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Modeling the role of marine protected areas on the recovery of shallow rocky reef ecosystem after a catastrophic submarine volcanic eruption

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ABSTRACT

Modeling is a useful approach to learn about the capacity of the systems to recover after disturbances. In October 2011, a submarine volcanic eruption in The Punta Restinga–Mar de Las Calmas Marine Protected Area (RMC-MPA) caused catastrophic mass mortality. We modeled the recovery dynamics of the fully protected (no-take zone), partially protected (buffer zone), and unprotected (fished zone) areas to evaluate their resilience and their potential to restore fishing resources. Recovery varied with species and levels of protection. Benthic macroalgae and parrotfish populations recovered the fastest. Piscivore fishes, macroinvertebrate feeders, and macroinvertebrate detritivores required more extended recovery periods. The levels of protection played a significant role in recovery, with the no-take zone showing more resilience than the buffer and fished zones. Our results suggest that no-take zones are crucial in the recovery process after catastrophic events. Regular monitoring of benthic communities provided the necessary data to model these communities and to point to the regulation of the artisanal fleet activity in restricted fishing areas as a mechanism to further enhance the recovery of fishing stocks.

1. Introduction

The vulnerability of marine ecosystems, the value of the services they provide, and the need for different approaches in understanding and managing human activities that affect oceans have recently received much attention (Halpern et al., 2015). The capacity of ecosystems to keep functioning even when disturbed has generated a growing interest in scientific communities and it is essential to contribute to the knowledge of the resilience of ecosystems in an already much-disturbed world. Resilient social-ecological systems incorporate the capacity to cope with unexpected disturbances using appropriate management responses (Adger et al., 2005). The challenge for resilient systems is to enhance the adaptative capacity to face uncertainty in vulnerable ecosystems in response to natural disturbances.

Currently, much evidence demonstrates the adequacy of marine protected areas (MPAs) as effective fishery reserves that conserve biodiversity and enhance targeted species biomass (Halpern et al., 2003; Claudet et al., 2010; Green et al., 2014). Consequently, MPAs also contribute to maintaining populations in adjacent fished areas through larval recruitment and spillover of adult fish (Abesamis et al., 2005; Halpern et al., 2009). However, MPAs are vulnerable to the impact of extreme disturbances events, which are predicted to increase in the next decades (Rahmstorf and Coumou, 2011; Thompson et al., 2013). Thus, to ensure future ocean services, it is important to consider and to test the resilience capacity of MPAs and other protective measures against catastrophic events. Natural catastrophes can transform marine ecosystems, thereby reducing population viability to extinction (Mangel and Tier, 1994). However, the no-take marine reserves have the capacity to mediate the population response to catastrophes (e.g., Lauck et al., 1998; Mangel, 2000; Allison et al., 2003).

Ecological modeling tools have been recently used globally to analyze marine ecosystems and their trophic dynamics, exploring responses to human and natural disturbances (Christensen and Walters, 2004; Plagányi, 2007). This holistic approach allows scientists to explore multi-species assessment models and identify ecosystem properties using a temporal and spatial scale (Walters et al., 1999). Overall, most ecological models are focused on analyzing the functioning of marine food webs and fisheries (Colléter et al., 2015). However, catastrophic phenomena (such as the one addressed in this paper) constitute an unusual opportunity to study the resilience and service-restoring potential of coastal marine ecosystems. Additionally, spatial modeling tools can test for MPA network designs to minimize catastrophic

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disturbances in vulnerable marine areas. Understanding catastrophic impacts on marine communities, the dynamics of recolonization processes, and the patterns of species recovery from a natural mass mortality scenario will also contribute to promoting improved management actions of marine resources (e.g., Jones et al., 2017).

The Ecopath with Ecosim (EwE) software approach has been applied in worldwide ecosystems and is currently one of the most frequently used modeling tools (Polovina, 1984; Christensen and Pauly, 1992; Pauly et al., 2000; Christensen and Walters, 2004, 2011). The capacity of EwE to characterize the structure of an ecosystem and run dynamic simulations over time allows evaluation of the impact of natural and human disturbances. Thus, in our study, we used the dynamic temporal and spatial modeling routines of the EwE software to explore the ecological impacts of a recent submarine volcano eruption. As a case study, we focused on the Punta Restinga–Mar de Las Calmas Marine Protected Area (RMC-MPA). This MPA is located on the south-western coast off El Hierro Island (Canary Islands), which was established in 1996 to promote the sustainable use of fishing resources by local fishermen and to safeguard marine biodiversity.

The Canarian Archipelago is located on the eastern Atlantic Ocean. The islands show some remnant volcanic activity, and over time, they have been subjected to intensive and catastrophic volcanic episodes (Whittaker and Fernández-Palacios, 2007). The most recent episode started in October 2011, with a submarine volcanic eruption strongly impacting the underwater biodiversity, marine resources, and the economic activities of the RMC-MPA (Brito et al., 2012; De la Cruz and Pascual, 2013). During the eruption process, extreme environmental conditions resulting from low oxygen concentrations caused mass mortality of almost all marine organisms and the emigration of pelagic species to the clear waters (De Paz et al., 2013) that were not affected by the volcano. The first evident effect of the eruption was on species targeted by artisanal fishing. The volcano eruption process lasted more than 3 months, and in September 2012, a 6-month temporal fishing closure was established in the El Hierro waters to benefit the natural recovery of species (BOC 2012/192; BOE-A-2012-11887). Recent survey data suggest a rapid restoration of fish biomass in the RMC-MPA for some trophic groups (authors personal observation). Thus, it has been hypothesized that the fertilization caused by the eruption, in the form of large amounts of nutrients expelled during the eruptive phase, was rapidly and strongly diluted by the efficient renewal of clear waters in the area (Gómez-Letona et al., 2018), which could contribute to the rapid recovery of some trophic groups. However, only monitoring studies based on responses of the local phytoplankton community (Fraile-Nuez et al., 2012), macroalgal species (Betancor et al., 2014; Sangil et al., 2016), and pelagic biota (Ariza et al., 2014) have been published, and these are not sufficient to assess the restoration of an entire ecosystem after the eruption. There is a need to explore the recovery process using an ecosystem-based approach to better understand the consequences of the impact, considering species interactions.

The EwE software capacities could allow us to address the challenging task of modeling the ecosystem reaction to the volcano eruption scenario. Thus, we have previously built a steady-state ecosystem model of the RMC-MPA (2003) that was fitted to the available time data from 1990 to 2015. Then, we used the balanced RMC-MPA model to simulate the effects of the volcanic eruption that took place during October 2011. With this approach, we were able to: (1) explore and discuss the temporal and spatial recovery trajectories of the main functional groups up to the pre-volcanic biomasses; (2) test the accuracy of the model comparing post-volcanic predicted and observed data for main fishery functional groups; and (3) use the Ecospace routine to compare the resilience potential of the three levels of protection of the RMC-MPA (no-take, buffer, and restricted fishing area) in promoting the restoration of fishing resources.

2. Material and methods

2.1. Study area

El Hierro Island is located on the western end of the Archipelago, and it is surrounded by oligotrophic and warm waters, which are comparable to the open ocean subtropical gyres (De León and Braun, 1973; Braun, 1980; Hernández, 2016). A short basin surrounds the whole island, reaching great depths. Coastal submarine ecosystems are mostly characterized by a subtidal lava rocky bottom and a few sandy patches. The study area covers 7.46 km^2 and represents a shallow rocky reef community that is up to 40 m deep in the RMC-MPA (Fig. 1). This protected area is characterized by high biodiversity and abundant fishing resources (Bortone et al., 1991), where the artisanal fisheries of La Restinga operate (except in the no-take area). The buffer area has particular fishing gear restrictions (traps) for the artisanal fleet involving some functional groups (morays and *Sarpa salpa*). The restricted fishing areas are defined for coastal recreational fishermen. Monitoring the abundance of marine organisms in the RMC-MPA ecosystem using scuba diving surveys has been ongoing since 1997. Catches and fishing efforts on El Hierro Island have also been registered on specific monitoring studies after the creation of the MPA.

2.2. Modeling the RMC_MPA

The EwE modeling approach version 6.6 (Christensen and Walters, 2004; Christensen et al., 2008; Heymans et al., 2016) was used to simulate a temporal catastrophic scenario in a spatial distribution model. The mass balance model (Ecopath) of the RMC-MPA was built previously to develop a baseline scenario representing the year 2003, before the submarine volcano eruption. The year chosen is the one with the best available data about the local species biomass and fishing catches because of the sampling effort and quality. The Ecopath model was parameterized to represent the ecological dynamics of rocky-bottom ecosystems above 40 m of depth, where the major fishing resources of the RMC-MPA are concentrated. This approach excluded some functional groups such as birds, sharks, or marine mammals. These exclusions from the model were related to the non-occurrence of these trophic levels during the sampling methodology in the model area, mainly because these individuals may be extremely scarce or inhabit the open ocean. The RCM-MPA balanced model was composed of 22 functional groups, including two of primary producers, two zooplanktonic groups, seven of benthic invertebrates, ten bony fish groups, and one group for detritus (Table A1). Each species included in the model were aggregated into these functional groups, based on the similarity of their ecological role, but also, when appropriate, considering biological (feeding habits) data that were available. The multi-species artisanal fleet was included in the analysis from the 2003–2005 fishery catch data. More details on the functional input data source, references of parameters estimation methods, and the prebalancing (PREBAL) analysis (Link, 2010) are provided in the appendix (Table A1) and supplementary data.

The Ecopath module provides a snapshot of an ecosystem for a given time period, based on assumptions of mass balance and a system of linear equations describing the average flows of mass and energy between functional groups.

The first Ecopath master equation (1) describes the production term for each functional group, as follows:

$$\text{Production} = \text{predation mortality} + \text{fishing mortality} + \text{other mortality} + \text{biomass accumulation} + \text{net migration}$$

The energy balance of each trophic group is given by the second Ecopath equation (2), as follows:

$$\text{consumption} = \text{production} + \text{respiration} + \text{unassimilated food}$$

A full description of the equation's parameters is explained in

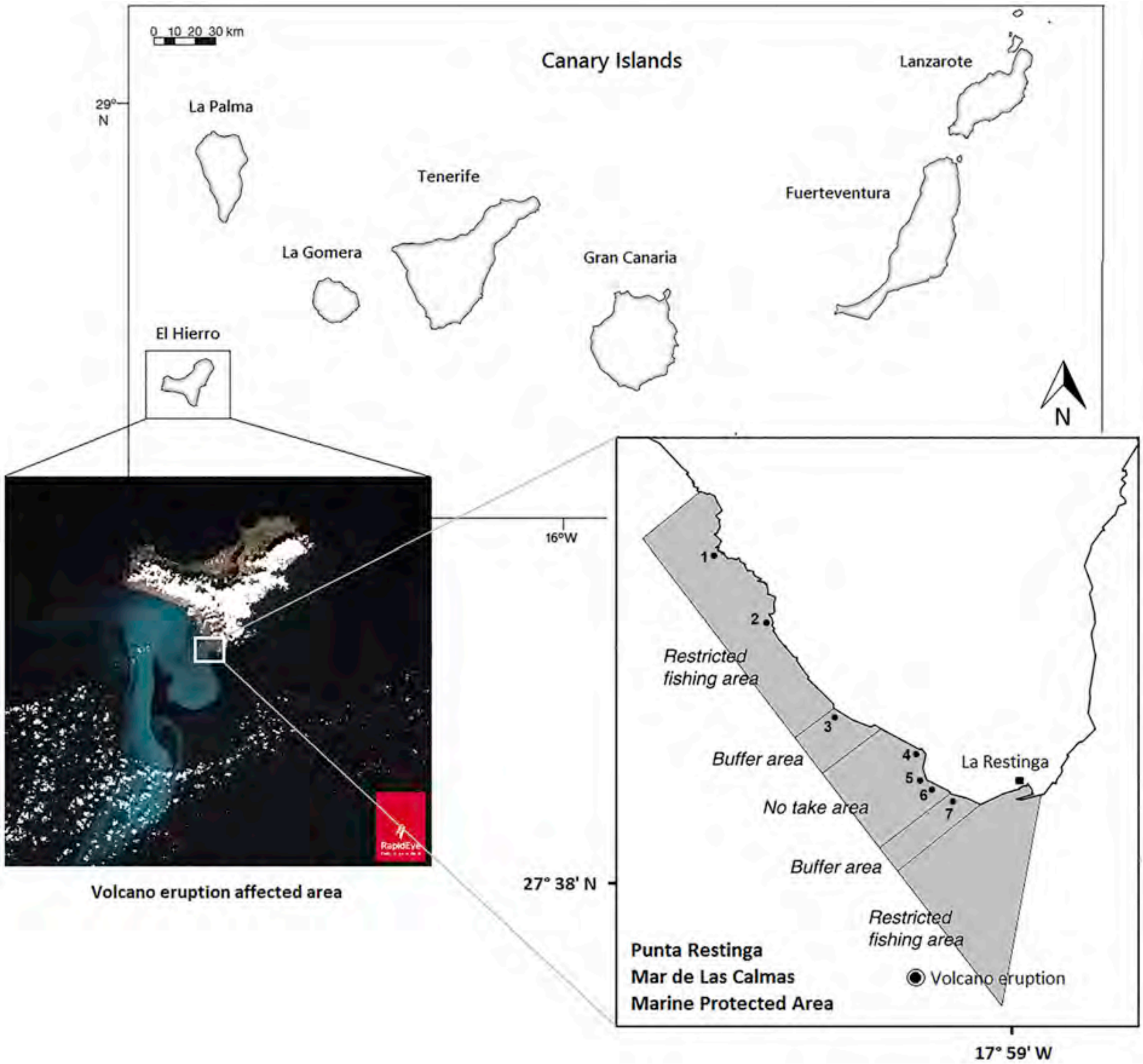

Fig. 1. Map of the Canary Islands, showing the location of the Punta Restinga–Mar de Las Calmas MPA. In grey, the Ecopath modeled area. The black circle indicates the epicenter of the volcanic submarine eruption (October, 2011). Numbered dots correspond to the different sampling sites (1: Tacorón, 2: Pta. Las Lapillas, 3: Pta Las Cañas, 4: Roque Chico, 5: Punta de los Frailes, 6: Cueva de los Frailes, 7: La Herradura). A satellite photograph of El Hierro Island is included, showing the area to the southwest of the island affected by the eruption. Satellite image courtesy of RapidEye (www.rapideye.com).

Christensen and Walters (2004) and Heymans et al. (2016).

The Ecosim module consists of time-dynamic simulations using the set of linear equations implemented in Ecopath and represented as a system of differential equations (Walters et al., 1997; Christensen and Walters, 2004). These equations describe how the biomass of each organism group in the ecosystem changes over time, which provides information on the dynamics of the ecosystem. Therefore, Ecosim simulations are especially sensitive to the "vulnerability" (v) parameter, which incorporates density-dependency and expresses how far a group is from its carrying capacity (Christensen and Walters, 2004; Christensen et al., 2008). Further details about the Ecosim equations are presented in the supplementary data.

To explore the temporal changes, the RCM-MPA model was fitted to the time series data in the Ecosim module (Walters et al., 1997), using the "Stepwise fitting procedure" tool (Scott et al., 2016). Time series of catches data (1990–2015) for all fished functional groups were used to calibrate the model. Temporal dynamic changes were driven by time series of fishing effort (1990–2017) and phytoplankton biomass data (1997–2015). Please refer to supplementary data for further details on the fitting procedure.

The Ecospace routine was developed using the RMC-MPA trophic model that had been previously built to simulate a volcanic eruption scenario. It incorporates the Ecopath and Ecosim dynamics across a two-dimensional spatial grid to regulate functional groups and fishing effort spatial distribution patterns (Christensen et al., 2008; Martell, 2005; Walters et al., 1999). The spatial grid comprises cells that are assigned to land or water and to a specific habitat type. Additionally, areas of enhanced primary production, advection patterns, or fishing fleet/gear restrictions (MPA) can be mapped. Each spatial cell represents a biomass pool of functional groups that move in the spatial grid as trophic flows. The space-time pattern in the Ecospace module is based on the Eulerian approach, which treats movement as "flows" of organisms among fixed spatial reference points or cells. Ecospace identifies each grid cell as being a "preferred" or "non-preferred" habitat for a given functional group, by setting differential dispersal rates. Therefore, movement into the adjacent cells is determined by the following: (1) the base dispersal rate of a functional group; (2) the type of habitat in the adjacent cell; (3) food availability; and (4) predation risk.

The fishing mortality rates per species in each cell depends on the distribution of fishing effort. The fishing effort spatial distribution pattern is distributed by a gravity model (Caddy, 1975; Walters et al., 1999). For each time step in the Ecospace routine, Ecosim simulations were run for every cell, and the biomass for functional groups was estimated. The mechanisms and equations involved in movement among spatial cells are explained in more detail by Walters et al. (1999).

2.2.1. Submarine volcano eruption scenario

The impact of the submarine eruption of 2011 was simulated in the mass balance model to estimate the hypothetic recovery of biomass levels for each functional group. To explore the resilience of the RCM-MPA ecosystem to the submarine eruption perturbation, responses of functional groups were analyzed, focusing on macroinvertebrates and fished functional groups.

Once the RCM-MPA model was fitted, the best available way to recreate the volcanic scenario was to introduce volcanic mortality. The input data representing the mortalities that resulted from the effect of the eruption were obtained from the annual monitoring of marine organism abundance in the RMC-MPA. Thus, catastrophic mortalities were calculated using sampled functional groups biomasses before (2010) and just after the volcanic eruption (2012). For some invertebrate groups with no available information in 2010, we assumed pre-volcano biomasses from the baseline year (2003). Volcanic mortalities (Z_v) for each group were expressed as the difference in the survival rates as follows:

$$-Z_v = \ln(S_2) - \ln(S_1)$$

where S_2 and S_1 are the survival rates before (2010) and after (2012) the volcanic eruption, respectively, and ln is the Napierian logarithm. Volcanic mortalities for each functional group were represented in the model as a forced "fishing mortality" time series, thereby setting up the volcano eruption scenario. This forced "fishing mortality" time series included a 6-month period for a biological recovery period where no fishing activity was allowed, right after the volcanic eruption. We assumed a fishing mortality (F) = 0 to represent the temporarily closed fishing season in the time series. The Ecosim temporal trends for the next years were analyzed to determine recovery periods of the relative biomass levels before the volcano eruption process. Finally, two available biomass data sets (observed) of fished functional groups from the most recent post-volcano samplings (2012 and 2014) were included in the results to compare with predictions and explore the accuracy of the model.

2.2.2. Spatial dynamic parameterization

In our study, we developed a basemap representing the RCM-MPA as a spatial grid that was 7.5 km^2 (Fig. 2). First, grid cells were assigned to land or water. Second, each cell on the basemap was associated with two different habitat types (Table 1). Habitat types were defined based on the shallow rocky bottom ecosystem of the RCM-MPA. Functional groups were also assigned to preferred habitat type(s). The dispersal movements of species to adjacent cells are governed by the following: (1) the dispersion rate of each functional group in terms of habitat; (2) the relative dispersal rate in non-preferred habitats; and (3) the relative feeding rate in the non-preferred habitat by functional group. These movement parameters were assigned based on ecological knowledge (Chen et al., 2009; Fouzai et al., 2012; Martell et al., 2005) or recommended default values (Christensen et al., 2008). In our model, we used two values (3 and 30 km $year^{-1}$) to represent invertebrates or low-mobility species and fish groups, respectively (Table 1). For the relative dispersal rate in unsuitable habitats, we assumed this to be a multiplication factor from 1 to 5, according to the base dispersal rate. We used the default value of 2 to represent the relative vulnerability to predation or grazing in non-preferred habitats. Moreover, the spatial RCM-MPA model assumed that there was an implementation error by species dynamics and temporal migration responses induced by the volcanic eruption beyond the limits of the modeled area. However, evidence on the efficient recovery of normal environmental factors levels (Gómez-Letona et al., 2018) should minimize the spatial distribution estimation error in short-term predictions.

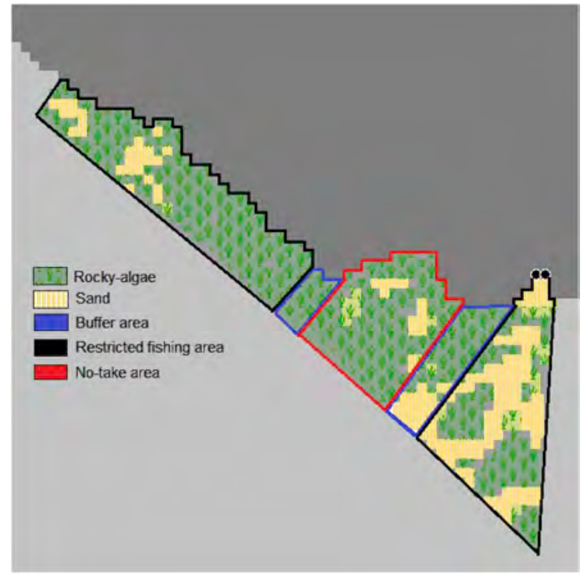

Fig. 2. Sectorization of protection zones in the Punta Restinga–Mar de Las Calmas marine protected area and habitats distribution. The dark grey area represents land; the light grey area is excluded from the model (outside from MPA boundaries).

The study area was not exposed to predominant winds, and surface water circulation was very low. Therefore, we assumed no differences in relative primary production between cells. For the same reason, we did not use the current advection tool in the Ecospace module (Christensen et al., 2008).

Finally, we defined three levels of fishing restrictions across the basemap, representing the RMC-MPA sectorization (no-take, buffer, and fishing restricted areas). Closed areas for fishing were assigned to the artisanal fleet for each level of protection. We previously split the artisanal fleet into two types of fishing gear (hook-and-line and traps) to define the fishing restrictions in the three levels of protection. However, both types of fishing gear are allowed to operate in all specific habitats (rocky-macroalgae and sand).

A spatial scenario was tested under the forced volcanic mortality from the calibrated Ecosim RMC-MPA model. The temporal distribution of the main functional groups in the three restricted areas was explored from 2010 (before volcano eruption) to 2025 to test the recovering capacity among the RMC-MPA sectorization. The results presented in this study consisted of four temporal snapshots of biomass distribution: 2010-year, 2011-year, 2019-year, and 2025-year, which represent pre-volcanic eruption, volcanic eruption, post-volcanic eruption, and community biomass recovery predictions, respectively. This spatial scenario was used to investigate the role of the three levels of the MPA to improve ecosystem restoration after a natural catastrophe.

3. Results

The baseline model (2003) results highlighted the rather low complexity of the food web, which was approaching a developmental-stage ecosystem. The RCM-MPA ecological indicators indicated a moderated maturity of the system related to the capacity to compensate for the effects of environmental impacts. Further details on the structure, ecological indicators, balancing model procedure, and fitting to time-series results of the RCM-MPA model are displayed in the supplementary data.

Table 1
Input parameters for habitat assignation (+) and dispersal movements by a functional group used in the Punta Restinga–Mar de Las Calmas marine protected area.

	Functional group	All habitats	Rocky-algae	Sand	Base dispersal rate (km/year)	Relative dispersion in non-preferred habitat
1	Phytoplankton	+			3	1
2	Benthic macroalgae		+		-	-
3	Bacterioplankton	+			3	1
4	Mesozooplankton	+			3	1
5	Benthic meiofauna		+		3	2
6	Macroinvertebrates detritivores	+			3	2
7	*Diadema africanum*		+		3	3
8	*Coscinasterias tenuispina*		+		3	3
9	Macrocrustaceans	+			3	3
10	Mollusca	+			3	3
11	Cephalopods	+			30	4
12	*Sarpa salpa*	+			30	5
13	Sparids	+			30	5
14	*Sparisoma cretense*	+			30	5
15	Planktivorous fishes	+			30	5
16	Microinvertebrate feeders	+			30	5
17	Microinvertebrate feeders and piscivorous	+			30	5
18	Macroinvertebrate feeders	+			30	5
19	Small macroinvertebrate feeders and piscivorous	+			30	5
20	Macroinvertebrate feeders and piscivorous	+			30	5
21	Morays		+		30	5
22	Detritus	+			-	-

3.1. Temporal volcanic eruption simulation

The forced catastrophic scenario showed the collapse of almost all groups and different recovery responses. Results from benthic macroalgae and macroinvertebrates showed different trends when we simulated the volcanic scenario (Fig. 3). Benthic macroalgae had a lower impact on the volcanic eruption and faster recovery of the initial biomass. However, detritivorous macroinvertebrates and *Coscinasterias tenuispina* had a longer recovery period.

For the fish groups, low trophic level species such as *Sparisoma cretense* had shorter recovery periods after the volcanic disturbance. However, higher trophic levels, such as macroinvertebrate feeders and piscivorous fishes, had a more extended recovery time to reach their initial biomass (Fig. 4). Recovery trends of the fish groups were compared with the last two post-volcanic sampled data points that determined the accuracy of the model. The predicted initial trends of these groups after the volcanic eruption were well explained by the observed data. In contrast, some observed points indicated uncertainty about the accuracy of the model. For example, predicted values for *S. cretense* in 2012 were under-estimated compared with observed values. However, predicted values for morays were overestimated, while sparids and microinvertebrate feeders showed the best fit of the observed values compared to the predicted trends.

3.2. Spatial volcano eruption scenario

The spatial RMC-MPA simulation, driven by the Ecosim scenario, showed a four-step distribution of the trophic guilds from the pre-volcanic data until the community reached the initial biomass levels. The distribution of the fishery groups in 2010 illustrates a generally higher concentration of biomass in the no-take and buffer areas compared to the restricted fishing area (Fig. 5). This result was most significant in fishery functional groups with a higher fishing mortality rate. Following the volcanic temporal process for this functional group,

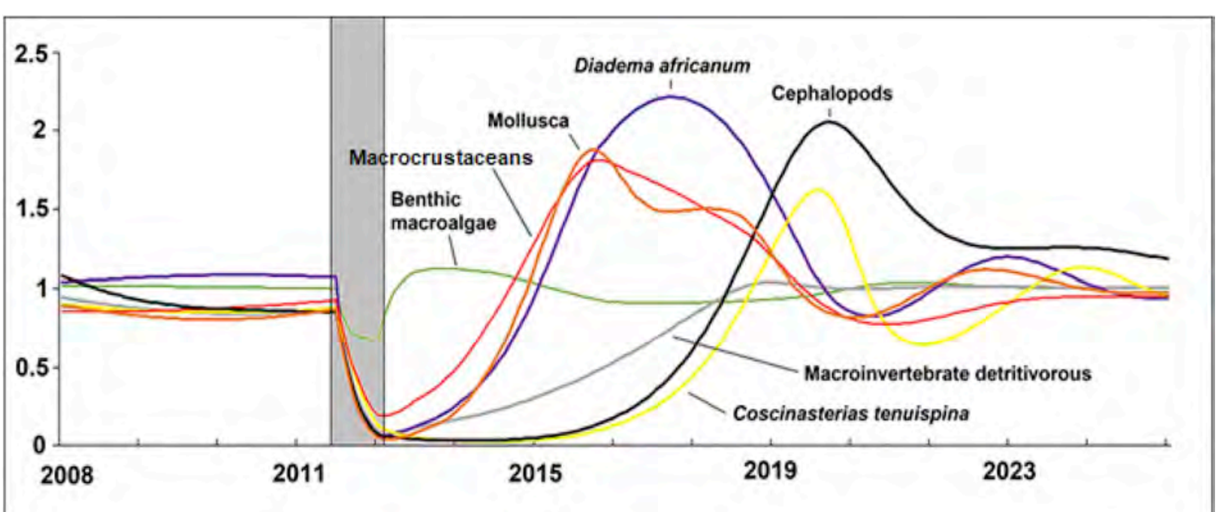

Fig. 3. Relative biomass trends for other functional groups in a volcanic eruption scenario of the Punta Restinga–Mar de Las Calmas marine protected area model. The ecosystem responses were estimated setting volcanic eruption mortalities (October, 2011) and subsequent no fishing activity (from September, 2012 to March, 2013) for each functional group. The volcanic eruption process is shown in grey. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

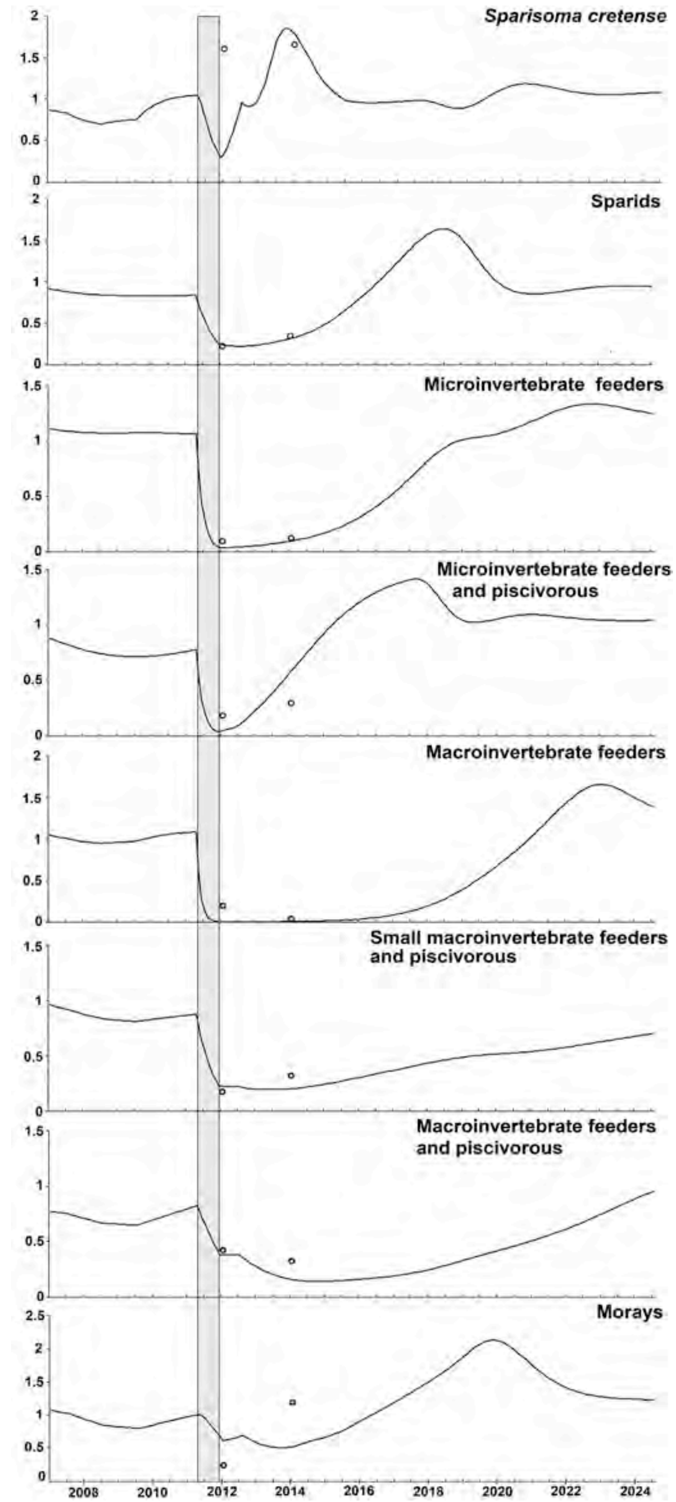

Fig. 4. Relative biomass trends of functional fish groups in a volcanic eruption scenario of the Punta Restinga–Mar de Las Calmas MPA model. Ecosystem responses were estimated, setting volcanic eruption mortalities (October, 2011) and subsequent no fishing activity (from September, 2012 to March, 2013) for each functional group. The volcanic eruption process is shown in grey. Dots represent observed values (2012 and 2014).

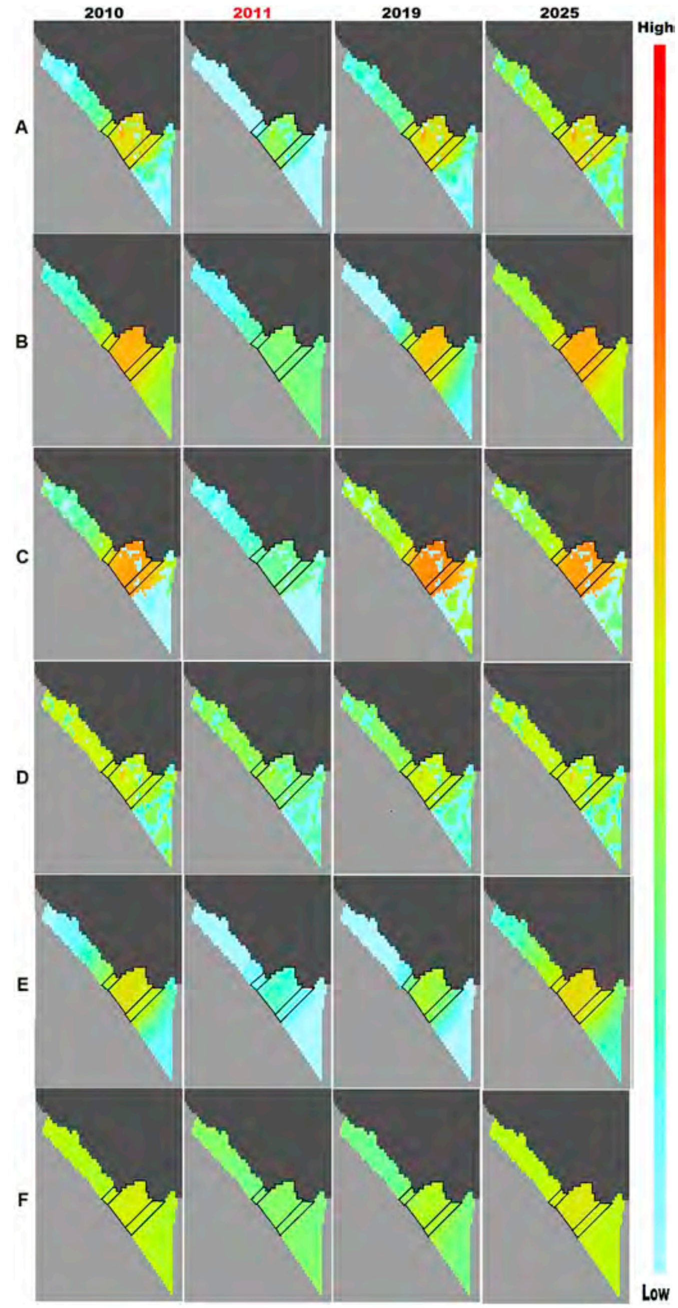

Fig. 5. Ecospace predictions of the volcano eruption scenario (from 2010 to 2025) for target fishing groups of the Punta Restinga–Mar de Las Calmas marine protected model. The color scale represents the spatial distribution of the biomass of represented trophic groups from the baseline model (2003). Red and blue coloring on the scale indicates an increase or decrease in relative densities, respectively. **A**: *Sparisoma cretense;* **B**: Macroinvertebrate feeders and piscivorous; **C**: Morays; **D**: Macroinvertebrate feeders, **E**: *Sarpa salpa,* **F**: Small macroinvertebrate feeders and piscivorous. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

the start of eruption (2011) caused a large decrease in the biomass density compared to baseline in 2003. The RMC-MPA did not show clear differences in biomass distribution between protection zones when the volcano submarine eruption was active. For a snapshot of 2019, after the catastrophic event and fishing closure period, biomass accumulation was restored in the no-take and buffer areas at lower levels compared to 2003. Finally, the last trend of the recovery process simulation (2025) reached the pre-volcanic biomass and distribution levels for the fishery functional groups.

When the differences in biomass levels were examined between the no-take and buffer areas, the results were less significant. However, the restricted fishing area showed lower biomass levels because of the artisanal fishing activity. Other groups such as morays or *Sarpa salpa* were affected by fishing restrictions in the buffer area (traps), which showed benefits beyond the limits of this area.

4. Discussion

The outcomes of this model demonstrate the importance of fishing restrictions inside MPAs to restore the pre-catastrophic conservation state of the studied ecosystem. Generally, temporal simulations, combined with the spatial distribution of functional groups trends after the volcanic eruption, have shown faster recovery trends inside the no-take and buffer zones compared to control areas. These results highlight the essential role of MPA designs for regions that are more susceptible to damage from natural catastrophes. For example, in our case, the RMC-MPA would have benefited from including more fishing restriction areas as a protected marine network. This may have improved the restoration of the depleted fished groups in the adjacent control areas, and it should be considered for future updates of the MPA design.

This study also represents the first attempt to perform a catastrophic scenario in an MPA using the EwE software, despite the assumptions and limitations of representing a submarine volcanic eruption scenario with a model. Several other Ecopath models have been constructed on nearby Eastern Atlantic waters, such in the Atlantic coast of Morocco (Stanford et al., 2001), Azores archipelago, Portugal (Guénette and Morato, 2001), Cabo Verde archipelago (Stobberup et al., 2004), the Gulf of Cadiz (Torres et al., 2013), and the Canary Islands (Moreno and Castro, 1998; Couce-Montero et al., 2015). However, none have applied the effects of a natural disturbance event or built a temporal-spatial dynamics simulation. In this sense, our model represents a step forward in using modeling to describe a shallow rocky reef ecosystem in our region.

This modeling approach, however, has been a challenging task because it attempts to force a mass mortality that is similar to what occurred in October 2011. This is particularly difficult after a natural catastrophe, when uncertain parameters are involved, and complex interaction between factors occurs during the recovery process. Modeling a natural catastrophic disturbance, such as a submarine volcanic eruption, requires taking into account these altered parameters of the ecosystem that occur in a relatively short period of time. The follow-up of the eruption process showed unusual values of production, pH, and oxygen levels in the studied area (Fraile-Nuez et al., 2012; Santana-Casiano et al., 2013). Additionally, our understanding of the impact of each of the altered parameters is limited. Therefore, the complexity of estimating how cumulative altered factors, such as oxygen concentration or pH, affects each functional group requires accepting some model assumptions. For the purpose of this paper, we assumed that the impact of the volcanic eruption was catastrophic mortality to build a reliable scenario. This mass mortality approach allows us to use the survival rates for each functional group to describe the recovery trends of species and the ecosystem compared with pre-mortality values. The RMC-MPA model shows the expected responses to a mass mortality event despite not including specific environmental factors that are strongly involved in species mortality, such as oxygen or pH, in the chosen parameterization of the volcanic scenario. Regardless, this assumption and the limitation of the input data, the capabilities of the EwE software to develop an environmental driving force, have opened the door for future studies about developing single or multiple stressors as an alternative to building a more feasible catastrophic scenario. For example, in recent years, knowledge and database resources (e.g., AQUAMAPS) (Kaschner et al., 2013) of species responses/preferences, for different abiotic factors, have been growing robustly. For example, modeling studies about the effects of climate change on marine ecosystems have been using these database resources to apply temperature-forcing functions onto future scenarios (e.g., Niiranen et al., 2013).

4.1. Effects of the volcanic eruption on the RMC-MPA marine ecosystems

After the severe species mortality was forced on the model, which was analogous to what actually occurred, the Ecosim predictions for functional group responses were consistent with the trends that were observed in post-volcanic samplings. For macroinvertebrates, there was a rapid recovery trend of macrocrustaceans, mollusks, and the sea urchin *Diadema africanum*, which may be related to the good state of the macroalgae forest that was not affected by the eruption (Sangil et al., 2016). This could be corroborated by the high settlement survival that was observed for *D. africanum* (Clemente et al., 2014) and some mollusks (author's personal observations). The absence of predators could also have benefited the high survival of these species. Alternatively, the starfish *C. tenuispina* and the cephalopod group showed a slower recovery trend. However, the slowest trend was detected for detritivorous macroinvertebrates, which were mainly represented by holothurians in biomass. Holothurians are characterized by low metabolism (Pawson, 1966), and this attribute could explain their slow recovery rates following the eruption. For the crucial role of these species on detritus and nutrient recycling in oligotrophic shallow ecosystems (Purcell et al., 2016), and although it was not tested here, the impact of its absence must be taken into consideration in future studies for possible indirect effects on the functioning of post-volcanic shallow rocky reefs.

For the fished groups, a trend where lower trophic levels recovered faster than higher trophic levels was observed with no detectable effect of the artisanal fishery activity after the fishing closure. The recovery of the RMC-MPA could have been supported by biomass imports from adjacent areas that were not affected by the volcano or the result of a higher swimming capacity of certain species that allowed them a rapid escape response from the catastrophic scenario and higher initial survival. For example, the mottled grouper (*Mycteroperca fusca*) was observed to form large schools outside the affected area (author's personal observation). This first approach of the post-volcanic scenario was consistent with the following previous observations: benthic macroalgae revealed a high resistance to extreme life conditions, as registered after the eruption (Sangil et al., 2016), and therefore, it showed a faster recovery rate of biomass; the impacted area was initially colonized by vertebrate species; and the main evidence of the initial recovery trend was that low trophic level fish groups were observed in aggregated breeding groups (microinvertebrate feeders). However, the recovery trend results for *S. cretense* and morays do not coincide with post-volcanic values. For *S. cretense*, a high biomass of juveniles was observed in 2012, which was not predicted by the model. However, the biomass of *S. cretense* registered in 2014 perfectly matches the predicted trend. For morays, volcanic mortality seems to have underestimated the observed data for the 2012 sampling. This issue could be related to the cryptic habits of young morays that may have kept them hidden from visual census and, consequently, initial biomasses were underestimated.

Focusing on higher trophic levels, some species with low representation in the functional groups (in terms of biomass) were absent on post-volcanic samplings, such as *Bodianus scrofa* or *Seriola dumerili.* These species with low representation remain masked on time dynamic simulations when they are included in functional groups, although they are target species for the artisanal fishery. Furthermore, regarding the ecological consequences of the volcanic eruption, the depletion of the adult fraction of top predatory species implies a reduction in the breeding capacity of certain populations, such as long-lived fish from the RMC-MPA (e.g., *Epinephelus marginatus* and *M. fusca*). Although it is important to establish the complete recovery of the pre-volcanic abundances, this result has few implications on the local fishery because these species are not among the most fished species. However, for the grouper *E. marginatus*, other socioeconomic indicators must be taken into account because of their emblematic value for underwater photographers and diving centers.

4.2. Testing the spatial sectorization of the MPA on the recovery trends of fished groups

The primary goal of the volcanic eruption model was to explore the recovery of the main functional groups. However, under the recovery process, we have also considered the influence of the RMC-MPA sectorization. The fishing restrictions in the three areas of protection that were studied have produced clear differences in biomass restoration. The Ecospace approach has been a useful modeling tool to generate an overview of marine resource distribution in different MPA management approaches, and it allows alternative scenarios to be designed (Salomon et al., 2002; Walters et al., 1999). In our case, we aimed to test the functional groups' distribution in the current sectorization of the RMC-MPA under a previous Ecosim volcanic eruption simulation.

The results, through a "four-step process", showed a high recovery capacity in the no-take area in the 7 years after the volcanic eruption. Macroinvertebrate feeders and piscivorous fishes, which were mainly represented by long-lived species (e.g., *E. marginatus* and *M. fusca*), exhibited clear benefits that were gained from the no-take area. This higher distribution of biomass in the no-take area allows the spillover effect of the buffer to adjacent areas to increase. The moray group and *Sarpa salpa* also showed a markedly spatial difference. More biomass was detected in the no-take area and in the buffer area, which can be because of fishing gear restrictions (traps) for these species in the buffer area. Generally, for these species, special attention should be paid to mid-low biomass that is found in the fished area. Additionally, in these areas, there is no information about available catches on coastal recreational fishing activity, and the fishing effort is clearly underestimated. Therefore, our study only highlights the poor state of the area compared to the no-take and the buffer zones and the need for better management. The non-marked differences between the three levels of protection for the rest of the fished groups could be related to sustainable fishing mortality. Among these fished groups, species such as *Oblada melanura* or *Pseudocaranx dentex* are defined as complementary species in the total catches by the artisanal fleet.

While it seems obvious that a solely managed MPA can do little to mitigate the initial impact of a catastrophic event on a local scale (McGilliard et al., 2011), the results of our study should be examined using a large scale, well-connected MPA network. Our study has shown that fishing restriction on the no-take and buffer areas has been very useful to speed up the recovery of important functional groups. This result was confirmed using assumptions from other modeling tools that were tested by McGilliard and collaborators (2011), where a population managed within a no-take area in addition to catch regulations is more resilient than a population that is well-managed without no-take areas. Thus, a more complex MPA network, including several no-take areas, seems more effective to face catastrophic events, such as the one described here. More no-take and buffer zones will assure faster recovery of larger biomasses, which in turn, benefit the adjacent fished areas. Future MPA planning in El Hierro Island or other volcanic active areas that are subject to this catastrophic event should consider the inclusion of other no-take and buffer areas that will help to mitigate the ecological and social outcomes of these dramatic situations.

5. Conclusions

(1) This is the first ecological model of an MPA of the Canary Islands that allowed us to understand the trophic interactions and functioning of a shallow rocky reef ecosystem that was subjected to a submarine volcanic eruption. Our results have shown the contrasting resilience of the three levels of protection in the RMC-MPA, under a catastrophic high mortality scenario, and the temporal biomass projections after this natural disturbance.

(2) Our results have highlighted a continuous recovery in the RMC-MPA under the current management restrictions. However, the long-term view of the volcanic effects on the RMC-MPA ecosystem suggests the need for continuous monitoring of long-lived species such as detritivorous macroinvertebrates or macroinvertebrates feeders and piscivorous fishes. Furthermore, the slow recovery trend of top predator species and biomass distribution suggests the need to control the artisanal fishing landings to preserve the sustainability of these marine resources and prevent a fishery decline.

(3) From the spatial surveys before the volcano eruption, it can be concluded that the no-take area had a higher concentration of biomass, as did the adjacent areas as a result of the spillover effect. Moreover, the RMC-MPA resilience of the no-take area and buffer zone have supported the volcanic recovery process from the artisanal fleet activity of La Restinga.

(4) These modeling findings, combined with field surveys, can be useful to re-evaluate the accuracy of the model by comparing future post-volcanic samplings with the already predicted trends. Moreover, the temporal-spatial model obtained in this study can be successfully applied to evaluate the potential effects of other MPA designs and management policies to ensure a good conservation state and the recovery of the marine ecosystems in the region, and to be better prepared for future natural catastrophes.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

José Carlos Mendoza: Conceptualization, Methodology, Writing - original draft. **Sabrina Clemente:** Supervision. **José Carlos Hernández:** Investigation, Writing - review & editing, Supervision.

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Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2020.104877.

Appendix A

Table A1
Description of input data and references by functional group of the Punta Restinga–Mar de Las Calmas Marine Protected Area model. Biomass is given in tonnes km^{-2}, P/B: Production/Biomass, Q/B: Consumption/Biomass and U/Q: Unassimilated food/ Consumption are given in year^{-1}. Landings (tonnes per km^{-2}). Percentages represent the functional group species composition in terms of weight.

FUNCTIONAL GROUP	SOURCES AND REFERENCES
1. Phytoplankton	
Biomass	- Arístegui et al. (2001)
	Conversion factor used to transform carbon units to organic matter (Dalsgaard and Pauly, 1997)
P/B	- Arístegui et al. (2001)
Time series data: 1997–2015 (forced)	- Satellite MODIS-A images, from the Global Marine Information System (GMIS, http://gmis.jrc.ec.europa.eu/)
	- Conversion factor used to transform chlorophyll (Chl)-A to organic matter (APHA, 2012)
2. Benthic Macroalgae	
100% *Lobophora variegata*	Habitat area in the model: 84.5%
Biomass	- From scuba diving surveys (2003) (quadrat method 50 × 50 cm −0.25 cm^2) in the modeled area to obtain the percent cover of algae and wet weight per area (Tuya and Haroun, 2006). 10 replicates covering the modeled depth range in each sampling site.
P/B	- Hernández (2016)
3. Bacterioplankton	
Biomass	- Estimated from BOC/POC (Bacterial organic carbon/Phytoplankton organic carbon) ratio in the Canary Islands (Arístegui et al., 2001). Conversion factor used to transform carbon units to organic matter (Sherr and Sherr, 1984).
P/B	- Bode et al. (2001)
Q/B	- Estimated by P/Q = 0.4
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Arístegui et al. (2001)
4. Mesozooplankton	
82.5–87% Copepods	
12% Appendiculariaceans	
8% Ostracods	
≤1% Cladocerans, pteropods and euphausiid larvaes	
Biomass	- Arístegui et al. (2001)
P/B	- Huggett et al. (2009)
Q/B	- Hernandez-León et al. (2001)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Arístegui et al. (2001)
5. Benthic meiofauna	
56.50% Polycheta	
24.08% Decapoda	
19.42% Echinoidea	
Biomass	- From scuba diving surveys in the modeled area.
P/B	- Brey (2001)
Q/B	- Estimated from Moens and Vincx (1996)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Estimated from Moens and Vincx (1996)
6. Macroinvertebrates detritivores	
98.95% *Holoturia sanctori*	
1.05% *Hermodice carunculata*	
Biomass	- Estimated from Ortega et al. (2009) (densities in el Hierro Island); Navarro et al. (2013) (mean body weight in Gran Canaria Island); Conand (1993) (length-weight relationship for *Holoturia atra*)
P/B	- Brey (2001)
Q/B	- Pauly et al. (1993); Opitz (1996)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Assumption: feeds exclusively on detritus
7. *Diadema africanum*	
Biomass	- From scuba diving surveys (transect line) in the modeled area (densities and length) and weight-length relationship (Hernández et al., 2005). 10 replicates covering the modeled depth range in each sampling site.
P/B	- Ebert (1985)
Q/B	- Tuya et al. (2001)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Assumption: Feeds exclusively on macroalgaes.
8. *Coscinasterias tenuispina*	
Biomass	- From scuba diving surveys (transect line) in the modeled area (densities) and weight-length relationship sampled in a similar area (Tenerife Island – Canary Islands).
P/B	- Brey (2001)
Q/B	- Brey (2001)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Estimated from Ortega et al. (2011)
9. Macrocrustaceans	
22.38% *Percnon gibbesi*	
77.62% *Stenorhynchus lanceolatus*	
Biomass	- Estimated from Ortega et al., 2009 (densities in El Hierro Island); Robinson et al. (2010) (weight-length relationship); Sciberras and Schembri, 2008 (mean body weight per specie).

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Table A1 (*continued*)

FUNCTIONAL GROUP	SOURCES AND REFERENCES
P/B	- Brey (2001)
Q/B	- Pauly et al. (1993); Opitz (1996)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Sciberras and Schembri, 2008
10. Mollusca 83.16% *Pagurus prideaux* 11.25% *Stramonita haemastoma* 5.59% *Dardanus sp.*	
Biomass	- Estimated from Ortega et al. (2009) (densities in El Hierro Island)
P/B	- From other model (Couce-Montero et al., 2015)
Q/B	- From other model (Couce-Montero et al., 2015)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Ramsay et al. (1996)
11. Cephalopods 50% *Octopus vulgaris* 50% *Sepia officinalis*	
Biomass	- Estimated from Ortega et al. (2009) (densities in El Hierro Island); Lopez (2000) (weight-length relationship and mean body weight in Gran Canaria Island)
P/B	- From other model (Couce-Montero et al., 2015)
Q/B	- From other model (Couce-Montero et al., 2015)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Castro and Guerra (1990); López (2000)
12. *Sarpa salpa*	
Biomass	- From scuba diving surveys in the modeled area (visual census for estimate abundance). Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias in 2005.
P/B	- P/B = Z = F + M where F=C/B and M calculated from empirical equation (Pauly, 1980). L∞ and K from Villamil et al. (2002)
Q/B	- From empirical equation of Pauly et al. (1990). W∞ from Villamil et al. (2002)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Havelange et al. (1997)
Landings	- Estimated from technical reports (2003–2005) in La Restinga artisanal fishing monitoring (Martín-Sosa et al., 2010).
Time series data:	
1990–2010 (catches)	- Technical reports in the Canary Islands Marine Protected Areas monitoring (Spanish Institute of Oceanography and Universidad de La Laguna, Martín-Sosa et al., 2010)
2010–2015 (catches)	- Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias in 2015
13. Sparidae 59.40% *Diplodus vulgaris* 22.71% *Diplodus cervinus* 16.45% *Diplodus sargus* 1.42% *Diplodus puntazzo*	
Biomass	- From scuba diving surveys in the modeled area (visual census for estimate abundance). Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias in 2005
P/B	- P/B = Z = F + M where F=C/B and M calculated from empirical equation (Pauly, 1980). L∞ and K from Pajuelo and Lorenzo (2002); Pajuelo and Lorenzo (2003); Pajuelo et al. (2003); Domínguez-Seoane et al. (2006)
Q/B	- From empirical equation of Pauly et al. (1990). W∞ from Pajuelo and Lorenzo (2003), Pajuelo and Lorenzo (2002) and Domínguez-Seoane et al. (2006)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Clemente et al. (2010); Mann and Buxton (1992); Gonçalves and Erzini (1998)
14. Sparisoma cretense	
Biomass	- From scuba diving surveys in the modeled area (visual census for estimate abundance). Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias in 2005.
P/B	- P/B = Z = F + M where F=C/B and M calculated from empirical equation (Pauly, 1980). L∞ and K from González (1993)
Q/B	- From empirical equation of Pauly et al. (1990). W∞ from González (1993)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- From local individuals stomach contents analysis.
Landings	- Estimated from technical reports (2003–2005) in La Restinga artisanal fishing monitoring (Martín-Sosa et al., 2010).
Time series data:	
1990–2010 (catches)	- Technical reports in the Canary Islands Marine Protected Areas monitoring (Spanish Institute of Oceanography and Universidad de La Laguna, Martín-Sosa et al., 2010)
2010–2015 (catches)	- Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias in 2015
15. Planktivorous fishes 67.91% *Boop boops* 30.30% *Chromis limbata* 1.79% *Atheryna presbyter*	
Biomass	- From scuba diving surveys in the modeled area (visual census for estimate abundance). Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias in 2005.
P/B	- P/B = Z = F + M where F=C/B and M calculated from empirical equation (Pauly, 1980). L∞ and K from Pajuelo and Lorenzo (2000)
Q/B	- From empirical equation of Pauly et al., 1990. W∞ from Morato et al. (2001), Pajuelo and Lorenzo (2000) and Monteiro et al. (2006)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Randall (1967)

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Table A1 (*continued*)

FUNCTIONAL GROUP	SOURCES AND REFERENCES
16. Microinvertebrate feeders	
84.26% *Thalassoma pavo*	
14.06% *Similiparma lurida*	
1.01% *Canthigaster capistrata*	
0.43% *Gnatholepis thompsoni*	
0.16% *Apogon imberbis*	
0.08% *Sphoeroides marmoratus*	
Biomass	- From scuba diving surveys in the modeled area (visual census for estimate abundance). Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias in 2005.
P/B	- P/B = Z = F + M where F=C/B and M calculated from empirical equation (Pauly, 1980). L∞ and K from Clemente et al. (2010)
Q/B	- From empirical equation of Pauly et al. (1990). W∞ from Raventós, 2007
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Randall (1967); Clemente et al. (2010); Mancera-Rodríguez and Castro-Hernández (2004); Marnane and Bellwood (2002)
17. Microinvertebrate feeders and piscivorous	
82.91% *Oblada melanura*	
16.67% *Kyphosus sectatrix*	
0.42% *Trachinotus ovatus*	
Biomass	- From scuba diving surveys in the modeled area (visual census for estimate abundance). Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias in 2005.
P/B	- P/B = Z = F + M where F=C/B and M calculated from empirical equation (Pauly, 1980). L∞ and K from Mora (2013) and Pallaoro et al. (1998)
Q/B	- From empirical equation of Pauly et al., 1990. W∞ from Mora (2013) and Pallaoro et al. (1998)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Moreno and Castro (1995); Silvano and Güth (2006); Lenfant and Olive (1998)
Landings	- Estimated from technical reports (2003–2005) in La Restinga artisanal fishing monitoring (Martín-Sosa et al., 2010)
Time series data:	
1990–2010 (catches)	- Technical reports in the Canary Islands Marine Protected Areas monitoring (Spanish Institute of Oceanography and Universidad de La Laguna, Martín-Sosa et al., 2010)
2010–2015 (catches)	- Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias in 2015
18. Macroinvertebrate feeders	
48.75% *Canthidermis sufflamen*	
24.39% *Aluterus scriptus*	
19.11% *Chilomycterus reticulatus*	
5.69% *Heteropriacanthus cruentatus*	
1.51% *Scorpaena maderensis*	
0.43% *Stephanolepis hispidus*	
0.12% *Coris julis*	
Biomass	- From scuba diving surveys in the modeled area (visual census for estimate abundance). Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias in 2005.
P/B	- P/B = Z = F + M where F=C/B and M calculated from empirical equation (Pauly, 1980). L∞ and K from Alarcón et al. (2017), Clemente et al. (2010), Brito and Falcon (1990), Ghosh et al. (2011) and Mancera-Rodríguez and Castro-Hernández (2004)
Q/B	- From empirical equation of Pauly et al. (1990). W∞ from Brito and Falcon (1990) and Clemente et al. (2010)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Clemente et al. (2010); Brito and Falcon (1990); La Mesa et al. (2007)
Landings	- Estimated from technical reports (2003–2005) in La Restinga artisanal fishing monitoring (Martín-Sosa et al., 2010)
Time series data:	
1990–2010 (catches)	- Technical reports in the Canary Islands Marine Protected Areas monitoring (Spanish Institute of Oceanography and Universidad de La Laguna, Martín-Sosa et al., 2010)
2010–2015 (catches)	- Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias in 2015
19. Small Macroinvertebrate feeders and piscivorous	
59.30% *Pseudocaranx dentex*	
31.79% *Aulostomus strigosus*	
3.10% *Serranus atricauda*	
2.21% *Sphyraena viridensis*	
2.08% *Balistes capriscus*	
1.37% *Caranx latus*	
0.15% *Synodus synodus*	
Biomass	- From scuba diving surveys in the modeled area (visual census for estimate abundance). Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias (2005).
P/B	- P/B = Z = F + M where F=C/B and M calculated from empirical equation (Pauly, 1980). L∞ and K from Tuset et al. (2004), Froese et al. (2013) and Clemente et al. (2010)
Q/B	- From empirical equation of Pauly et al. (1990). W∞ from Kulbicki et al. (2005)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Randall (1967); Morato et al. (2000); Golani (1993); Barreiros et al. (2002)
Landings	- Estimated from technical reports (2003–2005) in La Restinga artisanal fishing monitoring (Martín-Sosa et al., 2010)
Time series data:	
1990–2010 (catches)	- Technical reports in the Canary Islands Marine Protected Areas monitoring (Spanish Institute of Oceanography and Universidad de La Laguna, Martín-Sosa et al., 2010)
2010–2015 (catches)	- Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias in 2015
20. Morays	

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Table A1 (*continued*)

FUNCTIONAL GROUP	SOURCES AND REFERENCES
46.03% *Muraena augusti*	
53.97% *Gymnotorax unicolor*	
Biomass	- From scuba diving surveys in the modeled area (visual census for estimate abundance). Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias (2005).
P/B	- P/B = Z = F + M where F=C/B and M calculated from empirical equation (Pauly, 1980). L∞ and K from Jimenez et al. (2007)
Q/B	- From empirical equation of Pauly et al. (1990). W∞ from Bustos-Leon (2009) and Ferreira et al. (2008)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Matic-Skoko et al. (2010); Randall (1967)
Landings	- Estimated from technical reports (2003–2005) in La Restinga artisanal fishing monitoring (Martín-Sosa et al., 2010)
Time series data:	
1990–2010 (catches)	- Technical reports in the Canary Islands Marine Protected Areas monitoring (Spanish Institute of Oceanography and Universidad de La Laguna, Martín-Sosa et al., 2010)
2010–2015 (catches)	- Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias in 2015
21. Macroinvertebrate feeders and piscivorous	
43.31% *Epinephelus marginatus*	
40.88% *Mycteroperca fusca*	
8.79% *Seriola dumerili*	
7.02% *Bodianus scrofa*	
Biomass	- From scuba diving surveys in the modeled area (visual census for estimate abundance). Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias (2005).
P/B	- P/B = Z = F + M where F=C/B and M calculated from empirical equation (Pauly, 1980). L∞ and K from Bustos-Leon (2009), Clemente et al. (2010) and Harmelin and Harmelin-Vivien (1999)
Q/B	- From empirical equation of Pauly et al. (1990). W∞ from Bustos-Leon (2009) and Ferreira et al. (2008)
U/Q	- Assumption (Christensen et al., 2008)
Diet	- Linde et al. (2004), Clemente et al. (2010); Bustos-Leon (2009)
Landings	- Estimated from technical reports (2003–2005) in La Restinga artisanal fishing monitoring (Martín-Sosa et al., 2010)
Time series data:	
1990–2010 (catches)	- Technical reports in the Canary Islands Marine Protected Areas monitoring (Spanish Institute of Oceanography and Universidad de La Laguna, Martín-Sosa et al., 2010)
2010–2015 (catches)	- Report from Universidad de La Laguna and Viceconsejería de Pesca del Gobierno de Canarias in 2015
22. Detritus	
Biomass	- Estimated from the empirical equation of Pauly et al. (1993): Log D = 0,954 log PP + 0,863 log * E - 2,41 E = 40 m PP= Primary production (from phytoplankton estimated value)

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