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Experimental analysis of the effects of extreme events of mechanical disturbance on rocky shore algal and invertebrate assemblages in the Bagnoli-Coroglio post-industrial area and in reference sites in the Gulf of Naples.

Tesi di laurea in Alterazione e conservazione dei sistemi costieri

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1. INTRODUCTION

1.1 General contest

Marine systems are increasingly threatened by natural and anthropogenic disturbances, especially in coastal areas (Bryant et al. 1996; Hixon et al. 2001; Burbridge and Humphrey 2003). Assessing the ecological impacts of such disturbances and the recovery ability of marine populations and assemblages is a main topic of current ecological research, with important implications for assessing and predicting biodiversity dynamics, the relationship between biodiversity and ecosystem functioning, and providing scientifically-based and robust information for the sustainable exploitation of marine biological resources (Botsford et al. 1997; Castilla 2000; Hooper et al. 2005; Lotze et al. 2006; Halpern et al. 2008). Indeed, increased urban and industrial development and environmental contamination due to growing human population and activities cause alterations of habitats and may affect biodiversity at all levels of biological organization (Vitousek et al. 1997; Agardy et al. 2005; Spalding et al. 2014; Neumann et al. 2015). Actual biological and ecological impacts, however, depend on the regime of disturbance, including its intensity, spatial and temporal extent, the interaction of multiple disturbances, and the interaction of all these factors with the life-history traits of affected organisms (Halpern et al. 2007). The Mediterranean Sea, in particular, is one of the historically most impacted marine regions of the world (Costello et al. 2010), where current impacts are exacerbated by climate change (Airoldi and Beck 2007; Claudet and Fraschetti 2010; Lejeusne et al. 2010; Coll et al. 2012; Micheli et al. 2013).

In spite of large available evidence of relationships between changes in intensity and timing of different disturbances, including scouring (Shanks and Wright 1986; McQuaid and Dower 1990; McCook and Chapman 1993; Van Tamelen 1996; Vaselli et al. 2008), heat extremes (Menge and Sutherland 1987) and storms (Dayton 1971; Alvarado et al. 2001), and patterns of convergence of the structure of assemblages in disturbed areas towards that of assemblages in adjacent undisturbed areas (Underwood 1989), context-dependent processes make the generalization and prediction of spatial and temporal patterns of recovery of disturbed assemblages quite challenging. In this respect, manipulative experiments are essential to understand and predict the magnitude and direction of responses of natural assemblages to disturbance under a range of environmental settings. Under the logistic difficulties up to the virtual impossibility of manipulating the large-scale environmental variables and the broad scenario of possible chronic alterations of the background system within which current disturbances may operate, a good alternative to investigate how the responses of populations and assemblages to current disturbance are modulated by the local environment is that of

performing the same type of experiment in areas characterized by different conditions (e.g., Wernberg et al. 2010, 2012). This 'comparative experimental approach' (Menge et al. 2002) is also critically important to examine links between ecological processes operating over a range of scales (Underwood and Chapman 1996; Thrush et al. 2000). Under such an approach, a comprehensive understanding of the recovery ability of organisms to disturbance should focus not just on average values of response variables (e.g., Sousa 1980; Hawkins 1981; Keough 1984; Kim and De Wreede 1996; McCabe and Gotelli 2000; Mackey and Currie 2001; Shea et al. 2004; Vaselli et al. 2008a), but also on their temporal trajectories (e.g., Collins 1992, 2000; Bertocci et al. 2005; Araújo et al. 2009). This is essential, for example, to predict trends in functional traits of natural systems, including their stability under different driving processes acting on a range of scales (Micheli et al. 1999; Lundberg et al. 2000; Inchausti and Halley 2003).

The present work was carried out within such a general framework, comparing the recovery ability to physical disturbance of rocky shore assemblages between a site located within the post-industrial area of Bagnoli-Coroglio (Gulf of Naples) and reference sites located outside it.

1.2 The environmental issue of post-industrial areas

Pressures on the marine environment are constantly and globally increasing due to the increasing human exploitation of marine abiotic and biological resources for a range of valuable services. As a result, marine systems may be drastically altered (Halpern et al. 2008), although the net effect of multiple disturbances depend on their spatial and temporal extent, intensity and complex interactions (Daily 1997; Halpern et al. 2008; Bertocci et al. 2019).). Marine habitats and organisms are among the most exploited and disturbed systems on Earth, and only recently the need to develop appropriate conservation and management strategies has emerged coupled with the identification of actual and new sources of stress and disturbance (Steele 1985; Underwood 1995; Schmitt and Osenberg 1996; Botsford et al. 1997).

Among the anthropogenic impacts on coastal marine ecosystems, industrial activities and their post-industrial inheritance of environmental contamination play a large role. Main contaminants widely found in industrial and post-industrial areas include, in particular, heavy metals that are normally present in the marine environment, but that can reach toxic concentrations for marine organisms and be of concern for human health (Strömgren 1982; Bryan 1984; Munda and Hudnik 1986; Beaumont et al. 1987; Barreiro et al. 1993; Blackmore et al. 1998; Fichet et al. 1998). High concentrations of polycyclic aromatic hydrocarbons (PAHs) are also widely reported in industrial and post-industrial areas, where they can be

incorporated by marine organisms from the water through the body surface or the gills, or through the diet (Neff and Burns 1996; Peterson et al. 2003). For example, a number of studies have investigated the carcinogenic effects of PAHs on fish (Beyer et al. 1997; Hylland et al. 1996; Sandvik et al. 1997). There is evidence, however, that vertebrates generally tend to metabolise PAHs more efficiently than invertebrates, which may lead these organic compounds not to bioaccumulate in marine food webs and in fish tissues, although relatively high concentrations of their metabolites can be found in the bile (Aas 2000, Hylland et al. 2006). For these reasons, restoring marine habitats impacted by previous industrial activities and returning healthy and usable marine habitats to the local communities is a main goal of current research at the political, societal and scientific level (McGrath 2000; Amekudzi 2004; Alberini et al. 2005; Kaufman and Cloutier 2006). The achievement of such an objective is complicated by the occurrence of current natural and/or anthropogenic disturbances that are necessarily superimposed to the presence of chronic conditions of contamination (Meyer 2000; Bishop et al. 2002; Fraschetti et al. 2006).

The coastal area of Bagnoli-Coroglio in the Gulf of Naples, in particular, has hosted a large iron and steel factory for about a century, until its closure in 1990. As documented by numerous studies since 1999, the former industrial activities have left an important local contamination by PAHs and heavy metals (e.g., Romano et al. 2009). In 2000, this led to classify the Bagnoli-Coroglio area as a SIN (Site of National Interest) by the Italian Parliament (Italian Parliament 2000), and, in 2001, to include it among the areas to be environmentally characterized in detail and possibly recovered (Ministry of Environment and of the Territory Protection, 2001). In this respect, it is essential to understand not just whether the chronic contaminated conditions are associated with possible differences in the structure of assemblages compared to reference conditions (Keough 1984; Breitburg 1985; Reed 1990; Airoldi 2000; Benedetti-Cecchi 2000; Bertocci et al. 2005), but also whether they affect their functional characteristics, including the ability to recover once an additional concomitant disturbance has occurred and eventually ceased (Underwood et al. 1983; Blanchette 1996; Bevilacqua et al. 2006; Oliveira et al. 2011, 2015). This last property is related, although not necessarily linearly (e.g., Cervin et al. 2005), to the regime of the 'new' disturbance (Carr et al. 2012), and is likely to interact with other local abiotic and biological processes.

1.3 Natural and anthropogenic disturbance

Disturbance can be defined as a discrete event that determines the total or partial removal of one or more individuals (or colonies) and that, by doing so, indirectly creates an opportunity for new individuals (or colonies) to settle (Sousa 1984). Biomass removal can take place directly, with the death of one or more organisms, or indirectly, with enough damage to affect the abundance of other species in a positive or negative way. It is one of the main determinants of the structure of natural assemblages, of which it may drastically modify the patterns of distribution, abundance and diversity (Paine and Levin 1981; Sousa 1984; Picket and White 1985; Petraitis et al. 1989; Underwood 1999; Shea et al. 2004; Bertocci et al. 2005; Micheli et al. 2013).

Coastal marine ecosystems are exposed to a wide range of natural and anthropogenic disturbances, whose eventual and net effects depend on their own characteristics, including the spatial and temporal extent, and the life-history traits of exposed organisms. Natural abiotic disturbances on rocky shores include, among the others, desiccation due to aerial exposure (Connell 1961; Sutherland 1970; Branch 1975; Menge 1978a, 1978b; Sousa 1979; Underwood 1980; Turner 1983; Bertocci et al. 2007), osmotic stress associated with evaporation and freshwater inputs (Taylor and Andrew 1988), the emersion / immersion dynamics, typically associated with tidal cycles, which determine large variations in a range of physical factors to which coastal organisms may be subject (Connell 1970; Paine 1974). Furthermore, the exposure to the wave motion contribute to dictate vertical and horizontal gradients of distribution of organisms (Grant 1977; Raffaelli and Hawkins 1996; Underwood 1980, 1998, 1999), either directly through the effect of wave forces, or indirectly through the transportation of solid material, such as boulders and trunks that can hit the shore and detach the organisms to create free patches of substrate (Denny 1995; Bertocci et al. 2005) Finally, the transportation and deposition of sediment may cause scouring or burial of organisms (D'Antonio 1986; Airoldi 1998; Vaselli et al. 2008a). Major natural biotic disturbances include, for example, the foraging activity of grazers (e.g., Navarrete 1996; Adler et al. 2001; Benedetti-Cecchi et al. 2005) and predators (e.g., Fairweather 1988; Butler 1989). Especially on coastal assemblages, anthropogenic disturbances are represented, for example, by the mechanical impact associated with trampling (e.g., Brosnan and Crumrine 1994; Keough and Quinn 1998; Milazzo et al. 2004; Casu et al. 2006; Araújo et al. 2009; Plicanti et al. 2016), the removal of organisms for food, bait or collection (e.g., Addessi 1994; Airoldi et al. 2005; Atkinson et al. 2010; Brosnan

and Crumrine 1994), and the direct and indirect effects of climate-related events, including periods of extreme temperatures (e.g., Jackson et al. 2008), changes in sea level (e.g., Benedetti-Cecchi et al. 2006; Vaselli et al. 2008b) and modifications of the regime of meteorological processes (e.g., Bertocci et al. 2005 and references therein).

A range of effects of different types of disturbance have been widely reported (see Sousa 2001 for a review), but in most cases single disturbances were taken into account. It is evident, however, that natural systems are exposed to simultaneous multiple disturbances interacting with each other and with the life-traits of organisms in complex ways (Martone and Wasson 2008; Clark and Johnston 2011; Pincebourde et al. 2012; Bertocci et al. 2017). A consequence of such a complexity is that it is very difficult, or even practically impossible, to predict biological responses to compounded disturbances just by extrapolating results from separate studies that have focused each on a single disturbance (Paine et al. 1998; Bertness et al. 1999; Albert et al. 2008). Addressing such an issue under realistic scenarios requires to perform, where logistically feasible, combined experimental manipulations of more than one disturbance (e.g., Oliveira et al. 2014; Bertocci et al. 2017), or to carry out the same type of treatment involving a single disturbance along environmental gradients potentially spanning different levels of realized impacts from previous/extant disturbances (Menge et al. 2002). This last approach is particularly important where current acute and discrete disturbances, potentially amenable to experimental manipulation, are superimposed to the extant effects of chronic disturbances (Underwood 1996; Crowe 2000).

With particular reference to the responses of populations and assemblages to disturbance, a key concept is that of resilience (Holling 1973). In ecology, resilience (reviewed by Gunderson 2000) defines the ability and speed of a system to react to a disturbing event, without losing functions and services. The concept includes two main components, i.e., resistance and recovery, defining, respectively, the extent of the disturbance that the system can absorb without change, and the ability to return to a given reference state once modified by a disturbance that has then ended (Walker et al. 2004). Depending on the specifically addressed issue, ecological context and scale of observation, the reference state may be either represented by the pre-disturbance condition of the affected system, or by the present state of a system analogous to the affected one for all possible factors, but the occurrence of disturbance (e.g., Chapman and Underwood 1998 and references therein).

The ability of species and assemblages to recover depend on several factors. First, the moment in which the disturbance occurs can influence the patterns of recolonization and succession, depending on its possible concomitance and interaction with key phases of the life cycles of

organisms and/ or the presence of relevant abiotic limiting conditions (Benedetti-Cecchi and Cinelli 1993, 1994, 1996; Kim and De Wreede 1996; Chapman and Underwood 1998).

Second, the intensity and spatial extent of disturbance may play a crucial role in shaping the patterns of recovery and the eventual diversity of assemblages. Only the most intense events of disturbance, in particular, can remove all organisms from a given area, while most disturbance is likely to remove some organisms, for example those that are weakly attached to the substrate, leaving others in place (Sousa 1985; Foster and Sousa 1985; Huston 1994; Connell et al. 1997). This may crucially affect patterns of recovery since, for example, intertidal assemblages subject to the partial removal (mild disturbance) of algal cover may converge faster, in terms of species composition and abundance, towards unmanipulated assemblages compared to assemblages subject to complete removal (extreme disturbance) (Underwood 1998; Airoldi 1998). Such effects may also depend directly or indirectly on the size of the disturbed patch. For instance, large disturbed patches of substrate deprived by organisms and isolated from the surrounding assemblages are potentially subject to receive a larger number, per unit of time, of drifting propagules compared to still isolated smaller areas (Kay and Keough 1981). Potentially dominant competitors, however, may recruit in lower abundance in such small areas, which, therefore, could represent a sort of spatial refuge for those species that in large areas are likely to be competitively excluded (Keough 1984). If, instead, the disturbed patches are not isolated from the surrounding assemblage, their recolonization would occur mainly through vegetative growth from the edges to the centre, and it would be faster and more effective in small patches (that have a relatively higher perimeter to area ratio) than in large patches, contrarily to what happens in isolated patches (Keough 1984; Connell and Keough 1985; Raimondi 1990; Dye 1993; Minchinton 1997). Such processes can also interact with other biological processes, such as grazing (Sousa 1984).

Third, the temporal frequency, possibly combined with the intensity, of disturbance may drastically affect the diversity of assemblages at a range of scales, as postulated, for example, by the Intermediate Disturbance Hypothesis according to which low levels of species diversity would occur under undisturbed or very weak/infrequent disturbance (due to competitive exclusion) and under very intense and frequent disturbance (due to the survival of only the most resistant species). 'Intermediate' levels of disturbance intensity/frequency, instead, would allow a relatively high number of species due to the availability of a mosaic of resources allowing the coexistence of both strong and weak competitors and both more resistant and less resistant species (Connell 1978). It is worth noting, however, that the temporal regime of disturbance include relevant components other than frequency, including variance over a given time scale (e.g., Bertocci et al. 2005; Pausas et al. 2006; García-Molinos and Donohue 2010; Buckley and

Kingsolver 2012), as well as the spatial regime of disturbance is not limited to the affected size, but also includes spatial heterogeneity (e.g., Benedetti-Cecchi et al. 2006a) and correlation (e.g., Banitz et al. 2008; Tamburello et al. 2014).

1.4 Rocky shore habitats and organisms as study system

Rocky intertidal habitats are found worldwide and host diverse algal and invertebrate assemblages mostly represented by small, sessile and short-living species that are distributed across clear vertical gradients of physical factors. Such environmental gradients are primarily driven by tidal cycles associated with the alternation of periods of aerial exposure and submersion of organisms, and by the coastal morphology producing strong gradients of wave energy (e.g. Benedetti-Cecchi and Trussell 2014).

Indeed, the documentation of strong vertical and horizontal physical gradients is at the core of the traditional interpretation of observed patterns of spatial zonation of organisms on rocky shores (Lewis 1964; Stephenson and Stepehenson 1972). Desiccation and thermal stress, in particular, typically increase with tidal height, and rocky intertidal species have developed physiological, morphological and behavioural adaptations to tolerate such progressively harsher conditions (e.g., Chapman 1997 and references therein) and their combination with changes in hydrodynamic forces (e.g., Denny and Wethey 2001). The importance of biological interactions as determinants of the patterns of distrbution, abundance and diversity of intertidal organisms, however, has also been increasingly demonstrated since early experimental studies that documented the importance of consumer pressure and competition for resources and the relative importance of biological and abiotic factors for shaping the distribution of species across the shore (Connell 1961a, 1961b).

The particular combination of physical and biological gradients occurring on scales amenable to experimental manipulations makes rocky intertidal habitats ideal natural laboratories for empirical studies the findings of which have provided a great contribution to the progress of Ecology as a science (Paine 2002) and to the development of ecological concepts extended beyond the field of marine ecology alone. For example, the predator removal experiment by Robert Paine (1966) showed the importance of predator control of superior competitors on the maintenance of diverse assemblages, providing the basis for the keystone species and the trophic cascade concept and for the recognized importance of indirect biological interactions. A further crucial contribution to such broad concepts was provided by Lubchenco (1978) with her experiments on the effects of grazing by herbivorous snails on the diversity of algal assemblages on intertidal rock pools.

Moreover, the recognized importance of variation in recruitment for rocky shore dynamics made this issue a major focus of ecological research ('supply-side ecology': Underwood and Denley 1984; Roughgarden et al. 1987). Concomitantly, post-settlement mortality due to physical or biological factors can also determine large variations of rocky shore assemblages (Underwood and Denley 1984; Connell 1985; Gaines and Roughgarden 1985). This notion, combined with the knowledge of the effects of the density of organisms for modulating the strength of biological interactions, including predation, grazing and competition, and, eventually, the structure of intertidal assemblages (e.g., Underwood and Keough 2001), contributed to the development of broad conceptual models of community organization. For example, Menge and Sutherland (1987) proposed that physical factors, competition and predation should be increasingly important drivers of the structure of assemblages across gradients of increasing environmental stress, but that such effects should mainly occur under high levels of recruitment. By contrast, under low recruitment competition should become less relevant. Observations, theories and experiments in this field led to the construction of interaction webs suited to describe how direct and indirect species interaction vary in extent and direction over a range of spatial and temporal scales (Menge 1995; Berlow et al. 1999). However, not only top-down forces such as those primarily involved in the Menge and Sutherland model, however, control the structure of rocky intertidal communities. The availability of algal food, namely drifting algae, to limpets, for example, was reported as an explanation for large differences in the structure of coastal assemblages between the western and the eastern coast of South Africa, where strong upwelling occurs and is virtually absent, respectively (Bustamante et al. 1995 a, 1995b). On a wider perspective, the recognition of the relative importance of bottom-up and top-down processes and of its variation with recruitment and environmental conditions has fuelled a considerable part of recent ecological research, not just in the marine context.

Finally, a key and historical question in ecology is how patterns and processes are linked across multiple scales (Pianka 1966; Holling 1992; Levin 1992; Denny and Benedetti-Cecchi 2012). Important advances in this field have been allowed by research done on rocky intertidal systems at least in three main interlinked directions: the comparison of multiple scales of variation in space and time of the distribution, abundance and diversity of species, the investigation of the role of deterministic and stochastic processes for the regulation of communities, and the analysis of the strength of biological interactions across environmental gradients (reviewed by Benedetti-Cecchi and Trussell 2014).

1.5 Thesis objectives

As previously illustrated, the separate and interactive effects of multiple traits of disturbance and of concomitant disturbances, combined with the life-traits of affected organisms, can drastically affect not just the structure of intertidal assemblages (Keough 1984; Breitburg 1985; Reed 1990; Airoldi 2000; Benedetti-Cecchi 2000; Bertocci et al. 2005), but also their functioning, including their ability to recover once the disturbance is over (Underwood et al. 1983; Blanchette 1996; Bevilacqua et al. 2006; Oliveira et al. 2011). This last property is modulated by features of the specific disturbance of concern and by its possible interaction with other extant processes and environmental conditions. Relatively few previous studies, however, have involved manipulations of multiple disturbances or of single discrete disturbances across extant conditions of chronic disturbance to experimentally assess their effects of patterns of recovery of assemblages and individual taxa (but see Tamburello et al. 2014; Oliveira et al. 2015). The lack of knowledge is especially evident when recovery is examined not just in terms of convergence of the structure and abundance of disturbed assemblages and individual taxa towards those of reference assemblages (e.g., Underwood 1989), but also in terms of temporal trajectories, i.e., the shape of the curves describing temporal fluctuations in the same variables (e.g., Bevilacqua et al. 2006; Oliveira et al. 2015). Moreover, the complex abiotic and biological context within which such processes occur makes the direction of recovery difficult to predict. In principle, organisms historically subject to chronic contamination may respond better and faster to a present discrete and acute disturbance compared to organisms from reference areas not affected by the same chronic contamination due to their adaptation and resistance to harsh conditions. But, by contrast, the same organisms could be relatively more sensitive to the new disturbance if the chronic contaminated conditions have made them to live close to their tolerance limits.

To fill, at least in part, such gaps, a manipulative experiment was performed involving the removal of organisms from replicate rocky shore patches within the post-industrial area of Bagnoli-Coroglio (disturbed site) and at sites (reference sites) located, northward and southward, out of it. The patterns of subsequent recovery of whole assemblages, the richness of taxa and the abundance of individual taxa, examined in terms of both mean response variables and temporal trajectories, were then compared between the disturbed site and the average of the reference sites. While the overall study is expected to cover a recovery period of at least one year suited to span the annual dynamics of most organisms, the present thesis presents results from the early phases, i.e. the first six months since experimental disturbance, of recovery.

2. MATERIALS AND METHODS

2.1 Study area

The study area is located within the Gulf of Naples, southern Tyrrhenian Sea, and spans about 15 km of coast centered around the Bagnoli-Coroglio post-industrial area (Figure 2.1).
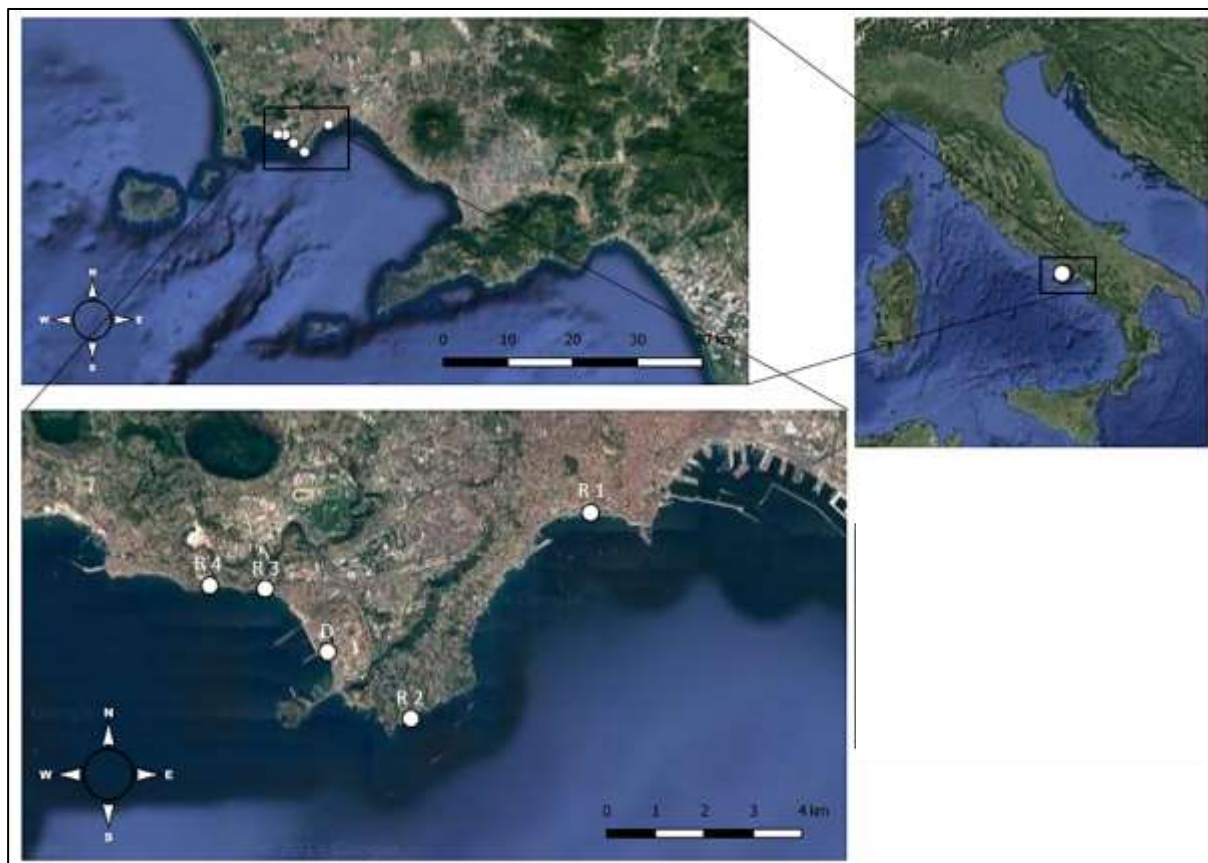

Figure 2.1. Map of the Bagnoli-Coroglio study area reporting the location of experimental sites. From R1 to R4 indicate the four reference sites (R1=Napoli Chiaia, R2=Marechiaro, R3=Via Napoli Bagnoli, R4 =Via Napoli Pozzuoli), while D is the disturbed site (Bagnoli-Coroglio, see insert Figure 2.1.1).

Figure 2.1.1. Bagnoli-Coroglio

As part of the Campi Flegrei volcanic district, the area is characterized by an intense volcanic activity, with gas emission and bradyseism (Bertocci et al. 2019), and an alternation of marine and alluvial deposits (De Pippo et al. 1988; Russo et al. 1998; Arienzo et al. 2017). The water circulation of the Gulf of Naples is related to the general circulation of the Tyrrhenian Sea (Carrada et al. 1980; Trifuoggi et al. 2017). During the winter, a clockwise circulation occurs in the inner part of the gulf, while a main northward current flows offshore. During the summer, the prevailing internal circulation shows an anti-clockwise deviation and the main off-shore currents are to the south (Pennetta et al. 1998; Trifuoggi et al. 2017).

The Gulf of Naples is affected by intense coastal development and anthropogenic activities (Pugnetti et al. 2006; Trifuoggi et al. 2017). The Bagnoli-Coroglio area, in particular, is a site of national interest (SIN) according to the Italian law due to local industrial contamination associated with the past activity of one of the largest steel plants in Italy, now disused. The SIN definition is primarily based on concerns for local biodiversity, ecosystem functioning and human health. For this reason, such an area is the focus of an ongoing multidisciplinary project (ABBaCo, see http://www.gazzettaufficiale.it/eli/id/2017/03/08/17A01736/sg%20) that ultimately aims at the environmental restoration of the contaminated marine environment and its revitalization, and within which the present experimental study was performed.

The first industrial plant in the Bagnoli-Coroglio area dates back to 1905 and was active for almost a century for the full-cycle production of steel from iron ores and limestone that were carried as raw materials to the coast by ships and then processed on land. These activities were interrupted only between 1943 and 1946 for the second world war. In parallel with increasing production demand, the plant was expanded in 1930 with the construction of two long piers: a northern one for allowing the docking and delivering of raw materials by large ships, and a southern one where the final products were loaded on the outgoing ships. Moreover, between 1962 and 1964, the marine area between the two pears was partially filled with contaminated soil from the plant as a result of further enlargement works (Romano et al. 2009; Bertocci et al. 2019).

Previous studies conducted in this area found high sediment concentrations of heavy metals (Cu, Fe, Hg, Mn, Pb and Zn), polychlorinated biphenyls (PCBs), PAHs and dichlorine diphenyl trichlorethane (DDT) (Damiani et al. 1987). Similarly, anomalous high concentrations of Ag, As, Cd, Co, Cr, Cu, Hg, Ni, Pb and Zn were found in sediments between the two long piers (Sharp and Nardi 1987), with contamination by Cd, Pb, Zn and Mn mainly restricted to the southern side of the plant, and contamination by Fe and Mn spread over the entire area (Romano

et al. 2004). In addition, there were PAH concentrations in the sediments three to four orders of magnitude higher than those reported from several marine benthic habitats (Arienzo et al. 2017).

At present, the study area is characterized by a low coastline with frequent sandy beaches that have often been protected by artificial barriers made of boulders of natural (mainly basalt or tuff, consistently with the most common natural rocky substrates around) or artificial (concrete) origin (Romano et al. 2004).

2.2 Experimental design

The study started in May 2018, when total five sites, a few km apart each other, were selected: one ('disturbed' = D) within the Bagnoli-Coroglio post-industrial area (40° 48'24.3'' N, 14°10', 16.7'' E), and four ('reference') located out of it, two southward (Napoli Chiaia = R1 and Marechiaro = R2, located at 40°49'54.9'' N, 14°14'6.7'' E and 40°47'39.7''N, 14°11'32.0''E, respectively), and two northward (Via Napoli Bagnoli = R3 and Via Napoli Pozzuoli = R4, located at 40°49'4.0'' N, 14°9'19.4'' E and 40°49'5.9'' N, 14°8'36.3'' E, respectively: see Fig. 2.1).

Each site was some hundred metres long and included two stretches (indicated as areas, each about 50 m long, about 100 m apart: Fig. 2.2) of artificial barrier made of natural rock. Under the practical impossibility to find a really 'pristine' reference condition, the four reference sites were intended to capture the variability among sites due to the various abiotic and biological processes, other than those strictly related to the presence of the post-industrial contamination, that are likely to occur in the Gulf of Naples, including the potential effects of main currents that could transport contaminants away from the disturbed site. All sites and areas, however, were chosen as to be comparable for a number of factors, including dominant organisms (articulated coralline algae), gently sloping substrate, ease of access, lack of any implemented protection, and the same low shore height sampled.

In each area, total ten 30 x 30 plots (tens cm apart) were marked at corners with epoxy putty at the beginning of the study. After a preliminary sampling and analysis aimed at assuring that all plots hosted initially comparable assemblages (see following sections), five out of ten plots were assigned at random to the treated condition and interspersed among the remaining five plots which were left unmanipulated as control (Fig. 2.2). The treatment was done only once at the beginning of the experiment and consisted in removing all the erect organisms by hand using hammer and chisel, a paint scraper and an iron brush. The resulting effect was comparable to that of major sources of disturbance on rocky shores, such as storms and sediment scouring (e.g., Paine and Levin 1981; Sousa 1985; Vadas et al. 1992; Benedetti-Cecchi 2000; Vaselli et al. 2008a), which can remove organisms from the substrate and open gaps. Encrusting organisms, mainly represented by encrusting coralline algae, were not completely removed as their growth form and strength of adhesion to the substrate would have required, to produce patches of bare rock, to chisel the substrate as strongly as to critically modify the topography of the substrate in an undesired way.
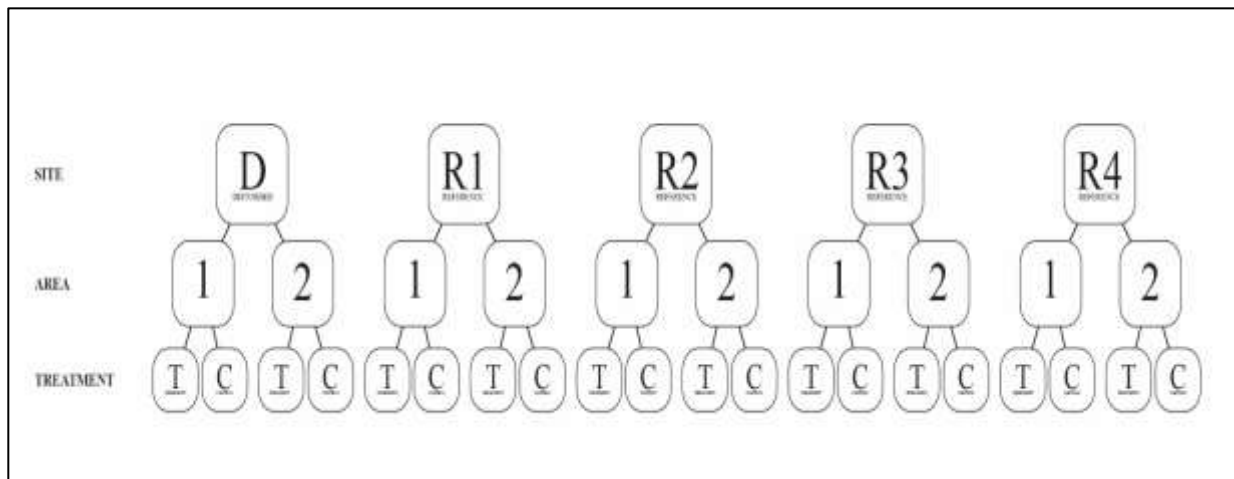
Fig 2.2. Diagrammatic representation of the experimental design, including a disturbed site (D = Bagnoli-Coroglio) and four reference sites (R1=Napoli Chiaia, R2=Marechiaro, R3=Via Napoli Bagnoli, R4 =Via Napoli Pozzuoli), with two areas in each site. In each area, interspersed replicate plots were allocated (n=5) to the removal treatment of organisms (T) or were left unmanipulated as control (C).

2.3 Collection of data

Before the experimental manipulation, the abundance of benthic taxa in all marked plots was visually sampled to exclude initial chance differences of assemblages that could have confounded the effect of the subsequent treatment. The cover of sessile organisms was estimated by superimposing in the centre of each plot a 20 x 20 cm (to avoid edge effects) frame divided into twenty-five 5 x 5 cm sub-quadrats, then assigning to each taxon in each sub-quadrat a score ranging between 0 (absence) and 4 (entire sub-quadrat covered), summing over all sub-quadrats, and expressing final values as percentages (Dethier et al. 1993). Mobile animals were quantified as number of individuals in each 20 x 20 cm quadrat. Organisms were identified to the finest level of taxonomic resolution obtainable visually, in some cases combining different species into higher taxa or morphological groups.

To assess the recovery ability of assemblages and individual taxa, the same procedures were used, on the same treated and control plots in each area and site, at each of five times of sampling interspersed over a total period of six months since experimental disturbance (Times 1 to 5, corresponding to one, two, three and a half, four and a half, and six months of recovery, respectively).

2.4 Data analyses

2.4.1. Preliminary checking

Before the experimental manipulation, permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) based on Bray-Curtis untransformed dissimilarities was used to compare the structure of assemblages between the plots allocated at random to the treated condition and the plots allocated to the control condition in each area within each site. A separate analysis was done for each site and was based on a two-way model including the crossed factors 'Area' (random, two levels) and 'Treatment' (fixed, two levels: treated vs. control), with the five replicate plots established in each area providing the replicates.

2.4.2. Multivariate and univariate average responses at subsequent times of recovery

PERMANOVA was used to compare the structure of whole assemblages between treated and control plots in each area and site at each of the five sampling times established over total six months of recovery. Since the same experimental units were sampled at subsequent times, a separate analysis was done for each time to avoid temporal non-independence problems (Underwood 1997). Each analysis was based on a Bray-Curtis matrix of untransformed dissimilarities and a three-way overall model including the factors 'Site' (five levels), 'Area' (random, two levels, nested within Site), and Treatment (fixed, two levels, crossed with both Site and Area), with five plots as replicates. The 'Site' source of variation was then partitioned into a fixed 'Disturbed site vs. reference sites' contrast and the 'Among reference sites' variation. Analogously the 'Area (Site)' term was partitioned into the 'Area (Disturbed)' and the 'Area (Reference)' quantifying, respectively, the variability between areas within the disturbed site, and the variability between areas within the reference site. The same rationale and procedure were applied to the terms involving the interaction of 'Site' and 'Area' with 'Treatment', and for the residual variability, which was finally partitioned into the variability among replicate plots established within the disturbed site and the variability among replicate plots established within the reference sites.

Following the main working hypothesis specifically relating to comparisons between the disturbed site and the reference sites in terms of recovery ability of assemblages, multivariate patterns were visually represented by calculating, separately for each sampling time, the centroids of assemblages for the treated and the reference condition in each site. For this purpose, since the semi-metric feature of the Bray-Curtis index (Legendre and Anderson 1999) prevents to obtain centroids as simple arithmetic averages of such dissimilarities (Anderson 2001), principal coordinates were calculated from the Bray-Curtis dissimilarity matrix of raw

data. Centroids were then obtained by averaging principal coordinates over 10 treated and 10 control plots (five per condition in each of two areas) in each site (McArdle and Anderson 2001). Finally, non-metric multidimensional scaling (nMDS) ordination based on Euclidean distances was displayed.

The total richness of sampled taxa and the abundances of the most common single taxa, namely articulated coralline algae, filamentous algae of the Ceramiales order, encrusting coralline algae, the mussel *Mytilus galloprovincialis*, and the limpet *Patella aspera*, were analysed with analysis of variance (ANOVA) based on the same model and procedures as those described above for PERMANOVA. Before each ANOVA, the assumption of homogeneity of variances was checked with Cochran's *C* test, log-transforming the data when necessary. When heterogeneous variances could not be stabilised by transformation, the analysis was done on untransformed data and results considered robust if either non-significant (at $p > 0.05$), as the probability of Type II error is not affected by significant heteroscedasticity, or significant at $p < 0.01$, to compensate for increased probability of Type I error (Winer et al. 1991; Underwood 1997). Analogously to multivariate patterns, univariate patterns were graphically visualized by plotting average abundances calculated separately over ten treated and ten control plots in each site, at each time of sampling.

2.4.3. Temporal heterogeneity of whole assemblages and individual response variables

Differences in temporal trajectories of recovering whole assemblages were tested by calculating measures of multivariate pseudo-variance over the five sampling times, following the approach illustrated in detail by Terlizzi et al. (2007). Specifically, multivariate pseudo-variance components over time were obtained from Bray-Curtis dissimilarities calculated for each replicate plot separately.

Analogously, temporal variances of the total richness of taxa and of the abundance of five single taxa, were obtained by calculating the variance over the five sampling times of the values of each variable separately for each experimental plot.

The obtained multivariate and univariate variance components were analysed with a three-way ANOVA model as above illustrated, including the same partitioning of terms and checking of the assumption of homogeneity of variances and corresponding procedures in case of its significant violation.

3. RESULTS

Total 43 taxa (25 algal and 18 animal taxa) were identified and used for multivariate analyses (Table 3.1).

Table 3.1. List of macroalgal and animal sampled taxa.

Rhodophyta

Articulated coralline algae[a]

Asparagopsis taxiformis (Delile) Trevisan

Ceramiales[b]

Encrusting Corallinales

Gastroclonium clavatum (Roth) Ardissone

Halymenia spp.

Hypnea musciformis (Wulfen) J.V.Lamouroux

'*Jania/Haliptilon*'[c]

Laurencia spp.

Porphyra sp.

Pterocladiella capillacea (S.G.Gmelin) Santelices & Hommersand

Undetermined coarsely branched algae

Undetermined filamentous red algae

Undetermined red crust

Ochrophyta

Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier

Dictyopteris membranacea (Stackhouse) Batters

Dictyota spp.

Halopteris scoparia (Linnaeus) Sauvageau

Padina pavonica (Linnaeus) Thivy

Ralfsia verrucosa (Areschoug) Areschoug

Chlorophyta

Bryopsis sp.

Caulerpa cylindracea Sonder

Ulva spp.

Undetermined filamentous green algae

Valonia utricularis (Roth) C.Agardh

Cyanobacteria

Rivularia spp.

Porifera
Cliona celata Grant, 1826
Undetermined massive black sponge

Cnidaria
Undetermined actinians

Annelida
Undetermined serpulids

Mollusca
Columbella spp.

Fissurella spp.

Mytilus galloprovincialis (Lamarck)

Ocenebra edwardsii complex[d]

Patella aspera Röding, 1798

Phorcus turbinatus (Born, 1778)

Rocellaria dubia (Pennant, 1777)

Spondilus sp.

Stramonita haemastoma (Linnaeus, 1767)

Vermetus triquetrus Bivona-Bernardi, 1832

Crustacea

Balanus spp.

Chthamalus stellatus (Poli, 1791)

Undetermined hermit crabs

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[a] mainly, *Ellisolandia elongata* (J.Ellis & Solander) K.R.Hind & G.W.Saunders.

[b] mainly *Ceramium spp.*

[c] including *Jania rubens* (Linnaeus) J.V. Lamouroux and *Jania virgata* (Zanardini) Montagne.

[d] see Barco A., Houart R., Bonomolo G., Crocetta F., Oliverio M. (2013). Molecular data reveal cryptic lineages within the northeastern Atlantic and Mediterranean small mussel drills of the *Ocinebrina edwardsii* complex (Mollusca: Gastropoda: Muricidae). Zoological Journal of the Linnean Society 169: 389-407.

3.1. Preliminary analysis

Besides a large and significant variability between areas within all sites but R1 (Napoli Chiaia), at all sites the sampled assemblages did not differ significantly between the plots randomly allocated to the unmanipulated control condition and the plots allocated to the removal treatment, before the experimental manipulation (D: $MS_{AreaxTreatment} = 238.7$, pseudo-$F_{1,16} = 0.54$, $p = 0.679$, $MS_{Treatment} = 238.7$, pseudo-$F_{1,1} = 1.47$, $p = 0.365$; R1: $MS_{AreaxTreatment} = 103.7$, pseudo-$F_{1,16} = 0.33$, $p = 0.877$, $MS_{Treatment} = 190.0$, pseudo-$F_{1,1} = 1.83$, $p = 0.277$; R2:

$MS_{Area x Treatment} = 112.6$, pseudo-$F_{1,16} = 0.42$, p = 0.653, $MS_{Treatment} = 139.2$, pseudo-$F_{1,1} = 1.24$, p = 0.438; R3: $MS_{Area x Treatment} = 277.2$, pseudo-$F_{1,16} = 0.41$, p = 0.799, $MS_{Treatment} = 1221.6$, pseudo-$F_{1,1} = 4.41$, p = 0.087; R4: $MS_{Area x Treatment} = 249.3$, pseudo-$F_{1,16} = 1.21$, p = 0.295, $MS_{Treatment} = 532.5$, pseudo-$F_{1,1} = 2.14$, p = 0.177).

3.2. Average responses at each time of sampling since experimental disturbance

3.2.1. Structure of whole assemblages

At the first time of sampling, corresponding to one month of recovery after experimental disturbance, treated and unmanipulated plots differed for the structure of whole assemblages with patterns variable among sites, especially the reference ones (Table 3.2). The nMDS plots, however, showed a clear separation between the centroids of treated and control plots within each site, including the disturbed one, suggesting that the significant 'Treatment x Site' and 'Treatment x Reference sites' interactions were mainly driven by differences in their multivariate dispersion rather than location (Figure 3.1).

No site-specific or main effects of the treatment were found at the subsequent sampling time (two months of recovery), where only within-site, i.e., among areas, treatment-associated differences resulted at the disturbed and the reference sites (Table 3.2 and Figure 3.1).

Any treatment effects disappeared since the third time of sampling, corresponding to three months and a half of recovery. At this time, only a significant variation at both the site and the area within site scale, independently of the experimental manipulation, was shown by the structure of assemblages from all sites. At the later phases of recovery, however, this variable became comparable among all sites, while the significant variability at the smaller, i.e., among areas, scale remained until the last sampling established six months since experimental disturbance (Table 3.3 and Figure 3.1).

Table 3.2. PERMANOVA comparing the recovery of total assemblages between treated and control plots in each of two areas within a disturbed site (Bagnoli-Coroglio) and four reference sites (Napoli Chiaia, Marechiaro, Via Napoli Bagnoli, and Via Napoli Pozzuoli), at one month and two months of recovery since experimental disturbance (Time 1 and Time 2, respectively).

Source of variation	df	MS	pseudo-F	p	MS	pseudo-F	p	Denominator for pseudo-F
		Time 1			Time 2			
Site	4	15819.3	1.40	0.258	10755.5	2.89	**0.004**	Area(Site)
Dist. vs. Ref. sites	1	9462.6	2.25	0.091	2942.7	0.79	0.559	Area(Site)
Among ref. sites	3	4726.7	1.16	0.383	13359.7	5.78	**0.001**	Area(Reference)[a]
Area(Site)	5	4210.9	3.30	**0.001**	3723.5	3.32	**0.001**	Residual
Area(Disturbed)	1	4697.7	2.23	0.072	9371.1	7.01	**0.002**	Quadrats(Disturbed)[b]
Area(Reference)	4	4089.3	3.83	**0.001**	2311.6	2.16	**0.008**	Quadrats(Reference)[c]
Treatment	1	22098.1	6.47	**0.037**	7888.1	2.55	0.881	Treatment x Site
Treatment x Site	4	3416.15	2.36	**0.042**	3094.3	1.06	0.433	Treatment x Area(Site)
Treatment x Disturbed	1	1474.0	1.02	0.387	3489.0	1.20	0.329	Treatment x Area(Site)
Treatment x Reference	3	4063.53	2.79	**0.041**	2962.8	1.19	0.373	Treatment x Area(Reference) [d]

Source	df	MS		p	MS		p	Denominator
Treatment x Area(Site)	5	1450.04	1.14	0.321	2906.5	2.59	**0.001**	Residual
Treatment x Area(Dist.)	1	1424.65	0.68	0.625	4565.7	3.41	**0.013**	Quadrats(Disturbed)[b]
Treatment x Area(Ref.)	4	1456.4	1.36	0.156	2491.7	2.33	**0.010**	Quadrats(Reference)[c]
Residual	80	1275.4			1122.9			
Quadrats (Disturbed)	16	2101.9			1337.6			
Quadrats (Reference)	64	1068.7			1069.2			

[a] Total 10 areas used as permutable units, but only areas within reference sites used for calculating the denominator MS.

[b] All replicate quadrats used as permutable units, but only quadrats within disturbed sites used for calculating the denominator MS.

[c] All replicate quadrats used as permutable units, but only quadrats within reference sites used for calculating the denominator MS.

[d] Total 20 Treatment x Area(Site) combinations used as permutable units, but only Treatment x Reference areas used for calculating the denominator MS.
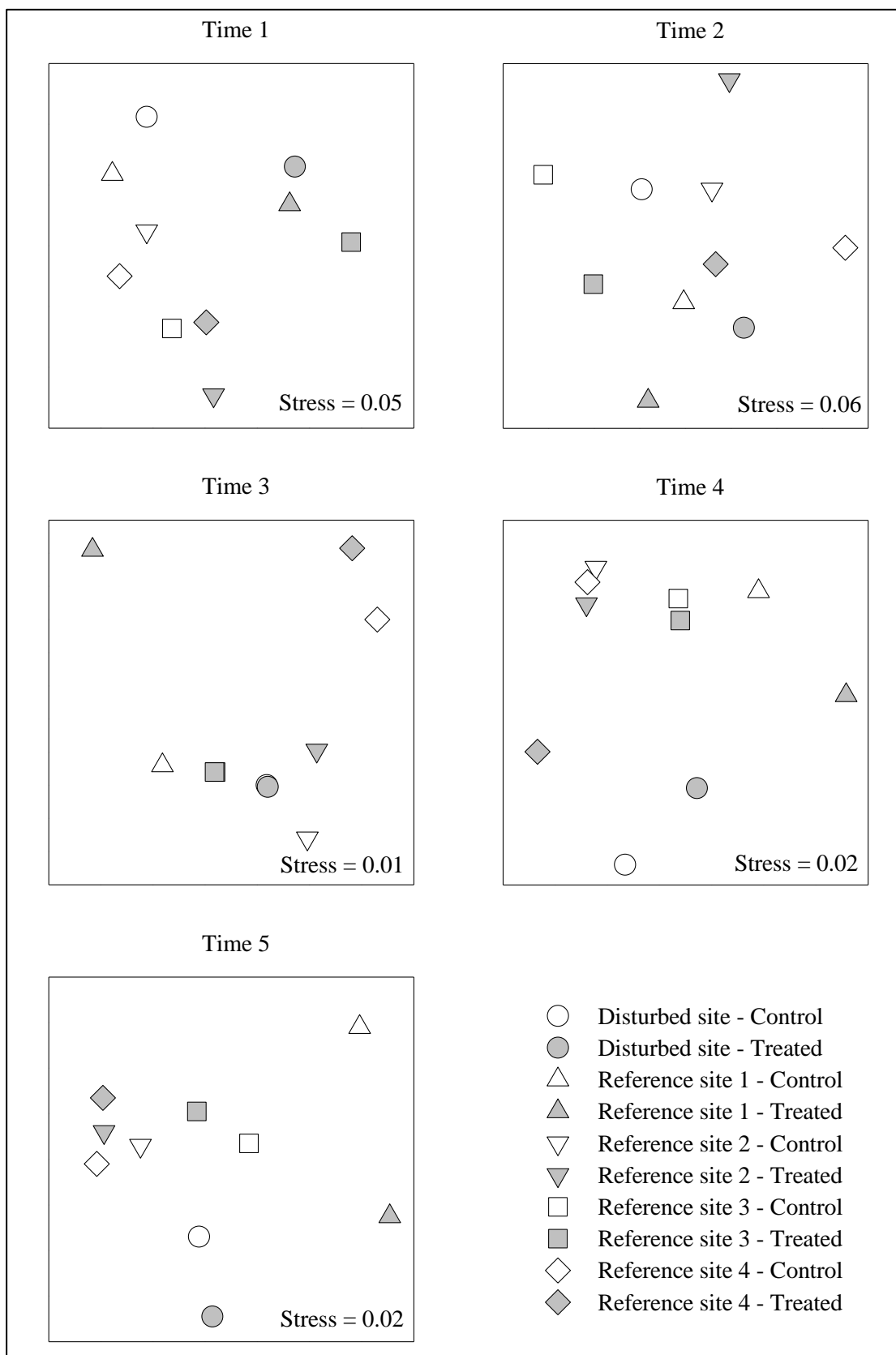
Figure 3.1. Non-metric multidimensional scaling (nMDS) ordinations of centroids of assemblages calculated, from principal coordinates, over replicate plots and areas for the treated and the control condition at the disturbed site and four reference sites, at each of five times of sampling (recovery time as in Tables 3.2 and 3.3).

Table 3.3. PERMANOVA comparing the recovery of total assemblages between treated and control plots in each of two areas within a disturbed site (Bagnoli-Coroglio) and four reference sites (Napoli Chiaia, Marechiaro, Via Napoli Bagnoli, and Via Napoli Pozzuoli), at three and a half, four and a half, and six months of recovery since experimental disturbance (from Time 3 to Time 5, respectively). Denominators as in Table 3.2.

Source of variation	df	Time 3			Time 4			Time 5		
		MS	pseudo-F	p	MS	pseudo-F	p	MS	pseudo-F	p
Site	4	15819.3	3.52	**0.012**	10027.3	2.09	**0.049**	5281.6	2.47	0.093
Dist. vs. Ref. sites	1	5553.4	1.23	0.267	11077.1	2.31	0.069	2550.9	1.19	0.338
Among ref. sites	3	19241.3	4.46	**0.010**	9677.4	3.43	**0.004**	6191.9	7.00	**0.005**
Area(Site)	5	4498.9	3.14	**0.001**	4790.7	3.79	**0.001**	2140.1	3.34	**0.001**
Area(Disturbed)	1	5234.0	3.53	**0.008**	12663.6	7.69	**0.001**	7164.2	6.53	**0.003**
Area(Reference)	4	4315.2	3.04	**0.001**	2822.4	2.42	**0.002**	884.1	1.68	0.050
Treatment	1	6469.5	3.09	0.880	3429.7	1.61	1.000	957.0	1.47	0.733
Treatment x Site	4	2093.1	1.85	0.075	2128.6	1.28	0.285	651.4	1.26	0.318
Treatment x Disturbed	1	2097.1	1.86	0.148	2076.1	1.25	0.276	628.6	1.21	0.309

Treatment x Reference	3	2091.8	2.11	0.062	2146.1	1.80	0.118	659.0	1.44	0.294
Treatment x Area(Site)	5	1129.3	0.79	0.800	1661.4	1.31	0.167	517.5	0.81	0.707
Treatment x Area(Dist.)	1	1688.6	1.14	0.317	3535.9	2.15	0.068	754.5	0.69	0.607
Treatment x Area(Ref.)	4	989.4	0.69	0.860	1192.7	1.02	0.433	458.2	0.87	0.575
Residual	80	1433.5			1264.3			640.5		
Quadrats (Disturbed)	16	1480.7			1647.4			1096.9		
Quadrats (Reference)	64	1421.7			1168.5			526.4		

3.2.2. Total richness and abundance of individual taxa

Not surprisingly, at the first time of sampling the total richness of sampled taxa was significantly higher in the unmanipulated than in the treated condition, independently of all other factors (Table 3.4 and Figure 3.2 A). The main effect of the experimental manipulation was not yet found one month later, when treated and control plots differed for the number of taxa within the reference sites only (Table 3.5), although the disturbed site still showed a trend towards a relatively higher richness in the control condition (Figure 3.3 A). The same general pattern of differences was displayed by almost all reference sites excepted R2, where richness was similar between treated and control plots and, actually, slightly higher in the former compared to the latter (Figure 3.3 A). No treatment-related significant effects on the richness of taxa were found at the later stages of recovery (Tables 3.6 and 3.8, and Figures 3.4 A and 3.6 A), with the only exception of sampling time 4 (Table 3.7), when the control plots hosted consistently more taxa than the treated plots, although with mean differences at each site of just 1-2 taxa (Figure 3.5 A).

Articulated coralline algae were the dominant component of the examined assemblages and showed a clear, and rather obvious, initial treatment effect in terms of consistently larger abundance in the unmanipulated compared to the treated condition (Table 3.4 and Figure 3.2 B). The response of this taxon to the experimental treatment differed at the between-areas scale at two months of recovery (Table 3.5). Such differences resulted into a relatively larger abundance in control plots at two of the four reference sites, namely R1 and R4, and comparable abundances between control and treated plots at the other two reference sites and the disturbed site (Figure 3.3 B). A main effect of the experimental treatment, however, resulted again at the third time of sampling (Table 3.6), when articulated corallines were, on average, generally more abundant in the unmanipulated than in the control condition (Figure 3.4 B). With the only exception of significant variation between areas, no significant differences in the abundance of this taxon were found since four months and a half of recovery (Tables 3.7 and 3.8, and Figures 3.5 B and 3.6 B).

The filamentous algae of the Ceramiales order did not show treatment-related significant differences at both the first and the third time of sampling (Tables 3.4 and 3.6, and Figures 3.2 C and 3.4 C). At Time 2, instead, their abundance differed between treated and control plots with patterns inconsistent at the scale of areas within the reference sites (Table 3.5). These resulted into overall slightly larger percentage cover values of this taxon in control

Table 3.4. ANOVA comparing the total richness of taxa and the abundance of individual taxa between treated and control plots in each of two areas within a disturbed site (Bagnoli-Coroglio) and four reference sites (Napoli Chiaia, Marechiaro, Via Napoli Bagnoli, and Via Napoli Pozzuoli), at one month of recovery since experimental disturbance. Denominators for F as in Table 3.2. * $p<0.05$, ** $p<0.01$, *** $p<0.001$, ns = not significant.

Source of variation	df	Richness		Artic. corallines		Ceramiales		Encr. corallines		*M. galloprovincialis*	
		MS	F	MS	F	MS	F	MS	F	MS	F
Site	4	12.93	15.6 **	1440.6	0.6	5303.8	2.1	6.68	2.8	234.5	2.1
Dist. vs. Ref. sites	1	0.01	0.01	97.0	0.04	2763.9	1.1	0.01	0.0	90.3	0.8
Among ref. sites	3	17.23	18.6 **	1888.4	0.9	2539.8	0.8	8.90	4.5	282.6	3.8
Area(Site)	5	0.83	0.4	2595.1	5.6***	2494.0	4.0 **	2.35	2.1	111.2	0.8
Area(Disturbed)	1	0.45	0.2	4929.8	9.9**	217.8	0.3	3.88	2.9	259.2	0.8
Area(Reference)	4	0.93	0.5	2011.5	4.4**	3063.0	5.0 **	1.97	1.8	74.2	0.8
Treatment	1	65.61	195.9***	23134.4	51.1**	6.8	0.0	34.18	17.0*	655.4	2.9
Treatment x Site	4	0.34	1.1	452.6	0.5	3435.4	4.8	2.01	1.5	224.3	1.9
Treatment x Disturbed	1	0.09	0.3	238.7	0.3	32.5	0.05	0.01	0.01	94.1	0.8
Treatment x Reference	3	0.42	1.5	523.9	0.5	4569.7	5.1	2.67	1.6	267.8	3.3
Treatment x Area(Site)	5	0.31	0.2	899.1	1.9	717.3	1.2	1.38	1.2	117.5	0.8
Treatment x Area(Dist.)	1	0.45	0.2	480.2	1.0	33.8	0.05	0.28	0.2	259.2	0.8
Treatment x Area(Ref.)	4	0.28	0.1	1003.8	2.2	888.2	1.4	1.65	1.5	82.1	0.8

Residual	80	2.06	463.7	622.8	1.13	144.4
Quadrats (Disturbed)	16	2.35	497.4	653.4	1.32	319.1
Quadrats (Reference)	64	1.98	455.3	615.2	1.08	100.8
Cochran's test		$C = 0.097$, ns	$C = 0.158$, ns	$C = 0.116$, ns	$C = 0.127$, ns	$C = 0.530$**
Transformation		None	None	None	Ln(x+1)	None

Table 3.4, continued   *Patella aspera*

Site	4	22.24	1.8
Dist. vs. Ref. sites	1	19.80	1.6
Among ref. sites	3	23.05	1.5
Area(Site)	5	12.50	2.2
Area(Disturbed)	1	0.05	1.0
Area(Reference)	4	15.61	2.2
Treatment	1	17.64	1.1
Treatment x Site	4	15.67	1.9
Treatment x Disturbed	1	5.52	0.7
Treatment x Reference	3	19.05	1.9
Treatment x Area(Site)	5	8.06	1.4
Treatment x Area(Dist.)	1	0.05	1.0

Treatment x Area(Ref.)	4	10.06	1.4
Residual	80	5.57	
Quadrats (Disturbed)	16	0.05	
Quadrats (Reference)	64	6.95	

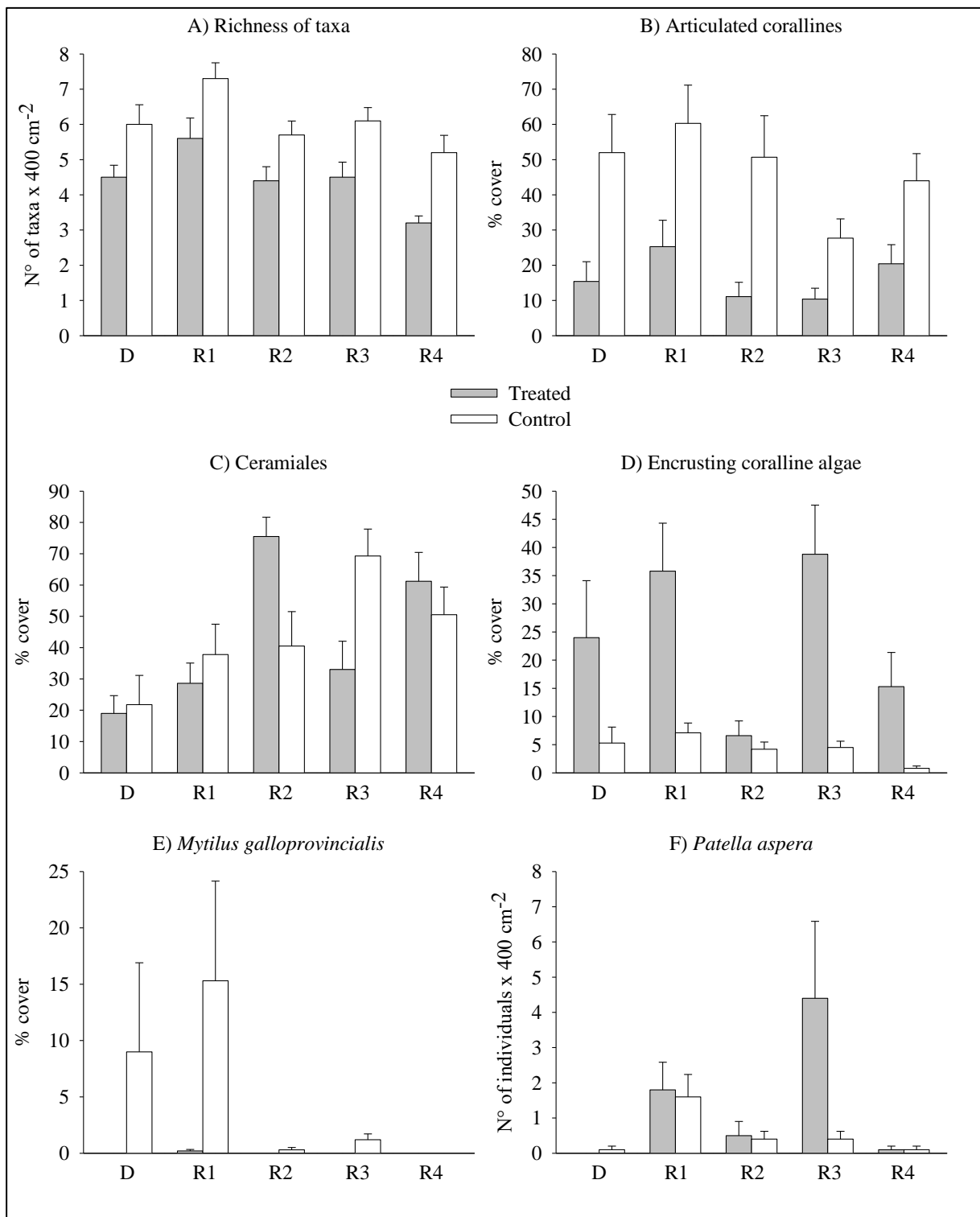|	
Cochran's test	$C = 0.725**$
Transformation	None

Figure 3.2. Mean (+SE) richness of taxa and abundance of individual taxa in treated and control plots within a disturbed site (D: Bagnoli-Coroglio) and four reference sites (R1: Napoli Chiaia, R2: Marechiaro, R3: Via Napoli Bagnoli, and R4: Via Napoli Pozzuoli), at one month of recovery since experimental disturbance. Data averaged over five replicate plots and two areas.

Table 3.5. ANOVA comparing the total richness of taxa and the abundance of individual taxa between treated and control plots in each of two areas within a disturbed site (Bagnoli-Coroglio) and four reference sites (Napoli Chiaia, Marechiaro, Via Napoli Bagnoli, and Via Napoli Pozzuoli), at two months of recovery since experimental disturbance. Denominators for F as in Table 3.2. * $p<0.05$, ** $p<0.01$, *** $p<0.001$, ns = not significant.

Source of variation	df	Richness		Artic. corallines		Ceramiales		Encr. corallines		M. galloprovincialis	
		MS	F	MS	F	MS	F	MS	F	MS	F
Site	4	9.74	3.0	6673.4	5.4*	6175.1	2.1	10.66	5.0	289.5	2.2
Dist. vs. Ref. sites	1	9.92	3.0	374.4	0.3	51.1	0.01	0.41	0.2	8.4	0.1
Among ref. sites	3	9.68	3.1	8773.5	7.3	8216.4	5.2	14.08	15.7*	383.2	2.6
Area(Site)	5	3.28	1.1	1238.3	2.2*	2970.6	5.8***	2.14	3.3	129.4	1.2
Area(Disturbed)	1	4.05	0.4	1411.2	1.7	8487.2	15.4**	7.12	11.0**	61.3	0.8
Area(Reference)	4	3.09	2.4	1195.1	2.5	1591.5	3.2*	0.90	1.4	146.4	1.2
Treatment	1	25.00	5.9	2052.1	1.3	2106.8	0.8	19.69	12.0*	930.3	4.4
Treatment x Site	4	4.25	3.8	1623.4	0.6	2494.1	1.6	1.65	1.0	213.2	1.2
Treatment x Disturbed	1	1.56	1.4	2878.3	1.1	3428.1	2.2	0.24	0.1	4.0	0.02
Treatment x Reference	3	5.15	13.3*	1205.1	0.9	2182.7	1.1	2.11	2.0	282.9	1.4
Treatment x Area(Site)	5	1.12	0.4	2609.7	4.7***	1585.8	3.1*	1.68	2.6*	173.8	1.6
Treatment x Area(Dist.)	1	4.05	0.4	7605.0	9.0**	51.2	0.1	4.19	6.5*	76.1	1.0
Treatment x Area(Ref.)	4	0.39	0.3	1360.9	2.8*	1969.4	3.9**	1.05	1.6	198.2	1.7

Residual	80	2.93	557.2	511.2	0.66	109.0
Quadrats (Disturbed)	16	9.48	847.7	551.9	0.65	75.9
Quadrats (Reference)	64	1.29	484.6	501.0	0.66	117.3
Cochran's test		$C = 0.106$, ns	$C = 0.133$, ns	$C = 0.166$, ns	$C = 0.136$, ns	$C = 0.665**$
Transformation		None	None	None	Ln(x+1)	None

Table 3.5, continued   *Patella aspera*

Site	4	8.59	2.4
Dist. vs. Ref. sites	1	1.82	0.5
Among ref. sites	3	10.85	2.4
Area(Site)	5	3.61	1.8
Area(Disturbed)	1	0.20	0.2
Area(Reference)	4	4.46	2.0
Treatment	1	0.09	0.02
Treatment x Site	4	3.79	2.9
Treatment x Disturbed	1	1.82	1.4
Treatment x Reference	3	4.45	2.8
Treatment x Area(Site)	5	1.29	0.6
Treatment x Area(Dist.)	1	0.01	0.01

Treatment x Area(Ref.)	4	1.61	0.7
Residual	80	2.05	
Quadrats (Disturbed)	16	1.30	
Quadrats (Reference)	64	2.24	

Cochran's test $C = 0.371**$

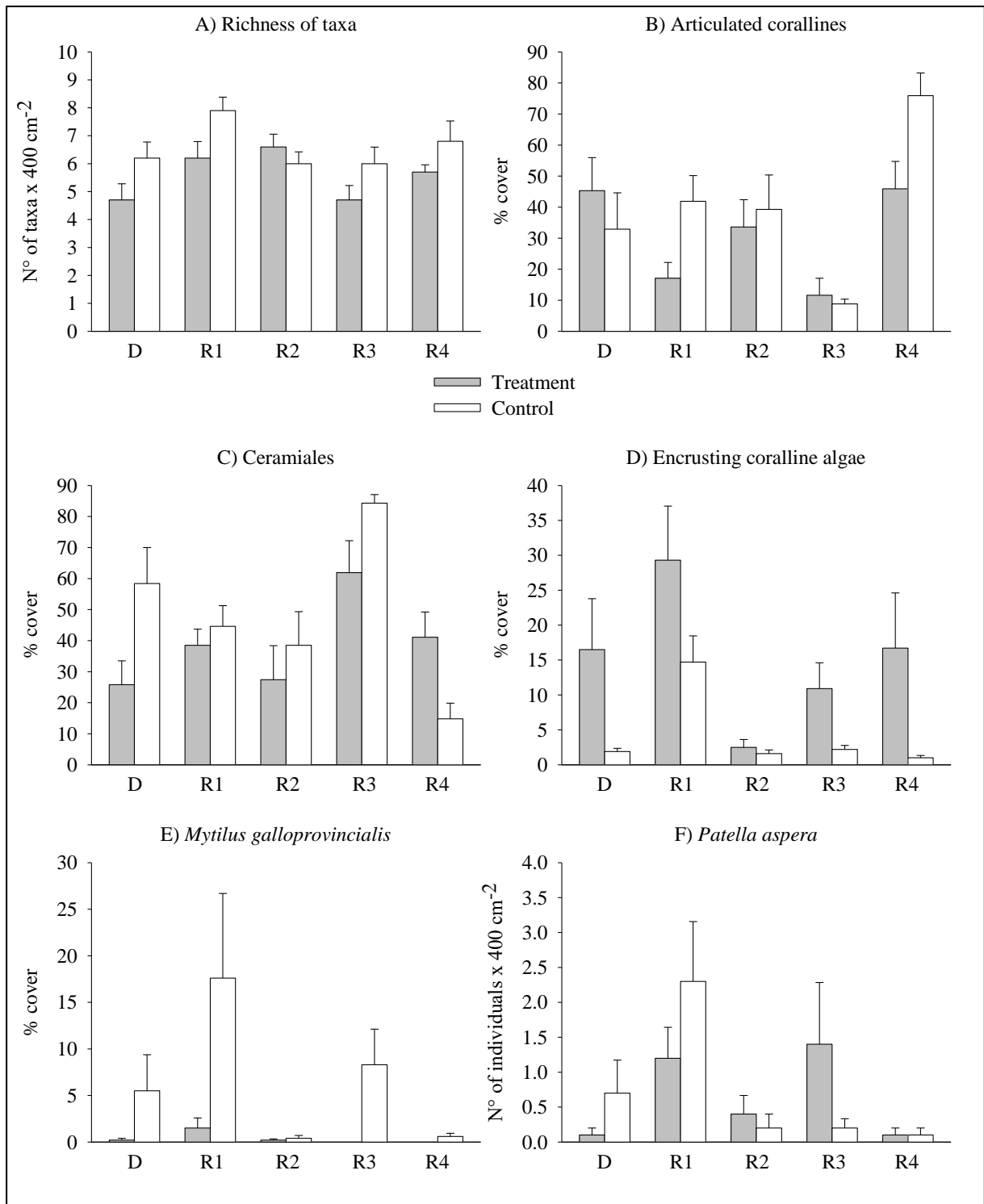Transformation   None

Figure 3.3. Mean (+SE) richness of taxa and abundance of individual taxa in treated and control plots within a disturbed site (D: Bagnoli-Coroglio) and four reference sites (R1: Napoli Chiaia, R2: Marechiaro, R3: Via Napoli Bagnoli, and R4: Via Napoli Pozzuoli), at two months of recovery since experimental disturbance. Data averaged over five replicate plots and two areas.

Table 3.6. ANOVA comparing the total richness of taxa and the abundance of individual taxa between treated and control plots in each of two areas within a disturbed site (Bagnoli-Coroglio) and four reference sites (Napoli Chiaia, Marechiaro, Via Napoli Bagnoli, and Via Napoli Pozzuoli), at three months and a half of recovery since experimental disturbance. Denominators for F as in Table 3.2. * p<0.05, ** p<0.01, *** p<0.001, ns = not significant.

Source of variation	df	Richness		Artic. corallines		Ceramiales		Encr. corallines		*M. galloprovincialis*	
		MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Site	4	6.49	1.5	5394.7	1.3	3.92	0.6	9.29	3.4	417.5	20.2**
Dist. vs. Ref. sites	1	14.82	3.5	5738.1	1.4	5.93	0.9	1.29	0.5	208.8	10.1*
Among ref. sites	3	3.71	0.8	5280.2	2.0	3.25	0.5	11.95	5.7	487.0	18.8**
Area(Site)	5	4.25	1.6	4074.3	5.4***	6.15	5.2***	2.72	4.1	20.7	0.2
Area(Disturbed)	1	1.80	1.0	9990.5	14.6**	2.12	1.6	5.24	5.1	0.01	1.6
Area(Reference)	4	4.86	1.7	2595.3	3.4*	7.16	6.2***	2.09	3.6	25.9	0.2
Treatment	1	4.41	1.8	6336.2	10.4*	0.68	0.3	0.04	0.3	767.3	1.9
Treatment x Site	4	2.51	0.7	607.4	3.1	2.01	1.1	0.12	0.1	406.3	17.2**
Treatment x Disturbed	1	0.003	0.0	602.7	3.1	0.02	0.01	0.00	0.0	191.8	8.1*
Treatment x Reference	3	3.35	1.1	609.0	4.9	2.67	1.2	0.16	0.6	477.7	16.2*
Treatment x Area(Site)	5	3.53	1.3	194.1	0.3	1.87	1.6	1.25	1.9	23.6	0.2
Treatment x Area(Dist.)	1	5.00	2.8	470.5	0.7	0.47	0.4	5.17	5.1	0.01	1.6
Treatment x Area(Ref.)	4	3.16	1.1	125.1	0.2	2.22	1.9	0.27	0.5	117.9	0.2

	DF					
Residual	80	2.63	748.9	1.18	0.66	129.9
Quadrats (Disturbed)	16	1.78	682.2	1.31	0.02	0.01
Quadrats (Reference)	64	2.84	765.6	1.15	0.58	162.3
Cochran's test		$C = 0.171$, ns	$C = 0.081$, ns	$C = 0.119$, ns	$C = 0.186$, ns	$C = 0.634$**
Transformation		None	None	Ln(x+1)	Ln(x+1)	None

Table 3.6, continued   *Patella aspera*

	DF	MS	F
Site	4	27.87	17.6**
Dist. vs. Ref. sites	1	16.81	10.6*
Among ref. sites	3	31.55	16.0**
Area(Site)	5	1.58	0.6
Area(Disturbed)	1	0.01	1.6
Area(Reference)	4	1.97	0.6
Treatment	1	1.00	0.8
Treatment x Site	4	1.28	0.2
Treatment x Disturbed	1	0.25	0.03
Treatment x Reference	3	1.62	0.2
Treatment x Area(Site)	5	7.46	2.6*
Treatment x Area(Dist.)	1	0.01	1.6

Treatment x Area(Ref.)	4	9.32	2.6*
Residual	80	2.83	
Quadrats (Disturbed)	16	0.01	
Quadrats (Reference)	64	3.53	

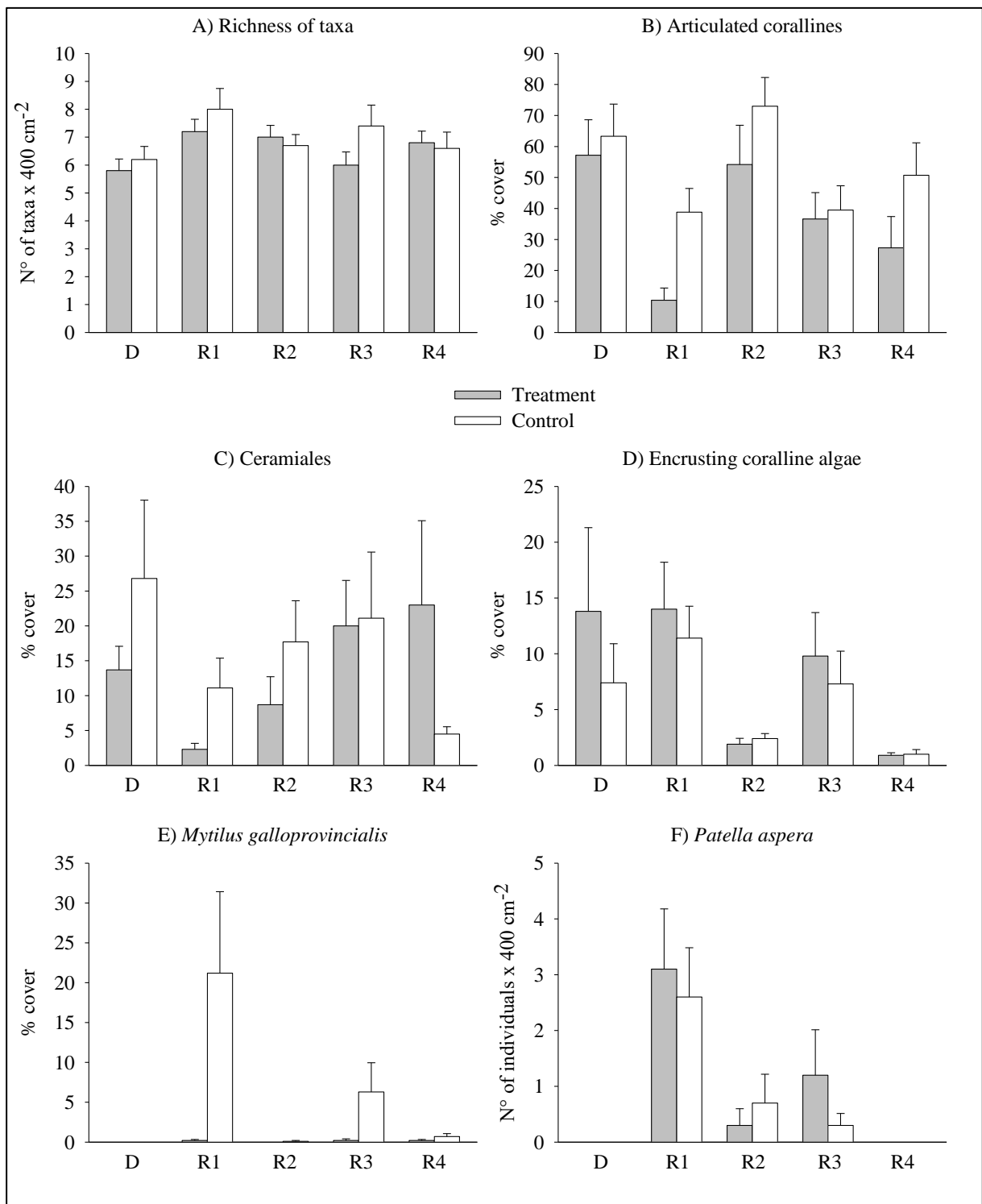|	
Cochran's test	$C = 0.342**$
Transformation	None

Figure 3.4. Mean (+SE) richness of taxa and abundance of individual taxa in treated and control plots within a disturbed site (D: Bagnoli-Coroglio) and four reference sites (R1: Napoli Chiaia, R2: Marechiaro, R3: Via Napoli Bagnoli, and R4: Via Napoli Pozzuoli), at three months and a half of recovery since experimental disturbance. Data averaged over five replicate plots and two areas.

compared to treated plots in all reference sites, but R4, where an opposite trend was displayed (Figure 3.3 C). However, a trend toward relatively larger cover of Ceramiales in the control condition was evident also for the disturbed site at the same time of sampling (Figure 3.3 C). A consistent negative effect of the treatment on the abundance of Ceramiales was then evident at four and a half months of recovery (Tables 3.7 and Figure 3.5 C). At the last time of sampling, however, the response of recovering Ceramiales to experimental disturbance were again variable between areas within reference sites (Table 3.8), with resulting patterns among sites generally analogous to those observed at Time 2 with the only exception of R4 being now consistent with the other sites (Figure 3.6 C).

The cover of encrusting coralline algae was consistently larger in the treated compared to the control plots one month after experimental disturbance (Table 3.4 and Figure 3.2 D). A similar response was observed at the subsequent time of sampling, although under a significant 'Treatment x Area(Disturbed)' interaction that was associated with a peculiar pattern of comparable abundance of this taxon, independently of the treatment, at R2 (Table 3.5 and Figure 3.3 D). No effects of any of the examined factors were generally detected for encrusting corallines further later during the recovery period (Tables 3.6, 3.7 and 3.8, and Figures 3.4 D, 3.5 D and 3.6 D). The only small exception occurred in the sampling done four months and a half since experimental disturbance, when the significant 'Treatment x Area(Reference)' interaction was associated with comparable cover of encrusting corallines between treated and control plots among all sites, but R1, where these algae were relatively more abundant in the control (Figure 3.5 D).

Both the animal species analyzed individually, the mussel *M. galloprovincialis* and the limpet *P. aspera*, were not affected by any of the examined factors until the second time of sampling included (Tables 3.4 and 3.4, Figures 3.2 E and 3.3 E for *M. galloprovincialis*, Figures 3.2 F and 3.3 F for *P. aspera*). At Time 3, the mussels showed treatment-related patterns variable among sites (Table 3.6), being comparably low abundant, where not completely absent, at the disturbed site and at the reference sites R2 and R2, and more abundant in the control than in the treated condition at the other two reference sites (Figure 3.4 E). Such patterns remained virtually the same at Time 4 (Figure 3.5 E), although in the presence of a significant 'Treatment x Area(Disturbed)' interaction (Table 3.7), and at Time 5, when the difference between the control and the treated condition observed at the two preceding times of sampling in the cover of *M. galloprovincialis* at R3 was eroded (Table 3.8 and Figure 3.6 E). Three and a half months after the removal treatment, *P. aspera* was completely absent at the disturbed site and at reference site R4, while tended to occur in relatively larger numbers in treated plots established

in reference sites R1 and R3, and in control plots established in R2 (Table 3.6 and Figure 3.4 F). These effects disappeared at Time 4, where only large variation among sites independently of the treatment was detected (Table 3.7 and Figure 3.5 F). Finally, at six months since experimental disturbance, limpets were still completely or almost absent at sites D and R4, equally represented in treated and control plots at site R3, and more numerous in treated than in control plots at both R1 and R3 (Table 3.8 and Figure 3.6 F).

Table 3.7. ANOVA comparing the total richness of taxa and the abundance of individual taxa between treated and control plots in each of two areas within a disturbed site (Bagnoli-Coroglio) and four reference sites (Napoli Chiaia, Marechiaro, Via Napoli Bagnoli, and Via Napoli Pozzuoli), at four months and a half of recovery since experimental disturbance. Denominators for F as in Table 3.2. * $p<0.05$, ** $p<0.01$, *** $p<0.001$, ns = not significant.

Source of variation	df	Richness MS	F	Artic. corallines MS	F	Ceramiales MS	F	Encr. corallines MS	F	M. galloprovincialis MS	F
Site	4	1.27	0.2	5741.3	1.3	5.43	1.9	8.92	4.5*	152.9	1.9
Dist. vs. Ref. sites	1	0.16	0.02	7344.5	1.7	13.89	4.9	0.00	0.0	62.4	0.8
Among ref. sites	3	1.63	0.2	5206.9	2.6	2.61	0.7	11.90	12.8	183.1	1.8
Area(Site)	5	8.15	4.0**	4379.2	5.5***	2.81	2.2	1.99	5.4***	81.3	1.3
Area(Disturbed)	1	0.45	0.2	13992.1	24.3***	0.01	0.01	6.23	9.6**	0.0	0.0
Area(Reference)	4	10.08	5.2**	1976.0	2.3	3.51	2.7*	0.93	3.1*	101.6	1.3
Treatment	1	6.25	10.9*	1608.0	1.3	3.80	13.8*	0.79	25.0**	219.0	1.5
Treatment x Site	4	0.58	0.4	1253.6	1.0	0.27	0.8	0.03	0.04	145.3	1.8
Treatment x Disturbed	1	0.25	0.2	2052.1	1.6	0.00	0.01	0.12	0.2	54.8	0.7
Treatment x Reference	3	0.68	0.4	987.4	0.8	0.36	0.9	0.00	0.0	175.4	1.7
Treatment x Area(Site)	5	1.63	0.8	1279.5	1.6	0.33	0.3	0.78	2.1	81.8	1.3
Treatment x Area(Dist.)	1	0.45	0.2	1496.5	2.6	0.00	0.0	0.00	0.1	0.01	16.0**
Treatment x Area(Ref.)	4	1.93	1.0	1225.3	1.4	0.42	0.3	0.98	3.3*	102.3	1.3

	df					
Residual	80	2.04	800.7	1.31	0.37	65.0
Quadrats (Disturbed)	16	2.35	576.0	1.28	0.65	0.0
Quadrats (Reference)	64	1.96	856.9	1.31	0.30	81.3
Cochran's test		$C = 0.128$, ns	$C = 0.090$, ns	$C = 0.118$, ns	$C = 0.141$, ns	$C = 0.955$**
Transformation		None	None	Ln(x+1)	Ln(x+1)	None

Table 3.7, continued   *Patella aspera*

	df	MS	F
Site	4	23.55	5.9*
Dist. vs. Ref. sites	1	14.06	3.5
Among ref. sites	3	26.71	5.3
Area(Site)	5	4.01	1.1
Area(Disturbed)	1	0.001	1.6
Area(Reference)	4	5.01	1.1
Treatment	1	18.49	2.9
Treatment x Site	4	6.39	4.4
Treatment x Disturbed	1	4.62	3.2
Treatment x Reference	3	6.98	3.9
Treatment x Area(Site)	5	1.45	0.4
Treatment x Area(Dist.)	1	0.001	1.6

Treatment x Area(Ref.)	4	1.81	0.4
Residual	80	3.59	
Quadrats (Disturbed)	16	0.001	
Quadrats (Reference)	64	4.89	

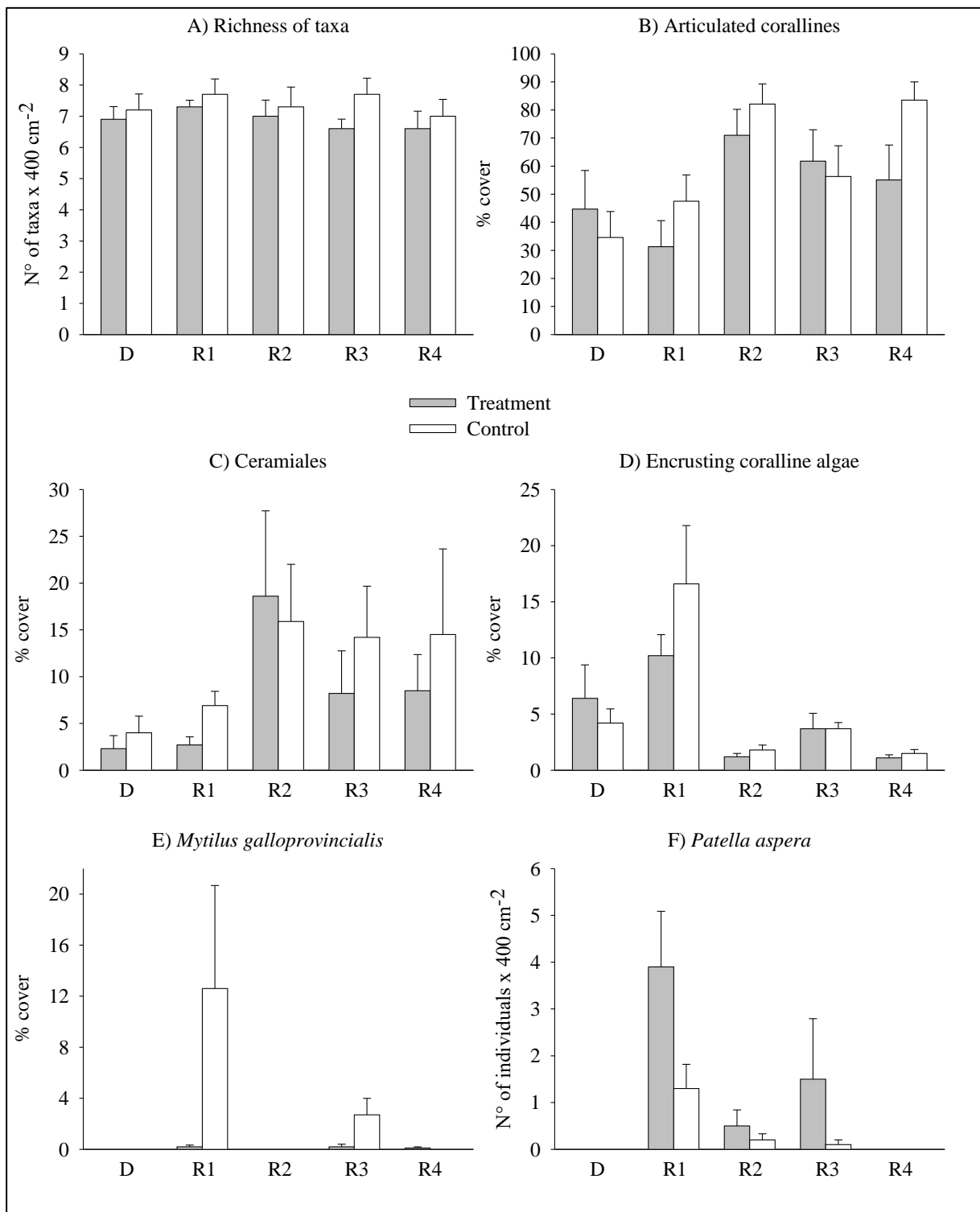|	
Cochran's test	$C = 0.471$**
Transformation	None

Figure 3.5. Mean (+SE) richness of taxa and abundance of individual taxa in treated and control plots within a disturbed site (D: Bagnoli-Coroglio) and four reference sites (R1: Napoli Chiaia, R2: Marechiaro, R3: Via Napoli Bagnoli, and R4: Via Napoli Pozzuoli), at four months and a half of recovery since experimental disturbance. Data averaged over five replicate plots and two areas.

Table 3.8. ANOVA comparing the total richness of taxa and the abundance of individual taxa between treated and control plots in each of two areas within a disturbed site (Bagnoli-Coroglio) and four reference sites (Napoli Chiaia, Marechiaro, Via Napoli Bagnoli, and Via Napoli Pozzuoli), at six months of recovery since experimental disturbance. Denominators for F as in Table 3.2. * $p<0.05$, ** $p<0.01$, *** $p<0.001$, ns = not significant.

Source of variation	df	Richness		Artic. corallines		Ceramiales		Encr. corallines		*M. galloprovincialis*	
		MS	F	MS	F	MS	F	MS	F	MS	F
Site	4	14.19	2.6	6034.7	1.9	3.99	5.4*	782.3	4.0	67.76	44.3***
Dist. vs. Ref. sites	1	1.10	0.2	1075.8	0.3	0.00	0.0	3.6	0.02	18.49	12.1*
Among ref. sites	3	18.55	2.7	7687.7	11.7*	5.31	5.9	1041.9	7.2	84.18	44.3**
Area(Site)	5	5.46	2.2*	3197.5	8.0***	0.74	1.1	197.2	1.5	1.53	0.1
Area(Disturbed)	1	0.05	0.02	13364.5	30.7***	0.11	0.1	405.0	1.4	0.05	1.0
Area(Reference)	4	6.81	2.7	655.8	1.7	0.90	1.4	145.2	1.6	1.90	0.1
Treatment	1	1.00	0.4	7.3	0.03	4.90	5.0	27.0	0.2	44.89	1.0
Treatment x Site	4	2.43	0.5	221.5	1.2	0.97	0.5	114.8	1.0	46.69	126.2***
Treatment x Disturbed	1	0.56	0.1	92.2	0.5	1.49	0.8	338.6	3.1	12.96	35.0**
Treatment x Reference	3	3.05	0.8	264.6	1.2	0.80	0.4	40.2	1.0	57.93	128.7***
Treatment x Area(Site)	5	4.70	1.9	190.4	0.5	1.93	2.9*	110.3	0.8	0.37	0.02
Treatment x Area(Dist.)	1	8.45	4.0	92.5	0.2	1.17	1.5	387.2	1.3	0.05	1.0
Treatment x Area(Ref.)	4	3.76	1.5	214.9	0.6	2.12	3.3*	41.1	0.5	0.45	0.02

Residual	80	2.45	397.5	0.67	130.2	17.60
Quadrats (Disturbed)	16	2.13	435.5	0.79	288.5	0.05
Quadrats (Reference)	64	2.53	388.0	0.64	90.6	21.99
Cochran's test		$C = 0.129$, ns	$C = 0.133$, ns	$C = 0.176$, ns	$C = 0.438$**	$C = 0.559$**
Transformation		None	None	Ln(x+1)	None	None

Table 3.8, continued   *Patella aspera*

Site	4	43.02	4.4
Dist. vs. Ref. sites	1	18.92	1.9
Among ref. sites	3	51.05	4.1
Area(Site)	5	9.86	2.3
Area(Disturbed)	1	0.05	1.0
Area(Reference)	4	12.31	2.3
Treatment	1	19.36	2.3
Treatment x Site	4	8.54	0.8
Treatment x Disturbed	1	3.80	0.4
Treatment x Reference	3	10.11	0.8
Treatment x Area(Site)	5	10.18	2.3*
Treatment x Area(Dist.)	1	0.05	1.0

Treatment x Area(Ref.)	4	12.71	2.3
Residual	80	4.35	
Quadrats (Disturbed)	16	0.05	
Quadrats (Reference)	64	5.42	

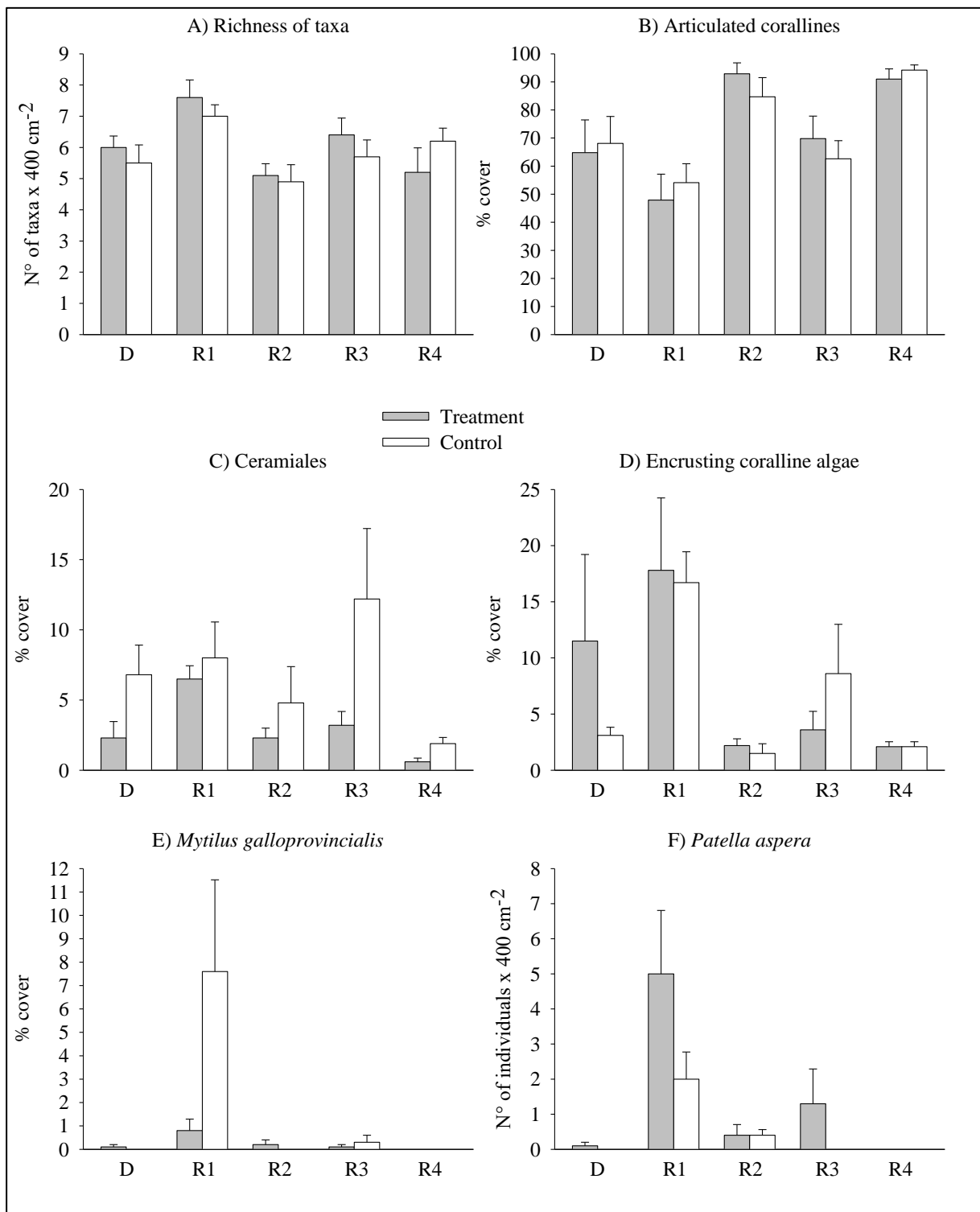|	
Cochran's test	$C = 0.559**$
Transformation	None

Figure 3.6. Mean (+SE) richness of taxa and abundance of individual taxa in treated and control plots within a disturbed site (D: Bagnoli-Coroglio) and four reference sites (R1: Napoli Chiaia, R2: Marechiaro, R3: Via Napoli Bagnoli, and R4: Via Napoli Pozzuoli), at six months of recovery since experimental disturbance. Data averaged over five replicate plots and two areas.

3.3. Multivariate and univariate temporal trajectories of recovery

The trajectories of recovery of the structure of whole assemblages differed only at the scale of areas within sites, irrespectively of all other examined factors (Table 3.9), as visually confirmed by the nMDS ordination plot which did not display any evident differences in the curves describing the temporal fluctuations of assemblages in the treated and the control condition in each of the total five sites (Figure 3.7).

Analogously, the temporal fluctuations of the total richness of taxa and of the abundance of the filamentous red algae of the order Ceramiales and of limpets did not show any significant differences (Table 3.10, and Figures 3.8 A, 3.8 C and 3.9 C, respectively). The recovery trajectories of articulated coralline algae were also not affected by the experimental treatment, while varied naturally among reference sites and between areas within the disturbed site (Table 3.10 and Figure 3.8 B). On the contrary, the removal treatment affected the recovery trajectories of encrusting coralline algae independently of the treated *vs.*control condition and the site (Table 3.10). Specifically, in spite of large natural variation among sites, the treated plots showed overall temporal fluctuations of these algae larger compared to the unmanipulated plots (Figure 3.9 A). finally, the recovery trajectories of *M. galloprovincialis* were affected by the experimental treatment only at the reference sites (Table 3.10), being the temporal fluctuations of mussels larger in the control than in the treated plots at R1, R3 and R4, and comparably very small at both conditions at R2, analogously to D (Figure 3.9 B).

Table 3.9. ANOVA comparing the temporal heterogeneity of the structure of assemblages between treated and control plots in each of two areas within a disturbed site (Bagnoli-Coroglio) and four reference sites (Napoli Chiaia, Marechiaro, Via Napoli Bagnoli, and Via Napoli Pozzuoli), over a period of six months of recovery (five times of sampling) since experimental disturbance. Denominators for F as in Table 3.2. * $p<0.05$, ** $p<0.01$, *** $p<0.001$, ns = not significant.

| Source of variation	df	MS	F
Site	4	13839270.6	0.6
Dist. vs. Ref. sites	1	5387598.1	0.2
Among ref. sites	3	16656494.7	0.9
Area(Site)	5	24558076.2	5.0***
Area(Disturbed)	1	48353347.3	8.3*
Area(Reference)	4	18609258.4	4.0**
Treatment	1	127324819.5	6.0
Treatment x Site	4	21076128.7	2.2
Treatment x Disturbed	1	45209352.0	4.7
Treatment x Reference	3	13031720.9	1.3
Treatment x Area(Site)	5	9536827.0	1.9
Treatment x Area(Dist.)	1	6283317.1	1.1
Treatment x Area(Ref.)	4	10350204.5	2.2
Residual	80	4911724.0	
Quadrats (Disturbed)	16	5856821.1	
Quadrats (Reference)	64	4675449.8	
Cochran's test		$C = 0.085$, ns	
Transformation		None	
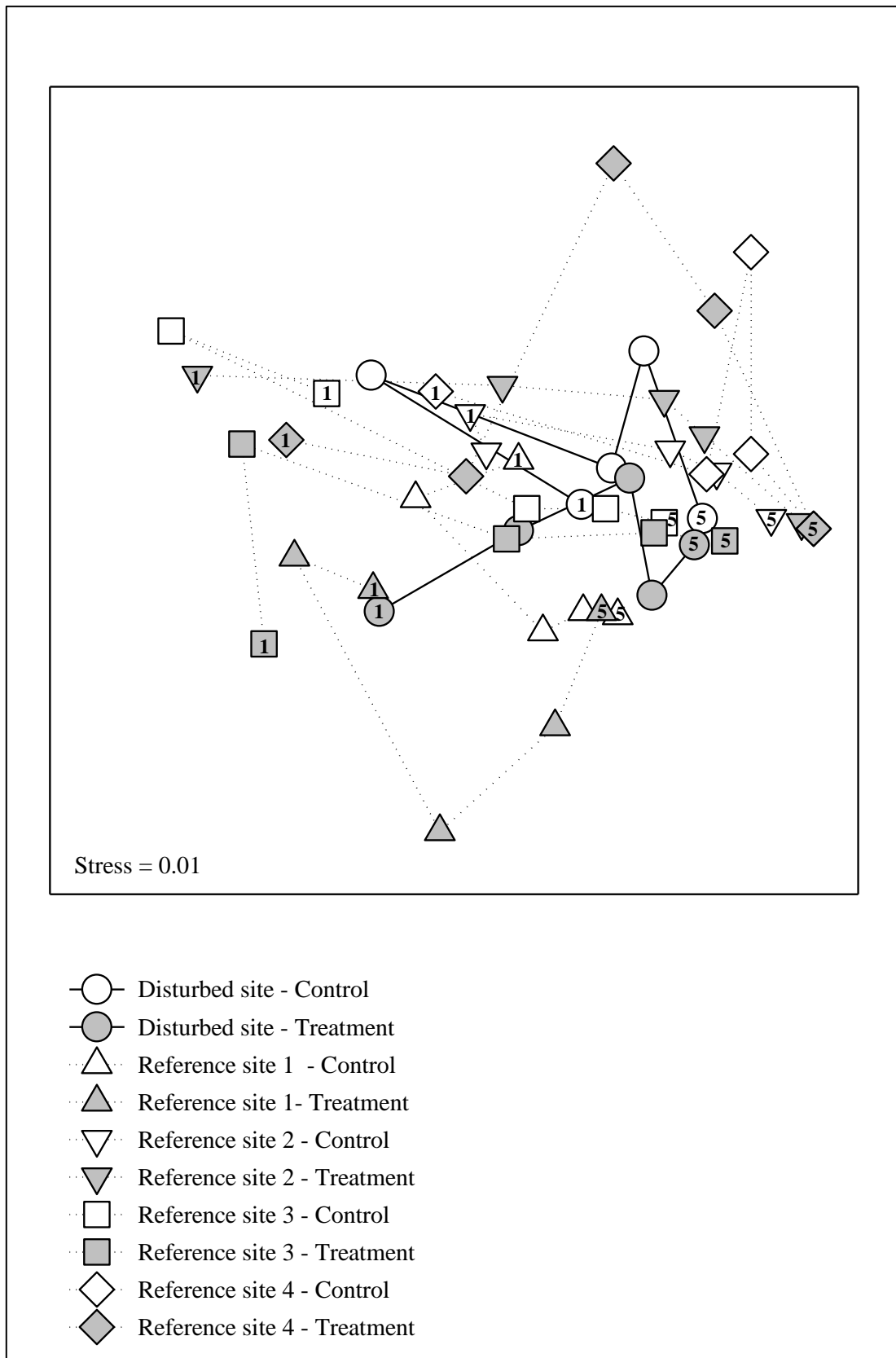
Figure 3.7. nMDS plots of the temporal trajectories of assemblages from the control and the treated condition in a disturbed site and four reference sites (centroids calculated over five replicate plots and two areas), sampled at each of five times since experimental disturbance (from 1 to 5: one, two, three and a half, four and a half, and six months of recovery, respectively).

Table 3.10. ANOVA comparing the temporal heterogeneity of the richness of taxa and the abundance of individual taxa between treated and control plots in each of two areas within a disturbed site (Bagnoli-Coroglio) and four reference sites (Napoli Chiaia, Marechiaro, Via Napoli Bagnoli, and Via Napoli Pozzuoli), over a period of six months of recovery (five times of sampling) since experimental disturbance. Denominators for F as in Table 1. * $p<0.05$, ** $p<0.01$, *** $p<0.001$, ns = not significant.

		Richness		Artic. corallines		Ceramiales		Encr. corallines		*M. galloprovincialis*	
Source of variation	df	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Site	4	0.56	1.2	1549821.3	4.3	1468552.1	2.8	27.80	12.8**	26511.5	1.5
Dist. vs. Ref. sites	1	0.04	0.1	83871.1	0.2	524458.4	1.0	0.18	0.1	24595.6	1.4
Among ref. sites	3	0.73	1.4	2038471.3	12.5*	1783250.0	3.6	37.01	16.9**	27150.1	11.7*
Area(Site)	5	0.47	2.2	360461.7	2.1	515637.1	2.1	2.17	0.8	18104.3	0.7
Area(Disturbed)	1	0.30	1.6	1151040.2	7.6*	570206.5	2.9	2.10	0.4	81217.5	1.0
Area(Reference)	4	0.51	2.3	162817.1	0.9	501994.8	1.9	2.19	1.0	2326.0	0.2
Treatment	1	0.01	0.1	990164.3	2.3	339271.3	0.2	76.28	31.5**	107538.1	4.2
Treatment x Site	4	0.20	0.9	425495.3	1.7	2259221.9	4.1	2.42	0.9	25313.3	1.4
Treatment x Disturbed	1	0.21	0.9	1311906.8	5.1	3330314.8	6.1	0.14	0.1	25475.4	1.4
Treatment x Reference	3	0.20	1.7	130624.8	0.4	1902191.0	2.9	3.18	1.0	25259.3	9.4*
Treatment x Area(Site)	5	0.23	1.1	256075.2	1.5	548146.1	2.2	2.66	0.9	18447.9	0.7
Treatment x Area(Dist.)	1	0.69	3.6	31.8	0.0	143549.6	0.7	0.71	0.1	81472.6	1.0

	df	MS	F	MS	F	MS	F	MS	F	MS	F
Treatment x Area(Ref.)	4	0.12	0.5	320086.1	1.8	649295.3	2.5	3.14	1.4	2691.7	0.2
Residual	80	0.22		170959.9		249702.6		2.81		25264.5	
Quadrats (Disturbed)	16	0.19		151801.5		199582.2		5.02		81749.4	
Quadrats (Reference)	64	0.22		175749.5		262232.7		2.26		11143.2	
Cochran's test		$C = 0.141$, ns		$C = 0.148$, ns		$C = 0.137$, ns		$C = 0.130$, ns		$C = 0.647**$	
Transformation		Ln(x+1)		None		None		Ln(x+1)		None	

Table 3.10, continued   *Patella aspera*

	df	MS	F
Site	4	235.8	1.8
Dist. vs. Ref. sites	1	158.4	1.2
Among ref. sites	3	261.6	1.6
Area(Site)	5	127.9	1.3
Area(Disturbed)	1	0.1	0.1
Area(Reference)	4	159.9	1.3
Treatment	1	278.6	2.0
Treatment x Site	4	136.8	0.9
Treatment x Disturbed	1	89.2	0.6
Treatment x Reference	3	152.7	0.8
Treatment x Area(Site)	5	152.2	1.6

Treatment x Area(Dist.)	1	0.1	0.1
Treatment x Area(Ref.)	4	190.2	1.6
Residual	80	96.8	
Quadrats (Disturbed)	16	0.6	
Quadrats (Reference)	64	120.8	

Cochran's test	$C = 0.672**$
Transformation	None
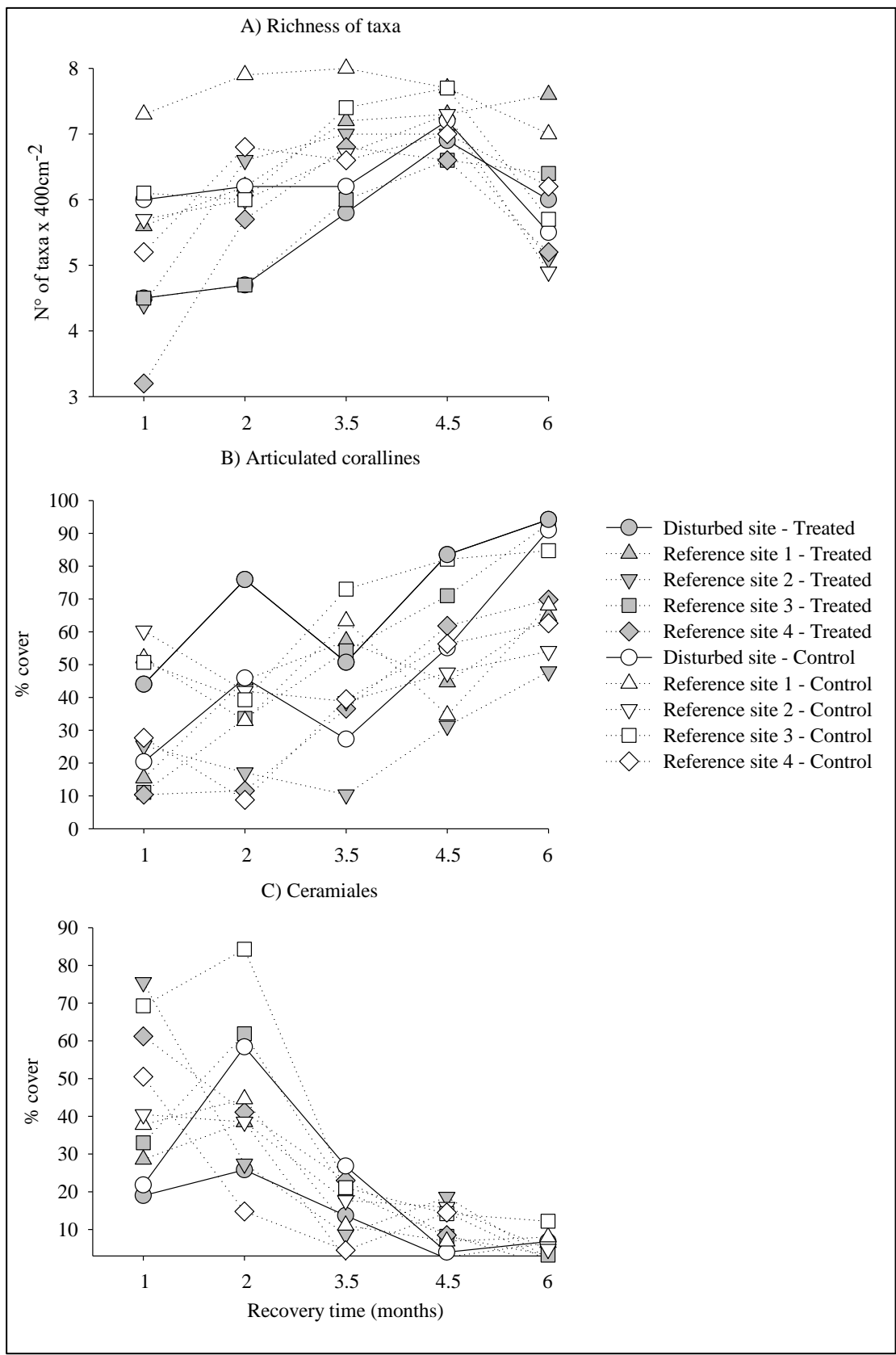
Figure 3.8. Temporal fluctuations of the total richness of taxa and of the abundance of individual taxa sampled at five times of recovery in treated and control plots at one disturbed and four reference sites. Data averaged over five replicate plots and two areas, but standard error bars were omitted for clarity.
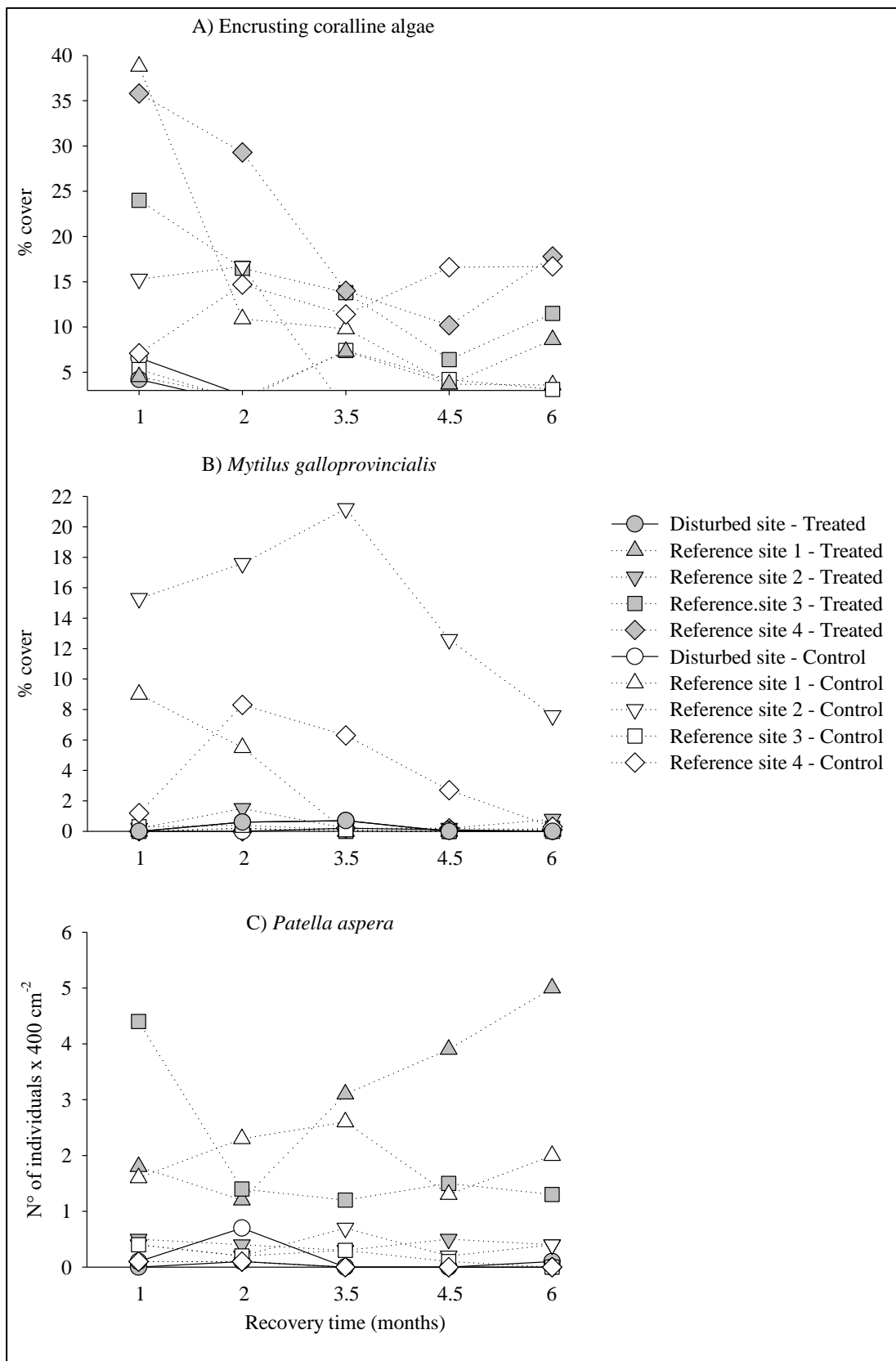
Figure 3.9. Temporal fluctuations of the abundance of individual taxa sampled at five times of recovery in treated and control plots at one disturbed and four reference sites. Data averaged over five replicate plots and two areas, but standard error bars were omitted for clarity.

4. DISCUSSION

This study was carried out to compare the ability of lowshore assemblages to recover from physical disturbance between the Bagnoli-Coroglio post-industrial site and four reference sites interspersed around it in the Gulf of Naples. In broad terms, two alternative predictions were tested: (i) organisms historically subject to chronic contamination may respond better and more quickly to a discrete and punctual disturbance compared to analogous organisms coming from reference sites putatively not influenced by the same contamination, due to their adaptation and developed resistance to environmental stressful conditions; (ii) by contrast, the organisms from the historically contaminated site may be relatively more sensitive to the new disturbance if the extant chronic stress maintained them close to their tolerance limits.

In general, the present findings suggest that the examined benthic assemblages were characterized by great ability to recover after a pulse-type disturbance, and that this ability was comparable between the post-industrial site and the reference sites. In fact, the most evident differences between the treated and the control plot occurred in the first recovery phases (up to two months after experimental disturbance), when the originally dominant organisms, namely articulated coralline algae, were obviously less abundant in the treated condition at all sites, while ephemeral filamentous algae of the Ceramiales order were found in large percentage cover. This pattern tended to reverse back in the subsequent sampling times, when articulated coralline algae begin to re-occupy and dominate again the treated plots. Such dynamics may be initially explained by the ability of ephemeral algae to take advantage of the resources, primarily space, released by the experimental removal of dominant algal competitors. The ability of filamentous macroalgae to grow on the surface of algal crusts, such as those that remained on the substrate after the removal treatment, may have played a role in this process (Figueiredo et al. 1996). At a later stage, however, it is likely that the cover of ephemeral algae facilitated the survival and growth of recruits of articulated coralline algae, as previously documented especially in intertidal habitats under intense stress associated with physical factors such as temperature, desiccation and wave action (Bertness and Leonard 1997). Such an effect may be driven by the amelioration, by ephemeral algae, of the abiotic conditions occurring on the substrate below them, which would result into an increased probability of survival of recruits of coralline algae (Coleman 2003). Similarly to articulated coralline algae, although never reaching large values, the abundance of invertebrates was also drastically reduced in the first months after disturbance, consistently with the previously reported effect of intense disturbance and harsh environmental conditions on these animals from rocky shores (Bertness 1999; Cimon and Cusson 2018). Instead, more surprising was the comparable ability of whole

assemblages and individual taxa to quickly recover at the Bagnoli-Coroglio site and at the reference sites. The present study was not designed to formally test for any specific processes involved in the recovery dynamics of the examined organisms, but some, not mutually exclusive, explanations can be proposed for such a result.

First, intertidal algal and invertebrate assemblages such as the present ones are known to possess great abilities to recover quickly and effectively after disturbance, which may have made any concomitant factors that were likely to differ between the contaminated site and the reference sites virtually unable to affect the recovery process. Indeed, several algal groups that are common in rocky intertidal habitats have been described as capable of very rapid recovery after a disturbance regardless of concomitant processes varying in both space and time (Airoldi 2000). Coralline algae, in particular, play an important role in the functioning of marine ecosystems, including the resilience of intertidal assemblages (Gattuso et al. 1998, Couto et al. 2012). A major contribution to this ability is due to their content in calcium carbonate in the form of calcite, which provides physical resistance and makes these algae one of the most important structural elements in coastal rocky areas. Moreover, the same macroalgae may be highly resistant to chemical contamination. They are often used as bioindicators of metal pollution due to their ability to accumulate metals (Mohamed and Khaled 2005; Wallenstein et al., 2009; Couto et al., 2010). Such a characteristic may have allowed such algae to recover at the historically contaminate site as well as at the references sites. Good recovery abilities are reported also for sessile invertebrates such as mussels, which are strong competitors for space in rocky intertidal habitats and can attain large cover soon after disturbance events, especially in periods of high larval supply (Holt et al., 1998). Sessile invertebrates, however, normally show longer recovery time due to their complex life cycles and relatively slow growth rates (Vance 1973; Watling and Norse 1998; Bevilacqua et al., 2006).

Second, this study was done in the highly urbanized and man-made environment of the Gulf of Naples. Therefore, even if the Bagnoli-Coroglio site is unique in terms of the presence of the former industrial plant, the reference sites are exposed to a range of other disturbances that are likely to occur all over the Gulf. Assessing the realized impacts of such disturbances and their underlying mechanisms was beyond the goals of this work, but it may be hypothesized that they could determine high 'background' levels of environmental and anthropogenic stress at the reference sites too. If the combined and potentially synergistic effects of such disturbance was such as to overwhelm the peculiar effects of chronic contamination at the post-industrial site, that would explain the comparable patterns of recovery of assemblages between such a site and, on average, the reference site. A possible relevant contribution to such a circumstance could

have been provided by the fact that the resilience of natural populations and assemblages depends not only on the nature of disturbance, but also and more importantly on the number of compounded factors to which they are subject and likely to respond in complex, often nonlinear and unexpected ways (Underwood 1989; Paine et al. 1998; Cimon and Cusson 2018).

In this respect, the relatively 'simple' and not very diverse structure of lowshore assemblages at all five experimental sites may actually suggest the occurrence of consistent harsh environmental conditions able to maintain a low diversity within and between functional groups. It is worth noting, however, that such an extant feature of the examined assemblages would have led to predict even stronger, rather than weaker, effects of further stressful conditions. In fact, the co-occurrence of species that play similar ecological roles may potentially provide alternative ways to maintain key ecosystem functions under severe stress, allowing assemblages to more effectively resist by reorganizing and maintaining their biological interactions and dynamics, and to more quickly recover after disturbance-induced changes by taking advantage of a range of alternative options for development and evolution (Nyström et al. 2000). Such processes would obviously be jeopardised by an already depressed diversity of assemblages, as reported, for example, in eutrophic systems where nutrient enrichment alone may stimulate the growth and the abundance of several algal species, but can also determine slower resilience when combined with other stressors (e.g., Littler and Murray 1975, 1978). Analogously, in terrestrial systems, it was reported a progressive reduction of the resistance and recovery ability of organisms with increasingly severe disturbance, due to its destabilization of assemblages (Collins 2000; Fraterrigo and Rusak 2008). So, it can also not be excluded that the chronic contamination at the Bagnoli-Coroglio site did not exert any large effects on assemblages from lowshore rocky habitats. In spite of the available evidence that a severe contamination by heavy metals and PAHs exists in shallow-water sediments all over the post-industrial area (Sharp and Nardi 1987; Romano et al. 2004, 2009; Arienzo et al. 2017; Trifuoggi et al. 2017), and that contaminated sediments may be largely re-worked, re-suspended and potentially spread to adjacent habitats by wave action during storms (e.g., Sunamura and Kraus 1985; Sherman et al. 1994), it may be that the actual main impacts of such a contamination remained limited within sediments themselves and associated organisms, exerting very limited effects on nearby rocky systems even if periodically exposed to it.

Third, and strictly linked to the previous point, the reference sites were not chosen to represent any 'pristine' environmental conditions that were logistically impossible to find, but, following the logic and requirements of sampling and experimental designs suited to assess environmental impacts, were intended to capture as much as possible the variability of sites as much as possible

similar biologically, ecologically, geographically and geologically to the post-industrial one, with the exception of the local presence of the former industrial plant (Underwood 1991, 1992, 1993, 1994; Benedetti-Cecchi 2001). Under such circumstances, the documented large and often significant variability both among- and within-sites may have, at least in part, masked any actual effects of the performed experimental treatment and their differences between the disturbed site and the reference sites. Indeed, the intrinsic variability existing at the reference sites would have required that the responses of assemblages from the Bagnoli-Coroglio site were very different than those of similar assemblages from the reference sites, since such difference, to be detected as significant, should have been large enough to overwhelm the degree of 'natural' (i.e., not directly related to the presence of the former industrial plant and associated contamination) variability characterizing the reference sites and also the disturbed site at smaller (among areas) scale. Considerable spatial variation over a spatial scale comparable to that spanned by the present experimental sites was documented by previous studies that have compared the responses and recovery patterns of rocky intertidal assemblages to physical disturbance between sites located a few kilometres apart and characterized by very similar abiotic conditions (Oliveira et al. 2014, 2015). Among the possible driving processes of large natural variation at such a scale, there is, for example, the large and almost unpredictable variation in the larval supply, dispersal and colonization of sessile organisms (e.g., Raimondi 1990).

Finally, it is worth noting that the present thesis spanned only the first six months of recovery since experimental disturbance. Further effects of the removal treatment, potentially differing between the disturbed site and, on average, the reference sites, may become evident at later stages of the ongoing research, when the examined period will have covered the full range of the yearly cycle of most of the examined organisms and of their underlying processes.

5. CONCLUSION

As far as just a relatively short period since a physical disturbance able to remove all erect organisms is concerned, the present findings suggest that lowshore assemblages from the Bagnoli-Coroglio system have fast recovery ability that are comparable with those of analogous assemblages from nearby sites located outside the historically most contaminated area. This was initially unexpected, but it may indicate that the most severe and ecologically relevant contamination and associated impacts are 'limited' to the sediments located within the post-industrial area, and do not propagate considerably to the adjacent rocky habitats. Alternatively, however, the background environmental conditions of the whole Gulf of Naples could have been already as altered, especially along the mainland, by several human activities as to overwhelm any specific effects of the chronic contamination existing at Bagnoli-Coroglio, eventually leading to maintain the local biodiversity virtually under the same stressful environmental conditions. Separating such two alternatives would be a key objective of future research as it would bear important implications for the direction and scale of possible future management and restoration strategies in this area. Independently of what the next answer to such a question is going to be, the present findings highlight the need for taking into careful consideration the natural variability of the examined system in any future interventions, to guarantee a proper representation of the whole range of variation of the target organisms and of the underlying processes (e.g., Chapman et al. 1995; Bishop et al. 2002; Benedetti-Cecchi et al. 2003; Terlizzi et al. 2005a, 2oo5b; Fraschetti et al. 2006; Bertocci et al. 2019). This principle should be applied even if such processes were not yet known. Nevertheless, it is recommended that future research will be based on specifically designed experiments suited to test alternative hypotheses on the abiotic and biological processes, either specifically related to the chronic post-industrial contamination or to other concomitant factors, that can affect populations and assemblages at the Bagnoli-Coroglio site and at adjacent sites.

Finally, this study emphasizes the need for not considering natural variability as 'noise' to be a-priori eliminated, but a main component of the studied system that should be properly included in any sampling and experimental design aimed at assessing the impact of any disturbance over and above the variability due to other sources. In a system such as Bagnoli-Coroglio, it is evident that any environmental impact assessment that would involve, as too often done, the comparison between a single disturbed site with a single control site, would likely detect significant differences, but would easily and necessarily lead to confound the intended impact with the effect of other natural and/or anthropogenic processes (Benedetti-Cecchi 2001). This may have undesired and further negative consequences if, as expected,

management and conservation measures that have important ecological and societal implications were based on conclusions drawn from biased empirical evidence.

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