frontiers in Marine Science

BRIEF RESEARCH REPORT
published: 09 February 2021
doi: 10.3389/fmars.2021.620866

Mass Mortality of Foundation Species on Rocky Shores: Testing a Methodology for a Continental Monitoring Program

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Global concern around substantial losses of biodiversity has led to the development of a number of monitoring programs. Networks were established to obtain appropriate data on the spatial and temporal variation of marine species on rocky shores. Recently, the Marine Biodiversity Observation Network Pole to Pole of the Americas (MBON P2P) program was established and is coordinating biodiversity surveys along coastal areas throughout the continent. The goal of this paper was to test the usefulness and adequacy of a methodology proposed for the MBON P2P program. Changes in benthic assemblage cover were studied on monitored sites in northern Patagonia before and after the 2019 austral summer. Long-term dynamics of mussel bed is described based on existing data. Results showed that assemblages before the 2019 austral summer were different from assemblages after it. Thus, a mussel mass mortality event could be detected with this methodology. It took less than a year for mussel cover to drop from 90 to almost 0%; even where substantial changes in mussel bed cover were not registered in the previous ∼20 years at the study area. This simple methodology is an adequate tool for monitoring rocky intertidal habitats. Yearly monitoring is needed, as a minimum, to perceive this kind of process timely. Real-time detection offers the opportunity of properly understanding the causes that lead to the loss of key community components, such as these foundation species. Furthermore, it would provide early warning to decision-makers enhancing the chances of conservation of natural environments and their ecosystem services.

Keywords: benthos, disturbance, conservation, mussels, ecosystem services, intertidal

Edited by:
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Specialty section:
This article was submitted to Ocean Observation, a section of the journal Frontiers in Marine Science

Received: *23 October 2020*
Accepted: *15 January 2021*
Published: *09 February 2021*

Citation:
Mendez MM, Livore JP, Márquez F and Bigatti G (2021) Mass Mortality of Foundation Species on Rocky Shores: Testing a Methodology for a Continental Monitoring Program. Front. Mar. Sci. 8:620866. doi: 10.3389/fmars.2021.620866

INTRODUCTION

Rocky shores are one of the most widely distributed coastal habitats throughout the world (Thompson et al., 2002). Different human stressors, including introduction of species, physical modification of the coast, contamination, recreation, and the changes in climate are continuously threatening these habitats (Halpern et al., 2015; Duffy et al., 2019). Several efforts have been made to build coordinated international monitoring networks across the world aimed at obtaining temporal data on biodiversity, community structure, and dynamics of rocky shores (Canonico et al., 2019; Duffy et al., 2019). Starting with the Marine Biodiversity and Climate Change Project (MarClim) in 1950 on the coast of United Kingdom and France, different programs have been developed with this premise around the world.

The history of monitoring networks in South America is relatively short; with three main efforts recorded in the last 20 years. The Natural Geography in Shore Areas (NaGISA) project of the Census of Marine Life (CoML) program (2000–2010) and its sequel the South American Research Group on Coastal Ecosystems (SARCE) (since 2011), together monitored rocky shores over more than 60° of latitude across 150 sites. Such monitoring described and analyzed biodiversity patterns across latitudinal gradients and linked them with ecosystem functioning and human stressors (Miloslavich et al., 2016; Cruz Motta et al., 2020). Lastly in 2016, the Pole to Pole project of the Marine Biodiversity Observation Network (MBON P2P) was established with a goal of using common methods for the collection of biological information in coastal habitats throughout the American continent (Canonico et al., 2019; Duffy et al., 2019).

Argentinean Patagonia (41–55°S; 63–70°W) rocky intertidal shores were included as sampling sites since 2007 in the NaGISA and SARCE projects (Miloslavich et al., 2016; Cruz Motta et al., 2020) and are currently being included in MBON P2P. One of the most important features on these shores is the extreme desiccation that intertidal organisms are exposed to through a combination of strong dry winds, low humidity and scarce rainfall (Bertness et al., 2006). Scorched mussel beds of the mid intertidal are a distinctive component of the shores and a dense matrix of the two species, *Brachidontes rodriguezii* and *Perumytilus purpuratus*, dominate the physiognomy of the rocky shore communities (Bertness et al., 2006; Silliman et al., 2011; Miloslavich et al., 2016). These communities are unique because almost all mid intertidal organisms are unable to survive outside of the mussel bed; hence community structure and its diversity along with ecosystem function in these shores are obligately dependent on these foundation species (Bertness et al., 2006). Historically, mussel beds from this region show simple structure, uniform appearance and disturbance-generated bare space throughout the bed is strikingly rare (Bertness et al., 2006; Adami et al., 2018). However, losses in cover of scorched mussels were visually observed at different monitored sites after the 2019 austral summer. The goal of this paper was to test the usefulness and adequacy of a simple, low-cost, low-tech methodology proposed for the recently established MBON P2P program (Livore et al., 2021). To do this, we compare the mid intertidal benthic assemblage before and after the 2019 austral summer using this methodology. A description of the long-term cover dynamics of the mid intertidal foundation species is given in order to provide a context of the temporal scale of natural fluctuations in the study area.

MATERIALS AND METHODS

Study Sites and Sampling Design

The study was performed at three rocky shores (Punta Cuevas: PC, Punta Este: PE and Punta Loma: PL; **Figure 1**) on the southwest coast of Golfo Nuevo, Chubut, Patagonia Argentina. Sites have similar slope, and semidiurnal tides with mean amplitude of ∼4 m, which exposes a sedimentary rock platform (consolidated mudstone). The characteristic three-level biological zonation of Patagonian rocky shores (Bertness et al., 2006; Rechimont et al., 2013; Miloslavich et al., 2016) was present at the three studied sites. The high intertidal zone has a large proportion of bare soil, being the invasive barnacle *Balanus glandula* and the limpet *Siphonaria lessonii* abundant. The mid-intertidal is typically dominated by matrix of scorched mussels, *Brachidontes rodriguezii* and *Perumytilus purpuratus*. The low intertidal level is characterized by several ephemeral algal species and a large proportion of the calcareous alga *Corallina officinalis*. PC and PE were monitoring sites of the SARCE project and the three sites are currently part of the MBON P2P program.

As mentioned in the Introduction, losses in scorched mussel cover were visually observed in the mid intertidal at several sites along the coast of Golfo Nuevo after the 2019 austral summer (**Figure 1**). Thus, we compare the mid intertidal benthic assemblage in two different times: before and after this event using data collected through a simple, low-cost, low-tech methodology proposed for the MBON P2P program. For the before samplings, data was obtained from previous surveys performed in October 2014 (at PL site) and in October 2018 (at PC and PE sites). After samplings were conducted in June 2019 at the three sites. A specifically designed protocol to study changes in rocky shore communities was used in all sampling events (adapted from Ocean Best Practices: http://dx.doi.org/10.25607/OBP-5). Briefly, percentage cover of benthic organisms was estimated inside 25 × 25 cm photoquadrats haphazardly placed on the substrate (n = 5–10 per sampling; N = 50). Recently, this methodology was compared to a previously used *in situ* visual methodology and both similarly detected spatial and temporal variability of rocky shores assemblages (Livore et al., 2021). In the lab, 100 equidistant points were placed over the digital image using the free software Coral Point Count (CPCe V 4.1, Kohler and Gill, 2006) and organisms observed under each point were determined to the lowest possible taxonomic level.

Non-metric multi-dimensional scaling (nMDS) was used to visualize multivariate patterns in benthic assemblages. Percentage covers of benthic taxa were analyzed using permutational analysis of variance (PERMANOVA). Similarity matrices based on Bray-Curtis measure were generated for the analyses, which used 9,999 permutations of residuals under a reduced model. PERMANOVA model had two factors: sites (Si, fixed, three levels: PC, PE, and PL) and Time (Ti, fixed, two levels: before and after). Pairwise comparisons were performed among all pair of sites for the two times levels. A similarity percentage analysis (SIMPER) was performed to determine the taxa responsible for the similarities among sites and the dissimilarities between times. All the multivariate analysis were performed using PRIMER v6.1.7 software.

To describe the long-term natural dynamics of mid intertidal foundation species we collected historical data from Punta Cuevas. This intertidal is located at the southern end of the

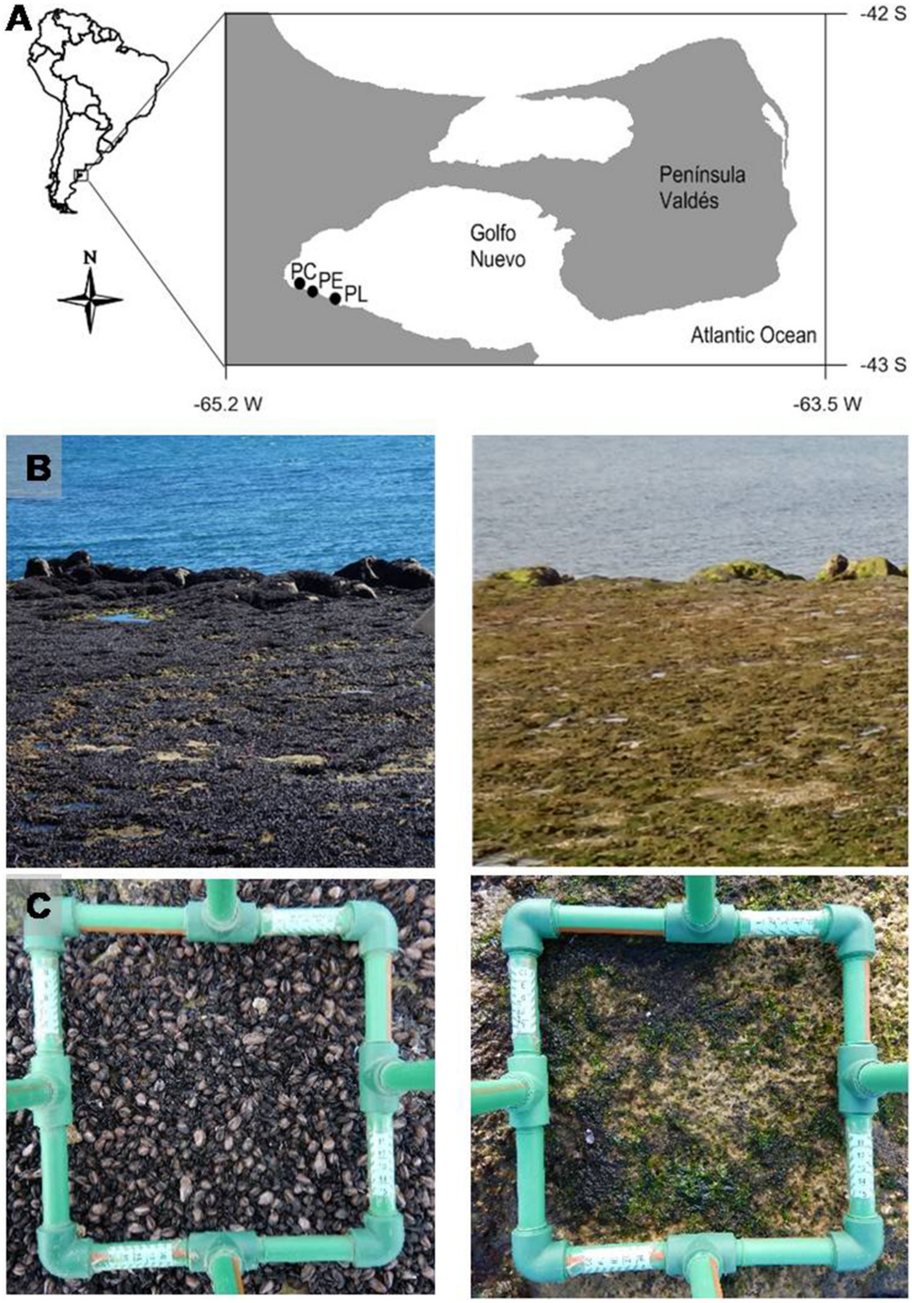

FIGURE 1 | (A) Map of South America showing the location of the study sites. PC, Punta Cuevas; PE, Punta Este; and PL, Punta Loma. **(B)** Punta Loma mid intertidal rocky shore showing the typical cover of the mussel bed in February 2018 (left) and in May 2019 (right). **(C)** Plots in the mid intertidal of Punta Cuevas in October 2018 (left) and after the mass mortality event, when mussels were absent on all horizontal surfaces in June 2019 (right).

city of Puerto Madryn, 500 meters from the CCT CONICET-CENPAT and the Universidad Nacional de la Patagonia (the authors' workplaces). Both scientist and biology professors, from these institutions, regularly use the site for academic and scholar field trips. Thus, quantitative (for example, percentage cover) and qualitative (for example, panoramic photographs) data was obtained almost annually for the last ~20 years to examine the stability and resilience of the mid intertidal. Due to the heterogeneity in the nature of the data a qualitative description of mussel cover at Punta Cuevas over the past ~20 years was obtained. Landscape photographs, occurrence data and percentage cover data of organisms at the site were considered (for details see **Table 2**). From these sources, scorched mussel cover was estimated into three categories: <50, 50–80, and >80%. Large bare soil patches (>10 m^2) in photographs, if present, were recorded.

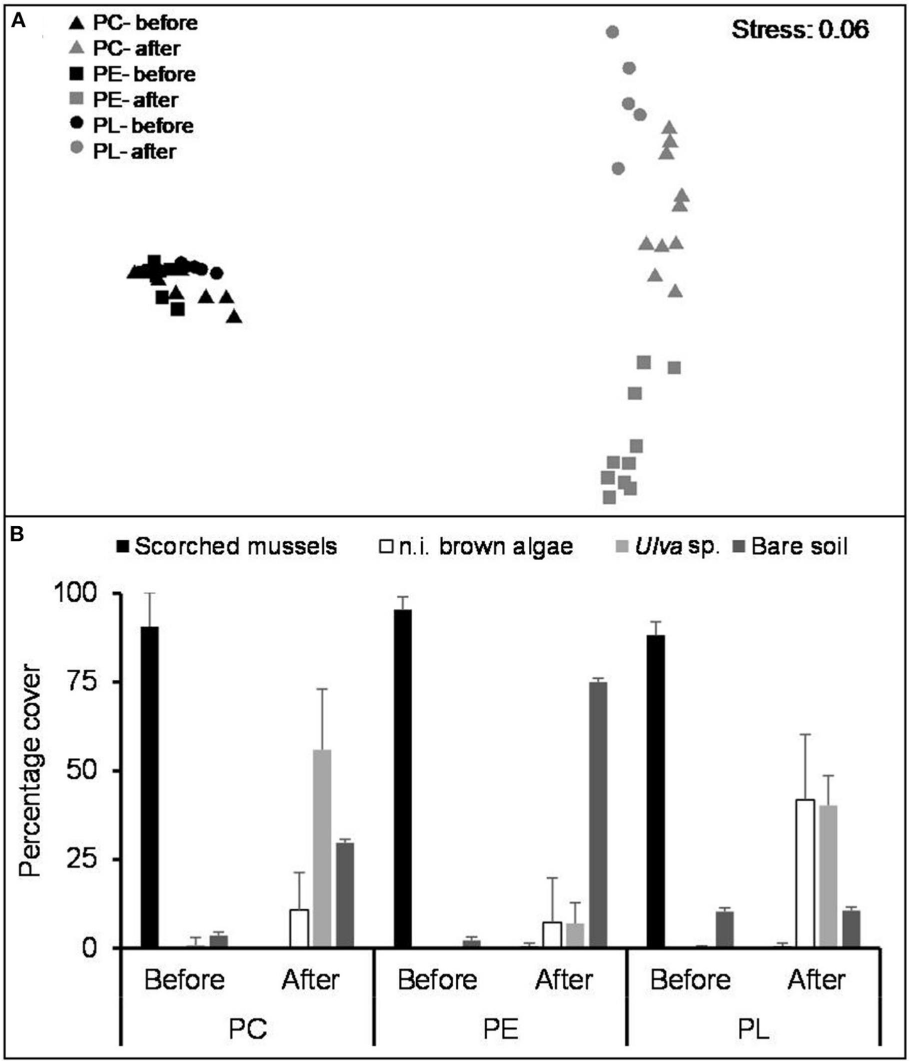

FIGURE 2 | (A) Two-dimensional MDS ordination comparing benthic assemblages associated with the three sites before and after the 2019 austral summer. **(B)** Mean (SD) scorched mussel, not identified (n.i.) brown algae, *Ulva* sp., and bare soil cover for the three samplings sites before and after the 2019 austral summer. These taxa explain >90% of the observed differences in the assemblages between sampling times (SIMPER analysis, **Table 1**).

RESULTS

Benthic assemblages before the 2019 austral summer were dissimilar to assemblages after it (**Figure 2A**). No clear separation between sites was distinguished in the before samplings, but samples were grouped by sites in the after samplings (**Figure 2A**). The assemblages before the 2019 austral summer were significantly different from the assemblages after it and among sampling sites [PERMANOVA. SixTi: pseudo-$F = 29.14$, $df = 2$, $p(\text{perm}) < 0.05$]. Pairwise comparisons showed that for the before samplings, PC = PE, PC = PL [$p(\text{perm}) > 0.05$] and PE $\neq$ PL [$p(\text{perm}) < 0.05$]. For the after samplings, instead, all sites were different from each other [$p(\text{perm}) < 0.05$]. SIMPER analysis showed that scorched mussels were responsible for most of the similarity between sites in the before samplings (**Table 1**). Cover of bare soil, *Ulva* sp., and a not identified brown algae, mostly contribute to the similarities between sites after the 2019 summer (**Table 1**). When before and after samplings were compared, scorched mussels, bare soil, *Ulva* sp., and a not identified brown algae cover explain the high dissimilarity found between times (**Table 1** and **Figure 2B**).

The examination of the available occurrence and cover data and photographs suggests that the natural dynamics of the mid intertidal at the studied site is very stable and uniform through time. Throughout the last ~20 years, mussel cover was >80%, and no substantial changes in cover were registered at the site (**Table 2**). Furthermore, bare soil patches >10 m^2 were not observed in the mussel bed during this period.

TABLE 1 | SIMPER routine results showing taxa with the greatest contributions to similarity among sites and the dissimilarities between times.

	Contrib%	Cum.%
Time: before (average similarity: 92.11%)		
Scorched mussels	96.56	96.56
Time: after (average similarity: 75.30%)		
Bare soil	54.32	54.32
Ulva sp.	34.24	88.55
n.i. brown algae	8.01	96.56
Before vs. after (average dissimilarity = 94.60%)		
Scorched mussels	48.72	48.72
Bare soil	23.5	72.21
Ulva sp.	16.91	89.13
n.i. brown algae	6.71	95.83

n.i., not identified.

TABLE 2 | Natural dynamics of Punta Cuevas mussel bed between 1998 and 2020.

Period	Sampling	Mussel bed cover estimation
1998–2001	Occurrence frequency[1] and landscape photographs	>80%
2002–2005	Occurrence frequency[1] and landscape photographs	>80%
2006–2009	Occurrence frequency[2] and landscape photographs	>80%
2010–2013	Cover data,[3,4] occurrence frequency,[2] and landscape photographs	>80%
2014–2017	Cover data,[3,4] occurrence frequency,[2] and landscape photographs	>80%
2018–2020	Cover data,[5] occurrence frequency,[2] and landscape photographs	No mussels after 2019 summer

Data collected from: [1]Torres and Caille (2009), [2]"Community ecology" samplings (Prof. A. Bisigato, UNPSJB), [3]"Malacology" sampling (Prof. G. Bigatti, UNPSJB), [4]SARCE samplings, [5]MBON samplings and a vast photographic record of the site.

DISCUSSION

This study shows how a simple low-cost and non-extractive methodology was able to detect changes in mid intertidal rocky shore assemblages, as a scorched mussel mass mortality event on Patagonian coasts. Anthropogenic pressure on coastal areas is increasing worldwide, and detecting temporal and spatial changes in rocky shore biodiversity is critical for its conservation (Duffy et al., 2019). Those sites suffering significant changes in biodiversity are considered degraded or unhealthy ecosystems. This equates to risks to different ecosystem services for billions of people, some as essential as human nutrition and health, recreation attractions or public safety (Canonico et al., 2019). One way to detect biodiversity changes is the implementation of monitoring programs. Although the history of these programs is quite young in South America, the present study provides empirical evidence on the efficacy of their methodologies in detecting rapid biodiversity changes. In the study area, dense beds of scorched mussels are a distinct component and the foundation species in the mid intertidal (Bertness et al., 2006; Miloslavich et al., 2016; Adami et al., 2018). In the present work, we found that mussel bed cover at different sites of Golfo Nuevo was close to 90% before the 2019 austral summer. However, almost no scorched mussels were registered at the sites after the 2019 summer, being replaced with bare soil and different algae (**Figure 1**).

In northern Patagonian rocky shores, desiccation plays a fundamental role in community structure (Bertness et al., 2006). Only a few habitat-forming species are capable of tolerating the extreme physical conditions. Several studies have described in detail the role of scorched mussels as ecosystem engineer species and in the provision of habitats and refuge for other organisms (Bertness et al., 2006; Silliman et al., 2011; Rechimont et al., 2013; Arribas et al., 2014, 2019). These studies report that more than 40 invertebrate species live associated with mussel beds avoiding environmental stress. In order to prevent the removal of living organisms and degradation of natural sites, global monitoring programs try to incorporate non-destructive sampling methodologies, like the one used here. Undoubtedly, there are some limitations related to this type of sampling, such as not detecting organisms associated with mussel beds. In this sense, the present work aimed at studying changes in cover on the dominant sessile intertidal species. However, the observed loss of the mussel cover and its replacement by ephemeral algae and bare soil would likely have important indirect effects on the associated assemblage through the absence of tens of species.

Our examination of the natural dynamics of Punta Cuevas mid intertidal showed that scorched mussel beds are highly stable and resistant to disturbance, as was suggested by Bertness et al. (2006) for central Patagonian rocky shores. This contrasts with mussel beds on the Atlantic and Pacific coasts of North America, for example, where disturbance-generated patches are common (Paine and Levin, 1981). The registered stability could be related to the small size of scorched mussels (usually about 0.20 cm long) and its strong byssal attachment strength (Bertness et al., 2006; Mendez et al., 2019). The pattern described in this study suggests that the drastic decline of scorched mussel cover observed at the study sites was not a consequence of the natural dynamics of the mussel bed and that this event was not part of the baseline fluctuations of the mid rocky shore assemblage.

From a conservation perspective, it is essential to consider the recovery time needed by a given community to reestablish after drastic changes in foundation species cover as the one detected here. Although *B. rodriguezii* has been observed to recruit continuously during the year in northern Atlantic Patagonia (Arribas et al., 2015), it would take up to a decade to reach the full recovery of the mussel bed (Bertness et al., 2006; Mendez et al., 2017). In this sense, the possibility of natural recovery from this event will depend on different processes related to larval recruitment, including larvae arrival from unaffected areas, and the reproduction of individuals in the affected areas (Kersting et al., 2020). We found that after the mass mortality event of scorched mussels, different opportunistic algae and bare soil dominated the mid intertidal. The switch in species dominance at the sites (i.e., algae and bare soil replacing mussels) could last several years and would influence local biological interactions with important consequences for community structure. Furthermore, the assemblages of the studied sites responded differently to mussel losses. After the 2019 austral summer, heterogeneity of the assemblages increased among sites and samples. This suggests that the effects of the mussel mortality are site-specific and could be hard to predict. Thus, in systems exposed to high physical stress where foundation species are dominant, management and conservation efforts should be focused on the foundation species instead of charismatic organisms that live associated to them (Bertness et al., 2006).

When massive mortalities occur, there is a need to study the causes of the event. Fungi, parasites, bacteria, viruses or toxic blooms have been reported as responsible agents for this kind of events in bivalves (Peperzak and Poelman, 2008; Vázquez et al., 2016; Kersting et al., 2020). More recently, several studies documented how extreme weather events (e.g., heatwaves) can be responsible for mass mortalities in dominant organisms (Zamir et al., 2018), including mytilids (Seuront et al., 2019; Lupo et al., 2021). The fact that the changes in mussel cover were detected after a summer suggests that mortality could be related to weather conditions. Even though no extraordinary storm events were registered in the 2019 summer, the loss of scorched mussels cover coincided with high atmospheric temperature (>35°C) and strong winds (>30 knots) occurring simultaneously during low tides that exposed these organisms to prolonged thermal and desiccation stress over several continuous days (Mendez et al., 2020). These atmospheric conditions also coincided with sea surface temperature anomalies exceeding 1°C occurring in Golfo Nuevo, indicating the presence of heatwaves during the 2019 austral summer (Mendez et al., 2020). Also, different parasites and viruses were reported in the area, several of them directly affecting local bivalve species (Vázquez et al., 2020). Thus, different drivers or a combination of them can be causing the registered mortality of scorched mussels (Lupo et al., 2021). At the time of publication, potential causes for this sudden mass mortality are being studied, and none of them could be completely ruled out.

In this work a scorched mussel mass mortality event was detected, taking <6 months (summer 2019) for the mussel beds to decline from 90% to losing all of its cover (**Figure 1**). Significant effort is spent on debating sampling frequency in monitoring programs; our results contribute empiric evidence that highlights the need to have at least yearly monitoring. It is important to note that without periodic monitoring, this mortality case would not have been detected in its beginnings and the causes that led to it could not have been appropriately studied. The immediacy of the detection gives us the opportunity to study the changes in the community from the start and to follow the entire recovery process, whilst considering the concomitant effects on ecosystem function. Studies of this nature, derived from monitoring programs, can give an early alarm to decision-makers and provide a timely response action that mitigates the impacts on coastal zones and preserves rocky shore environments and their ecosystem services.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

MMM analyse the data and wrote the manuscript with contribution from all authors. All authors conceived the project and participated in data collection in the field.

FUNDING

Field work was partially financially supported by ANPCyT-FONCyT (PICT 2018-0969). Field work was also supported by Total Foundation (SARCE program) and NASA under the A.50 AmeriGEO Work Program of the Group on Earth Observations with grant number 80NSSC18K0318 (Laying the foundations of the Pole-to-Pole Marine Biodiversity Observation Network of the Americas [MBON Pole to Pole]).

ACKNOWLEDGMENTS

We were grateful to all the colleges and friends that kindly share information and photographs of Punta Cuevas. We thank Pepe Ojeda for technical support. The manuscript was greatly improved by the comments of two reviewers. This was publication #142 of the Laboratorio de Reproducción y Biología Integrativa de Invertebrados Marinos (LARBIM).

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.