

THE ROLE OF WAVE-EXPOSURE AND HUMAN IMPACTS IN REGULATING THE
DISTRIBUTION OF ALTERNATIVE HABITATS ON SHALLOW ROCKY REEFS IN THE NW
MEDITERRANEAN

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Abstract

The global decline of canopy-forming macroalgae has stimulated research on the mechanism regulating shifts among alternative habitats on rocky reefs. The effects of sea urchin grazing and alterations of environmental conditions are now acknowledged as the main drivers of shifts between canopy-formers and encrusting coralline barrens and algal turfs, respectively. The conditions under which these mechanisms operate remains, however, somewhat elusive. This is mostly a consequence of the fact that our current understanding has been generated by envisioning habitat shifts as dichotomic, at odds with rocky reef landscapes being composed by mosaics of habitats and with evidence of strong interactions among the species that compose each of the alternative habitats. Using data from a long-term sampling program and path analysis, we investigated how wave-exposure and human-induced degradation of environmental conditions regulate the mechanisms maintaining algal canopies formed by *Cystoseira brachycarpa*, barren habitats and algal turfs as alternative states on subtidal reefs in the NW Mediterranean. In the Tuscan Archipelago, wave-exposure had positive effects on sea urchins, which, likely due to their low density, had weak effects on each of the alternative habitats. Canopy-forming macroalgae resulted, instead, to exert strong negative effects on the abundance of algal turfs. Since data from the Tuscan Archipelago did not explain any of the variation in the abundance of *C. brachycarpa* canopies, a further analysis was performed including data from the coast of Tuscany to assess the role of cumulative human impacts in regulating habitat shifts. This showed that degradation of environmental conditions directly cause the decline of macroalgal canopies, indirectly favouring the dominance of algal turfs. Our study suggests that management of human impacts should be considered a priority for preserving subtidal canopies formed by *Cystoseira* in the NW Mediterranean and that conservation efforts based exclusively on the control of sea urchin populations would be deemed to failure.

1. Introduction

25 Subtidal macroalgal forests are among the most diverse and productive coastal marine systems
(Steneck and Johnson 2014). Understanding the causes of the current global decline of canopy-forming
macroalgae, either Laminariales or Fucooids (Vogt and Schramm, 1991; Benedetti-Cecchi et al., 2001;
Lilley and Schiel, 2006; Airoidi and Beck, 2007; Mangialajo et al., 2008; Gorman and Connell 2009;
Strain et al., 2014; Thibaut et al., 2015) has, thus, become a priority for marine ecologists. A
30 considerable research effort has produced general consensus over some of the mechanisms
underpinning shifts in dominance from macroalgal canopy beds to alternative habitats, such as those
characterized by the dominance of encrusting corallines, generally referred to as barren grounds, or
algal turfs. Sea urchin grazing is now widely acknowledged as the main driver of shifts in dominance
from erect algal forms to barrens (Lawrence, 1975; Fletcher, 1987; Andrew, 1993; Andrew and
35 Underwood, 1993; Benedetti-Cecchi et al., 1998; Bulleri et al., 1999; Sivertsen, 2006; Hereu et al.,
2008; Hernandez et al., 2008; Norderhaug and Christie, 2009; Feehan et al., 2012; Ling et al., 2008,
2009; Filbee-Dexter and Scheibling, 2014; Perreault et al., 2014). By contrast, alterations in abiotic
conditions, such enhanced sediment deposition and nutrient loading (Gorgula and Connell, 2004;
Airoidi and Beck, 2007; Gorman and Connell, 2009; Tamburello et al., 2012; Alestra and Schiel, 2014;
40 Balata et al., 2015), have been identified as the main drivers of shifts in dominance from canopy-
formers to algal turfs.

 The conditions under which these mechanisms operate remain, however, somewhat elusive. This
is mostly a consequence of the fact that our current understanding has been generated envisioning
habitat shifts as dichotomic. The vast majority of studies has focused on pair-wise habitat interactions
45 and on single external drivers, either biotic or abiotic, that is shifts between macroalgal canopies and
barrens regulated by herbivore pressure (reviewed by Filbee-Dexter and Scheibling, 2014) or shifts
between macroalgal canopies and algal turfs regulated by alterations in environmental conditions

(reviewed by Airoidi and Beck, 2007). This is at odds with subtidal landscapes being often characterized by multiple habitat mosaics, including canopy-formers, algal turfs and encrusting coralline barrens (Jones and Andrew, 1990; Bulleri and Benedetti-Cecchi, 2006; Tamburello et al., 2012), and with 50 compelling evidence of strong interactions among the species that compose each of them (Breitburg, 1984; Kennelly, 1987; Airoidi, 2000; Bulleri et al., 2002; Gorgula and Connell, 2004; Alestra and Schiel, 2014).

Life-traits, such as timing and prevalent mode of reproduction (e.g., sexual *versus* vegetative, size 55 and toughness of thallus) of the macroalgae that compose alternative habitats influence their ability to retain or acquire space, as well as their susceptibility to herbivory (Santelices, 1990; Airoidi, 1998; Lauzon-Guay and Scheibling, 2007; Agnetta et al., 2015). For instance, most of the Laminariales or Fucoids that form canopies reproduce annually and are fertile within a short temporal window (Brawley and Johnson, 1992; Gianni et al., 2013), whilst species composing algal turfs are generally 60 fertile throughout the year and can also acquire space via vegetative propagation (Airoidi, 1998, 2000; Connell et al., 2011). Algal turfs, in virtue of their opportunistic life-traits, may take advantage of natural fluctuations in grazing pressure, due to either declines in urchin populations or shifts in their feeding habit from active to passive, more readily than canopy-forming species (Bulleri, 2013). Recovery of macroalgal canopies following decreases in grazing pressure may be, therefore, prevented 65 when turf-forming species are present within regional pools. Likewise, the ability of sea urchins to form and maintain barrens is likely to vary according to the life-traits that are dominant in erect macroalgal assemblages. Easier handling may allow sea urchin to maintain higher consumption rates of algal turfs in respect to canopy-formers (Lauzon-Guay and Scheibling, 2007; Bulleri, 2013; Felbee-Dexter and Scheibling, 2014; Agnetta et al., 2015). On the other hand, more efficient re-colonization of 70 space by algal turfs may require grazing pressure to be constant to avoid barren swamping when these algal forms are dominant within the local pool (Bulleri, 2013).

Further complexity is generated by the fact that competitive and consumptive interactions that regulate habitat shift dynamics are influenced by environmental factors. For instance, the outcome of competition between canopy- and turf-forming species depends on water quality, with shifts in dominance from canopy-formers to algal turfs been documented worldwide (Gorman and Connell, 2009; Benedetti-Cecchi et al., 2001; Mangialajo et al., 2008). Likewise, mechanical disturbance due to hydrodynamic forces can promote the formation or the persistence of encrusting dominated barrens, either directly, by dislodging erect macroalgae (Dayton et al., 1992; Byrnes et al., 2011) or reducing their settlement or early-stage survival (Santelices, 1990). Wave-action can, by the other hand, constrain sea urchin foraging activity (Himmelman and Steele, 1971; Benedetti-Cecchi et al., 1998; Lauzon-Guay and Scheibling 2007; Konar, 2000; Feehan et al., 2012; Gianguzza et al., 2013), promoting the persistence of erect algal stands, at expense of encrusting forms. Trade-off between negative and positive effects of wave-exposure on erect macroalgae is, therefore, likely to determine the net effect of wave-action on contrasting habitats on shallow rocky reefs.

This evidence suggests that a comprehensive understanding of the mechanisms that regulate the spatial and temporal distribution of different habitats on rocky reefs cannot be achieved without simultaneously taking into account the complex web of interactions among the species that form each of the alternative habitats and the way they are modified by exogenous biotic and abiotic drivers. Here, using data from a long-term sampling program and path analysis, we investigated how wave-exposure and human-induced degradation of environmental conditions regulate the mechanisms maintaining algal canopies, barren habitats and algal turfs as alternative states on subtidal reefs in the Tuscan Archipelago and along the main coast of Tuscan (Italy). On shallow rocky reefs of islands in the Tuscan Archipelago, canopy stands formed by the Furoid, *Cystoseira brachycarpa* J. Agardh alternate with patches of either algal turfs or encrusting coralline barrens (Micheli et al., 2005; Tamburello et al., 2012). Two species of sea urchins, *Paracentrotus lividus* and *Arbacia lixula*, co-exist on these rocky

reefs (Benedetti-Cecchi et al., 1998; Bulleri et al., 1999; Micheli et al., 2005). Two alternative models were proposed to assess how wave-exposure can influence directly or indirectly the distribution of alternative habitats (Fig. 1).

Although there is some evidence indicating that the abundance of both sea urchin species tends to increase with decreasing wave-exposure (Micheli et al., 2005), some studies have documented large *P. lividus* abundances along wave-swept coasts (Benedetti-Cecchi et al., 1998; Bulleri et al., 1999; Jacinto et al., 2013). Likewise, there is no detailed information on how the abundance of *C. brachycarpa* varies with wave-exposure, although it is generally reported to occur at moderately exposed sites (Thibaut et al., 2015). The direction of the effects of wave-exposure on the distribution of both sea urchins and *C. brachycarpa* remains, therefore, unresolved and was not set *a priori* in our models. In the first model (M1; Fig. 1), we assumed wave-exposure to directly regulate the distribution of sea urchins (treated as a guild), but not that of alternative habitats. In addition, sea urchin effects on the distribution of alternative habitats would take place exclusively via direct negative control of *C. brachycarpa*, the stronger macroalgal competitor for space. Hence, wave-exposure and sea urchins could influence habitats alternative to the canopy only indirectly. In the second model (M2 Fig. 1), wave-exposure directly regulates the distribution of both sea urchins and that of alternative habitats. In this scenario, direct negative effects of sea urchins are not limited to canopy stands, but extend to algal turfs. Following competitive hierarchies, macroalgal canopies can have direct negative effects on both barrens and algal turfs. Differently, direct negative effects of algal turfs are limited to barrens.

Since the best fitting model did not explain any variation in the abundance of canopy-forming species (see Results section), two further conceptual models were fitted including data from the coast of Tuscany to assess the influence of environmental degradation on this macroalgal group. In the first model (M3; Fig. 1), we assumed negative effects of habitat degradation on canopy-formers, indirectly

facilitating algal turfs. By contrast, in the second model (M4; Fig. 1), negative and positive direct
120 effects of habitat degradation are envisioned for both canopy-formers and algal turfs, respectively.

2. Materials and Methods

2.1. Study sites

We used data from two surveys carried out at several islands in the Tuscan Archipelago and
125 along the coasts of Tuscany (NW Mediterranean; Fig. 2). Such a regional approach enabled us to
encompass sites exposed to a wide gradient of wave-exposure and human activities, ranging from
heavily urbanized or industrialized centres to totally protected areas (i.e., no entry zones in Marine
Protected Areas). In the Tuscan Archipelago, benthic assemblages and sea urchin populations were
sampled along the coasts of the islands of Montecristo, Giannutri, Pianosa and Capraia, using a
130 hierarchical design. Between 2005 and 2013, assemblages were sampled three times along the islands
of Capraia and Giannutri, 2 times at Montecristo and 4 times at Pianosa. For each time of sampling, 9
sites (extending ~ 100 m alongshore) were sampled at Capraia and Giannutri, while 6 were sampled at
Montecristo and Pianosa (except for one time at which 10 and 5 sites were sampled at Giannutri and
Montecristo, respectively). Within each site, 5 pictures (20 × 15 cm) were taken at a depth of ~ 5 m in
135 each of two areas ~ 50 of m apart. Likewise, the density of sea urchins was recorded in 5 randomly
placed 50 x 50 cm plastic frames in each area. Both pictures and frames were meters apart one from
another. Pictures were analyzed visually on a PC screen to estimate the percentage cover of macroalgae
and sessile invertebrates. A grid of 25 subquadrats was superimposed onto each image, a score from 0
to 4% was given to each taxon in each subquadrat and the total percentage cover was obtained by
140 summing over the entire set of sub-quadrats. Organisms could generally be identified to the species
level, except for encrusting and filamentous algal forms. Taxa were grouped into three major
morphological groups describing alternative habitats: i) barrens made of encrusting corallines plus bare

rock, ii) canopies formed by *C. brachycarpa* and iii) algal turfs including the geniculate coralline algae *Corallina elongata* Ellis et Solander and *Haliptilon virgatum* (Zanardini) Garbary and Johansen, the
145 coarsely branched algae *Laurencia* spp. (Hudson) Lamouroux, *Chondria* spp. (De Notaris) De Toni and *Gastroclonium clavatum* (Roth) Ardissonne, and several species of filamentous algae (Benedetti-Cecchi et al., 2001).

Another extensive survey was carried out along the coasts of Tuscany (NW Mediterranean Sea) in summer 2008. According to prevailing human activities, 3 levels of decreasing human pressure were
150 identified: (1) urban reefs, (2) extra-urban reefs, (3) offshore reefs. Two locations were randomly selected for each of these conditions (Fig. 2). Two areas of 200×200 m and ~ 1 km apart, were randomly selected for each level of human influence at Livorno and Rosignano Solvay (urban, extra-urban and off-shore reefs). Four transects, 30×5 m wide, were randomly selected, 100s of meters apart, within each area. Ten pictures were taken at random along each transect and the percentage cover
155 of macroalgae and sessile invertebrates was estimated by means of the same techniques described above. Benthic assemblages and environmental conditions at these study sites have been fully described (Tamburello et al., 2012).

2.2. Wave exposure

160 The wind wave exposure level for each site was obtained by means of numerical approach. A phase averaging wind wave numerical model, the WWM (Hsu et al., 2005; Zanke et al., 2006; Roland et al., 2009), was implemented for the whole Western Mediterranean Sea, from the Sicily Channel to Gibraltar, including the Thyrreanean Sea and the Sardinia Sea. The model describes growth, decay, advection, refraction and diffraction of wind waves due to wind action, depth gradient and coastal
165 geometrical features. It was already used with success for both oceanographic and operational purposes to make prediction of the main wave statistical parameters in the Western Mediterranean Sea at both

coastal and off-shore areas (De Falco et al., 2011; Cucco et al., 2012; Olita et al., 2012; Coppa et al., 2013; Ferrarin et al., 2013; Simeone et al., 2014). The model uses finite elements unstructured meshes for representing the model domain. A finite element grid composed by 28321 nodes and 56456
170 triangular elements was implemented with a spatial resolution ranging from around 100 meters for the coastal areas of the whole Tuscan Archipelago and Livorno coastline to few km for the outer domain. The spectral space domain was reproduced by a discrete distribution of 32 regularly spaced frequency intervals ranging between 1 and 0.04 Hz with a relative frequency distribution of about 1.2 Hz, whereas the directional space domain is discretized using 24 regular intervals of 15°. The wind data
175 used for simulating the wave processes were provided by the high resolution meteorological forecasting system SKIRON (<http://forecast.uoa.gr>; Kallos et al., 1997; Kallos and Pytharoulis, 2005). A 2-year period model run was performed using as surface boundary conditions the hourly wind data fields computed by SKIRON for the year 2010 and 2011. As a result, the hourly spatial distribution of the Significant Wave Height (SWH) as well as of the other statistical parameters, were computed over
180 the whole model domain and for all the duration of the simulation. For each station, the time series of the computed SWH was obtained and the exposure level estimated as its maximum value.

2.3. Cumulative human impact score

For each study site, we extracted the cumulative human impact score estimated by Micheli et al.
185 (2013) for the Mediterranean Sea. This score, by combining 22 anthropogenic drivers, generates a single comparable estimate of cumulative human impact on 17 different ecosystems across the Mediterranean. This is similar to the human impact index developed for the global ocean by Halpern et al. (2008). Some shortcomings of the global index developed by Halpern et al. (2008) have been identified: overlapping human activities cannot spatially match up with areas of major impact (Heath,
190 2008) or interactive effects frequently displayed when multiple stressors co-occur (Crain et al., 2008)

cannot be accounted for. Similarly, the index by Micheli et al. (2013) does not incorporate interactions among multiple drivers and uses expert judgment rather than empirical quantification to weight ecosystem vulnerability to human impacts (Micheli et al., 2013). Nonetheless, this score represents the only synthetic measure of human impact for comparisons between sites at the Mediterranean scale.

195 Impact scores were sampled without interpolation by overlying the sampling sites onto the georeferenced raster map of Micheli et al. (2013), downloaded at <https://www.nceas.ucsb.edu/globalmarine/mediterranean#model>. When study sites did not spatially correspond with values in the cumulative human impact layer (e.g. sites close to the coastline), the value of the closest pixel was assigned without interpolation. This analysis used the ‘raster’ library in R
200 computing environment (Hijmans, 2015).

2.4. Statistical analyses

We used structural equation modelling (SEM) to distinguish between alternative potential causal pathways through which wave exposure and cumulative human impact can regulate the distribution of
205 sea urchins and alternative macroalgal habitats on shallow rocky reefs. The abundance of each of the three habitats was included as a continuous variable, estimated as the cover of canopy-formers, algal turfs and encrusting corallines plus bare rock. We started by fitting a full SEM to each of the hypothesized casual paths (Fig. 1). For each SEM, we subsequently excluded non-significant paths with the highest p -values in a stepwise procedure until all remaining links were statistically significant
210 and evaluated modification indices to identify important missing links (Grace et al., 2012). Final SEMs had satisfactory fits as indicated by lack of departure from a saturated model (i.e. consistency of the hypothesized model with the data), a low root mean square error approximation (RMSEA, between 0.01 and 0.07 with confidence intervals embracing zero) and large comparative fit index (larger than 0.9). SEMs were fitted using library ‘lavaan’ in R (Rosseel, 2012).

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3. Results

The density of both *P. lividus* and *A. lixula* was low at all study sites in the Tuscan Archipelago (Fig. 3). The density of *P. lividus* ranged between 0.2 and 0.6 individuals \times m^{-2} , with peak values of 1.8 ind. m^{-2} at exposed sites of the island of Giannutri. In general, densities of *A. lixula* were about three times higher than those of *P. lividus*, with peak values of 4.5 ind. m^{-2} found again at the most exposed sites of Giannutri.

M2 received greater support from the data than M1 (Table 1). Standardized regression coefficients were significant for all the linkages retained in the final model (Fig. 4). Wave-exposure had significant positive direct effects on the abundance of sea urchins and all alternative habitats. Effects on habitats, despite being significant were, however, weak (Fig. 4). Sea urchins had only weak negative effects on canopy formers (Fig. 4), which, in turn, had direct negative effects on the abundance of algal turfs. The fit of a model including directionality in the interaction between sea urchins and algal turfs was worse than that of a model not specifying a causal relationship between these pairs of variables (i.e., simply accounting for covariance). This model showed a positive correlation between the abundance of sea urchins and that of algal turfs and, although weaker, between barrens and algal turfs (Fig. 4).

For the second analysis, M3 received greater support than M4 (Table 1). The minimum adequate model for data from the coast of Tuscany showed negative direct effects of habitat degradation on the abundance of canopy-forming species which, in turn, reduced the abundance of algal turfs (Fig. 4). This resulted in indirect positive effects of habitat degradation on algal turfs (Fig. 4).

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4. Discussion

Wave-exposure had positive effects on the abundance of sea urchins along the coasts of the Tuscan Archipelago. Previous studies in the NW Mediterranean that have brought mixed evidence on

the role of wave-exposure in shaping patterns of distribution of sea urchins. For instance, Micheli et al. (2005), although not formally quantifying wave-exposure, reported a trend for *P. lividus* to be more abundant at wave-sheltered sites on some islands of the Tuscan Archipelago (Giannutri and Capraia). By contrast, large densities of both *P. lividus* and *A. lixula* have been found on more exposed coasts of mainland Tuscany (Benedetti-Cecchi et al., 1998; Bulleri et al., 1999), as well as along eastern Atlantic coasts characterized by higher mean wave-energy than the Mediterranean (e.g., Canary Islands, Tuya et al., 2007; Portugal, Jacinto et al., 2013). Both *P. lividus* and *A. lixula* have been shown to exhibit an upward migration after downward displacement, suggesting that they may have evolved a behavioural adaptation to dislodgement by waves (Chelazzi et al., 1997). Susceptibility to wave-action seems, however, smaller in *A. lixula* than *P. lividus* (Chelazzi et al., 1997; Bulleri et al., 1999). In particular, the force necessary to dislodge *A. lixula* from encrusting coralline dominated surfaces has been found to be 1/3 greater than that necessary to dislodge *P. lividus* (Gianguzza et al., 2010). The greater abundance of *A. lixula* than *P. lividus* in sea urchin assemblages may, thus, explain the trend for the abundance of sea urchins to increase, as a guild, with wave-exposure at sites along the coasts of Tuscan Archipelago.

Wave-exposure had weak effects on the distribution of all the alternative rocky reef habitats. *C. brachycarpa* has been previously described as typical of moderately exposed shores (e.g. Sales and Ballesteros, 2009; Thibaut et al., 2015). Although not explicitly defining wave-exposure, these studies suggest that this species thrives well in Mediterranean relatively high-energy environments. Encrusting corallines and species composing turfs, by virtue of their morphology, are likely to be little susceptible to wave-action. Thus, in contrast to findings from other temperate coasts (Byrnes et al., 2011; Filbee-Dexter and Scheibling, 2014 and references therein), variation in wave-exposure appears to play little role in shaping patterns of distribution of either primary producers or consumers on shallow rocky reefs in the NW Mediterranean.

Likewise, sea urchins had very weak effects on the distribution of alternative habitats. This is not surprising given that urchin densities were very low, with peak values of 6 ind. m⁻² (both species combined) in Giannutri. All of the islands included in the Tuscan Archipelago National Park are subjected to some form of protection. In particular, human activities are totally banned within a 1 nautical mile respect zone around the islands of Montecristo and Pianosa and along some stretches of coast of the islands of Giannutri and Capraia. Protection, by enhancing the abundance of large-sized predatory fishes, such as *Diplodus sargus*, may have caused the decline of sea urchins and, in particular, of *P. lividus*, the species more susceptible to predation (Guidetti, 2006).

Under no control by consumers, the distribution of alternative habitats seems to be directly regulated by competitive hierarchies among the species composing each of them. In oligotrophic water conditions, such as those found in the Tuscan Archipelago, Fucoids are stronger competitors for space than algal turfs (Benedetti-Cecchi et al., 2012). Algal turfs would be, however, able to recruit within barren areas, as suggested by the positive correlation between the abundance of these two habitats. By virtue of their opportunistic traits, even temporary decreases in grazing pressure might be sufficient for algal turfs to colonize space in barrens. Encrusting corallines, although able to reduce the recruitment of species composing algal turfs (Bulleri et al., 2002) are poor competitors for space and would, therefore, provide a suitable habitat for turf colonization in the absence of *Cystoseira*. This may ultimately generate a positive correlation between algal turf abundance and sea urchin density, given that the presence of these herbivores is generally restricted to barren areas.

Macroalgal canopies would indirectly regulate the abundance of sea urchins, likely by reducing the availability of the most suitable habitat and food items. Barrens provide *A. lixula* with suitable surfaces for attachment and movement, as well as preferred food items, including encrusting coralline macroalgae (Privitera et al., 2008) and sessile invertebrates (Wangensteen et al., 2011). Likewise, algal species composing turfs can represent an important source of food for *A. lixula* (Bulleri et al., 1999;

Bonaviri et al., 2011). Under these circumstances, macroalgal canopies, through the direct control of their main competitors for space (i.e., algal turfs), would be able to control the distribution of their grazers. Thus, our analysis suggests that causality in the relationship between sea urchins and
290 macroalgal canopies could switch according to the density of the formers: sea urchins would limit the distribution of macroalgal canopies when their density is high; by contrast, canopies would determine sea urchin distribution when their density is low. Whiplashing by kelps has been previously shown to be able to constrain the movement of sea urchins (Konar and Estes, 2003; Tamaki et al., 2009), thereby influencing their distribution. Although further experimental work is warranted to establish causality,
295 our analysis suggests that a similar mechanism may operate also on Mediterranean rocky reefs dominated by Fucoids.

Degradation of environmental conditions due to human agency seems, instead, the main cause of the collapse of algal canopies. There is an increasing body of evidence pointing to human impacts as the main drivers of the decline of canopy-formers worldwide (reviewed by Strain et al., 2014).
300 Canopies made by *Cystoseira* make no exception and have been widely shown to decline in urbanized areas as a consequence of multiple stressors, including enhanced nutrient loading and sediment deposition, heavy metal pollution and invasions (Rodriguez-Prieto and Polo, 1996; Benedetti-Cecchi et al., 2001; Mangialajo et al., 2008; Bulleri et al., 2010; Sales et al., 2011). The effects of these regional stressors can be exacerbated by global climate changes, such as rising of sea surface temperature and
305 ocean acidification (Falkenberg et al., 2013; Strain et al., 2014). Our analysis of coastal data is in accordance with this bulk of evidence and suggests that negative effects of degraded environmental conditions on macroalgal canopies are likely direct and not mediated by positive effects on algal turfs. This means that species composing algal turfs do not directly benefit from environmental degradation, but rather from decreased competition from canopy-forming species. For instance, filamentous algal
310 forms, by virtue of their opportunistic traits, including year-round sexual reproduction, vegetative

propagation, tolerance to sediment smothering and abrasion (Airoldi, 1998) and capability of using of extra inputs of nitrogen (Falkenberg et al., 2013), can readily exploit free space. Once established, algal turfs can then trigger positive feed-back mechanisms (e.g., trapping of sediments) that prevent the recovery of canopies.

315 Control of sea urchin populations, either through culling/harvesting programs or re-establishment of lost predatory interactions, has been identified as potential tool to conserve or restore canopies formed by Laminariales or Furoids (Guidetti, 2006; Shears and Babcock, 2002). Limited effects of sea urchins on the distribution of alternative habitats on shallow rocky reefs of the Tuscan Archipelago may be an indirect consequence of enhanced predation on *P. lividus*, elicited by the establishment of
320 Marine Protected Areas. Our results suggest, however, that management of human impacts should be considered a priority for preserving subtidal canopies formed by *Cystoseira* (Gianni et al., 2013). Direct effects of human impacts on macroalgal canopies suggest that conservation efforts based on the control of sea urchin populations would be deemed to failure. Finally, our study suggests that the distribution of alternative habitats is regulated by a complex web of direct and indirect interactions
325 involving primary producers, characterized by different life-traits, and their consumers. A comprehensive understanding of the underpinning dynamics requires, therefore, going beyond a dichotomic view of alternative habitat shifts, to include the whole set of life-traits and forces at play.

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335 Impact on Economic Sectors (VECTORS).

References

- 340 Agnetta, D., Badalamenti, F., Ceccherelli, G., Di Trapani, F., Bonaviri, C., Gianguzza, P., 2015. Role
of two co-occurring Mediterranean sea urchins in the formation of barren from *Cystoseira*
canopy. *Mar. Env. Res.* 152, 73–77.
- Airoldi, L. 1998. Roles of disturbance, sediment stress, and substratum retention on spatial dominance
in algal turf. *Ecology* 79, 2759–2770.
- Airoldi, L., 2000. Effects of disturbance, life-history and overgrowth on coexistence of algal crusts and
345 turfs. *Ecology* 8, 798–814.
- Airoldi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe. *Oceanogr.*
Mar. Biol. Annu. Rev. 45, 345–405.
- Alestra, T., Schiel, D.R., 2014. Effects of opportunistic algae on the early life history of a habitat-
forming fucoid: influence of temperature, nutrient enrichment and grazing pressure. *Mar. Ecol.*
350 *Prog. Ser.* 508, 105–115.
- Andrew, N.L., 1993. Spatial heterogeneity, sea urchin grazing, and habitat structure on reefs in
temperate Australia. *Ecology* 74, 292–302.
- Andrew, N.L., Underwood, A.J., 1993. Density-dependent foraging in the sea urchin *Centrostephanus*
rodgersii on shallow subtidal reefs in New South Wales, Australia. *Mar. Ecol. Prog. Ser.* 99, 89–
355 98.
- Balata, D., Piazzzi, L., Bulleri, F., 2015. Sediment deposition dampens positive effects of substratum
complexity on the diversity of macroalgal assemblages. *J. Exp. Mar. Biol. Ecol.* 467, 45–51.

- Benedetti-Cecchi, L., Bulleri, F., Cinelli, F., 1998. Density dependent foraging of sea urchins in shallow subtidal rocky reefs on the west coast of Italy (western Mediterranean). *Mar. Ecol. Prog. Ser.* 163, 203–211.
- 360
- Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P.S., Airoidi, L., Relini, G., Cinelli, F., 2001. Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. *Mar. Ecol. Prog. Ser.* 214, 137–150.
- Benedetti-Cecchi, L., Tamburello, L., Bulleri, F., Maggi, E., Gennusa, V., Miller, M., 2012. Linking patterns and processes across scales: the application of scale-transition theory to algal dynamics on rocky shores. *J. Exp. Mar. Biol. Ecol.* 215, 977–985.
- 365
- Bonaviri, C., Vega Fernandez, T., Fanelli, G., Badalamenti, F., Gianguzza, P., 2011. Leading role of sea urchin *Arbacia lixula* in maintaining barren state in southwestern Mediterranean. *Mar. Biol.* 158, 2505–2513.
- 370
- Brawley, S.H., Johnson, L.E., 1992. Gametogenesis, gametes and zygotes: An ecological perspective on sexual reproduction in the algae. *Brit. Phycol. J.* 27, 233–252.
- Breitburg, D.L., 1984. Residual effects of grazing: inhibition of competitor recruitment by encrusting coralline algae. *Ecology* 65, 1136–1143.
- Bulleri, F., Benedetti-Cecchi, L., 2006. Mechanisms of recovery and resilience of different components of mosaics of habitats on shallow rocky reefs. *Oecologia* 149, 482–492.
- 375
- Bulleri, F., Benedetti-Cecchi, L., Cinelli, F., 1999. Grazing by the sea urchins *Arbacia lixula* L. and *Paracentrotus lividus* Lam. In the Northwest Mediterranean. *J. Exp. Mar. Biol. Ecol.* 241, 81–95.
- Bulleri, F., 2013. Grazing by sea urchins at the margins of barren patches on Mediterranean rocky reefs. *Mar. Biol.* 160, 2493–2501.
- 380

- Bulleri, F., Bertocci, I., Micheli, F., 2002. Interplay of encrusting coralline algae and sea urchins in maintaining alternative habitats. *Mar. Ecol. Prog. Ser.* 243, 101–109.
- Bulleri, F., Balata, D., Bertocci, I., Tamburello, L., Benedetti- Cecchi, L., 2010. The seaweed *Caulerpa racemosa* on Mediterranean rocky reefs: from passenger to driver of ecological change. *Ecology* 91, 2205–2212.
385
- Byrnes, J.E., Reed, D.C., Cardinale, B.J., Cavanaugh, K.C., Holbrook, S.J., Schmitt, R.J., 2011. Climate-driven increases in storm frequency simplify kelp forest food webs. *Glob. Change Biol.* 17, 2513–2524.
- Chelazzi, G., Serra, G., Bucciarelli, G., 1997. Zonal recovery after experimental displacement in two sea urchins co-occurring in the Mediterranean. *J. Exp. Mar. Biol. Ecol.* 212, 1–7.
390
- Connell, S.D., Foster, M.S., Airoidi, L., 2011. What are algal turfs? Towards a better description of turfs. *Mar. Ecol. Prog. Ser.* 495, 299–307.
- Coppa, S., de Lucia, G.A., Magni, P., Domenici, P., Antognarelli, F., Satta, A., Cucco, A., 2013. The effect of hydrodynamics on shell orientation and population density of *Pinna nobilis* in the Gulf of Oristano (Sardinia, Italy). *J. Sea Res.* 76, 201–210.
395
- Cucco, A., Sinerchia, M., Ribotti, A., Olita, A., Fazioli, L., Sorgente, B., Perilli, A., Borghini, M., Schroeder, K., Sorgente, R., 2012. A high-resolution real-time forecasting system for predicting the fate of oil spills in the Strait of Bonifacio (western Mediterranean Sea). *Mar. Pollut. Bull.* 64, 1186–1200.
- Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol. Lett.* 11, 1304–1315.
400
- Dayton, P.K., Tegner, M.J., Parnell, M.E., Edwards, P.B., 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.* 62, 421–445.

- De Falco, G., De Muro, S., Batzella, T., Cucco, A., 2011. Carbonate sedimentation and hydrodynamic
 405 pattern on a modern temperate shelf: The strait of Bonifacio (western Mediterranean). *Estuar.
 Coast. Shelf Sci.* 93, 14–26.
- Falkenberg, L.J., Russell, B.D., Connell, S.D., 2013. Contrasting resource limitations of marine
 primary producers: implications for competitive interactions under enriched CO₂ and nutrient
 regimes. *Oecologia* 172, 575–583.
- 410 Feehan, C., Scheibling, R.E., Lauzon-Guay, J.S., 2012. Aggregative feeding behavior in sea urchins
 leads to destructive grazing in a Nova Scotian kelp bed. *Mar. Ecol. Prog. Ser.*, 444, 69–83.
- Ferrarin, C., Roland, A., Bajo, M., Umgiesser, G., Cucco, A., Davolio, S., Buzzi, A., Malguzzi, P.,
 Drofa O., 2013. Tide-surge-wave modelling and forecasting in the Mediterranean Sea with focus
 on the Italian coast. *Ocean Modelling* 61, 38–48.
- 415 Filbee-Dexter, K., Scheibling, R.E., 2014. Sea urchin barrens as alternative stable states of collapsed
 kelp ecosystems. *Mar. Ecol. Prog. Ser.* 495, 1–25.
- Fletcher, W.J., 1987. Interactions among subtidal Australian sea urchins, gastropods and algae: effects
 of experimental removals. *Ecol. Monogr.* 57, 89–109.
- Gianguzza, P., Bonaviri, C., Milisenda, G., Barcellona, A., Agnetta, D., Vega Fernandez, T.,
 420 Badalamenti, F., 2010. Macroalgal assemblage type affects predation pressure on sea urchins by
 altering adhesion strength. *Mar. Environ. Res.* 70, 82–86.
- Gianguzza, P., Bonaviri, C., Prato, E., Fanelli, G., Chiantore, M., Privitera, D., Luzzu, F., Agnetta, D.,
 2013. Hydrodynamism and its influence on the reproductive condition of the edible sea urchin
Paracentrotus lividus. *Mar. Environ. Res.* 85, 29–33.
- 425 Gianni, F., Bartolini, F., Airoidi, L., Ballesteros, E., Francour, P., Guidetti, P., Meinesz, A., Thibaut, T.,
 Mangialajo, L., 2011. Conservation and restoration of marine forests in the Mediterranean Sea
 and the potential role of Marine Protected Areas. *Adv. Oceanogr. Limnol.* 4, 83–101.

- Gorman, D., Connell, S.D., 2009. Recovering subtidal forests in human-dominated landscapes. *J. Appl. Ecol.* 46, 1258–1265.
- 430 Gorgula, S.K., Connell, S.D., 2004. Expansive covers of turf forming algae on human-dominated coast: the relative effects of increasing nutrient and sediment loads. *Mar. Biol.* 145, 613–619.
- Grace, J.B., Schoolmaster, D.R., Guntenspergen, G.R., Little, A.M., Mitchell, B.R., Miller, K.M., Schweiger, M. 2012. Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere* 3, art73. (doi:10.1890/es12-00048.1)
- 435 Guidetti, P., 2006. Marine reserves re-establish lost predatory interactions and cause community changes in rocky reefs. *Ecol. App.* 16, 963–976.
- Hereu, B., Zabala, M., Sala, E., 2008. Multiple controls of community structure and dynamics in a sublittoral marine environment. *Ecology* 89, 3423–3435.
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., et al., 2008. A global map of
440 human impact on marine ecosystems. *Science* 319, 948–952.
- Heath, M.R., 2008. Comments on “A global map of human impact on marine ecosystems”. *Science* 312, 1446.
- Hernandez, J.C., Clemente, S., Sangil, C., Brito, A., 2008. The key role of the sea urchin *Diadema*
445 *aff. antillarum* in controlling macroalgae assemblages throughout the Canary Islands (eastern subtropical Atlantic): a spatio-temporal approach. *Mar. Environ. Res.* 66, 259–270.
- Himmelman, J.H., Steele, D.H., 1971. Foods and predators of the green sea urchin *Strongylocentrotus droehachiensis* in Newfoundland waters. *Mar. Biol.* 9, 315–322.
- Hijmans, R.J., 2015. raster: Geographic data analysis and modeling. R package version 2.3-33.
<http://CRAN.R-project.org/package=raster>.
- 450 Hsu, T.-W., Ou, S.-H., Liau, J.-M., 2005. Hindcasting near shore wind waves using a FEM code for SWAN. *Coastal Engineering*, 52, 177–195.

- Jacinto, D., Bulleri, F., Benedetti-Cecchi, L., Cruz, T., 2013. Patterns of abundance, population size structure and microhabitat usage of *Paracentrotus lividus* (Echinodermata: Echinoidea) in SW Portugal and NW Italy. *Mar. Biol.* 160, 1135–1146.
- 455 Jones, G.P., Andrew, N.L., 1990. Herbivory and patch dynamics on rocky reefs in temperate Australasia: The roles of fish and sea urchins: *Aust. Ecol.* 15, 505–520.
- Kallos, G., Nickovic, S., Papadopoulos, A., Jovic, D., Kakaliagou, O., Misirlis, N., Boukas, L., Mimikou, N., Sakellaridids, G., Papageorgiou, J., 1997. The regional weather forecasting system Skiron: an overview. *Proceedings of the Symposium on Regional Weather Prediction on Parallel*
- 460 *Computer Environments, Greece, Athens*, pp. 109–122.
- Kallos, G., Pytharoulis, I., 2005. Short-term predictions (weather forecasting purposes). Anderson, M.G. (Ed.), *Encyclopedia of Hydrological Sciences*. Wiley, London, pp. 2791–2811.
- Kennelly, S.J., 1987. Inhibition of kelp recruitment by turfing algae and consequences for an Australian kelp community. *J. Exp. Mar. Biol. Ecol.* 112, 49–60.
- 465 Konar, B., 2000. Seasonal inhibitory effects of marine plants on sea urchins: structuring communities the algal way. *Oecologia*, 125, 208–217.
- Konar, B., Estes, J.A., 2003. The stability of boundary regions between kelp beds and deforested areas. *Ecology* 84, 174–185.
- Jacinto, D., Bulleri, F., Benedetti-Cecchi, L., Cruz, T., 2013. Patterns of abundance, population size
- 470 structure and microhabitat usage of *Paracentrotus lividus* (Echinodermata: Echinoidea) in SW Portugal and NW Italy. *Mar. Biol.* 160, 1135–1146.
- Lauzon-Guay, J.S., Scheibling, R.E., 2007. Seasonal variation in movement, aggregation and destructive grazing of the green sea urchin (*Strongylocentrotus droebachiensis*) in relation to wave action and sea temperature. *Mar. Biol.* 151, 2109–2118.

- 475 Lawrence, J.M., 1975. On the relationships between marine plants and sea urchins. *Oceanogr. Mar. Biol. Annu. Rev.* 13, 213–286.
- Ling, S.D., 2008. Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. *Oecologia* 153, 883–894.
- Ling, S.D., Johnson, C.R., Frusher, S.D., Ridgway, K.R., 2009. Overfishing reduces resilience of
480 kelp beds to climate-driven catastrophic phase shift. *Proc. Nat. Acad. Sci. USA* 106, 22341–22345.
- Ling, S.D., Scheibling, R.E., Rassweiler, A., Johnson, C.R., Shears, N., Connell, S.D., Salomon, A.K., Norderhaug, K.M., Pérez-Matus, A., Hernández, J.C., Clemente, S., Blamey, L.K., Hereu, B., Ballesteros, E., Sala, E., Garrabou, J., Cebrian, E., Zabala, M., Fujita, D., Johnson, L.E., 2015.
485 Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philos. T. Roy. Soc. B*, 370, 201269.
- Lilley, S.A., Schiel, D.R., 2006. Community effects following the deletion of a habitat-forming alga from rocky marine shores. *Oecologia*, 148, 672–681.
- Mangialajo, L., Chiantore, M., Cattaneo-Vietti, R., 2008. Loss of furoid algae along a gradient of
490 urbanisation, and structure of benthic assemblages. *Mar. Ecol. Prog. Ser.* 358, 63–74.
- Micheli, F., Benedetti-Cecchi, L., Gambaccini, S., Bertocci, I., Borsini, C., Osio, C.G., Romano, F., 2005. Cascading human impacts, marine protected areas and the structure of Mediterranean rocky-reef assemblages. *Ecol. Monogr.* 75, 81–102.
- Micheli, F., Halpern, B.S., Walbridge, S., Ciriaco, S., Ferretti, F., et al., 2013. Cumulative human
495 impacts on Mediterranean and Black Sea marine ecosystems: assessing current pressures and opportunities. *PLoS ONE* 8(12), e79889.
- Norderhaug, K.M., Christie, H.C., 2009. Sea urchin grazing and kelp re-vegetation in the NE Atlantic. *Mar. Biol. Res.* 5, 515–528.

- Olita, A., Cucco, A., Simeone, S., Ribotti, A., Fazioli, L., Sorgente, B., Sorgente R., 2012. Oil spill
 500 hazard and risk assessment for the shorelines of a Mediterranean coastal archipelago. *Ocean
 Coast. Mgmt.* 57, 44–52.
- Palacin, C., Giribet, G., Carner, S., Dantart, L., Turin, X., 1998. Low density of sea urchins influence
 the structure of algal assemblages in the western Mediterranean. *J. Sea Res.* 39, 281–290.
- Rodríguez-Prieto, C., Polo, L., 1996. Effects of sewage pollution in the structure and dynamics of the
 505 community of *Cystoseira mediterranea* (Fucales, Phaeophyceae). *Sci. Mar.* 60, 253–263.
- Perreault, M.C., Borgeaud, I.A., Gaymer, C.F., 2014. Impact of grazing by the sea urchin *Tetrapygus
 niger* on the kelp *Lessonia trabeculata* in Northern Chile. *J. Exp. Mar. Biol. Ecol.* 453, 22–27.
- Privitera, D., Chiantore, M., Mangialajo, L., Glavic, N., Kozul, W., Cattaneo-Vietti, R., 2008. Inter-
 and intra-specific competition between *Paracentrotus lividus* and *Arbacia lixula* in resource
 510 limited barren areas. *J. Sea Res.* 60, 184–192.
- Roland, A., Cucco, A., Ferrarin, C., Hsu, T.W., Liau, J.-M., Umgiesser, G., Zanke, U., 2009. On the
 development and verification of a 2d coupled wave-current model on unstructured meshes *J. Mar.
 Syst.* 78, S244–S254.
- Rosseel, Y., 2012. lavaan: An R package for structural equation modeling. *Journal of Statistical
 515 Software*, 48, 1-36. URL <http://www.jstatsoft.org/v48/i02/>.
- Sales, M., Ballesteros, E., 2009. Shallow *Cystoseira* (Fucales: Ochrophyta) assemblages thriving in
 sheltered areas from Menorca (NW Mediterranean): relationships with environmental factors and
 anthropogenic pressures. *Estuar. Coast. Shelf S.* 84, 476–482.
- Sales, M., Cebrian, E., Tomas, F., Ballesteros, E., 2011. Pollution impacts and recovery potential in
 520 three species of the genus *Cystoseira* (Fucales, Heterokontophyta). *Estuar. Coast. Shelf S.* 92,
 347–357.

- Santelices, B., 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanogr. Mar. Biol. Annu. Rev.* 28, 177–276.
- 525 Shears, N.T., Babcock, R.C., 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia*, 132, 131–142.
- Simeone, S., De Falco, G., Quattrocchi, G., Cucco, A., 2014. Morphological changes of a Mediterranean beach over one year (San Giovanni Sinis, western Mediterranean). *J. Coast. Res.*, 217–222.
- 530 Sivertsen, K., 2006. Overgrazing of kelp beds along the coast of Norway. *J. Appl. Phycol.* 18, 599–610.
- Steneck, R.S., Johnson, C.R., 2014. Kelp forests: dynamic patterns, processes, and feedbacks. In Bertness, M.D., Bruno, J.F., Silliman, B.R., Stachowicz, J. J. (Eds.), *Marine community ecology and conservation*. Sinauer Associates, Inc., Sunderland, MA, pp. 315–336.
- 535 Strain, E.M., Thomson, R.J., Micheli, F., Mancuso, F.P., Airoidi, L., 2014. Identifying the interacting roles of stressors in driving the global loss of canopy-forming to mat-forming algae in marine ecosystems. *Glob. Change Biol.* 20, 3300–3312.
- Tamaki, H., Kusaka, K., Fukuda, M., Arai, S., Muraoka, D., 2009. *Undaria pinnatifida* habitat loss in relation to sea urchin grazing and water flow conditions, and their restoration effort in Ogatsu Bay, Japan. *J. Water. Environ. Technol.* 7, 201–213.
- 540 Tamburello, L., Benedetti-Cecchi, L., Ghedini, G., Alestra, T., Bulleri, F., 2012. Variation in the structure of subtidal landscapes in the NW Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 457, 29–41.
- Thibaut, T., Blanfuné, A., Boudoresque, C., Verlaque, M., 2015. Decline and local extinction of Fucales in the French Riviera: the harbinger of future extinctions? *Medit. Mar. Sci.*, 16, 206–224.

- 545 Tuya, F., Cisneros-Aguirre, J., Ortega-Borges, L., Haroun, R.J., 2007. Bathymetric segregation of sea urchins on reefs of the Canarian Archipelago: role of flow-induced forces. *Estuar. Coast. Shelf S.* 73, 481–488.
- Vogt, H., Schramm, W., 1991. Conspicuous decline of *Fucus* in Kiel Bay (western Baltic): what are the causes? *Mar. Ecol. Prog. Ser.* 69, 189–194.
- 550 Zanke, U., Roland, A., Hsu, T.W., Ou, S.H., Liao, J.M., 2006. Spectral wave modeling on unstructured grids with the WWM (Wind Wave Model) II: the shallow water cases. In: Third Chinese-German Joint Symposium on Coastal and Ocean Engineering (JOINT2006), Tainan, Taiwan.
- Wangensteen, O.S., Turon, X., Perez-Portela, R., Palacin, C., 2011. A wolf in sheep's clothing: carnivory in dominant sea urchins in the Mediterranean. *Mar. Ecol. Prog. Ser.* 441, 117–128.

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Table 1. Structural equation models (SEMs) of alternative community state in subtidal rocky reefs. Evaluation criteria to select a minimum adequate model included: χ^2 test of the consistency of the hypothesized model with the data, root mean square error approximation (RMSEA) with associated confidence intervals (CIs), the comparative fit index and Akaike Information Criterion (AIC).

Final SEMs	[§] Consistency (χ^2)	df	RMSEA	90% CIs of RMSA	Comparative fit index	AIC
Exposure-Sea urchin model						
M1	45.7***	6	0.29	0.216-0.373	0.16	2259.2
M2	5.6	6	0.01	0.0-0.142	1.01	1824.9
Environmental quality model						
M3	1.4	1	0.069	0.0-0.299	0.99	891.6
M4	21.1***	1	0.473	0.311-0.658	0.72	911.3

[§]Significant values indicate lack of fit

Figure legends

Figure 1. Alternative conceptualizations describing dynamics among alternative habitats on shallow rocky reefs. Model 1 and Model 2 describe direct dependencies among wave exposure, sea urchins and alternative habitats (canopies, algal turfs and barrens); Model 3 and Model 4 describe direct dependencies among cumulative human impact, canopies and algal turfs.

Figure 2. Map of study sites in the Tuscan Archipelago and along the coast of Tuscany. Maximum values for significant wave height (expressed in meters) are reported for each study site, as a proxy for wave-exposure.

Figure 3. Abundance of the sea urchins, *Arbacia lixula* and *Paracentrotus lividus*, along the coasts of islands in the Tuscan Archipelago. Values are means \pm SE; *n*: Capraia = 540, Giannutri = 419, Montecristo = 320, Pianosa = 440.

Figure 4. SEM (best fit models) for the abundance of sea urchins and alternative habitats under the influence of wave-exposure (Model 2) or cumulative human impact (Model 3). Arrows, with width proportional to the standardized correlation ranging from -1 to 1, indicate the direction and strength of the relationship. Positive and negative effects are in blue and red, respectively. The percentage of variance explained by the model (R^2) is given under each of the variable label. ** $P < 0.01$; *** $P < 0.001$.

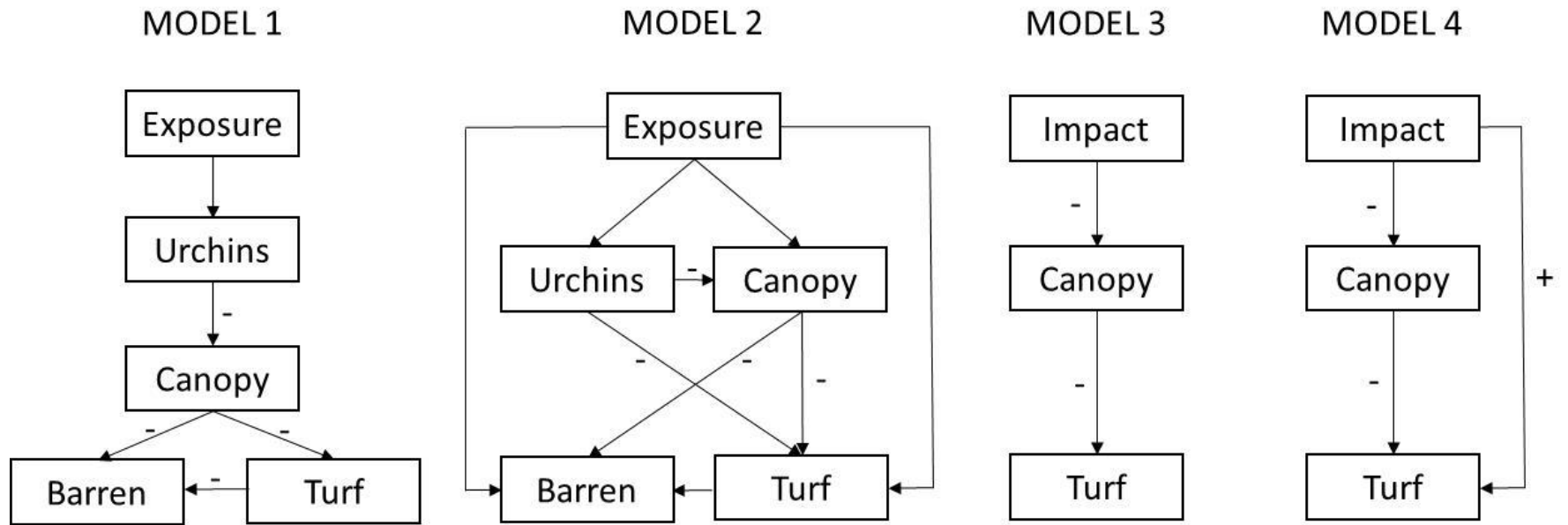


Figure 1

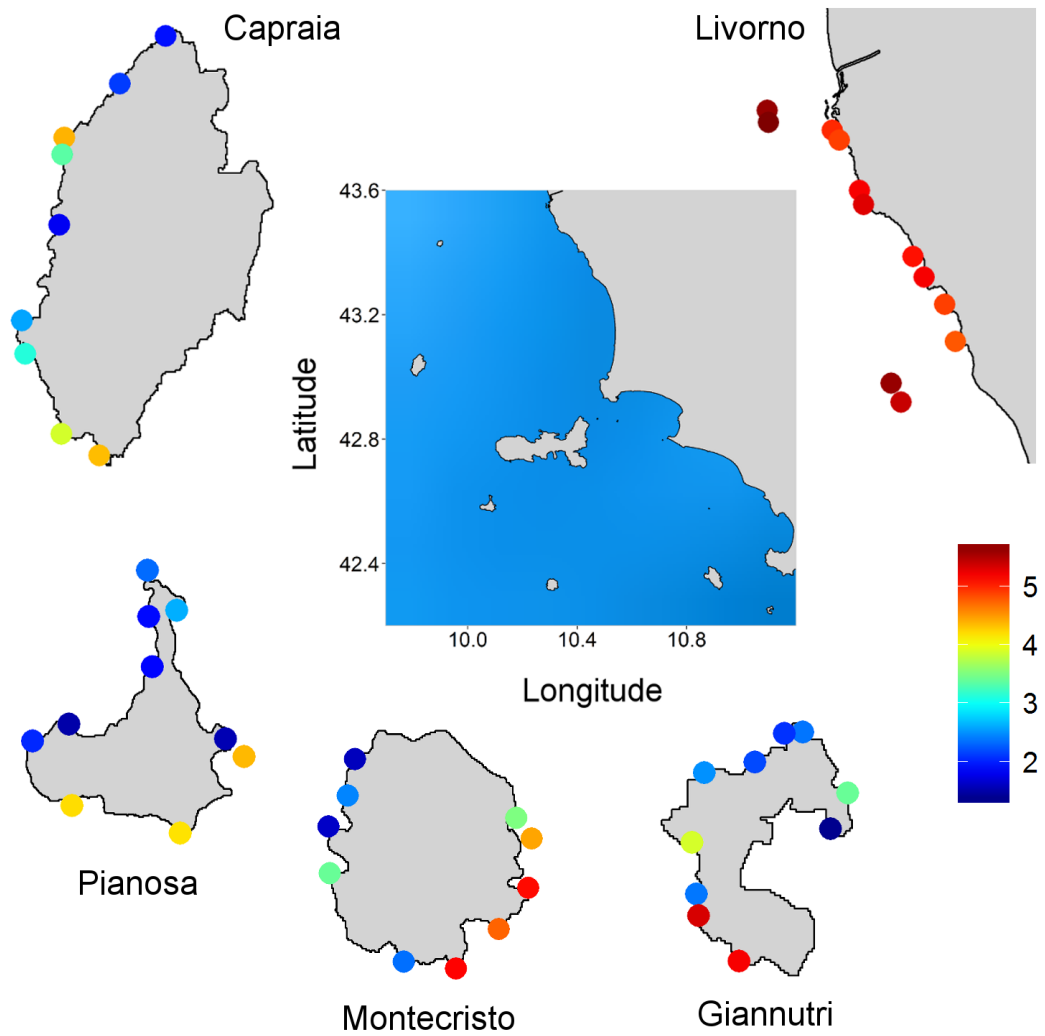


Figure 2

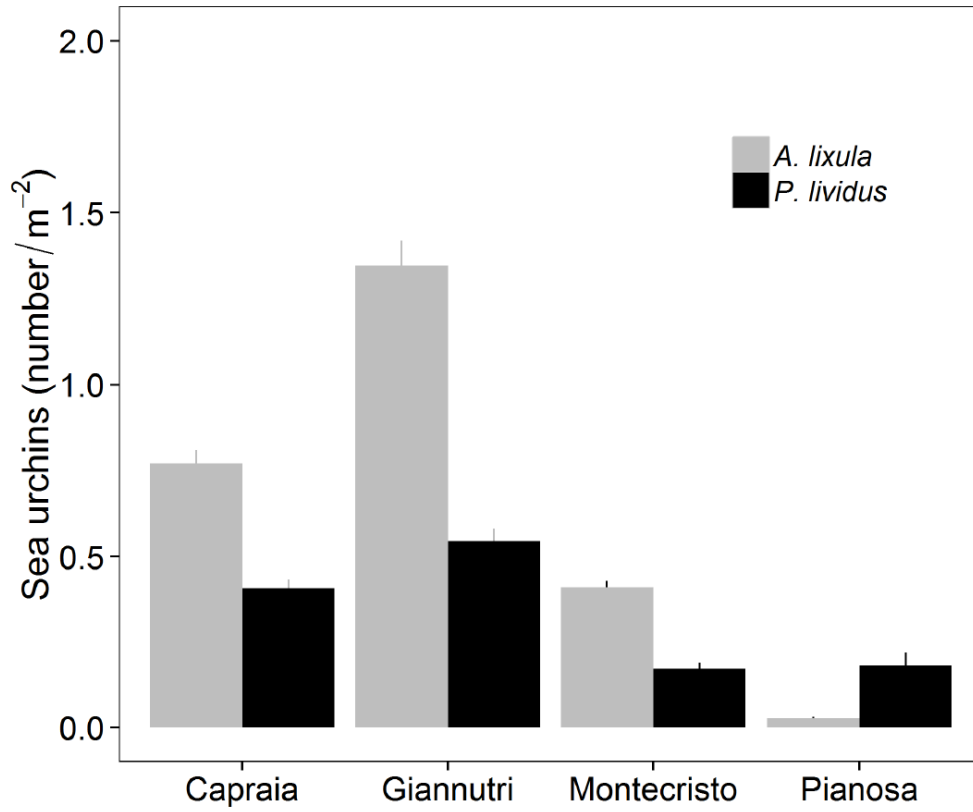


Figure 3

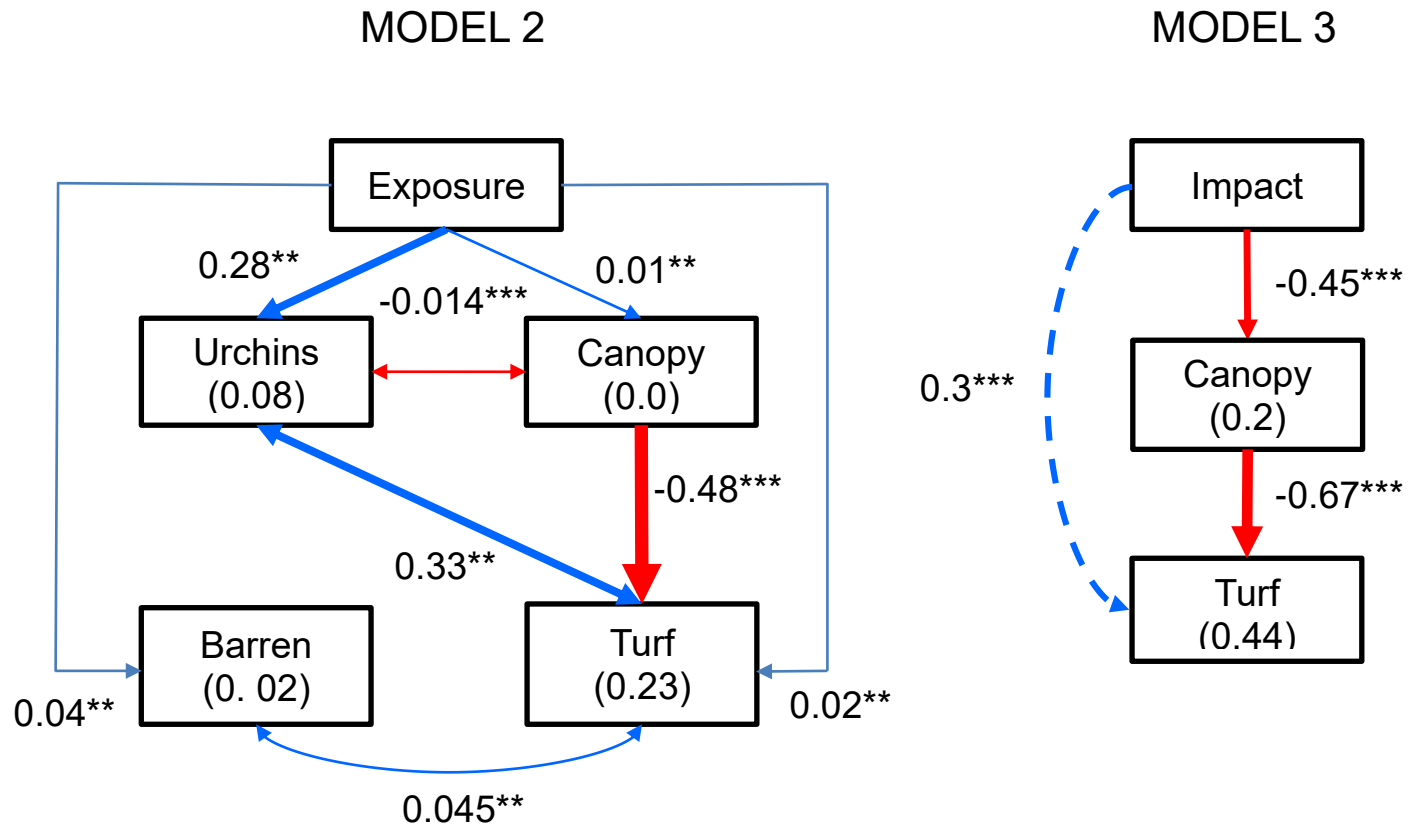


Figure 4