable and convergent, and as "contingent" when colonization processes are more variable and divergent. Similar to the facilitation and inhibition models, in the deterministic canalized succession early species have

strong effects on later species, while consistent effects of early events canalize subsequent successional changes. However, variation in developing community structure may be driven by “external” events, such as environmental conditions, propagule availability, and disturbance regimes, resulting in externally driven succession, this seemingly being more influential than species interactions (Sousa, 1979; Gaines & Roughgarden, 1985; Berlow, 1997; Petraitis & Dudgeon, 1999). In “contingent” succession, similar to the alternative stable state *sensu* Sutherland (1974), the strength of species interactions strongly depends upon the context in which they occur (Berlow, 1997). In this regard the succession pattern is determined from the timing and/or sequence of invading species and can produce multiple successional pathways that can diverge to alternative endpoints. A detailed knowledge of species interactions and how these interactions vary in space and time is needed to understand the resulting structure (Berlow, 1997). Thus, sequences of species colonization may be influenced by the temporal and spatial variability of propagule supply (Osman, 1977; Chalmer, 1982; Cifuentes *et al.*, 2010), so determining the occurrence of contingent patterns, or multiple stable points *sensu* Sutherland (1974). Recruitment is highly affected by season (Turner & Todd, 1993) and, consequently, the period in which succession begins affects community structure (Breitburg, 1985; Underwood & Anderson, 1994; Anderson & Underwood, 1994; Rico *et al.*, 2012). However, despite the presence of seasonality, macrobenthic communities may converge to a similar endpoint structure (Cifuentes *et al.*, 2010; Pacheco *et al.*, 2010; 2011).

Even though experiments are often limited in area and time (Bender *et al.*, 1984; Diamond, 1986; Underwood & Petraitis, 1993), small-scale experiments can be a powerful tool for characterizing contingencies and patterns of variation in successional processes (Dayton, 1971; Menge, 1991; Menge *et al.*, 1994; Berlow & Navarrete, 1997), also shedding light on the colonizers’ arrival sequence and competitive abilities as well as on interactions between recruits and resident population.

The comprehension of mechanisms acting during community development has recently received renewed interest, since such mechanisms remain a critical integrative concept; although central to ecology, it still awaits, however, a definitive solution. The study of succession is particularly helpful for understanding ecological phenomena such as biodiversity loss, climate change, invasive species, and ecological restoration (Maggi *et al.*, 2011; Prach & Walker, 2011).

We investigated the macrofouling succession in the Gulf of Taranto (Central Mediterranean Sea), an area recently attracting interest due to the establishment of numerous non-indigenous species (NIS) (Gravili *et al.*, 2010; Occhipinti-Ambrogi *et al.*, 2011), and where fouling assemblages seem to be dominated mainly by filter feeder invertebrates (Pierri *et al.*, 2010). In particular, we examined succession on artificial substrates in exper-

iments conducted in the Mar Grande of Taranto (Central Mediterranean Sea), a wide confined area recently attracting interest due to the establishment of numerous non-indigenous species (NIS) (Gravili *et al.*, 2010; Occhipinti-Ambrogi *et al.*, 2011; Lezzi *et al.*, 2017).

The fouling communities of the Gulf of Taranto have been previously investigated by several authors (e.g. Gherardi, 1973; Gherardi & Lepore, 1974; Tursi *et al.*, 1976; Tursi *et al.*, 1982 a, 1982 b; Tursi *et al.*, 1990; Cecere *et al.*, 1991; Pierri *et al.*, 2010). However, most of the studies concentrate only on the inner basins of the Taranto seas (Mar Piccolo). Moreover, most of these studies were conducted before the recent spread of alien species (Cecere *et al.*, 2015), while few of them focused on ecological successions and structural analysis.

The present work deals with two years of study examining four different starting times of the sessile invertebrate macrofouling succession in order to study the influence of the seasons in shaping the 12-month old assemblage endpoints, determining species recruitment periods and their influences during community development and so investigating the matching of the development pattern with contingency and/or convergence models.

Material and Methods

Field sampling and processing

The study was conducted in the south-west side of the Mar Grande of Taranto (40°25'56"N 17°14'19"E), in the north western Ionian Sea (eastern-central Mediterranean) (Fig. 1). The Mar Grande is semi-enclosed basin with an

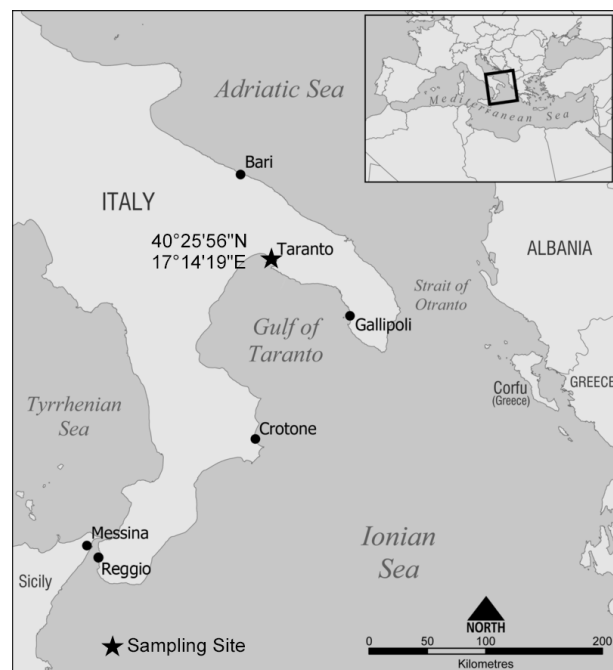


Fig. 1: Map of the Gulf of Taranto with indications of sampling site.

area of 35.5 sq. km and a maximum depth of 42 m and is limited by the Chéradi Islands on its western side. As regards the temperature, it shows seasonal variations typical of the coastal Ionian regions with an average annual value of about 18°C (Fig. 2); the salinity is about 38 ‰ and almost uniform over the year.

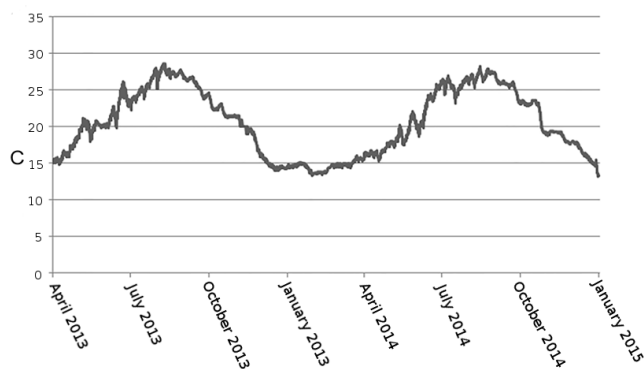


Fig. 2: Trend of temperature during the period of study.

immersion experiments were carried out. Four series, each consisting of 36 panels (4 collection times x 3 depth x 3 replicates), were deployed during spring (April = S1), summer (July = S2), autumn (October = S3) and winter (January = S4). Each series was surveyed at 3-month intervals (T1, T2, T3 and T4). During each sampling three replicate modules were randomly collected (Fig. 3).

A total of 144 panels were analysed. Each panel was first photographed *in vivo*. Sessile living organisms were then identified at species level when possible, using stereoscope and binocular microscope. Ascidians were extracted and anesthetized in menthol before preservation in 4% formaldehyde-seawater solution. Thereafter all the samples were fixed in 4% formaldehyde in seawater. Photograph from panels were then analysed using the software Image J (Abràmoff *et al.*, 2004) to obtain the covering matrices of each species detected. The central part of each panel was analysed (excluding an external frame of 1 cm wide so as to avoid sampling of potential edge effects, total surface 196 cm²) (Cifuentes *et al.*, 2010). A multi-layer coverage was analysed, with a potential coverage surface greater than 100%.

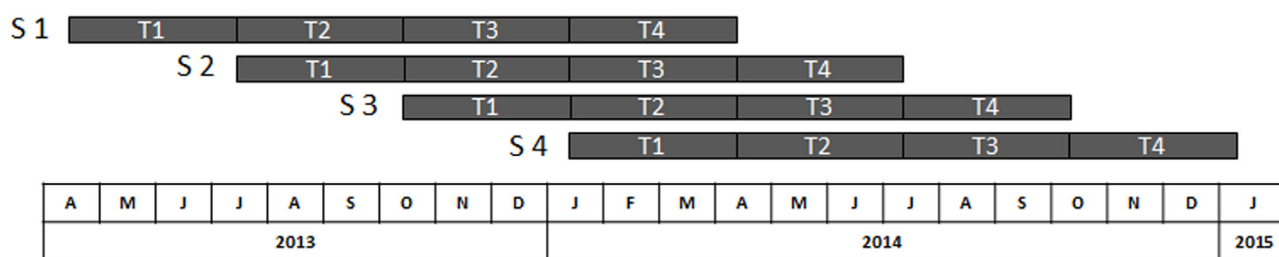


Fig. 3: Sampling scheme for the conducted study.

Experimental PVC artificial 15×15×0.5 cm² panels were used as macrofouling collectors (Sutherland & Karlson, 1977; Canning-Clode *et al.*, 2009). Each panel was previously roughened with sandpaper (grain 60) to facilitate larval settlement and to prevent the detachment of sessile organisms and then covered by a net of 1 cm mesh at each side. Several modules, constituted by three replicates located at different depths (0, 3 and 6 m) were placed in the water, tied to a vertical ballasted nylon rope anchored to an offshore floating rafts. The modules were deployed at 2-6 m intervals. In the sampling location water depth was about 9 m.

Only sessile macrobenthic components were considered in the present study, the fouling of the study site being characterized by filter feeder dominance (e.g. Parenzan, 1969; Gherardi, 1973; Gherardi & Lepore, 1974; Tursi *et al.*, 1977; Tursi *et al.*, 1979; Montanaro & Tursi, 1983; Pierri *et al.*, 2010).

To study the influence of the starting time in shaping the 12-month old assemblage endpoints, four different

Data analysis

Diversity expressed in terms of species number, Pielou's evenness and coverage was tested using PERMANOVA, in an approach similar to parametric ANOVA. Univariate PERMANOVA tests were run on Euclidean distances matrices with 9999 permutations (Anderson, 2001). Starting time (S, 4 levels) and depth (d, 3 levels) factors were used to detect differences among the endpoints of the macrofouling communities. When significant effects were detected (p<0.05), differences between levels within treatments were identified with post-hoc pairwise comparisons.

Multivariate analyses were used to compare the similarity of macrofouling communities developed on the panels. Non-metric multidimensional scaling (nMDS) via Bray-Curtis distances on square root data transformed was used to visualize changes in species composition. Permutational analysis of variance, PERMANOVA (Anderson, 2001) was used to test for differences in compo-

sition of the assemblage of the endpoints using the same model of ANOVA. Additional PERMANOVA was used to test for differences in the community development for each starting time using 3-month intervals survey (T, 4 levels) and depth (D, 3 levels) as factors. When significant effects were detected ($p < 0.05$), differences between levels within treatments were identified with post-hoc pairwise comparisons.

Where the number of possible permutable units was insufficient for a reasonable test by permutation, a p -value was obtained using a Monte Carlo random sample from the asymptotic permutation distribution (Anderson & Robinson, 2003).

The BVSTEP routine was used to select the subset of species of the endpoints which generates the same multivariate sample pattern as would the entire assemblage set (Clarke & Gorley, 2006). This analysis uses Spearman rank correlation to determine the minimum number of variables (i.e. taxa) that shows the highest correlation with the complete matrix. The subset of species was added as a vector overlay on the nMDS plot to better understand which species best characterize the sample clusters. Positive and negative correlations among the coverages of the subset's species were made in order to detect the co-occurring and dis-occurring species patterns.

PERMANOVA, nMDS, BVSTEP were conducted in PRIMERv6+PERMANOVA software (Anderson *et al.*, 2008).

Results

In total, 93 taxa were identified, most at species level (Table 1), 80 of these characterizing the endpoint stages. Among the collected species *Branchiomma boholense* (Grube, 1878), *B. luctuosum* (Grube, 1870), *Hydroides*

elegans (Haswell, 1883), *H. dirampha* Mörch, 1863, *Paraleucilla magna* Klautau, Monteiro and Borojevic, 2004, *Polyandrocarpa zorritensis* (Van Name, 1931), *Celleporaria brunnea* (Hincks, 1884), representing 7.5% of the assemblage, were recognized as NIS (Zenetos *et al.*, 2010; Zenetos *et al.*, 2012; Occhipinti-Ambrogi *et al.*, 2011) and were already recorded in previous years in the Gulf of Taranto (i.e. Cecere *et al.*, 2015).

The structure of assemblage relative to each series from different starting time, proved to be affected by immersion period (T) and depth (D) with a significant interaction between them (PERMANOVA, Table 2). The nMDS plots of community developments is shown in Figure 4. Four different developmental patterns could be enhanced for the four series; T1 and T2 samples appeared separated from T3 and T4 that were very close to each other in the four starting time panel sets, indicating a similarity of structure starting from 9-month old assemblage. This pattern was particularly evident in S1, S3 and S4, and less obvious in S2. This was confirmed by the pairwise analysis, which showed no significant differences for each panel set in T3 and T4 within the factor depth (Table 2).

Considering the endpoints (T4) of each series, the number of taxa was maximum in S2 and minimal in S1 (Fig. 5a), and seemed to be influenced by the Starting time (S) (PERMANOVA, $F=13.653$, $p = 0.00002$). By contrast a significant interaction between starting time (S) and Depth (D) was found for macrofouling coverage (PERMANOVA, $F=3.99$, $p=0.0065$). As is shown in the Figure 5b, coverage remained constant in all the series at 0 meters depth, decreasing at 3 and 6 m only in S3 and S4. Pielou's evenness is influenced by the Starting time (S) (PERMANOVA, $F=17.004$, $p= 0.001$) and Depth (D) (PERMANOVA, $F=43.96$, $p= 0.001$) with lower

Table 1. List of the collected macrobenthic taxa. The subset of species in the endpoints selected by BVSTEP routine are indicated in bold. Presences in each panels Set (S) is shown.

	Presence in the endpoints			
	S1	S2	S3	S4
<i>Aglaophenia picardi</i> Svoboda, 1979	-	X	X	X
<i>Aiptasia diaphana</i> (Rapp, 1829)	X	X	X	X
<i>Amathia verticillata</i> (delle Chiaje, 1822)	-	X	-	-
<i>Amphibalanus amphitrite</i> (Darwin, 1854)	-	-	X	X
<i>Amphitrite rubra</i> (Risso, 1826)	X	X	X	X
<i>Anomia ephippium</i> Linnaeus, 1758	X	X	X	X
<i>Aplidium coeruleum</i> Lahille, 1890	X	-	X	-
<i>Aplidium densum</i> (Giard, 1872)	-	-	-	X
<i>Arca noae</i> Linnaeus, 1758	-	X	-	-
<i>Ascidia conchilega</i> Müller, 1776	-	-	-	-
<i>Ascidia malaca</i> (Traustedt, 1883)	-	-	-	-
<i>Ascidiella aspersa</i> (Müller, 1776)	-	X	X	X
<i>Balanus trigonus</i> Darwin, 1854	-	-	X	X

(continued)

Table 1 continued

	Presence in the endpoints			
Botrylloides leachii (Savigny, 1816)	X	X	X	X
Botryllus schlosseri (Pallas, 1766)	X	-	-	X
Branchiomma boholense (Grube, 1878)	X	X	X	X
Branchiomma bombyx (Dalyell, 1853)	-	X	-	-
Branchiomma luctuosum (Grube, 1870)	X	X	X	X
Bugula neritina (Linnaeus, 1758)	X	X	X	X
Bugulina calathus (Norman, 1868)	X	X	X	X
Cardiidae ind.	X	X	X	-
Celleporaria brunnea (Hincks, 1884)	X	X	X	X
Chthamalus depressus (Poli, 1791)	-	-	-	-
Ciona intestinalis (Linnaeus, 1767)	-	X	-	X
Clathrina coriacea (Montagu, 1814)	-	X	X	X
Clavelina lepadiformis (Müller, 1776)	X	X	X	X
Crisia denticulata (Lamarck, 1816)	-	X	X	X
Crisia fistulosa (Heller, 1867)	-	-	-	-
Crisularia aperta (Hincks, 1886)	-	X	X	X
Cryptosula pallasiana (Moll, 1803)	X	-	-	-
Dasybranchus gajolae Eisig, 1887	-	-	X	-
Diplosoma listerianum (Milne Edwards, 1841)	-	-	-	-
Distaplia bermudensis Van Name, 1902	-	X	X	X
Ecteinascidia turbinata Herdman, 1880	-	X	-	-
Filograna implexa Berkeley, 1835	-	X	X	X
Fissurella nubecula (Linnaeus, 1758)	-	-	-	-
Hiatella rugosa (Linnaeus, 1767)	X	X	X	X
Hydroides nigra Zibrowius, 1971	-	-	X	-
Hydroides dianthus (Verrill, 1873)	-	X	-	-
Hydroides dirampha Mörch, 1863	-	X	X	X
Hydroides elegans (Haswell, 1883)	X	X	X	X
Hydroides helmatus (Iroso, 1921)	-	-	X	-
Hydroides stoichadon Zibrowius, 1971	X	-	-	-
Hydrozoa ind.	-	X	-	-
Limaria hians (Gmelin, 1791)	X	-	X	X
Limaria tuberculata (Olivi, 1792)	-	X	-	-
Lissoclinum perforatum (Giard, 1872)	X	X	X	X
Lissoclinum weigelei Lafargue, 1968	X	X	X	X
Microcosmus polymorphus Heller, 1877	-	X	-	-
Microcosmus squamiger Michaelsen, 1927	X	X	-	X
Mimachlamys varia (Linnaeus, 1758)	X	X	X	X
Modiolus barbatus (Linnaeus, 1758)	-	X	X	-
Musculus subpictus (Cantraine, 1835)	X	X	X	X
Mytilaster minimus (Poli, 1795)	-	X	-	-
Mytilus galloprovincialis Lamarck, 1819	X	X	X	X
Myxilla sp.	X	X	X	X
Nicolea venustula (Montagu, 1818)	X	X	X	X
Noetiidae ind.	-	-	-	-
Ostrea edulis Linnaeus, 1758	X	X	X	X
Paraleucilla magna Klautau, Monteiro & Borojevic, 2004	X	X	X	X
Parasabella langerhansi (Knight-Jones, 1983)	-	X	-	-

(continued)

Table 1 continued

	Presence in the endpoints			
<i>Parasabella tenuicollaris</i> (Grube, 1861)	-	X	-	-
<i>Perforatus perforatus</i> (Bruguière, 1789)	-	X	X	X
<i>Perophora multiclathrata</i> (Sluiter, 1904)	-	-	-	-
<i>Phallusia ingeria</i> Traustedt, 1883	-	-	-	X
Phallusia mammillata (Cuvier, 1815)	-	X	-	-
<i>Pinna nobilis</i> Linnaeus, 1758	-	-	-	-
<i>Pista cristata</i> (Müller, 1776)	-	-	-	-
<i>Polyandrocarpa zorritensis</i> (Van Name, 1931)	-	X	-	-
<i>Polycirrus</i> cf. <i>aurantiacus</i> Grube, 1860	-	X	-	-
<i>Polydora</i> ind.	-	X	-	-
<i>Sabella discifera</i> Grube, 1874	-	-	-	-
<i>Sabella pavonina</i> Savigny, 1822	X	-	-	-
Sabella spallanzanii (Gmelin, 1791)	-	X	X	X
<i>Savignyella lafontii</i> (Audouin, 1826)	-	X	X	X
<i>Schizobrachiella sanguinea</i> (Norman, 1868)	-	-	X	X
<i>Schizoporella errata</i> (Waters, 1878)	X	X	X	X
<i>Scopalina</i> ind.	X	X	-	-
<i>Scrupocellaria scruposa</i> (Linnaeus, 1758)	-	-	-	-
<i>Scrupocellaria bertholletii</i> Audouin in Savigny, 1826	X	X	X	X
<i>Serpula vermicularis</i> Linnaeus, 1767	X	X	X	X
<i>Serpula concharum</i> Langerhans, 1880	-	X	X	-
<i>Simplaria pseudomilitaris</i> (Thiriou-Quievreux, 1965)	-	X	X	-
<i>Spirobranchus lamarcki</i> (Quatrefages, 1866)	-	-	X	X
<i>Spirobranchus triquetus</i> (Linnaeus, 1758)	X	X	X	X
<i>Styela canopus</i> (Savigny, 1816)	-	-	-	-
<i>Styela plicata</i> (Lesueur, 1823)	-	-	X	X
<i>Terebella lapidaria</i> Linnaeus, 1767	X	-	-	-
<i>Timarete filigera</i> (Delle Chiaje, 1828)	-	-	X	-
<i>Trididemnum cereum</i> (Giard, 1872)	X	-	X	X
Trididemnum inarmatum (Drasche, 1883)	-	X	-	X
<i>Vermetus triquetus</i> Bivona-Bernardi, 1832	X	X	-	X
<i>Watersipora subtorquata</i> (d'Orbigny, 1982)	-	-	-	-

value at 0 meter depth in each panel set endpoint.

Multivariate analysis conducted on the assemblage structure of the 4 endpoints showed that both starting time (S) and Depth (D) affected the macrofouling structure with a significant interaction between them (PERMANOVA, Table 3). Pairwise comparison (Table 3) shows no significant differences among the communities of S1, S3 and S4 at 0 m depth, of S3 and S4 at 3-meter depth, and of S3 and S4 and S2 and S4 at 6-meter depth.

The relevance of both starting time and depth in terms of shaping the structure of endpoint assemblages is confirmed by the nMDS ordination plot (Fig. 6). The graphical model highlighted a depth gradient in the endpoint of each temporal series: in fact, the points referred to the shallow depths and those referred to the deeper ones were located respectively at the left and at the right side of the

nMDS plot. Moreover the groups containing the points of S1 and S2 series appeared to be separated, while the points referred to 3 and 6 m depth of the S3 and S4 series were placed on the right of the model; all this above enhances differences in the Starting time factor (S) along the depth gradient (Fig. 6). The nMDS pattern, notwithstanding the stress values are near 0.2, visually confirms what was observed in the PERMANOVA analysis.

The BVSTEP routine selected the subset of species explaining the pattern shown by the nMDS plot above described. This subset is composed by 17 species and generates the same multivariate pattern which emerges by examination of the entire assemblage set. The selected species are: *Mytilus galloprovincialis*, *Botrylloides leachi*, *Clavelina lepadiformis*, *Schizoporella errata*, *P. magna*, *Trididemnum inarmatum*, *Mimachlamys varia*,

Table 2. Results from PERMANOVA using Bray–Curtis distance matrices to test for immersion period (T) and depth (D) on assemblage structure of each Set (S). Significant p-values are given in bold.

S1								S2							
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)		
T	3	12162	17,151	0,001	8408,4	9,2408	0,001								
D	2	2458,9	3,4676	0,001	4145	4,5553	0,001								
TxD	6	1166,5	1,645	0,004	1236,7	1,3591	0,023								
Res	24	709,11			909,93										
Total	35														
Pairwise comparison															
Within level '0 m' of factor 'D'				Within level '0 m' of factor 'D'				Within level '0 m' of factor 'D'				Within level '0 m' of factor 'D'			
T1≠T2≠T3=T4				T1≠T2≠T3=T4				T1≠T2≠T3=T4				T1≠T2≠T3=T4			
Within level '3 m' of factor 'D'				Within level '3 m' of factor 'D'				Within level '3 m' of factor 'D'				Within level '3 m' of factor 'D'			
T1≠T2≠T3=T4				T1≠T2≠T3=T4				T1≠T2≠T3=T4				T1≠T2≠T3=T4			
Within level '6 m' of factor 'D'				Within level '6 m' of factor 'D'				Within level '6 m' of factor 'D'				Within level '6 m' of factor 'D'			
T1≠T2≠T3=T4				T1≠T2≠T3=T4				T1≠T2≠T3=T4				T1≠T2≠T3=T4			
S3								S4							
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)		
T	3	16954	15,794	0,001	20145	25,463	0,001								
D	2	3046,4	2,838	0,001	3130,9	3,9575	0,001								
TxD	6	1988,4	1,8524	0,001	1197,9	1,5141	0,012								
Res	24	1073,4			791,14										
Total	35														
Pairwise comparison															
Within level '0 m' of factor 'D'				Within level '0 m' of factor 'D'				Within level '0 m' of factor 'D'				Within level '0 m' of factor 'D'			
T1≠T2≠T3=T4				T1≠T2≠T3=T4				T1≠T2≠T3=T4				T1≠T2≠T3=T4			
Within level '3 m' of factor 'D'				Within level '3 m' of factor 'D'				Within level '3 m' of factor 'D'				Within level '3 m' of factor 'D'			
T1≠T2≠T3=T4				T1≠T2≠T3=T4				T1≠T2≠T3=T4				T1≠T2≠T3=T4			
Within level '6 m' of factor 'D'				Within level '6 m' of factor 'D'				Within level '6 m' of factor 'D'				Within level '6 m' of factor 'D'			
T1≠T2≠T3=T4				T1≠T2≠T3=T4				T1≠T2≠T3=T4				T1≠T2≠T3=T4			

B. boholense, *B. luctuosum*, *Aiptasia diaphana*, *Nicolea venustula*, *Phallusia mammillata*, *Myxilla* sp., *Crisularia aperta*, *Anomia ephippium*, *Limaria hians*, *Sabella spallanzanii*; of these, only *B. boholense*, *B. luctuosum* and *P. magna* are NIS. When such set of species was overlapped in the nMDS plot (Fig. 6), it was possible to observe how *M. galloprovincialis* characterized the entire set of S1 and the endpoints of shallow panels in all the series. Otherwise *B. boholense*, *C. aperta*, *S. spallanzanii* and *A. ephippium* typically characterized the deeper panels (3 and 6 m depth) of S2, S3 and S4. Lastly *S. errata*,

C. lepadiformis and *B. leachii* distinguished the S2 from the other series.

As shown by the nMDS plot, the trend of *M. galloprovincialis* appeared influenced by depth, although its coverage varied among the panels sets belonging to different temporal Series (Fig. 7). The trend graphs identified species characterizing single sets: for instance, *S. spallanzanii* for S3, *P. mammillata*, *B. leachii*, *S. errata* and *C. lepadiformis* for S2. Moreover, some structuring species (such as *Myxilla* sp., *B. boholense*, *B. luctuosum*, *A. ephippium* and *P. magna*) are abundant in S3 and S4,

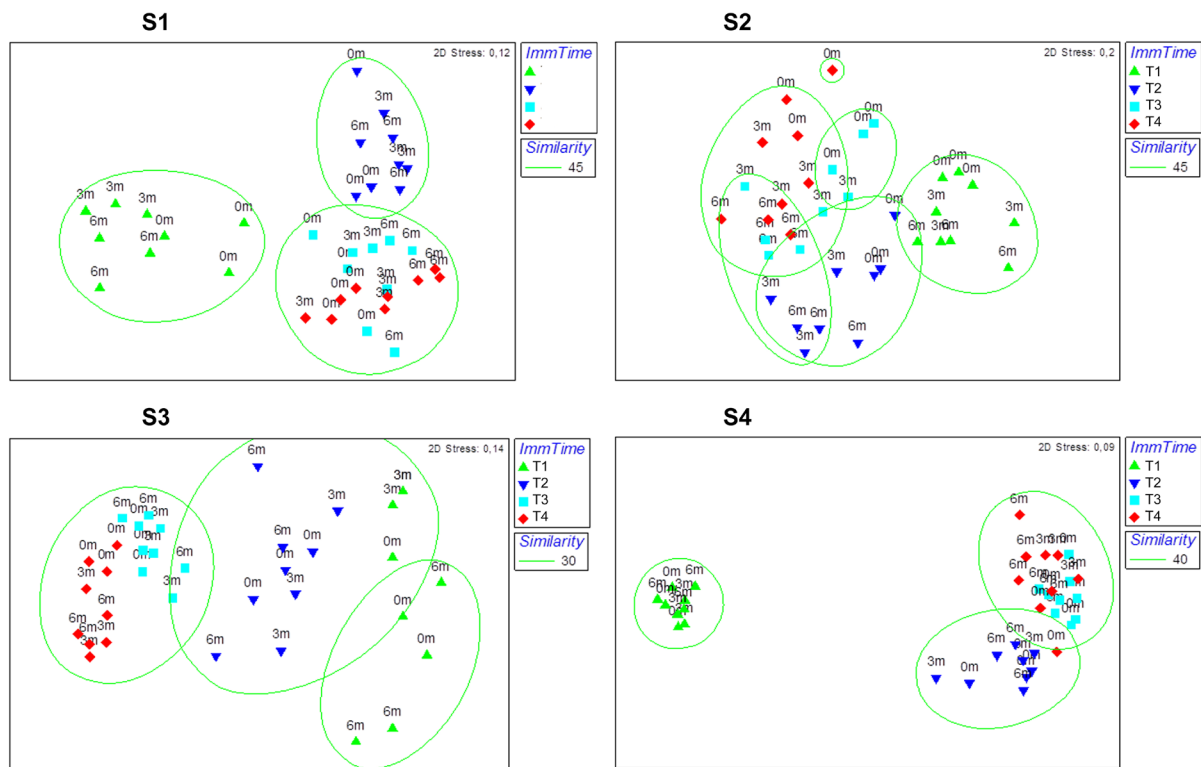


Fig. 4: NMDS plot based on Bray–Curtis distance of community development of each panel set. Solid lines represent the principal clusters' similarity.

and *B. boholense* is always more abundant according to depth.

The succession pattern of species subsets selected by BVSTEP can be tracked for each panel set (Supplementary Material Fig. S1), in order to explain the differences of endpoint assemblage.

In S1, *M. galloprovincialis*, which was the most abundant species in the endpoint (T4) recruited after the first immersion quarter (T1), grows gradually, covering most of the space in all the panels. First colonizers were also other species such as *B. leachii*, *C. lepadiformis*, *S. errata*, *P. magna*, which became scarce at the end of the succession (T3 and T4), even though their presence at the previous time point (i.e. T2) were relevant. Other species such as *B. boholense*, *B. luctuosum* and *N. venustula* settled on the panels mainly in T2 and remained during the subsequent time points.

In the development of S2 assemblage, a massive presence of alien species characterized the early colonization and *M. galloprovincialis* was less abundant at the end point T4 of this series if compared to the end point of S1, showing a massive recruitment at the last immersion time. Moreover *M. galloprovincialis* recruitment seemed to be influenced by depth: deeper panels appeared less covered by this mollusc. Other species such as *B. boholense*, *B. luctuosum*, *S. errata*, *C. lepadiformis*, *P. magna*, and *A. ephippium* remained in the S2 after their first recruitment at the starting time T1. Lastly, *S. spallanzanii*,

M. varia and *B. leachii* appeared at late successional times (T3 or/and T4).

In S3, in which the first colonizers were the colonial ascidians *D. listerianum* and *Botryllus schollerii*, while *M. galloprovincialis* appeared in T2, although a massive recruitment occurred in T3 at all the depths, with a slight decrease at the last immersion time (T4), thus resulting in a poor coverage of the species despite the growth of the recruits. Most of the species, e.g. *M. varia*, *B. boholense*, *B. luctuosum*, *A. ephippium*, *Myxilla* sp., *L. hians*, and *N. venustula*, appeared in the last succession time (T4) and others, e.g. *S. spallanzanii*, *P. magna*, in middle successional times.

Lastly, in S4 first colonizers were mainly *D. listerianum*. *M. galloprovincialis* recruited in the T2 and remained abundant during the succession only at 0 m depth, decreasing in coverage at 3 and 6 m depth after the third immersion quarter (T3); thus not appearing as a structuring component of the endpoint communities. The other species pattern is strongly depended upon their recruitment (i.e. *Branchiommata* spp., *P. magna*, *A. ephippium*, *L. hians* and *S. errata* which recruited in T3).

Matrix correlation of the abundances of the species subset designed by BVSTEP (Table 4), shows a significant negative correlation between *M. galloprovincialis* and *B. boholense*, *A. ephippium*, *L. hians*, and *S. spallanzanii*; while *A. ephippium*, *L. hians* and *S. spallanzanii* all prove to be positively correlated.

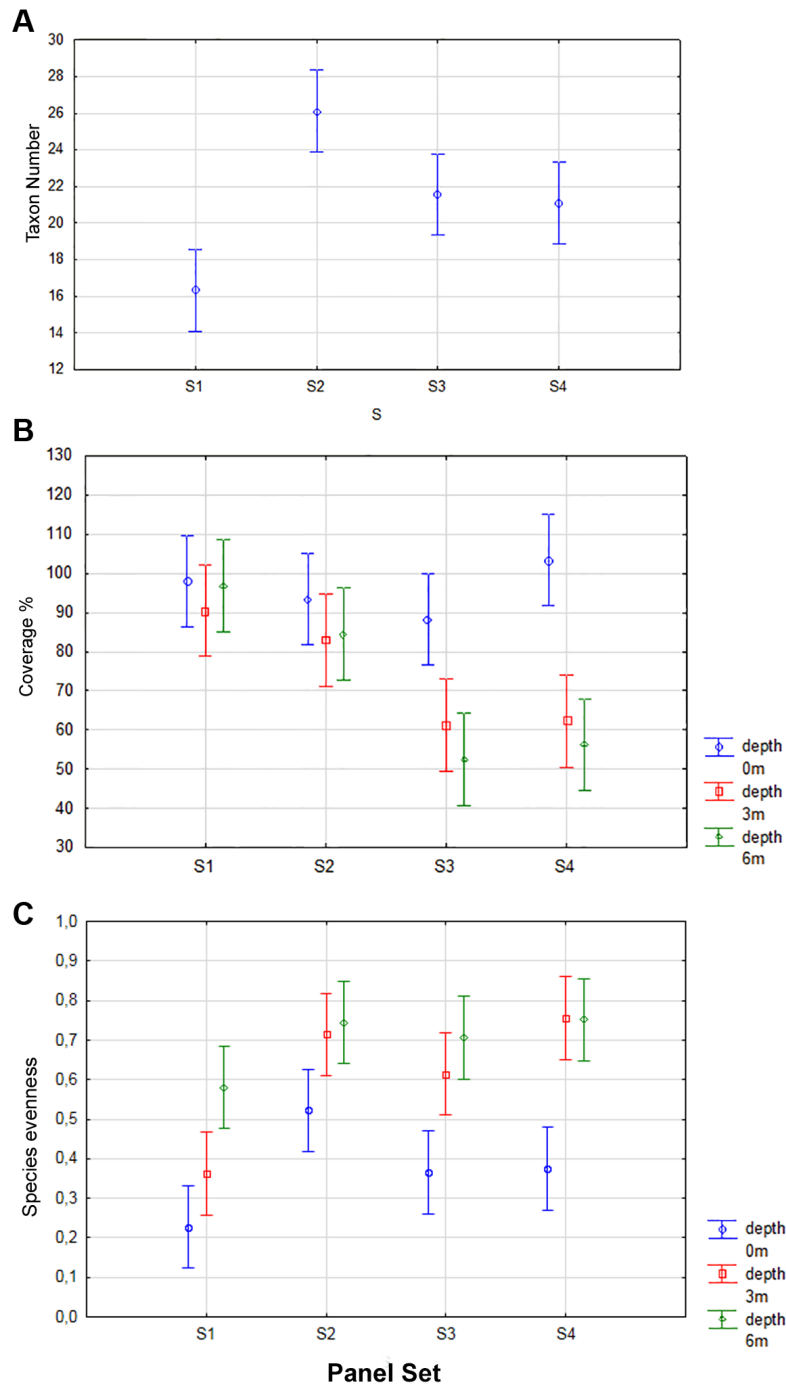


Fig. 5: Variability of (A) species richness, (B) macrofaunal coverage, and (C) species evenness (bars represent standard error) of each panel set (S) at the endpoint.

The observed development of the assemblages for each series with different starting times is summarized in Figure 8. The endpoint of S1 was characterized at all the depths by the strong dominance of *M. galloprovincialis*. The endpoints of S2 were characterized at all the depths by the highest number of species, *B. boholense*, *B. luctuosum*, *S. errata*, *C. lepadiformis*, *P. magna*, *A. ephippium*, *S. spallanzani*, *M. varia* and *B. leachii*. Finally, the endpoints of S3 and S4 at 0 meters depth were characterized

by the high dominance of *M. galloprovincialis*, in contrast to the deepest assemblages, which were characterized by *Branchiomma* spp., *A. ephippium*, *L. hians* and *S. spallanzanii*.

Discussion and Conclusion

The Gulf of Taranto's fouling assemblages were found to be dominated mainly by filter feeder invertebrates

Table 3. Results from PERMANOVA using Bray–Curtis distance matrices to test for Starting (S) and depth (D) on assemblage structure of each endpoints (T4). Significant p-values are given in bold.

Source	df	MS	Pseudo-F	P(perm)
S	3	5619,8	6,9884	0,001
D	2	5454,1	6,7823	0,001
SxD	6	1265,3	1,5735	0,003
Res	24	804,16		
Total	35			

Pairwise comparisons

Within level '0 m' of factor 'D'

S1≠ S2; S1=S3; S1=S4; S2=S3; S2=S4; S3=S4

Within level '3 m' of factor 'D'

S1≠S2; S1≠S3; S1≠S4; S2≠S3; S2≠S4; S3=S4

Within level '6 m' of factor 'D'

S1≠S2; S1≠S3; S1≠S4; S2≠S3; S2=S4; S3=S4

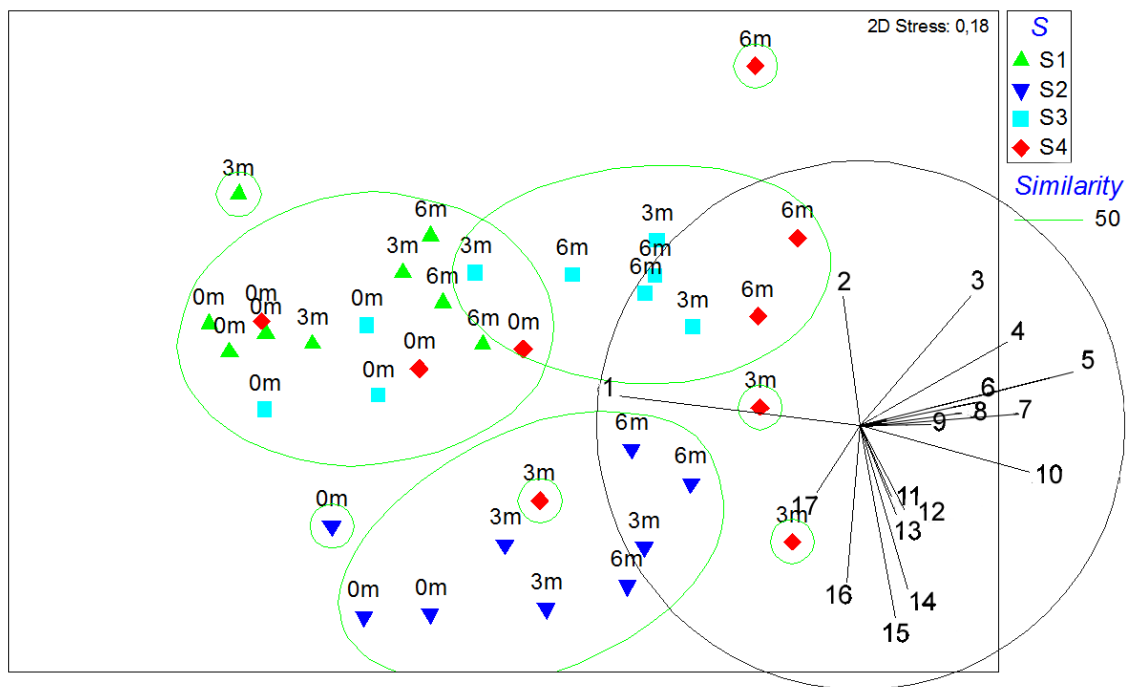


Fig. 6: NMDS plot based on Bray–Curtis distance of community development of each panel set (S) at the endpoint. Solid lines represent the principal clusters. Numbers used as abbreviations for the taxa variables: 1, *Mytilus galloprovincialis*; 2, *Nicolea venustula*; 3, *Limaria* sp.; 4, *Crisularia aperta*; 5, *Branchiomma boholense*; 6, *Mimachlamys varia*; 7, *Sabella spallanzanii*; 8, *Branchiomma luctuosum*; 9, *Paraleucilla magna*; 10, *Anomia ephippium*; 11, *Phallusia mammillata*; 12, *Myxilla* sp.; 13, *Trididemnum inarmatum*; 14 *Schizoporella errata*; 15, *Clavelina lepadiformis*; 16, *Botrylloides leachii*; 17, *Aiptasia diaaphana*.



Fig. 7: Coverage for species from BVSTEP in each panel set (S) and depth at the endpoint.

Table 4. Correlation among BVSTEP selected species in the endpoints. Significant values are highlighted in Green (positive) and Red (negative).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
<i>Mytilus galloprovincialis</i>	1	1.00																
<i>Botrylloides leachii</i>	2	-0.14	1.00															
<i>Clavelina lepadiformis</i>	3	-0.32	0.44	1.00														
<i>Schizoporella errata</i>	4	-0.27	0.29	0.42	1.00													
<i>Paraleucilla magna</i>	5	0.06	-0.07	-0.17	-0.08	1.00												
<i>Trididemnum inarmatum</i>	6	-0.15	-0.06	-0.04	0.08	-0.06	1.00											
<i>Mimachlamys varia</i>	7	-0.28	-0.08	-0.06	-0.05	-0.17	-0.08	1.00										
<i>Branchiomma bairdi</i>	8	-0.62	-0.12	0.15	-0.08	-0.08	-0.01	0.45	1.00									
<i>branchiomma luctuosum</i>	9	-0.13	-0.08	0.13	0.16	0.32	-0.22	-0.10	0.10	1.00								
<i>Aiptasia diaphana</i>	10	0.09	0.07	0.15	0.00	0.07	-0.08	-0.03	-0.25	-0.21	1.00							
<i>Nicolea venustula</i>	11	0.18	-0.22	-0.33	-0.14	-0.21	-0.14	0.01	0.03	0.30	-0.09	1.00						
<i>Phallusia mammillata</i>	12	-0.12	0.16	0.06	-0.07	0.22	-0.04	-0.03	0.11	0.34	-0.04	-0.11	1.00					
<i>Myxilla sp</i>	13	-0.17	0.22	0.21	0.09	0.13	-0.15	-0.05	0.18	0.39	-0.10	0.29	0.47	1.00				
<i>Crisularia aperta</i>	14	-0.30	-0.12	-0.17	-0.07	0.31	0.00	0.40	0.51	-0.05	-0.14	-0.16	-0.04	-0.13	1.00			
<i>Anomia ephippium</i>	15	-0.57	0.00	0.06	0.08	-0.05	-0.10	0.03	0.30	0.11	-0.19	-0.06	-0.06	0.10	-0.01	1.00		
<i>Limaria hians</i>	16	-0.33	-0.20	-0.34	-0.27	-0.17	-0.15	0.08	0.26	-0.16	-0.18	0.26	-0.11	-0.26	0.12	0.41	1.00	
<i>Sabella spallanzanii</i>	17	-0.43	-0.09	-0.12	0.04	-0.22	-0.11	0.04	0.15	0.00	-0.12	-0.06	0.03	-0.11	-0.02	0.45	0.57	1.00

(Pierri *et al.*, 2010). One year of successional changes in the Mar Grande showed how different times of panels' setup develops different structures of fouling assemblages, both in terms of total coverage and species diversity and abundance. Among the taxa characterizing the endpoints, some of them, such as *M. galloprovincialis*, *S. spallanzanii*, *C. lepadiformis*, and *S. errata*, are typical of fouling communities of Mediterranean harbor and eutrophic environments, and are already known as dominant species in the fouling of the presently studied area (Gherardi & Lepore, 1974; Tursi *et al.*, 1974; Pierri *et al.*, 2010). By contrast in the late stage of the community, the present study confirms the structural role of some relatively recent faunistic entries for the Gulf of Taranto, such as *P. magna* (Longo *et al.*, 2007) and *B. boholense* (Del Pasqua *et al.*, 2018).

Four different successional patterns relative to the four starting times were observed. However, independently of the starting times, each succession seems to reach the endpoint structure after just 9 months. Results arising from the present study suggest that the structure of 12-month endpoint fouling assemblages in the Gulf of Taranto is mainly controlled by colonizer time arrival and between-taxa interactions.

The endpoints are strictly influenced by two factors: first by the starting time, which in turn influences the incurred successional history, and second by depth, which determines the abundance and settlement pattern of several structuring species. Differing according to depth, the

recruitment of the players that contributes to community convergence or divergence of the different endpoints. In line with the findings of several authors for different bio-geographical areas (Underwood & Anderson, 1994; Brown & Swearingen, 1998; Maughan & Barnes, 2000; Cifuentes *et al.*, 2010), differences among panels immersed at different starting points and depths were observed taking into account the cover surface of the endpoint assemblages.

The main players are shown to be *M. galloprovincialis* and *B. boholense*. The former is generally the dominant species in most of the endpoints and appears negatively related to the depth. In both the years of study this species recruits massively during the April-July quarters. In S1, its recruitment occurs in the early stage of succession, determining a strong structuring weight in the late stages assemblage at all the depths by the monopolization of all the available substrate. When the recruitment of *M. galloprovincialis* occurs at later successional stages (i.e. T4 in S2, T3 in S3, T2 in S4), this does not rule a subsequent structuring role in the endpoint assemblage. Indeed, the already settled macro-invertebrates can affect the further recruitment pressure or/and can facilitate a set of species that results in a negative feedback for the *M. galloprovincialis*. This could have occurred in the panels S3 and S4 at 3 and 6 m depth, where after its settlement, *M. galloprovincialis* undergoes a decrease in coverage coupled with the development of other species, such as *B. boholense*, *A. ephippium*, *L. hians*, and *S. spallanzanii*, which prob-

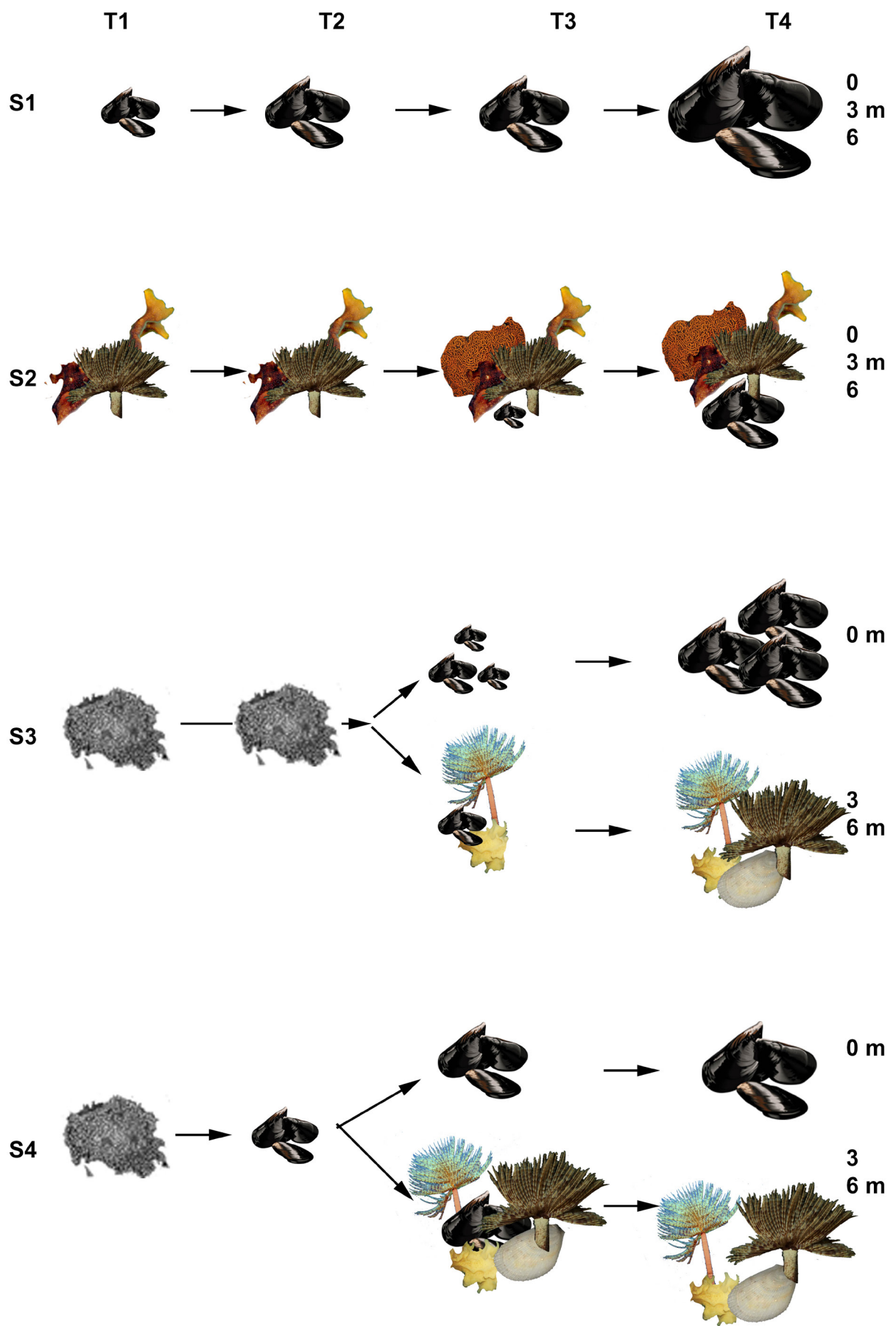


Fig. 8: Development model of the macrofaunal assemblages. Each Set (S), Immersion time (T) and depth are showed.

ably outcompete the mollusc, as the significant negative correlation with them showed. It was proved, for instance, that the canopy effect of the sabellids had an inhibitory effect, so altering the structure of benthic community (Holloway & Keough, 2002 a, 2002 b). This does not occur in the shallowest panels of S3 and S4 series, where the recruitment of *B. boholense*, *A. ephippium*, *L. hians*, and *S. spallanzanii* is lower than that recorded at 3 and 6 m depth and where a pattern similar to that described for all the depth of S1 is observed, being *M. galloprovincialis* the dominant species in the endpoint assemblage. The pattern observed at 3 and 6 m depth in S3 and S4 is linked more to biological events (species interactions, propagule pressure) altering the course of succession, and causing a community shift towards a more speciose endpoint than that dominated by *M. galloprovincialis*.

Finally, a different and more species-rich endpoint was observed in the S2 due to its successional history. Multivariate analysis shows that the endpoints of all the depths relative to S2 are characterized by high diversity communities, which involve species distinct from those of the other endpoints (i.e. *S. errata*, *C. lepadiformis*, *B. leachii*). All these species appear in the first succession time and remain in the community, so distinguishing it from the other previously discussed endpoints. The first succession time of this series is also coupled with the maximum of the diversity in the recruitment of macrofaunal foulers. It is characterized by the total absence of *Mytilus*, which, by contrast, appear in the late succession, when the community have already reached the end point structure, and therefore the mussels fail to colonize *en masse*. Moreover, in the starting time of the S2 a strong recruitment of alien species, particularly *P. zorritensis*, needs to be highlighted, most of them being seasonal taxa which decrease significantly during the following quarters (Lezzi *et al.*, 2018). On the contrary, *Mytilus galloprovincialis* appears only in T4 (April-July 2014) when the community is already structured. In S2, differences in communities according to depth are mainly due to the different recruitment pressure of *M. galloprovincialis*, *B. boholense*, *B. luctuosum* and *Myxilla* sp.

Independently of the starting time, ecological succession in the marine environment is gradual, continuous and directional (Pacheco *et al.*, 2011; Antoniadou *et al.*, 2011) and proceeds through stages recognized by the structure of the developing communities (Dean & Connell, 1987 a, 1987 b; Hirata, 1987; de Eston *et al.*, 1990). In this framework, as observed by Cifuentes *et al.* (2010), the pool of early colonizers may include both opportunistic and/or competitive taxa, that vary in abundance in accordance with their seasonal reproductive peaks. These early taxa can inhibit the arrival of others (i.e. *Mytilus* dominated the end point in S1) or not, determining a different direction in community succession.

Mytilus galloprovincialis is recognized as the dominant taxon in the stable state of fouling communities in the investigated area, as generally occurs in Mediterranean confined environments (Relini, 2001; Çinar *et al.*,

2008). Its importance as a structuring component was observed by Kocak *et al.* (1999), who highlighted a massive recruitment on artificial substrates during the winter quarter in the Izmir Bay (Western Mediterranean). The same pattern was observed by Pierri *et al.* (2010), who studied the succession on artificial substrates in different areas of the Mar Piccolo of Taranto, a more confined area compared to the Mar Grande. The same authors also found that succession was mainly driven by extrinsic factors, such as site features. Therefore, endpoints differed according to the physical characteristics of the sites and thus to larval availability.

In the same area Tursi *et al.* (1982) studied in 1980 the biological *facies* present on fouling panels immersed for 12 months from different seasonal starting times at different depths. The authors found no alternative end states to the *Mytilus* one (called *facies*), so demonstrating that the endpoints were characterized by similar sets of species within seasonal and depth factors. Moreover, the summer and spring panels (immersed in April and July, analogues to the S1 and S2 of the present study) were characterized by high densities of *M. galloprovincialis*, especially at the shallowest depths and a slower success rate of mussels in deep panels. Also the winter/autumnal series (analogues to the S3 and S4) tend to reach a *Mytilus* dominated endpoint, although this required more time due to a late recruitment of the mollusc during the successional history. The main differences between the cited study and the present one is the different role of *M. galloprovincialis* in the successional history and its recruitment pattern. Our results show that the mollusc dominance in the endpoints is due to early recruitment during the months of April-July. By contrast Tursi *et al.* (1982) found that *Mytilus* dominance derived from a late recruitment in November and June. Comparing our results with Tursi *et al.*'s study is difficult due to the different methods used and to the different environmental conditions of the two sites in the Gulf of Taranto. Nevertheless, we can still infer that the observed difference could be partly attributable to the difference in temperature and trophic regime between the two sites studied, but mainly to the difference in the player species pool which in turn characterizes the endpoints, also underlying the total absence of alien species in the studies mentioned above.

As far as this last point some considerations arise: the most abundant NIS in the studied biotopes were *B. boholense* and *P. zorritensis*. Whilst the second taxon shows a massive presence only in early assemblage during summer, the former one proved to be a persistent structural component in the endpoints. The presence of the NIS *B. boholense* in the endpoint can be considered of paramount importance in conditioning the community's structure. Thus it is important to focus on the alternative states during which the *M. galloprovincialis* loses its structural importance and *B. boholense* becomes dominant so being able to compete with the mollusc. In the present study, the presence of *B. boholense* at the primary succession led to the increase in the endpoint assemblage fouling

biodiversity. However, it must be considered that this species should be responsible for a change in ecosystem structure and in the loss of the goods and services due to the important commercial value of *M. galloprovincialis* (Beaumont *et al.*, 2007; Pejchar & Mooney, 2009).

Although our study concerns artificial substrates and succession, it is the first study within the Mediterranean area to be statistically supported, so underlining the influence of starting time on successional pattern. Our results show that during the experiment all the assemblages tend to converge towards multiple contingent communities, according to starting times and depths. In other words, differences are due to different propagule availability in time and depth, this in turn influencing further species interactions. The endpoint patterns are defined by a contingent community development (*sensu* Berlow, 1997) determined by the seasonal species pool and phenologies, by pre- and post- settlement events, and by species interaction.

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