

ARTICLE

Special Feature: Honoring Charles H. Peterson, Ecologist

Rapid recovery of depleted abalone in Isla Natividad, Baja California, Mexico

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Abstract

In the last decades, many marine invertebrates have experienced dramatic declines throughout many coastal marine ecosystems worldwide due to overfishing, disease outbreaks, and climate vulnerability. Despite extensive conservation and restoration effort, evidence of successful population recovery is rare. In this work, we document mass mortality events of pink and green abalone (*Haliotis corrugata* and *Haliotis fulgens*) in 2009–2010, and their subsequent rapid recovery following the continued enforcement and monitoring of two voluntary no-take reserves by the local fishing cooperative (2006–present) and a 6-year fishing closure (2012–2017) around Isla Natividad, Baja California Sur, Mexico. Age data collected from harvested abalone in 2019 suggest recruitment was maintained throughout the years when abundance was lowest following mass mortalities. The observed 6 to 8-year time frame for recovery is consistent with scenarios presented in previous modeling studies, where marine reserves and other measures aimed at protecting large spawners predicted the potential for rapid recovery of abalone populations. This case study supports the effectiveness of a portfolio of resilience strategies, which include combining climate refugia and marine reserves, adherence to conservative annual fishing quotas, fishing closures, minimum size limitations, and ecological monitoring. Importantly, this example showcases how close collaboration between fishers, resource managers, scientists, and non-governmental organization (NGOs) is critical for designing, implementing, and learning from conservation and management interventions to reverse marine population and ecosystem decline, reinforcing the legacy of Dr. Pete Peterson's life work on fully integrating ecology with marine management and restoration.

KEYWORDS

abalone, conservation, fisheries, marine protected areas, recovery, Special Feature: Honoring Charles H. Peterson, Ecologist

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INTRODUCTION

Globally, marine benthic broadcast spawners have struggled or failed to recover for decades following severe population declines (Coates et al., 2014; Hobday et al., 2000; Karpov et al., 2000; Rogers-Bennett et al., 2001; Trimble et al., 2009). At the same time, the catch share of invertebrates is rising globally relative to finfish (Anderson et al., 2011). Benthic invertebrates are often highly vulnerable to the compounded effect of high fishing pressure (Harley & Rogers-Bennett, 2004) with multiple environmental stressors, such as ocean acidification, hypoxia, heatwaves, food scarcity, and disease. Recovery is further hindered by reproductive failure at low adult population density (the Allee effect; e.g., Aalto et al., 2019).

Abalone (*Haliotis* spp.) is a model example of how the combined effect of sustained fishing pressure and environmental vulnerability can threaten populations and generate negative economic and social outcomes. The patchy spatial distribution of abalone makes them difficult to monitor and can distort fishery-dependent indicators such as catch per unit effort (Karpov et al., 2000; Rose & Kulka, 1999). The high economic value of abalone further exacerbates the risk of overexploitation by incentivizing harvest even as the costs of harvesting these resources increase (Hutchings & Reynolds, 2004). Seven species of abalone once supported a booming commercial fishery across the California Current Large Marine Ecosystem (CCLME). Overfishing, disease outbreaks, and climate-driven stressors have reduced regional populations dramatically, with some species and local populations at risk of extinction (Aalto et al., 2019; Morales-Bojórquez et al., 2009; Rogers-Bennett et al., 2001).

The heightened vulnerability associated with climate-driven stressors challenges the efficacy of local fishery management strategies such as the creation of marine protected areas and catch restrictions (Bruno et al., 2018). Previous empirical and modeling studies suggest that marine reserves may support population resilience by maintaining reproductive output and recruitment following mortality events (Aalto et al., 2019; Micheli et al., 2012; Roberts et al., 2017; Rossetto et al., 2015). Moreover, while large-scale forcing due to global climate change looms over local and regional adaptation and management strategies, there is evidence that small-scale marine microclimates may provide natural refuges that can be harnessed to increase resilience (Woodson et al., 2019). That is, when populations experience mass mortality events, natural refuges may buffer the effects and facilitate recovery by allowing some animals to survive. To date, however, few long-term studies have followed population trajectories and documented actual

recovery after mass mortality events in the presence of marine reserves. Thus, while short-term recruitment studies and models predict population recovery, the question of whether such outcomes occur under continued environmental variability and extremes, including recent marine heat waves (Arafeh-Dalmau et al., 2020, 2021; Beas et al., 2020), remains open.

Here, we examine 13 years of monitoring data from an adaptively managed abalone fishery around Isla Natividad, off the Baja California Peninsula of Mexico, where the local fishing cooperative has established and enforced voluntary no-take reserves. Our data span a mass mortality event (attributed to severe and prolonged hypoxia; Micheli et al., 2012), which resulted in the closure of the fishery, through the subsequent recovery and reopening of the fishery 6 years later. We present data for two species, green abalone (*Haliotis fulgens*) and pink abalone (*Haliotis corrugata*), to explore whether and how these relatively sedentary broadcast spawners prone to Allee effects may recover following mass mortality events. These data are complemented by a reconstruction of harvested green abalone age structure based on shell growth rings and 6 years of oceanographic monitoring (temperature, oxygen, and salinity) of marine microclimates around the island (temperature, oxygen, and salinity). We explore the interplay between natural refuges and the proactive and reactive fishery management strategies employed by local managers to consider what conditions might enable this uncommon recovery.

Study area

Abalone is a key economic species for many fishing cooperatives in Baja California, Mexico, and a valuable fishery of concern along the broader CCLME (Morales-Bojórquez et al., 2009; Rogers-Bennett et al., 2001). Isla Natividad and other locations along Baja California, Mexico, remain the sole commercial producers of wild abalone in the CCLME today. In addition to spatial management, the abalone fisheries in Baja California operate under minimum and maximum size regulations, seasonal fishing closure, annual quotas determined each year by government monitoring, and controls on fishing effort (number of fishing teams) set internally by the cooperative (McCay et al., 2014).

Since the 1980s, the fishing cooperative *Buzos y Pescadores de la Baja California* has maintained exclusive fishing rights for abalone within their concession around Isla Natividad. In 2006, the cooperative voluntarily established two marine reserves around the island accounting for approximately 8% of the total fishing

ground. These areas were officially established as fishery refuges in 2018 (DOF, 2018). This area is well monitored, and protection well enforced as illegal harvest is practically absent due to geographic isolation and the high level of organization of the cooperatives in this region (McCay et al., 2014). The reserves were strategically placed in areas that were known to have been historically productive abalone sites (Micheli et al., 2012). Although this was not known at the time of reserve establishment, subsequent studies revealed that reserves were placed within areas identified as natural local refuges from prolonged and spatially broader hypoxic and warming events, which impacted Isla Natividad during the study period (Boch et al., 2018; Woodson et al., 2019).

Abalone is a highly remunerative fishery, in 2006; despite making up only 9% of total harvest by weight, abalone accounted for an estimated 60%–80% of fishing revenue for the Isla Natividad cooperative (unpublished data). Following a prolonged decline in abundance and mass mortalities in 2009–2010, the abalone fishery in Isla Natividad was closed in August 2011, after the 2011 fishing season (Micheli et al., 2012). Since its reopening in 2017, the fishery is operating under conservative quotas below those from the pre-closure era, and 75% of the government set quota, or less, is harvested in each year.

METHODS

Ecological monitoring

Ecological monitoring was conducted from 2006 to 2019 for two marine reserve sites and two control sites with similar habitat characteristics but outside the reserves (Figure 1). The abundance was quantified by the number of abalone found per hour by trained local fishing cooperative divers conducting timed searches for abalone aggregations. The sizes of each abalone found were measured and recorded for the four sites around the island ($n = 345$ searches in total), and approximately six dives per site were conducted per year. Divers searched the reefs for abalone for approximately 60 min, pausing the clock to record shell length measurements and aggregation size. Aggregations were defined as at least two abalone less than 1 m apart. Field surveys were conducted once per year in July. Additionally, divers received refresher training each year prior to field surveys. The first year of monitoring (2006) revealed highly variable counts and outliers, and therefore, those data were excluded from analyses. To assess recovery, we define recovery as the time for the population to reach the lower bound of pre-closure abundance. We then compared our estimates of the recovery period with existing population models.

Differences in the size structure of the population through time were tested using the two-sample Kolmogorov–Smirnov test. The data were grouped into three periods marked by the mass mortality event, and closure and reopening of the fishery: (1) pre-closure (2007–2011); (2) decline/fishery closure (2012–2016); and (3) recovery/fishery reopening (2017–2019). For each species (*H. corrugata* and *H. fulgens*), size–frequency distributions were tested between time periods, and between reserve and fished sites within each period. All statistical tests were conducted using R (version 3.6.3).

Green abalone age determination

The age of individuals of the dominant species in the fishery catch, green abalone (*H. fulgens*) recently caught in the fishery, was estimated based on shell growth patterns, using methods previously developed and tested for red and black abalone (*Haliotis rufescens* and *Haliotis cracherodii*) in California, USA (Micheli et al., 2008). The shells of harvested green abalone ($n = 146$) were sampled haphazardly from the cooperative's 2019 catch. Individuals were harvested from six fishing areas around the island (A–F, Figure 1). Following methods outlined in Micheli et al. (2008), we ground down the apex of each shell with increasingly fine sandpaper grits on a Dremel rotary tool until a small hole appeared at the spire of the shell. This revealed annual growth rings, which were counted under a dissecting microscope. Counts were done in four perpendicular directions for each shell, starting from the spire, and the four counts were averaged for analysis. To validate that the growth rings coincide with annual growth, a sample of abalone shells of known ages ($n = 58$; age range: 2–5 years) was collected from two aquaculture facilities on the Baja Peninsula, from Isla Natividad and La Bocana (Figure 1). We regressed known age on the number of growth rings using simple ordinary least squares linear regression. The mean age estimates were compared across all sites with an ANOVA. Because prior studies have revealed distinct oceanographic conditions along the two sides of the island (Boch et al., 2018; Woodson et al., 2019), the mean age estimates were also compared between sites on the northeastern (A and B) and southwestern (C–F) sides of the island using a *t* test.

Oceanographic monitoring

Permanent oceanographic monitoring stations were established on the northeastern and southwestern sides of Isla Natividad in 2010 (Morro Prieto) and 2013 (Punta

Prieta; Figure 1). The sensors at these sites recorded temperature, dissolved oxygen (DO), and salinity at approximately 14-m depth, at 10-min intervals over an 8-year period from 2010 to 2018. Aanderaa DO and temperature (T) optodes (Aanderaa 3830) were used from 2010 to 2013. The DOT sensors were factory-calibrated from the manufacturing company (Aanderaa Data Instruments). Beginning in 2013, the Aanderaa sensors were replaced with Sea-Bird 37 CTDOs (Sea-Bird Scientific) and miniDOT (Precision Measurement Engineering, Inc.) DO and temperature sensors. Instruments were retrieved and cross-calibrated at 6-month intervals.

RESULTS

Long-term monitoring of pink and green abalone at four sites around Isla Natividad revealed recovery trends beginning from 6 to 8 years after the 2009–2010 mass mortality events (Figure 2). Following a 10-fold population decline between 2007 and 2016, pink abalone exhibited increasing trends in abundance starting in 2017 and have returned to the lower bound of pre-mortality levels both inside and outside the reserves (Figure 2). Following a steep decline in 2011, green abalone started to

recover in 2012 inside the marine reserves and few years later in the fished areas, and by 2017, green abalone had returned to pre-closure abundance both within the marine reserves and at control sites (Figure 2). Parallel trends are observed for the number of abalone aggregations of both species (two or more individuals within 1 m from each other) (Figure 3), which are critically important for successful reproduction in sedentary broadcast spawning marine invertebrates (Aalto et al., 2019).

Size distribution of both pink and green abalone shifted toward smaller and younger individuals in the recovery phase (Figure 4). Reserves on average tended to have larger individuals than fished sites through the study period. Both within and outside the reserves, the size structure has not returned to match the pre-closure distribution (Figure 4).

For the green abalone of known ages from aquaculture facilities (age range: 2–5 years), we found a roughly one-to-one relationship between average number of rings and age, intercept = 0.18 (± 0.16 , $p = 0.276$); slope = 0.90 (± 0.05 , $p < 0.01$), $R^2 = 0.85$. The age distribution of the shells from the 2019 green abalone catch (Figure 5) shows that a majority of individuals (75%, out of $n = 146$ in total) were recruited 6–8 years before, in 2011—immediately after the mortality event—and in the two

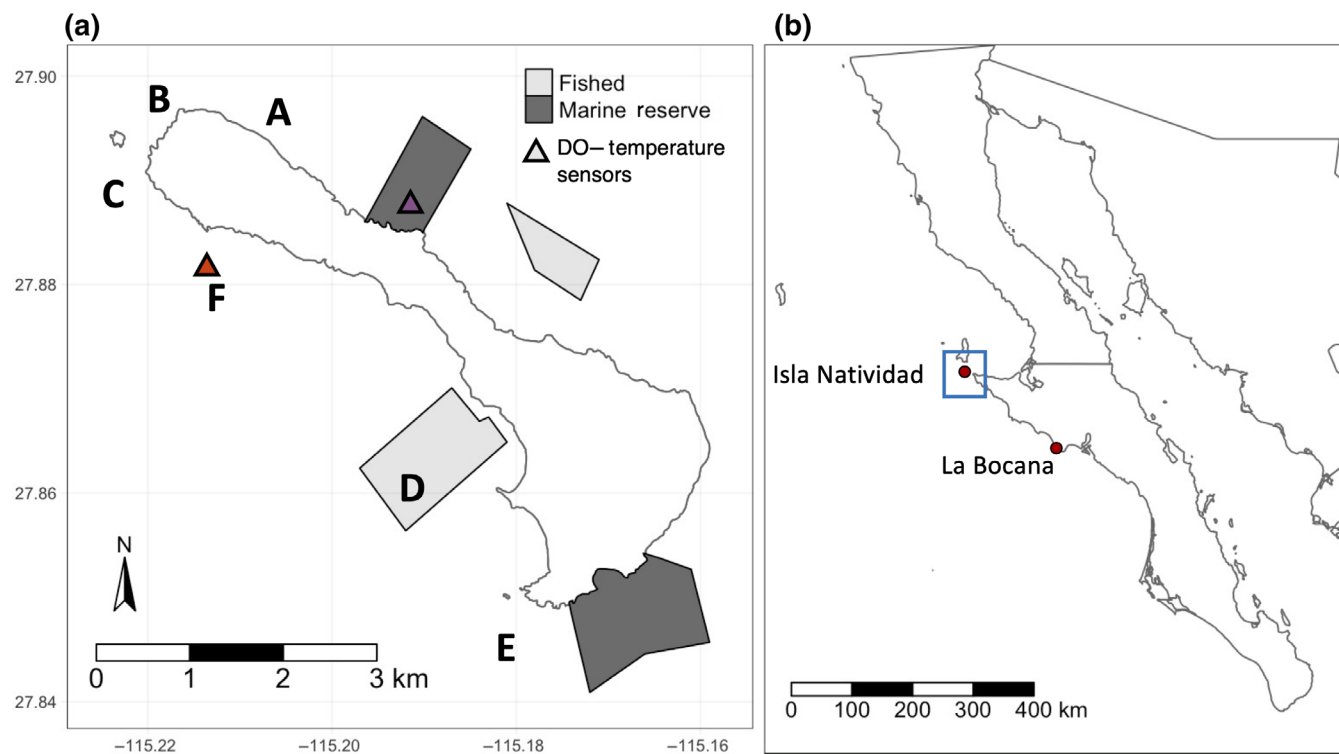


FIGURE 1 (a) Age sampling sites for harvested abalone (A–F) and the four ecological monitoring areas, reserves (dark gray), and fished sites (light gray). The triangles indicate the mooring locations of the temperature and dissolved oxygen (DO) sensors at Morro Prieto (orange) and Punta Prieta (purple). (b) Isla Natividad and La Bocana, Baja California Sur, Mexico

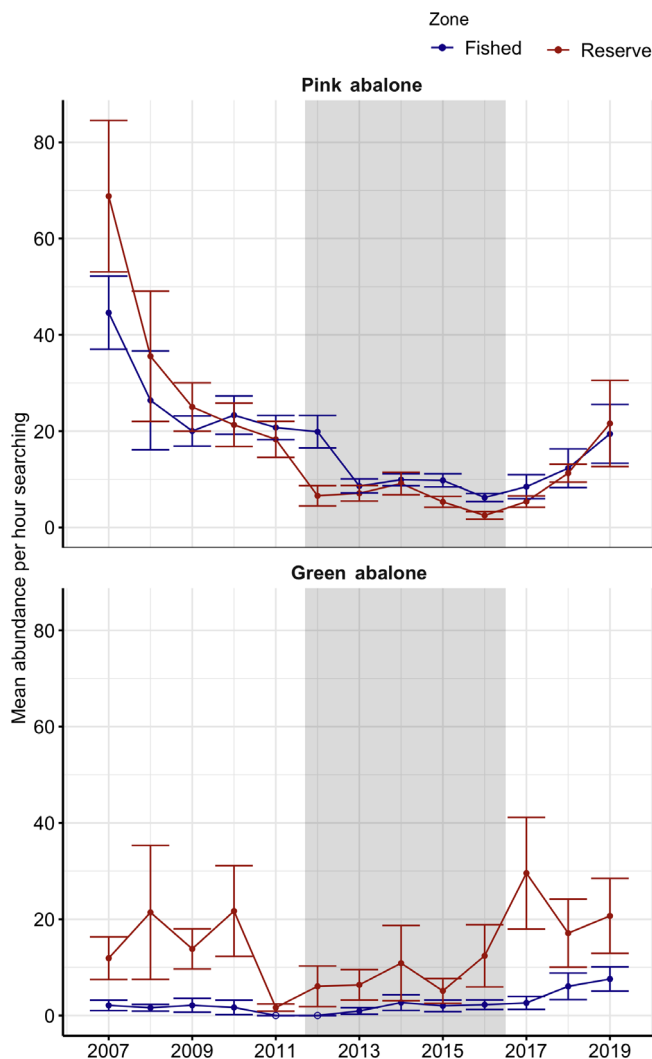


FIGURE 2 Mean abundance of abalone with SE (error bars) of pink (top) and green abalone (bottom) per hour of searching inside (red) and outside (blue) the reserves. The shaded region indicates years during which the fishery was closed. Hollow points indicate a value of zero

subsequent years (2012–2013). The youngest animals in the fishery, based on this sample, were 5 years old, and the oldest, 11 years old (Figure 5). Over 50% of the individuals in our sample were recruited between 2011 and 2012, the 2 years following the mass mortality events. The mean size of green abalone in the reserves over this period was 16.2 cm (ranging from 9.7 to 20.3 cm), while surveys conducted in fished areas during this time found no green abalone in these years. The sites sampled from the northeastern side of the island, which previous studies have identified as a potential local refuge from climate extremes (Boch et al., 2018; Woodson et al., 2019), had a significantly greater mean age ($M = 7.4$ years) than the southwestern sites ($M = 6.9$ years), $t(107.51) = 3.0264$, $p = 0.003$ (Figure 6). ANOVA and a post hoc Tukey test

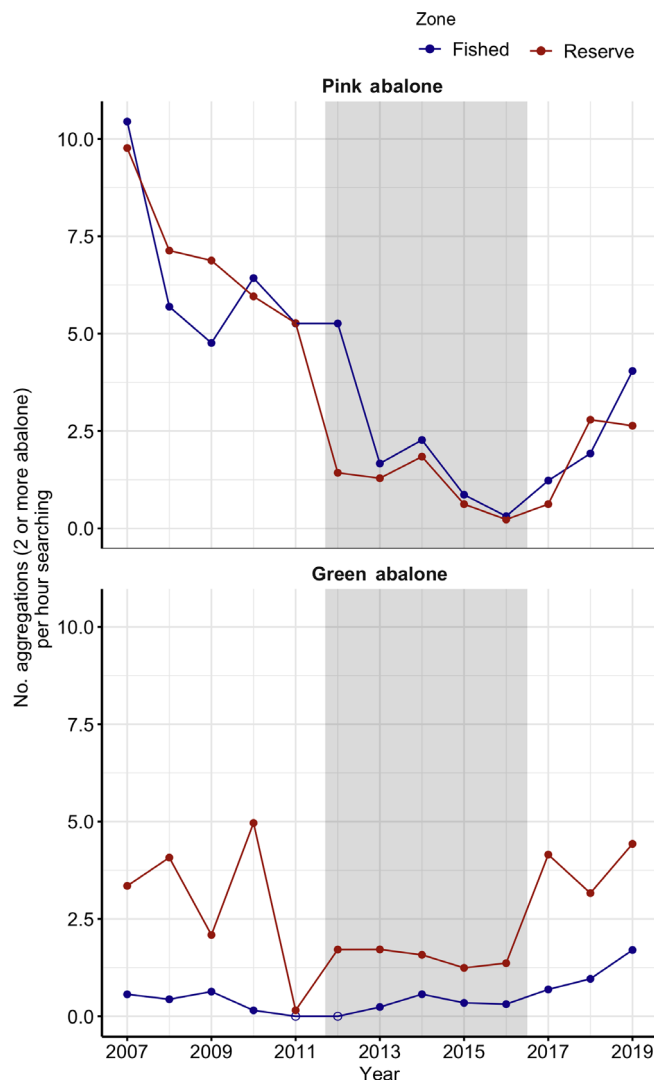


FIGURE 3 Number of aggregations (two or more abalone within 1 m from each other) of pink (top) and green abalone (bottom) per hour of searching inside (red) and outside (blue) the reserves. The shaded region indicates years during which the fishery was closed. Hollow points indicate a value of zero

showed that the mean age at Site E was significantly lower ($p < 0.05$) than at sites A and B, while the mean age at all other sites was intermediate and not significantly different (Figure 6). The oldest animals, 10–11 years old, were harvested primarily from the north-eastern sites (Figure 6), suggesting some survival through the prolonged hypoxia of 2010–2011 (Figure 7) at these sites.

The recovery of abalone around Isla Natividad occurred during a period of strong oceanographic variability including a marine heat wave from 2014 to 2016 and hypoxic events in 2011–2012 (Figure 7). In addition, recovery occurred on both sides of the island where

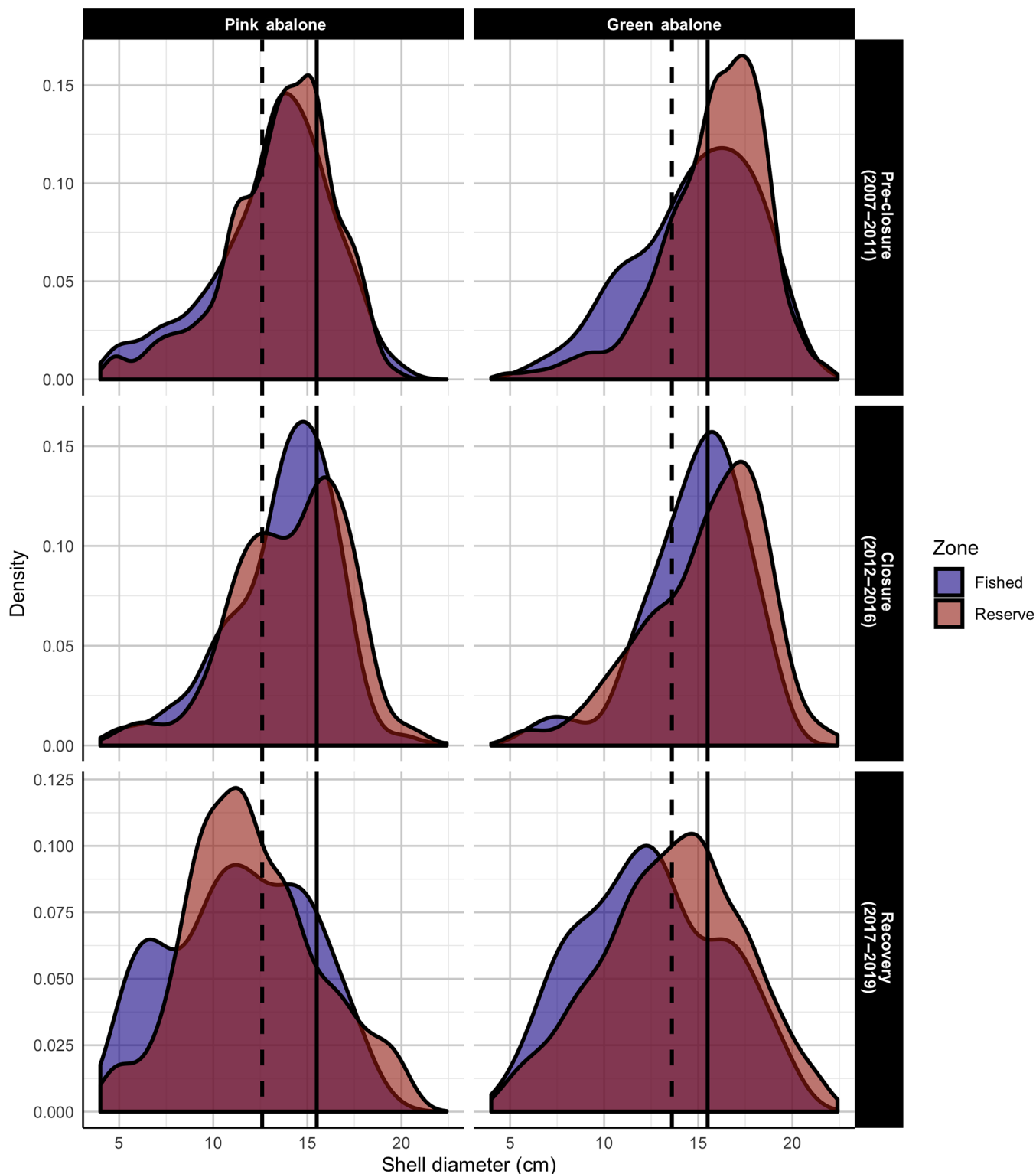


FIGURE 4 Overlapping size structure of pink (left) and green abalone (right) in reserve (red) and fished (blue) sites for each of the three time periods. The solid line indicates the minimum harvest size (15.5 cm), and the dashed line indicates size at sexual maturity (the size at which 50% of individuals are sexually mature) as reported in Rossetto et al. (2013)

environmental conditions are very different due to marine microclimates (Woodson et al., 2019). The southwestern side of the island experienced cooler

temperatures and periods of low oxygen during the recovery period, while the northeastern side was generally warmer and did not experience low oxygen conditions.

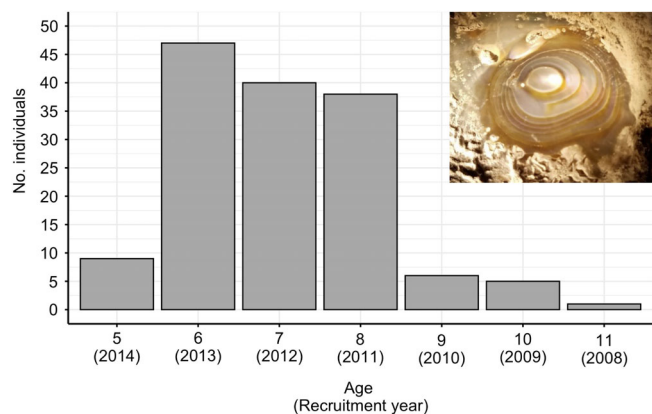


FIGURE 5 Age and recruitment year associated with each age class of all sampled green abalone ($N = 164$) from the 2019 fishing season. The inset image shows the spire of the abalone shell, ground down to reveal growth rings

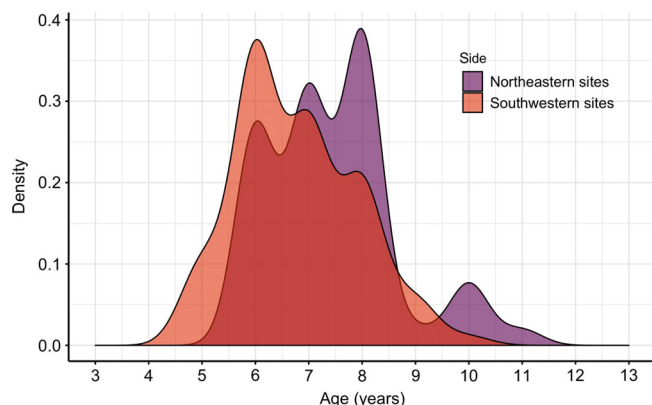


FIGURE 6 Overlapping density plots of estimated age distribution of harvested green abalone (*Haliotis fulgens*) from the northern (sites A–B) and southern (sites C–F) sides of Isla Natividad. The mean ages for the northeastern and southeastern sites were 7.4 and 6.8 years, respectively

DISCUSSION

To our knowledge, this study is the first to report the rapid recovery of a relatively sedentary benthic marine invertebrate following extreme population reductions within the CCLME. Previous studies have identified a suite of processes that can prevent recovery including Allee effects, predation, limited food availability, disease, climate stressors, habitat change, and continued fishing mortality (Micheli et al., 2008). Modeling studies with pink abalone have predicted recovery times of 20–30 years in the absence of marine reserves (Button & Rogers-Bennett, 2011). These projections were developed by using age-dependent growth and survival rate assuming no fishing mortality (i.e., fishing closure), but simulation scenarios did not include the effect of marine reserve

implementation. In contrast, modeling analyses based on stochastic stage-structured models of green abalone from Isla Natividad had projected much shorter recovery time frames (7–15 years) in the presence of networks of small marine reserves (Rossetto et al., 2015). A similar result was found by Aalto et al. (2019) by using a spatially explicit, integral projection model that accounted for Allee effects (i.e., reproductive failure at low adult density). The model was used to assess long-term fishery performance and population viability for alternative fishery management strategies and for a range of frequencies and intensity of mass mortality events. Aalto et al. (2019) found that, by protecting aggregations of large, highly fecund spawners, a network of marine reserves is expected to significantly reduce recovery time with respect to lengthy fishing closures. Reserve networks also buffered populations against the risk of collapse following catastrophic mortality events, compared with fishery strategies not based on spatial closures. The trends in abundance observed in Isla Natividad and the fast recovery rate of the population in the presence of marine reserves corroborate the modeling projections of Rossetto et al. (2015) and Aalto et al. (2019).

A 6 to 8-year time frame for recovery is further supported by the green abalone age determination data, which indicate that abalone from the 2019 fishing season were recruited 6–8 years before, between 2011 and 2013. Our data thus show that green abalone recruitment was maintained throughout the years when abundance was lowest (i.e., directly after the mass mortality events), likely thanks to the protection of aggregations of large and highly fecund individuals inside the marine reserves. Recovery of green abalone in the fishing ground took longer than in marine reserves and was likely fostered by the 2012–2016 fishing closure. Evidence of fast recovery derived from population age structure and increasing population trends thus provides an unprecedented validation of theoretical projections of population recovery in this system by previous studies (Aalto et al., 2019; Rossetto et al., 2015).

The slower recovery rate of pink abalone relative to the green abalone is likely a combination of biological and anthropogenic factors. Pink abalone has a slower growth rate than green abalone and a deeper depth range (Cox, 1962)—limiting access to shallow water refuges from hypoxia. Pink abalone experienced higher fishing pressure prior to the establishment of the reserves, and we observed fewer mature individuals in the reserve sites during the pre-closure period.

Recovery trends of both abalone species despite multiple consecutive years of marine heat waves and across sites with different environmental conditions are encouraging for conservation and management efforts in the face of a

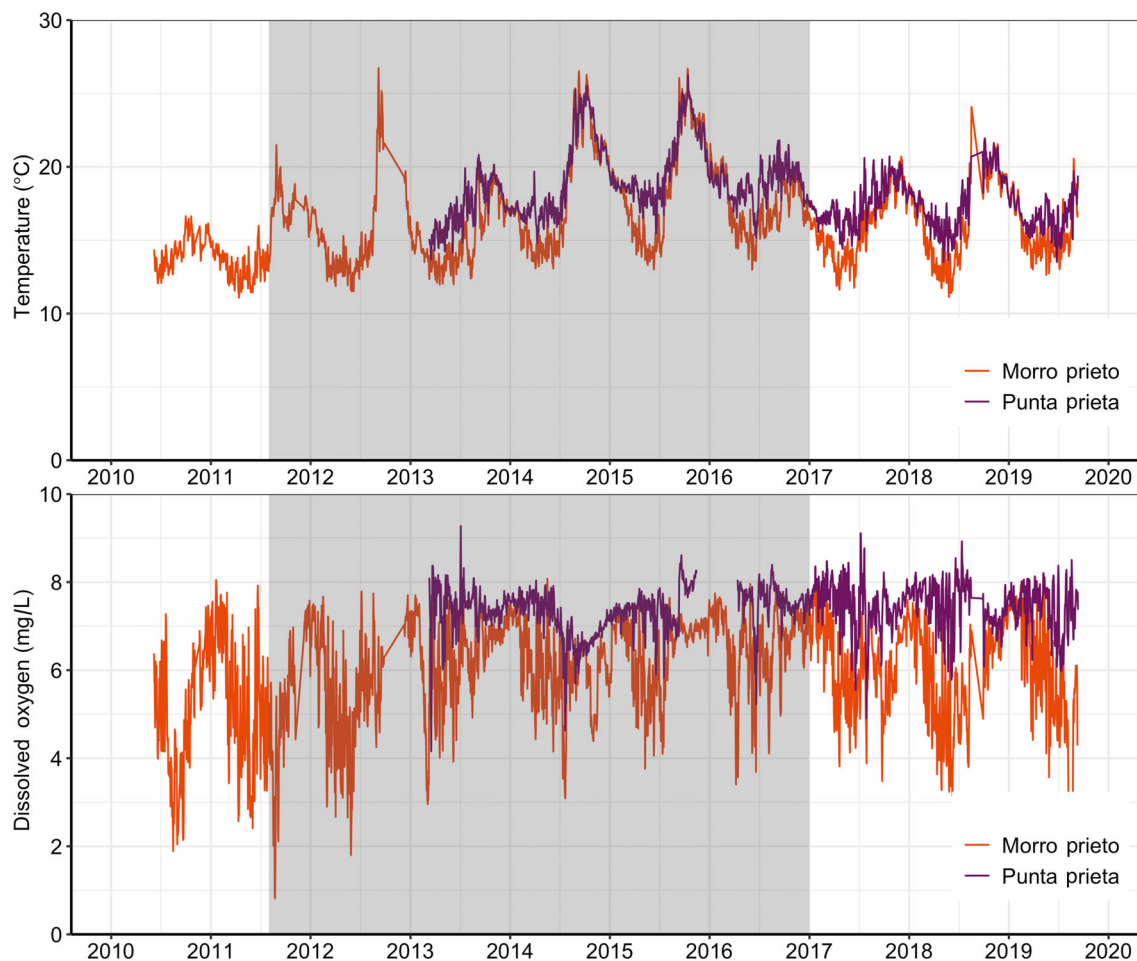


FIGURE 7 Average daily temperature (top) and dissolved oxygen (bottom) at Morro Prieto in 2010–2019 (orange) and Punta Prieta in 2013–2019 (purple). The fishing closure is noted by the shaded area

changing climate. It remains challenging to quantify the effects of protection provided by marine reserves (pre-fishery closure and following its reopening in 2017) on the observed recovery trends. However, recovery may be attributed to environmental and biological factors of the local ecosystem and understanding the interaction of these factors is likely critical for quantifying the effects of spatial management. For example, microclimates on the northeastern side of the island may have provided local climate refugia during frequent hypoxic events and unprecedented heatwaves in the CCLME. The remaining resilient abalone populations could thereby have maintained a spawning stock biomass, which allowed for replenishment of other nearby sites through larval dispersal (Micheli et al., 2012; Munguía-Vega et al., 2015). Alternatively, fishery closure could have solely led to population recovery; however, the short larval duration of abalone (~1 week) makes the possibility of long-distance reseedling of the population highly unlikely in such a short time frame (6–8 years). Without the protection placed on these areas historically known to be suitable habitats for abalone, the standing stock of

abalone would have been highly vulnerable to overfishing and continued ocean change. Thus, the establishment of reserves within known climate refuges may be critical for maintaining standing stocks of sedentary marine populations and for enhancing recruitment processes (Woodson et al., 2019). In spite of the inherent uncertainties about the contribution of any single measure for conservation of commercially exploited species in the face of climate change, the fast recovery of the abalone fishery in Isla Natividad shows the crucial role of a portfolio of resilience strategies, which include capitalizing on potential synergies between climate refugia and marine reserves, adherence to conservative annual fishing quotas, fishing closures, minimum size limitations, and ecological monitoring.

This long-term study was the result of a multi-stakeholder collaboration among fishing cooperatives, the NGO Comunidad y Biodiversidad, and research institutions. This partnership enabled the establishment, enforcement and monitoring of the reserves, and the implementation of oceanographic, population, and recruitment studies. Actions and investments into

maintaining and recovering coastal populations and ecosystems, and the important services they provide, require thorough assessments of their efficacy, and mechanisms to support learning and adaptive management in the face of changing conditions. Participatory science and multi-stakeholder partnership provide promising models for achieving such integration of insight and actions for promoting healthy ecosystems and sustainable fisheries. Dr. Pete Peterson and his many students and collaborators have pioneered this model for close integration of marine science with the management and restoration of marine populations and habitats. We dedicate this work to his memory and legacy.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Smith, 2021) are available from Figshare: <https://doi.org/10.6084/m9.figshare.13953566>.

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REFERENCES

- Aalto, E. A., F. Micheli, C. A. Boch, J. A. Espinoza Montes, C. B. Woodson, and G. A. De Leo. 2019. "Catastrophic Mortality, Allee Effects, and Marine Protected Areas." *The American Naturalist* 193: 391–408.
- Anderson, S. C., J. M. Flemming, R. Watson, and H. K. Lotze. 2011. "Rapid Global Expansion of Invertebrate Fisheries: Trends, Drivers, and Ecosystem Effects." *PLoS One* 6: e14735.
- Arafeh-Dalmau, N., K. C. Cavanaugh, H. P. Possingham, A. Munguia Vega, G. Montaña-Moctezuma, T. W. Bell, K. Cavanaugh, and F. Micheli. 2021. "Southward Decrease in the Protection of Persistent Giant Kelp Forests in the Northeast Pacific." *Communications Earth & Environment* 2: 119. <https://doi.org/10.1038/s43247-021-00177-9>
- Arafeh-Dalmau, N., D. S. Schoeman, G. Montaña-Moctezuma, F. Micheli, L. Rogers-Bennett, C. Olguin-Jacobson, and H. P. Possingham. 2020. "Marine Heat Waves Threaten Kelp Forests." *Science* 367: 635.
- Beas, R., F. Micheli, C. B. Woodson, M. Carr, D. Malone, J. Torre, C. Boch, et al. 2020. "Geographic Variation in Responses of Kelp Forest Communities of the California Current to Recent Climatic Changes." *Global Change Biology* 26(11): 6457–73.
- Boch, C. A., F. Micheli, M. AlNajjar, S. G. Monismith, J. M. Beers, J. C. Bonilla, A. M. Espinoza, L. Vazquez-Vera, and C. B. Woodson. 2018. "Local Oceanographic Variability Influences the Performance of Juvenile Abalone under Climate Change." *Scientific Reports* 8: 5501.
- Bruno, J. F., A. E. Bates, C. Cacciapaglia, E. P. Pike, S. C. Amstrup, R. van Hooedonk, S. A. Henson, and R. B. Aronson. 2018. "Climate Change Threatens the world's Marine Protected Areas." *Nature Climate Change* 8: 499–503.
- Button, C. A., and L. Rogers-Bennett. 2011. "Vital Rates of Pink Abalone *Haliotis corrugata* Estimated from Mark-Recapture Data to Inform Recovery." *Marine Ecology Progress Series* 431: 151–61.
- Coates, J. H., K. A. Hovel, J. L. Butler, and A. J. Bohonak. 2014. "Recruitment and Recovery of Pink Abalone (*Haliotis corrugata*) in a Historically Overexploited Kelp Forest: Are Local Populations Self-Sustaining?" *Journal of Experimental Marine Biology and Ecology* 460: 184–92.
- Cox, K. W. 1962. "Fish Bulletin No. 118. California Abalones, Family Haliotidae." *California Department of Fish and Game Fisheries Bulletin* 118: 1–133.
- Diario Oficial de la Federación. 2018. "Acuerdo Por El Que Se Establece Una Red de Dos Zonas de Refugio Pesquero Parciales Permanentes En Aguas Marinas de Jurisdicción Federal Adyacentes a Isla Natividad, Ubicada En El Municipio de Mulegé, En El Estado de Baja California Sur." https://www.dof.gob.mx/nota_detalle_popup.php?codigo=5525396.
- Harley, C., and L. Rogers-Bennett. 2004. "The Potential Synergistic Effects of Climate Change and Fishing Pressure on Exploited Invertebrates on Rocky Intertidal Shores." *California Cooperative Oceanic Fisheries Investigations Reports* 45: 98–110.
- Hobday, A. J., M. J. Tegner, and P. L. Haaker. 2000. "Over-Exploitation of a Broadcast Spawning Marine Invertebrate: Decline of the White Abalone." *Reviews in Fish Biology and Fisheries* 10: 493–514.
- Hutchings, J., and J. Reynolds. 2004. "Marine Fish Population Collapses: Consequences for Recovery and Extinction Risk." *Bioscience* 54: 297–309.
- Karpov, K., P. Haaker, I. Taniguchi, and L. Rogers-Bennett. 2000. "Serial Depletion and the Collapse of the California Abalone (*Haliotis* spp.) Fishery." *Canadian Special Publication of Fisheries and Aquatic Sciences* 130: 11–24.

- McCay, B. J., F. Micheli, G. Ponce-Díaz, G. Murray, G. Shester, S. Ramirez-Sanchez, and W. Weisman. 2014. "Cooperatives, Concessions, and Co-Management on the Pacific Coast of Mexico." *Marine Policy* 44: 49–59.
- Micheli, F., A. Shelton, S. Bushinsky, A. Chiu, A. Haupt, K. Heiman, C. Kappel, et al. 2008. "Persistence of Depleted Abalones in Marine Reserves of Central California." *Biological Conservation* 141: 1078–90.
- Micheli, F., A. Saenz-Arroyo, A. Greenley, L. Vazquez, J. A. E. Montes, M. Rossetto, and G. A. D. Leo. 2012. "Evidence that Marine Reserves Enhance Resilience to Climatic Impacts." *PLoS One* 7: e40832.
- Morales-Bojórquez, E., M. Muciño-Díaz, and J. Vélez-Barajas. 2009. "Analysis of the Decline of the Abalone Fishery (*Haliotis fulgens* and *H. corrugata*) along the West Central Coast of the Baja California Peninsula, Mexico." *Journal of Shellfish Research* 27: 865–70.
- Munguía-Vega, A., A. Sáenz-Arroyo, A. P. Greenley, J. A. Espinoza-Montes, S. R. Palumbi, M. Rossetto, and F. Micheli. 2015. "Marine Reserves Help Preserve Genetic Diversity after Impacts Derived from Climate Variability: Lessons from the Pink Abalone in Baja California." *Global Ecology and Conservation* 4: 264–76.
- Roberts, C. M., B. C. O'Leary, D. J. McCauley, P. M. Cury, C. M. Duarte, J. Lubchenco, D. Pauly, et al. 2017. "Marine Reserves Can Mitigate and Promote Adaptation to Climate Change." *Proceedings of the National Academy of Sciences* 114: 6167–75.
- Rogers-Bennett, L., P. Haaker, T. Huff, and P. Dayton. 2001. "Estimating Baseline Abundances of Abalone in California for Restoration." *California Cooperative Oceanic Fisheries Investigations Reports* 43: 97–111.
- Rose, G., and D. Kulka. 1999. "Hyperaggregation of Fish and Fisheries: How Catch-Per-Unit-Effort Increased as the Northern Cod (*Gadus morhua*) Declined." *Canadian Journal of Fisheries and Aquatic Sciences* 56: 118–27.
- Rossetto, M., G. A. D. Leo, A. Greenley, L. Vazquez, A. Saenz-Arroyo, J. A. E. Montes, and F. Micheli. 2013. "Reproductive Potential Can Predict Recruitment Rates in Abalone." *Journal of Shellfish Research* 32: 161–9.
- Rossetto, M., F. Micheli, A. Saenz-Arroyo, J. A. E. Montes, and G. A. De Leo. 2015. "No-Take Marine Reserves Can Enhance Population Persistence and Support the Fishery of Abalone." *Canadian Journal of Fisheries and Aquatic Sciences* 72: 1503–17.
- Smith, A. 2021. "abalone_recovery_ecosphere." Figshare. Data set. <https://doi.org/10.6084/m9.figshare.13953566.v1>.
- Trimble, A. C., J. L. Ruesink, and B. R. Dumbauld. 2009. "Factors Preventing the Recovery of a Historically Overexploited Shellfish Species, *Ostrea lurida* Carpenter 1864." *Journal of Shellfish Research* 28: 97–106.
- Woodson, C. B., F. Micheli, C. Boch, M. Al-Najjar, A. Espinoza, A. Hernandez, L. Vázquez-Vera, A. Saenz-Arroyo, S. G. Monismith, and J. Torre. 2019. "Harnessing Marine Microclimates for Climate Change Adaptation and Marine Conservation." *Conservation Letters* 12: e12609.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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