

Article

Abrupt Change in a Subtidal Rocky Reef Community Coincided with a Rapid Acceleration of Sea Water Warming

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Received: 27 September 2019; Accepted: 11 November 2019; Published: 13 November 2019



Abstract: Seawater warming is impacting marine ecosystems, but proper evaluation of change requires the availability of long-term biological data series. Mescio Reef (Ligurian Sea, Italy) offers one of the longest Mediterranean data series on sessile epibenthic communities, based on underwater photographic surveys. Photographs taken in four stations between 20 m and 40 m depth allowed calculating the percent cover of conspicuous species in 1961, 1990, 1996, 2008, and 2017. Multivariate analysis evidenced an abrupt compositional change between 1990 and 1996. A parallel change was observed in Ligurian Sea temperatures. Two invasive macroalgae (*Caulerpa cylindracea* and *Womersleyella setacea*) became dominant after 1996. Community diversity was low in 1961 to 1996, rapidly increased between 1996 and 2008, and exhibited distinctly higher values in 2008–2017. A novel community emerged from the climate shift of the 1990s, with many once characteristic species lost, reduced complexity, biotic homogenization, greater diversity and domination by aliens. Only continued monitoring will help envisage the possibility for a reversal of the present phase shift or for further transformations driven by global change.

Keywords: sea water warming; historical data series; phase shift; subtidal sessile epibenthos; coralligenous community; alien species; biotic homogenization; Mediterranean Sea

1. Introduction

Seawater warming is exerting an overwhelming impact on marine ecosystems and biota worldwide [1,2], with profound implications for the economic and social systems that depend upon them [3]. Together with ocean acidification and sea level rise, temperature increase is a major driver of ecological change and is leading to unprecedented biological shifts in the world's ocean [4], but further studies are needed to improve mechanistic understanding of how ocean warming will alter the structure and functioning of marine communities [5]. Sea water temperature influences marine organisms by a combination of direct (survival, reproduction, recruitment, etc.) and indirect effects, mediated by biotic interactions (predation, parasitism, diseases, etc.) or by the altered emphasis of marine current fluxes between adjacent basins, which may facilitate the arrival of allochthonous species [6,7]. While the earliest climate-related biological changes in the sea have been observed decades ago, the first unambiguous evidences of the effects of rising temperature on the marine ecosystems became clear in the 1990s [8–10], and a number of studies worldwide provided an abundant documentation in

the subsequent years [11–14]. The semi-enclosed nature of the Mediterranean Sea, together with its smaller inertia due to the relative short residence time of its water masses, makes it highly reactive to climate change [15–17], so that it ranks among the world’s regions for which the strongest warming rates are predicted [18]. The Mediterranean Sea is also a biodiversity hotspot [19,20], threatened by many anthropogenic impacts [21]. In addition to direct human impacts, climate change is driving the sensitive Mediterranean Sea ecosystems towards an unpredictable future [22–24]. A proper evaluation of ecosystem change requires the availability of long-time series [25,26], which are unfortunately rare in the Mediterranean Sea as well as worldwide [6,27]. The Ligurian Sea (NW Mediterranean) represents a partial exception, as historical data are available for a number of taxa and habitats [28].

There is growing evidence that a major shift in Ligurian Sea climate and ecosystem regime occurred around the 1980–90s [28,29], in coincidence with similar changes observed in other European seas and perhaps globally. Such changes were caused by complex ocean-atmosphere interactions and involved plankton, fish, and top predators [30–32].

Quantitative assessments of the ecological impact of climate change are scarce [17]. The rocky reef off Mesco Point offers one of the longest, although discontinuous, Mediterranean data series on epibenthic communities, which includes both qualitative and quantitative data ([33], and references therein). Qualitative, “naturalistic” observations are available since the 1930s [34], whereas quantitative data—obtained through underwater wire-frame still photography—are available since 1961 [35,36]. Combining observational information with quantitative data led to the conclusion that the epibenthic communities remained comparatively stable for nearly 60 years, then changed abruptly in the 1990s to assume a new configuration that in turn remained stable till 2008 [33].

The aim of the present paper is twofold: (i) updating the existing historical data series with new photographic surveys carried out in 2017, in order to see if the community remained stable for a further decade or returned to the previous situation; and (ii) to compare community trends with pre-existing sea water temperature data.

2. Materials and Methods

2.1. Study Area and Field Activity

Mesco Point is a rocky headland located in the eastern Ligurian Sea, composed by sandstones organised in strata, dipping SW as a plunging cliff. The rocky reef studied (hereafter, Mesco Reef) lies immediately off the point, between ca 15 m and ca 55 m depth (Figure 1), and hosts a typical coralligenous community [33,36]. Since 1997, Mesco Point and Mesco Reef have been included in the “Cinque Terre” Marine Protected Area (MPA): as a consequence, fishing has been banned and diving strictly regulated [37].

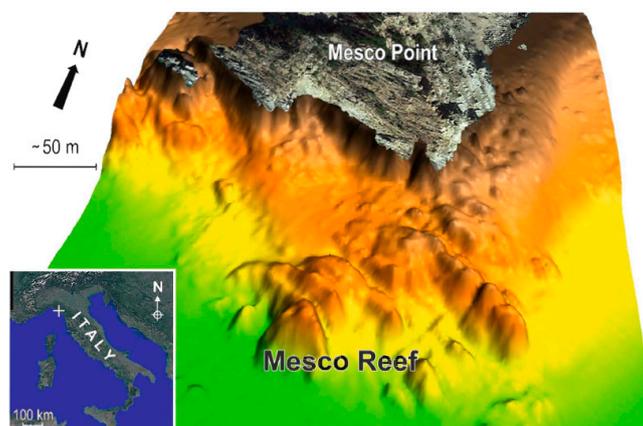


Figure 1. Geographical situation of the study area in Italy (cross in the inset) and three-dimensional reconstruction of Mesco Reef based on multibeam survey.

Fieldwork in 2017 [38] consisted in photographic surveys as already done in 1961 [36], 1990 [39], 1996 [40,41], and 2008 [42,43], always in summer. The original photostations of 1961 were relocated on the basis of published descriptions [35,36] and the personal detailed knowledge of Mesco Reef by one of the authors (AP). Four stations between 20 m and 40 m depth were selected (one at 20 m, one at 30 m and two at 40 m), with 3 replicates per station, for a total of 12 photoquadrats of 1 m² per year. Voucher specimens of non protected species were collected only when necessary to identify problematic organisms, especially turf/filamentous algae.

2.2. Temperature Data

As no time series of temperature data exist for Punta Mesco, we used the longest dataset available for the Ligurian Sea, i.e., that of Villefranche-sur-Mer, where measures of sea water temperature have been collected fortnightly in the water column between 0 m and 75 m depth since 1958 [44,45]. We took into account the data coming from 20 m and 40 m depth, where biological data also came, and from 0 m depth, to verify congruence with Ligurian sea surface temperature (SST) data derived from NOAA (US National Oceanic and Atmospheric Administration) satellite records and freely available at www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl [46].

2.3. Data Management

Yearly means of sea water temperature were calculated independently for each of the depths selected (0 m, 20 m, and 40 m). Time trends between 1960 and 2018, to cover the periods of biological data, were explored by smoothing yearly means with moving averages over seven-year periods [47]. Water temperature data measured at 0 m off Villefranche-sur-Mer were almost superimposable to SST data from satellite records, indicating that they can be an acceptable proxy of sea water temperatures at Mesco.

From the photoquadrats, the percent cover of all the sessile epibenthic conspicuous species was obtained. To assure comparability with the earliest study, cover data were transformed into the following indices: 0.1 = cover negligible (<0.5%); 1 = less than 5% of the surface; 2 = between 5% and 25% of the surface; 3 = between 25% and 50% of the surface; 4 = between 50% and 75% of the surface; 5 = more than 75% of the surface [36]. Transformed cover data were analysed both in R-mode (for species) and Q-mode (for stations). Species were clustered using Bray–Curtis similarity and complete linkage. To explore change with time in community composition, the data matrix (photoquadrats × years) × species was submitted to non-metric multidimensional scaling (NMDS), based on Euclidean distances. NMDS has been integrated with a 1-way permutational multivariate analysis of variance (PERMANOVA), using 9999 random permutations of species between year groups to test for significance of the pseudo-F value. The temporal rate of change of the whole coralligenous community of the rocky reef was assessed by computing the average (± standard error) Euclidean distance between the photoquadrats of a given year and the centroid of the photoquadrats of 1961, thus allowing direct comparison with a previous study [33]. Finally, the average (± standard error) Coefficient of Variation (CV%) of Euclidean distances was calculated for each year, lower CV values indicating biotic homogenization [48,49]. Change in community structure was analysed using primarily the Shannon–Wiener diversity index, computed with the natural logarithm \ln . However, as no single index adequately summarizes the diversity of a species assemblage, we also measured species richness, with Margalef index, and evenness, with Simpson index [50]. To assess the relative importance of richness and evenness in determining overall diversity, a graphical display was produced where each year was represented by its mean value (± standard error) in the richness-equitability plane [51]. All analyses were performed using the free software PaSt [52].

3. Results

3.1. Sea Water Temperature

An increase in water temperature between 1960 and 2018 was observed at all depths, but the increase was not gradual; rather, three main phases could be recognised: (1) a comparatively cool phase between 1960 and 1985; (2) a phase of rapid warming from 1985 to 1995; and (3) a warmer phase from 1995 to 2018 (Figure 2a). Accordingly, in the third phase sea water temperatures were on average 0.8 °C at 0 m, 0.7 °C at 20 m, and 0.4 °C at 40 m higher with respect to those of the first phase (Figure 2b); differences were significant at all depths (Student *t* test, $p < 0.001$).

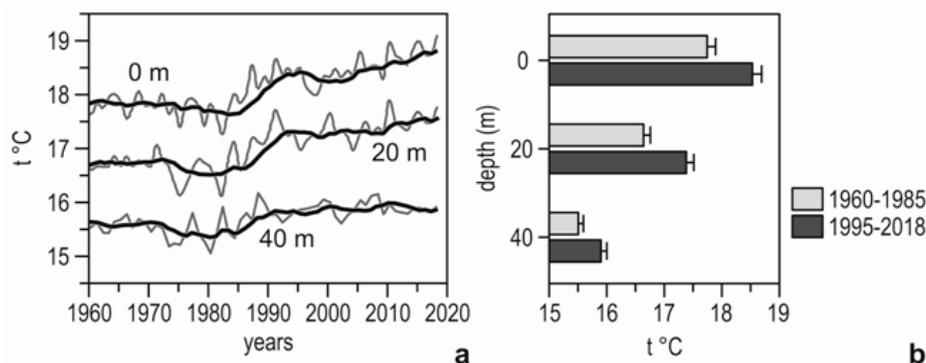


Figure 2. Trend in Ligurian Sea water temperatures, 1960 to 2018: (a) thin lines represent yearly averages at 0 m, 20 m, and 40 m, thick lines are 7-year moving averages (data from Villefranche-sur-Mer [44,45]); (b) comparison between mean (+ standard error) sea water temperatures at 0 m, 20 m, and 40 m in two time periods: 1960–1985 and 1995–2018.

3.2. Species and Species Groups

A total of 62 epibenthic sessile species was found (Supplementary Material Table S1). The 23 species that were recorded in a single year only have been excluded from any subsequent analysis to avoid noise and to reduce the number of zeros in the dataset (Supplementary Material Table S2). These 23 species are not to be considered “rare”, as all of them are common in Ligurian Sea subtidal reefs; rather, they are species that have been undersampled with the methodology adopted in this study. The remaining 39 species have been arranged in four groups by cluster analysis (Figure 3). Groups were apparently related to change over time of individual species cover. A group of 14 species increased or newly appeared after 1990 and were therefore named ‘winners’ (Figure 4a); beside a number of native species (e.g., the sponges *Axinella verrucosa* and *Crambe crambe*), they included two invasive alien macroalgae (*Caulerpa cylindracea* and *Womersleyella setacea*) that reached high cover values in recent years. On the contrary, ten species became scarcer (e.g., the gorgonian *Paramuricea clavata*) or even disappeared (e.g., the soft coral *Alcyonium coralloides* and the gorgonian *Eunicella singularis*) with respect to 1961, showing little or no sign of recent recovery, and were therefore named ‘losers’ (Figure 4b). Seven species (e.g., the sponges *Ircinia oros* and *Leucosolenia variabilis*, and the encrusting coralline alga *Lithophyllum stictiforme*) similarly reduced their cover after 1990, but then showed some sign of recovery, reaching in 2017 values comparable to those of 1961 (Figure 4c); they were therefore named ‘resilients’. Finally, a group of eight species (such as the sponge *Agelas oroides*, the hydroid *Eudendrium racemosum*, and the bryozoan *Smittina cervicornis*), absent or scarce in 1961, bloomed after 1990 but then decreased again in 2017 (Figure 4d); they were named ‘profiteers’ because apparently they took advantage of the reduction of the losers and the resilientes before the winners took place and resilientes recovered.

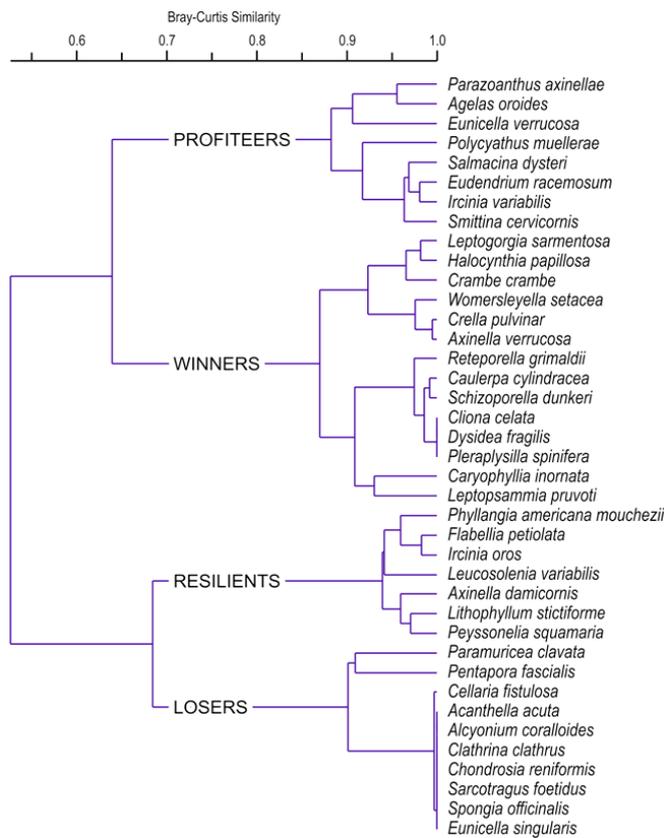


Figure 3. Species groups resulting from cluster analysis (Bray–Curtis similarity, complete linkage) in the sessile epibenthos of Mesco Reef. Groups’ names have been assigned according to change over time in species cover (see text for groups’ definition).

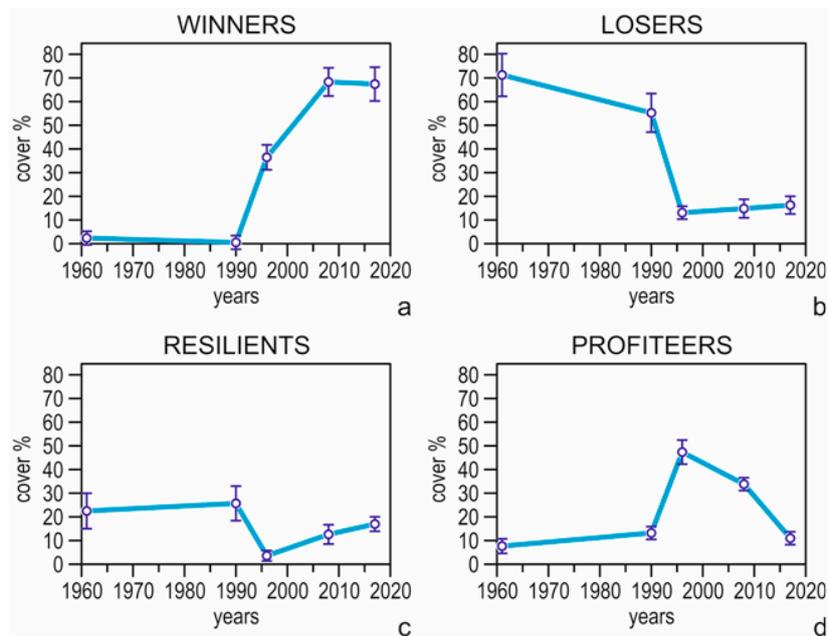


Figure 4. Change in mean (\pm standard error) total cover with time of the four groups of sessile epibenthic species identified by cluster analysis at Mesco Reef: (a) winners; (b) losers; (c) resilients; (d) profiteers; see text for groups’ definition.

3.3. Community Composition

Applying NMDS to the matrix of (12 photoquadrats \times 5 years) \times 39 species (Supplementary Material Table S2) produced a two-dimensional graph in which year-points were disposed in two major clouds (Figure 5): the first was located on the left side of the graph and included all the points for the years 1961 and 1990, with no apparent difference between the two years; the second was located on the right side of the graph and included all the points for the years 1996, 2008, and 2017. There was no overlap between the two point-clouds. The dispersion of individual photoquadrats around the relative year centroid was rather high in 1961 and 1990, and lower in 1996, 2008, and 2017.

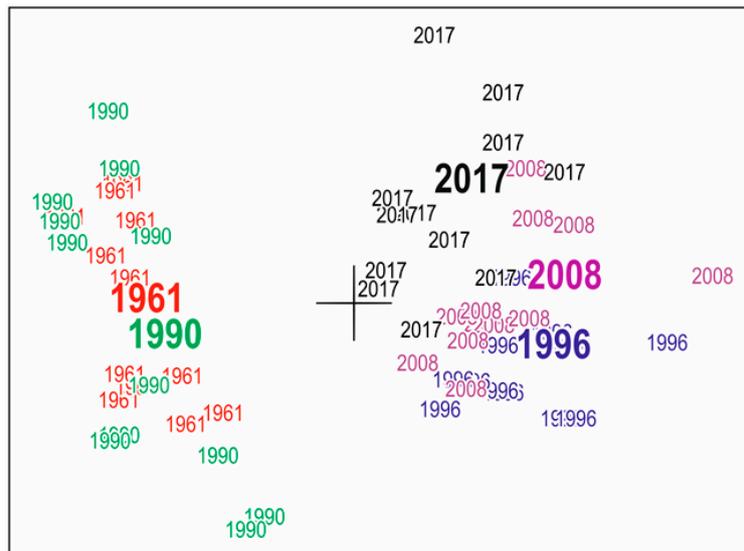


Figure 5. Two-dimensional NMDS plot of Mesco Reef photoquadrats. Stress = 0.1725. Small numbers represent individual photoquadrats of that year, large numbers the year centroids.

The sharp separation between 1961–1990 and 1996–2008–2017 points was indicative of a dramatic change in community composition at Mesco Reef. Results of 1-way PERMANOVA confirmed that the difference between these two-year groups was highly significant (pseudo-F = 10.52, $p < 0.0001$). Similarly, the trend of the average Euclidean distance between photoquadrats indicated little change between 1961 and 1990, a distinct acceleration of the rate of change between 1990 and 1996, and again little change between 1996 and 2017 (Figure 6a). On the contrary, the variability among assemblages (average Coefficient of Variation) declined monotonously over time, describing a gradual process of biotic homogenization, with decreasing difference among photoquadrats (Figure 6b).

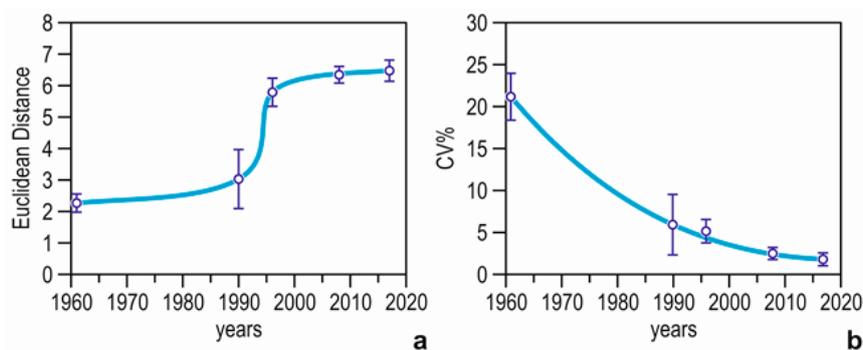


Figure 6. Quantitative change in community composition at Mesco Reef, 1961 to 2017: (a) Mean (\pm standard error) Euclidean distance among photoquadrats with respect to 1961; (b) Mean (\pm standard error) Coefficient of Variability (CV%) among photoquadrats in each year.

All analyses were consistent in indicating that a major change in community composition occurred between 1990 and 1996. The formerly flourishing coralligenous community of Mesco Reef experienced a severe reduction of the canopy of the gorgonian *Paramuricea clavata*, which even disappeared at the shallowest depths and implied the loss or diminution of the three-dimensional structure of the seascape; the assemblage of the basal layer also changed noticeably (Figure 7).



Figure 7. Change in the epibenthic sessile community of Mesco Reef. Note the high canopy of the purple red gorgonian *Paramuricea clavata* in 1990 and the abundance of encrusting sponges and of the zoantharian *Parazoanthus axinellae* in 2017. The two images were taken in the same station at 20 m depth.

3.4. Community Structure

Diversity (Shannon–Wiener index) increased over time in the coralligenous community of Mesco Reef. Once again, the increase was not gradual, and two phases could be distinguished: a low diversity phase between 1961 and 1996 and a comparatively high diversity phase in 2008 and 2017 (Figure 8a). Both species richness (Margalef index) and evenness (Simpson index) confirmed this pattern, exhibiting a sharp discontinuity between 1996 and 2008 (Figure 8b).

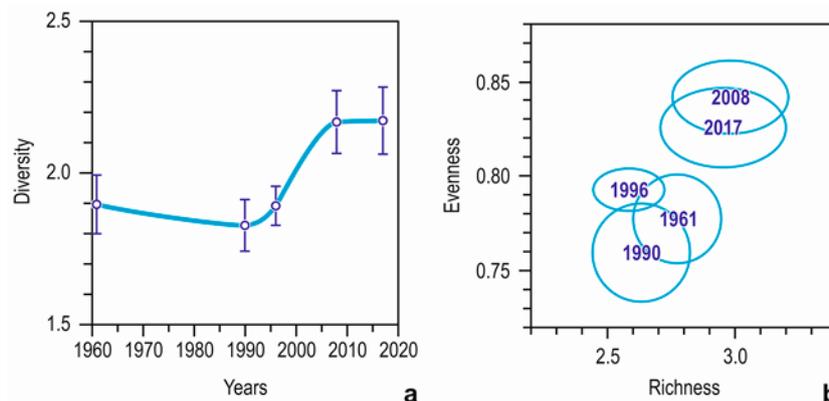


Figure 8. Change in community structure at Mesco Reef, 1961 to 2017: (a) Mean (\pm standard error) diversity (Shannon–Wiener index); (b) Position of year centroids in the richness–equitability plane, the axes of the ellipses being standard errors.

4. Discussion and Conclusions

The abrupt change in Ligurian Sea thermal regime in the 1990s determined a sea water temperature increase of 0.4–0.7 °C at the depths inhabited by the coralligenous community of Mesco Reef. Other recent analyses of sea water temperatures in the NW Mediterranean Sea evidenced a similar change [17,29,45,46,53], and its effects on marine communities were soon detected [54].

There might be other potential drivers of biotic change at Mesco Reef. Local human pressures have been increasing during the period of study: in the 1960s a small marina was built at the

western extremity of the beach of Monterosso (about 1 km from Mesco Reef), whereas between 1963 and 1974 a large embankment was created [33]; coastal works have probably been responsible for the increased water turbidity in the area, which must have surely affected sessile organisms [54]. Distinguishing environmental stress due to climate change from that due to human pressure is often difficult [19]. However, the major coastal works occurred well before 1990, while the community change occurred after 1990. In 56 years, underwater photographic technology changed radically, passing from Rolleimarin (in 1961) to Nikonos (in 1996 to 2008) to a housed digital Canon (in 2017), which might imply change in image resolution and accuracy of data extraction [43]. Observers also changed, but three of the authors (AP, CNB, and CM) participated in field and/or laboratory activities from 1990 to 2017. Therefore, change in sampling and analysis did not coincide with biological change.

At Mesco Reef, change in sea water temperature between 1990 and 1996 was paralleled by a similar abrupt change in species occurrence and cover [33]. Novel information obtained in 2017 indicated that the community composition established after 1996 in a warmer condition persisted almost unaltered for two decades. Theory predicts that regime shifts (i.e., changes in the factors that govern the dynamics of the ecosystem) cause corresponding phase shifts in the biotic communities [55], and this is apparently what happened at Mesco Reef, suggesting that the previous community as known in 1961 and 1990—and possibly little modified from that existing in the 1930s [33]—has not been capable to resist climate change. The community passed from a complex configuration with a dense canopy of large gorgonians (*Paramuricea clavata*), an understory dominated by long-lived calcified bryozoans (*Cellaria fistulosa*), and a basal layer of encrusting corallines (*Lithophyllum stictiforme*), to a simpler configuration with a reduced *P. clavata*'s canopy (due to the mass mortality induced by the heat waves of the 1990s [28]), an understory with soft corals (*Parazoanthus axinellae*) and a basal layer of filamentous algae (dominated by the alien species *Womersleyella setacea* and *Caulerpa cylindracea*). Reduced canopy and decreased abundance of calcified organisms implied loss of topographic complexity, with likely consequences on the whole associate community and ecosystem services [56,57]. The two alternative states remained comparatively stable for many years (1961 to 1990 the previous one, 1996 to 2017 the subsequent one), while the transition between them has been abrupt (between 1990 and 1996) and marked by the quantitative exuberance of a number of species we called 'profiteers'. The outburst of generalist species at the transition between two distinct species assemblages along a spatial gradient has been called 'Riou effect', from the name of an island near Marseilles, France [58]. What happened at Mesco Reef was apparently a Riou effect along a temporal gradient.

Updating the historical data series of Mesco Reef confirmed the trend in community composition already observed in previous analyses [33]. A hitherto unexplored aspect was structural change, in terms of community diversity. A phase shift was apparent also in this case, although the discontinuity was not between 1990 and 1996 but rather between 1996 and 2008. Why community structure responded with such a lag time to compositional change is unclear. In addition, it has been surprising to observe that the new community emerging from the regime shift of the 1990s was both richer and more equitable, notwithstanding reduced variability among photoquadrats. Although counterintuitive, the parallel increase in diversity and biotic homogenization after dramatic change in species composition may not be paradoxical [59]. The two phenomena (i.e., diversity and homogenization) concern different ecological scales, as the increase in the average photoquadrat diversity is an expression of α -diversity while homogenization implies a reduction of β -diversity, and the two may well be uncorrelated [16]. At Mesco Reef, reduced canopy might have offered space to the colonization by new taxa (especially the photophilic ones) or simply made understory species more visible in the photographs: as a result, and contrarily to global patterns [60], there have been more 'winners' than 'losers'. The 'winners' included alien species, such as *Womersleyella setacea* and *Caulerpa cylindracea*, two of the 'worst' invaders in the Mediterranean Sea [61]. Both species were first recorded in the Ligurian Sea in the 1990s [62,63]: the former was first detected at Mesco Reef in 1996, to become dominant in 2008 and 2017; the latter appeared in 2008 and increased dramatically in 2017, as observed in most of the Ligurian Sea [64]. Alien

invaders are known to induce homogenization in the recipient ecosystem [65], but their relationship with diversity may be either positive or negative, and no generalization is possible a priori [66].

In the same years when the aliens were arriving, the Cinque Terre MPA was established (1997). The protection measures implemented by the MPA might help the return of the species that used to characterise the coralligenous community of Mesco Reef in historical times [67] and mitigate the effects of climate change [68]; however, they will hardly eradicate the aliens [69].

Only a minority of species, which we called ‘resilients’, showed some recovery to date. The novel community that emerged from the climate shift of the 1990s, with many once characteristic species lost, reduced complexity, biotic homogenization, greater diversity, and domination by alien species, may be able to persist [70], and there is little opportunity to go back for ecosystems under altered regime [16]. Recent analyses of Ligurian Sea temperature suggest that another phase of rapid warming is occurring, 2014 to 2018 having been the warmest years on records [28,46], thus conforming to the expected further rapid warming over the whole Mediterranean Sea [71,72]. Only continued monitoring will help envisaging the possibility for a reversal of the present phase shift or for further directional transformations driven by sea water warming and other components of global change. The accumulation of data for nearly 50 years represents a precious heritage: long-term monitoring effort on Mesco Reef is a multi-generational deal and requires commitments by institutions that persist beyond the working lives of individuals [73]. We recommend MPA administrators and environmental managers to keep investigating Mesco Reef community in the years to come.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1424-2818/11/11/215/s1>, Table S1: Species list, Table S2: Data matrix.

Author Contributions: Conceptualization, C.N.B. and A.P.; methodology, A.P.; software, C.N.B. and V.P.; validation, C.N.B., C.M., A.A., and M.M.; formal analysis, C.N.B. and V.P.; investigation, A.A. and M.M.; resources, M.M.; data curation, C.N.B. and V.P.; writing—original draft preparation, C.N.B.; writing—review and editing, C.M.; visualization, C.N.B. and A.P.; supervision, C.N.B.; project administration, C.M.; funding acquisition, C.M. and M.M.

Funding: This research received no external funding.

Acknowledgments: This paper is dedicated to the memory of Gianni Roghi (1927–1967), pioneer in scuba diving and UW photography (www.gianniroghi.it). Luigi Piazzini (Sassari) identified *Womersleyella setacea*, Francesco Massa (Genoa) produced the 3D rendering of Mesco Reef based on multibeam data provided by Stefano Coppo and Corinna Artom of Regione Liguria (Genoa). The “Cinque Terre” Marine Protected Area authorised fieldwork at Mesco Reef.

Conflicts of Interest: The authors declare no conflict of interest.

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