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The two facets of species sensitivity: Stress and disturbance on coralligenous assemblages in space and time

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ABSTRACT

Marine coastal ecosystems are affected by a vast array of human-induced disturbances and stresses, which are often capable of overwhelming the effects of natural changes. Despite the conceptual and practical difficulty in differentiating between disturbance and stress, which are often used interchangeably, the two terms bear different ecological meanings. Both are external agents, but the former causes mortality or physical damage (subtraction of biomass), whereas the latter causes physiological alteration (reduction in productivity). Sensitivity of marine organisms may thus have a dual connotation, being influenced in different ways by disturbance and by stress following major environmental change. Coralligenous assemblages, which shape unique biogenic formations in the Mediterranean Sea, are considered highly sensitive to change. In this paper, we propose a method to differentiate between disturbance and stress to assess the ecological status of the coralligenous assemblages. Disturbance sensitivity level (DSL) and stress sensitivity level (SSL) of the sessile organisms thriving in the coralligenous assemblages were combined into the integrated sensitivity level of coralligenous assemblages (ISLA) index. Changes in the coralligenous status were assessed in space, along a gradient of stress (human-induced pressures) at several sites of the western Mediterranean, and in time, from a long-term series (1961–2008) at Mesco Reef (Ligurian Sea) that encompasses a mass mortality event in the 1990s. The quality of the coralligenous assemblages was lower in highly urbanised sites than that in sites in both marine protected areas and areas with low levels of urbanisation; moreover, the quality of the assemblages at Mesco Reef decreased during the last 50 years. Reduction in quality was mainly due to the increase in stress-tolerant and/or opportunist species (e.g. algal turfs, hydroids and encrusting sponges), the disappearance of the most sensitive macroalgae (e.g. Udoteaceae and erect Rhodophyta) and macro-invertebrates (e.g. *Savalia savaglia*, *Alcyonium coralloides* and *Smittina cervicornis*), and the appearance of invasive alien algal species. Although the specific indices of SSL or DSL well illustrated the changes in the spatial or temporal datasets, respectively, their integration in the ISLA index was more effective in measuring the change experienced by the coralligenous assemblages in both space and time.

1. Introduction

Most ecosystems are, directly or indirectly, under the human control (Crutzen, 2002). Heavy and unprecedented human-induced impacts are widespread today and often are capable of overwhelming the effects of natural change. Marine coastal ecosystems, in particular, are declining around the world across a broad range of spatial and temporal scales. In many regions, they have already been significantly altered by overfishing, pollution, eutrophication, global warming, ocean acidification and spread of invasive species (Thrush et al., 2009). Ecosystems are therefore affected by a large array of disturbances and stresses that undermine, either abruptly or gradually, their state of health.

A sharp and rigid distinction, both conceptual and practical, between disturbance and stress has been hardly achieved, and much depends on the intensity and duration of the external affectors involved. The terms disturbance and stress are also often used interchangeably; in fact, they have the general meaning of worry (Montefalcone et al., 2011). However, stress and disturbance have a different ecological connotation, and the most useful and clear definitions are those given by Grime (1977). He stated that both disturbance and stress are external factors (i.e. causes): subtraction (partial or total) of biomass is the primary effect of disturbance, whilst reduced production is the primary effect of stress. Effects of disturbance may be evidenced by a discrete and punctuated mortality, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity

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for new individuals (or colonies) to become established (Sousa, 1984). Stress may induce a condition of physiological alteration in organisms or populations in response to variations in the levels of environmental factors and occurs below the intensity that produces mortality and/or the time that allows adaptation (Levitt, 1972).

According to their biological characteristics (e.g. longevity, size, susceptibility to contaminants), organisms may show different levels of sensitivities to disturbance (i.e. the contrary of resistance) and stress (i.e. the contrary of tolerance) (García-Gómez, 2015). Sensitivity to disturbance refers to the susceptibility of organisms to be physically injured or killed by exposure to specific external factors (e.g. mechanical impacts, climate anomalies) and the ability of survivors to adjust to change and then recover. Sensitivity to stress refers to the capacity of an organism to tolerate and to cope with, and eventually adapt to, altered environmental quality (e.g. pollution, water turbidity). According to Grime (1977), extremely stressed environments favour communities composed of stress-tolerant species that withstand such conditions. Stress-tolerant species have low production ability because they have to spend energy to cope with the stress. It can be argued that stress implies the possibility of adaptation, and the metabolic cost of adaptation implies a limitation of production. External factors such as substratum loss, overfishing, anchoring, climate anomalies and spread of invasive species can conversely be viewed as disturbances. By coupling sensitivity to disturbance (or resistance) and sensitivity to stress (or tolerance), each species is characterised by its own resilience to environmental alterations. In ecology, resilience is a complex cluster of concepts that describes the stability of ecosystems and their responses to external perturbations, focussing in particular on their ability to recover (i.e. to return to its previous condition) after a perturbation (Holling, 1973; Montefalcone et al., 2011).

Species sensitivity is a commonly used descriptor in various ecological indices for assessing marine environmental quality, as requested by the most recent European Directives, i.e. the Water Framework Directive (WFD) (EC, 2000) and the Marine Strategy Framework Directive (MSFD) (EC, 2008) (García-Gómez, 2015; Leonardsson et al., 2015). A high sensitivity value implies that the species is seldom found in altered environments. On the contrary, a low sensitivity value implies that the species can be predominantly found in altered environments (Harmelin and Capo, 2002). Among the marine habitats adopted to monitor the health status of coastal waters, the coralligenous habitat is one of the most important habitats in the Mediterranean Sea because of its high biodiversity and the role it plays in the carbonate cycle (Laborel, 1961, 1987; UNEP, 2007). Being the main calcareous formation of biogenic origin in the Mediterranean, the coralligenous habitat was included among the 'special habitat types' that should be assessed under the MSFD (EC, 2008) through accurate monitoring plans. The coralligenous habitat is the typical rocky habitat of the circalittoral Mediterranean zone and is characterised by bioconstruction, primarily due to calcareous red algae belonging to Corallinales and Peyssonneliales and secondarily by cnidarians, polychaetes and bryozoans (Ballesteros, 2006; Martin et al., 2014). This habitat is maintained because of a delicate balance between bioconstruction and bioerosion, and this balance can be easily broken by extreme natural events or human-induced perturbations (Ballesteros, 2006, and reference therein). Thus, coralligenous assemblages are considered highly sensitive to stress following water quality alterations such as sedimentation, pollution and eutrophication and extremely sensitive to disturbances such as invasion by alien species, mechanical destruction by fishing or anchoring and global warming (Hong, 1983; Piazzi et al., 2012; Gatti et al., 2015a, 2015b). All these pressures act synergistically on coralligenous assemblages, modifying the patterns of spatial variability and causing shifts in the structure and composition of assemblages by decreasing the number of sensitive organisms and increasing the number of resistant and tolerant ones (Gray, 1997; Arevalo et al., 2007; Piazzi and Balata, 2011).

Previous indices that adopted the sensitivity of coralligenous species as a descriptor of ecological quality considered only the sensitivity to stress induced by water quality alteration and used macroalgae to evaluate responses of assemblages to human-induced stress (Balata et al., 2007a, 2007b, 2011; Piazzi et al., 2011, 2012, 2015; Cecchi et al., 2014). Although sessile macro-invertebrates are a dominant component of coralligenous assemblages (Ballesteros, 2006) and are also considered sensitive to different pressures (Garrabou et al., 1998, 2009; Cerrano et al., 2000; Balata et al., 2005, 2007a; Kipson et al., 2011; Deter et al., 2012; Gatti et al., 2012, 2015a, 2015b), their different responses to stress and disturbance have rarely been addressed. Macro-invertebrates have been widely used to evaluate the ecological quality of soft-bottom habitats (Borja et al., 2000; Simboura and Zenetos, 2002; Rosenberg et al., 2004; Teixeira et al., 2009), and only one method has been proposed for macro-invertebrates of shallow rocky bottoms (Orlando-Bonaca et al., 2012).

The aim of this paper is to propose a method to distinguish and measure the sensitivity to stress and the sensitivity to disturbance of the sessile organisms thriving in coralligenous assemblages. An integrated ecological index based on a biocoenotic approach and combining the two components of sensitivity was then elaborated to assess the ecological status of the coralligenous habitat. The following steps were performed:

i. a list of the main taxa or morphological groups of macroalgae and sessile macro-invertebrates of coralligenous assemblages was compiled;
ii. the sensitivity level of taxa/morphological groups to disturbance was evaluated using their biological traits;
iii. the sensitivity level of taxa/morphological groups to stress was evaluated using an expert judgment approach;
iv. sensitivity to disturbance and sensitivity to stress were combined into an integrated value of sensitivity level for each taxon/morphological group with respect to anthropogenic pressures, and the integrated sensitivity level of coralligenous assemblages (ISLA) index was thus defined to evaluate the ecological status of the coralligenous assemblages;
v. the effectiveness of the ISLA index in space and time was tested on two different datasets: (1) a 'spatial' dataset obtained from different sites in the western Mediterranean Sea along a gradient of human-induced pressure and (2) a 'temporal' dataset obtained from the long-term assessment (1961 to 2008), encompassing a mass mortality event in the 1990s, of the coralligenous assemblages at Mesco Reef (Ligurian Sea, NW Mediterranean).

2. Methods

2.1. Coralligenous assemblages

We compiled a list of the most characteristic macroalgae and sessile macro-invertebrates that can be found in coralligenous assemblages (Table 1), following Ballesteros (2006), Cecchi et al. (2014), Gatti et al. (2015b) and Piazzi et al. (2015). We also considered a number of operational taxonomic units (OTUs) that can be easily recognised on photographs, which lump taxa into morphological groups where all species show similar morphological features (see for instance Balata et al., 2011; Cecchi et al., 2014).

2.2. Disturbance sensitivity level

To evaluate the disturbance sensitivity level (DSL) of each taxon/morphological group, we considered the method proposed by Darling et al. (2012), who predicted how different benthic species respond to environmental disturbances by inferring their life-history strategies from biological traits. A trait-based classification approach was thus applied, and a total of 6 commonly available biological traits were used to classify the DSL of coralligenous taxa/groups: (1) individual/colony growth form, (2) reproductive mode, (3) individual/colony size, (4) growth rate, (5) bioconstruction potential and (6) generation time (Table 2). We specifically focused on traits that were expected to