Journal of Experimental Marine Biology and Ecology 570 (2024) 151962

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Effects of stalked barnacle harvest on a rocky shore intertidal community

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A R T I C L E I N F O

Keywords:
Pollicipes pollicipes
Intertidal community structure
Small-scale fisheries impacts
Succession

A B S T R A C T

A two-year experiment investigated the effects of *Pollicipes pollicipes* (Gmelin, 1791) harvest on intertidal community structure and ecological diversity, as well as the recovery potential of *P. pollicipes* aggregations. The experiment was conducted at three locations along the West Asturian coast (Northern Spain) from July 2017 to July 2019. More intense exploitation resulted in reduced *P. pollicipes* and *Mytilus* spp. coverage, while *Chthamalus* spp. and *Corallina* spp. increased during the two years. Initially, the extraction of *P. pollicipes* lowered the ecological diversity of space occupying species, but this increased over time due to succession. While the recovery of exploited *P. pollicipes* aggregations was highly variable and slow, their coverage increased by up to 80% under caged non-extracted conditions in two years, leading to decreased diversity of primary space occupiers. Based on our findings, we suggest implementing two-yearly harvest bans to promote sustainability of this fishery.

1. Introduction

Human-exclusion experiments have demonstrated that exploitation can alter the structure of intertidal communities (e.g. Castilla and Duran, 1985; Castilla, 1999; Duran and Castilla, 1989; Godoy and Moreno, 1989; Moreno, 1986; Moreno et al., 1984; Oliva and Castilla, 1986; Rius et al., 2006). The resilience of intertidal organisms to exploitation is influenced by the mobility and life history traits, such as reproductive strategies, age of maturity, and growth rate (Adams, 1980; Jennings et al., 1999; Roff, 1984). Additionally, interspecific interactions and trophic level can affect a species' ability to recover after exploitation (Jennings et al., 1995; Jennings and Polunin, 1996; Koslow et al., 1988; Pauly et al., 1998). Evaluating the impact of exploitation on target species and interspecific interactions is crucial for developing ecosystem-based fisheries management strategies (Crowder et al., 2008). This is essential particularly for small-scale fishing communities that heavily rely on local marine resources for their livelihoods and that may contribute to resource overexploitation (Muallil et al., 2014; Pomeroy, 2012).

In this study, we examine the sessile pedunculated cirripede, *Pollicipes pollicipes* (Gmelin, 1791 [in Gmelin, 1788–1792]) a stalked barnacle, and its associated marine community. The geographical distribution of *P. pollicipes* ranges from the southwestern coast of the UK down to Senegal in West Africa, where it typically grows on very exposed rocky shores in the shallow subtidal to the mid-intertidal zone (Cruz et al., 2022). The species forms dense clusters securely attached to the substrate by a cement-like substance (Rocha et al., 2019). *P. pollicipes* life cycle includes planktonic larval phases (nauplii and cypris) and a benthic adult phase (Kugele and Yule, 1996; Molares et al., 1994). *P. pollicipes* are cross-fertilizing, simultaneous hermaphrodites and larvae recruit heavily on conspecific adults (Cruz et al., 2010), rendering the species vulnerable to overexploitation (Rivera et al., 2017).

In Europe, particularly in Spain and Portugal, *P. pollicipes* has been harvested for thousands of years, dating back to the Mesolithic (Álvarez-Fernández et al., 2010; Cruz et al., 2022). Presently, this species is highly valued and intensively exploited, with approximately 500 t being harvested annually by around 2100 professional harvesters in Europe, generating revenues of 10 million € (2013–2016; Aguión et al., 2022). The depletion of local stalked barnacle stocks in various parts of Spain (Molares and Freire, 2003) has prompted the implementation of diverse management solutions. In the Basque Country, Bay of Biscay, a no-take marine reserve was established specifically to protect the *P. pollicipes* stocks (Borja et al., 2006), while in Galicia, a co-management system was introduced in the early 1990s. This co-management system involves regulated access through the utilization of Territorial User Rights for Fishing (TURFs) (Molares and Freire, 2003) and regular stock assessments since 1992 (Macho et al., 2013). A comparison of the overall governance and sustainability level among different stalked barnacle

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https://doi.org/10.1016/j.jembe.2023.151962
Received 2 April 2023; Received in revised form 2 October 2023; Accepted 19 October 2023
Available online 6 November 2023

fisheries in Europe showed that management in Galicia and Asturias-West are the most successful (Aguión et al., 2022).

In Asturias (Fig. 1), the management of the stalked barnacle fishery is carried out through a combination of general regulations applied throughout the entire region (Gobierno del Principado de Asturias, 2022), as well as an adaptive co-management system along the west coast since 1992 (Rivera et al., 2014). The general regulations include a designated harvest season (from October until the end of April), a limited number of licenses for professional harvesters, specific time restrictions for the harvest activity (2 h before high tide until 1 h after), individual harvest quotas (kilograms per person per day), restrictions on harvest tools, and a minimum commercial size for the stalked barnacles (≥18 mm Rostro-carinal length (RC); Sestelo and Roca-Pardiñas, 2007) (Gobierno del Principado de Asturias, 2022). Similar to Galicia, the co-management system in Asturias-West follows a regulated access approach using TURFs (Aguión et al., 2022; Rivera et al., 2014). Additionally, harvest bans are frequently implemented as a management strategy within the co-management system in Asturias (Gobierno del Principado de Asturias, 2022). Total bans involve the complete closure of specific areas for the entire season, while partial bans allow for a limited number of designated harvest days per season (Rivera et al., 2014). Stock assessments done on a yearly base, help to decide whether harvest bans need to be implemented in specific locations. This fishery has proved remarkable resilience and sustainability by employing adaptive management strategies, particularly during critical periods such as the economic crisis in 2008 (Rivera et al., 2017). It holds significant socio-economic importance for Asturias (García-de-la-Fuente et al., 2016; González-Álvarez et al., 2016; Rivera et al., 2014), contributing around 38–50 million € annually through the harvest of approximately 55 tons (2013–2016; Aguión et al., 2022). However, to date, no prior human exclusion experiment has been conducted to examine the ecological impact of this fishery on the intertidal community.

This study aims to investigate the effects of *P. pollicipes* harvesting on the structure and ecological diversity of the intertidal community along the West coast of Asturias. The objective is to determine the resilience of *P. pollicipes* to harvesting by evaluating the recovery potential of the species within a two-year period. Ultimately, the study aims to contribute to the development of ecosystem-based fisheries management strategies for the stalked barnacle fisheries to ensure ecological sustainability.

2. Material and methods

2.1. Study location

The experiment was conducted in Asturias, North Spain, at three locations on the south shore of the Bay of Biscay: *La Cruz* (43°33 N, 7°01 W), *Las Salsinas* (43°35 N, 6°14 W) and *Las Llanas* (43°33 N, 6°06 W) (Fig. 1). All locations were situated within co-managed TURF areas (Rivera et al., 2014), with Las Salsinas and Las Llanas in Cudillero-Oviñana TURF and La Cruz in Tapia-Figueras TURF.

2.2. Experimental design

The experiment was conducted on 35 × 35 cm square plots that were located within the middle of the vertical distribution of *P. pollicipes* populations, at the interface between the lower, algae-dominated intertidal and the mid invertebrate-dominated intertidal (Fig. 2). The plots were placed randomly among areas with an approximately uniform coverage of *P. pollicipes* (15–20%) and were required to include individuals of commercial size (Fig. 2). The approximate coverage of 15–20% was chosen to achieve a comparable coverage among plots and locations at the start of the experiment. Rock pools and deep crevices

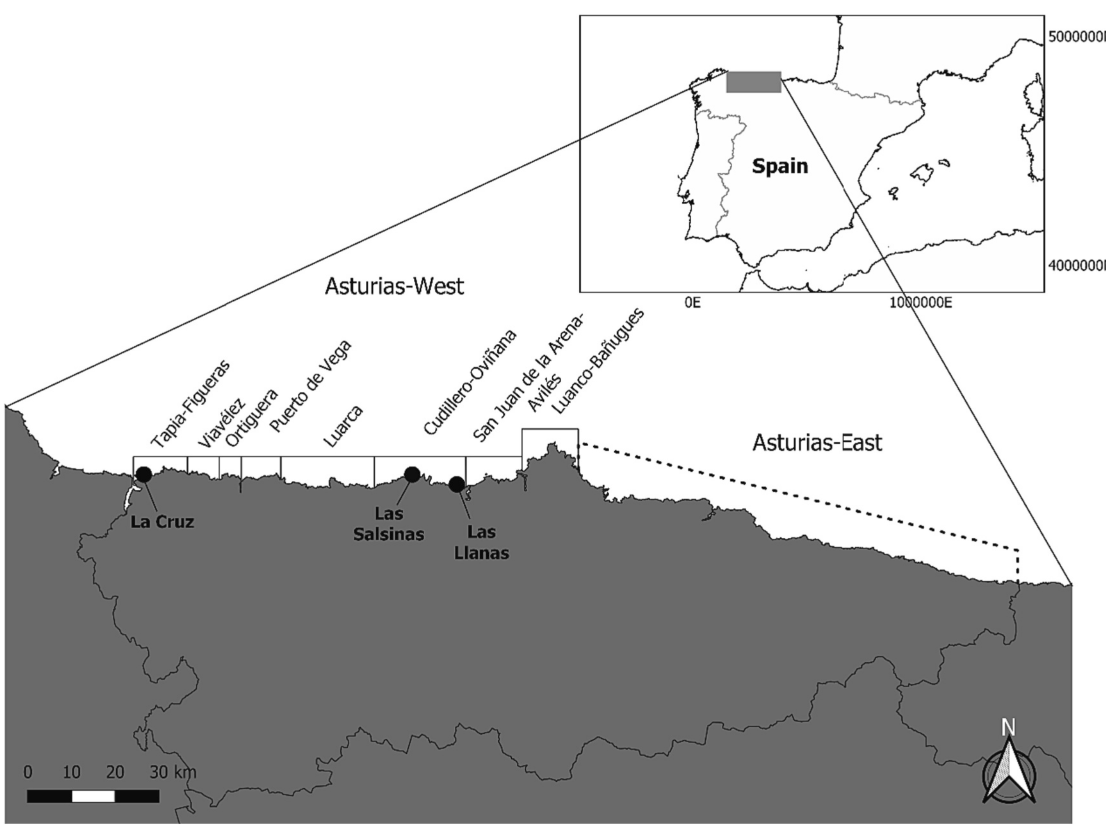

Fig. 1. Map of Asturias (North Spain) including the 8 TURFs located along the West coast. The three locations where the experiment took place are marked as black dots.

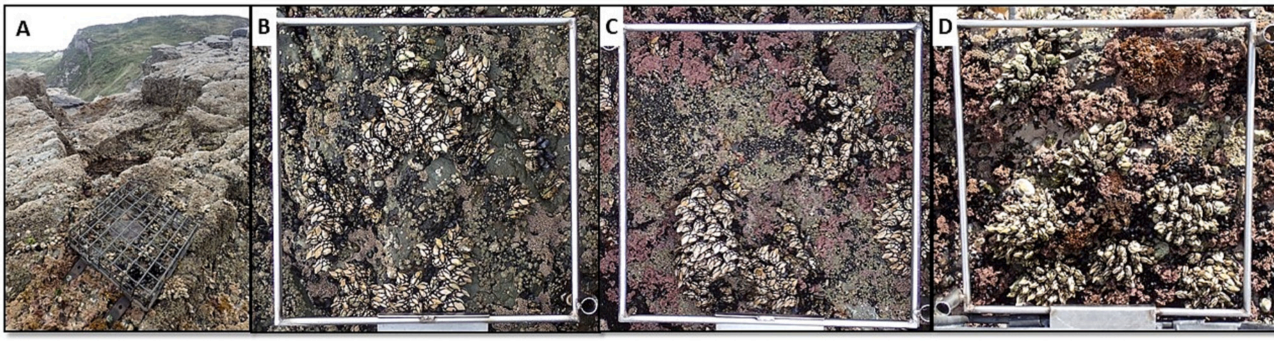

Fig. 2. Images of a cage (A) and examples of experimental plots with *P. pollicipes* aggregations (B: *Las Llanas*, C: *Las Salsinas*, D: *La Cruz*; Photos: Katja Geiger).

were avoided wherever possible. The experiment consisted of four factors:

2.2.1. Location (random factor)

The three locations (*La Cruz*, *Las Salsinas* and *Las Llanas*) were randomly chosen due to the following characteristics: good accessibility by foot, enough space to place 24 experimental plots with an appropriate coverage of *P. pollicipes*, and with suitable rock surface to firmly attach cages to withstand heavy wave action. Exposure to waves, harvest pressure, harvest bans, and other factors influencing the intertidal community in the selected locations may have varied, much like they would in any other randomly chosen location.

2.2.2. Experiment duration (fixed factor)

We used the same experimental setting in two different years and with distinct durations. The first setting started in July 2017 and ended in July 2019 (2-years experiment duration) (Fig. 3). The second setting started in July 2018 and also ended in July 2019 (1-year experiment duration).

2.2.3. Cage (fixed factor)

We covered half of the plots with cages to prevent exploitation (caged, *C*+) and left the other plots uncovered to allow for exploitation by harvesters (uncaged, *C*-). The cages were built with electro welded, galvanised steel wire mesh (4 mm diameter) to avoid decomposition by the salt water and were attached with heavy duty chemical bolts to withstand strong wave action. Cages measured 12 × 35 × 35 cm with a mesh size of 5 cm (Fig. 2). This gap allows the passage of scraping tools, but is sufficient to deter the harvest, because harvesters have limited time during the low tide.

2.2.4. Experimental extraction (fixed factor)

In half of the plots, both caged and uncaged, we conducted experimental extraction (*E*+). This experimental extraction conducted by us scientists was done as similarly as possible to the way professional harvesters harvest stalked barnacles in terms of methodology and timeframe. Only individuals above a minimum allowed harvest size were removed using a scraper, detaching the animals directly at the base where they attach to the rock to avoid damaging them. We conducted two experimental extraction events for the 2-years experiment. The first extraction was done in winter of 2017/2018 and the second extraction in winter 2018/2019, while the 1-year experiment duration plots were extracted experimentally only once, in winter 2018/2019. The exploitation intensity was not predetermined, but instead estimated retrospectively based on the removal of stalked barnacles detected through image analysis. We will use the term exploitation intensity referring to the degree of extraction of barnacles from experimental plots over the course of the experiment, based on the frequency and extent.

In Asturias the season for harvesting stalked barnacles opens in the beginning of October and closes at the end of April. Along the west coast, where the fishery is managed by TURFs (Fig. 1), areas can have more restricted harvest periods. As the experimental locations were situated within TURFs, the experimental extraction conducted by us scientists was conducted during the open period of these locations (Fig. 3).

The experimental design had 3 replicate plots for each combination of location, cage, extraction and duration, totalling 72 plots.

2.3. Hypothesis testing

The first step in the hypothesis testing examined whether the experimental extraction, done by scientists, was equivalent to that done by harvesters. To detect an extraction bias, open experimental plots in which only harvesters extracted (treatment *C-E-*) needed to be compared to other open experimental plots in which scientists and possibly harvesters extracted *P. pollicipes* (treatment *C-E*+). Treatment *C-E*+ also served to ensure exploitation in at least half of the open experimental plots, as we could not guarantee that harvesters would harvest in all open experimental plots.

If no statistically significant difference exists between the communities of treatments *C-E*+ and *C-E-*, the cage effect must be examined, testing *C*+*E*+ versus *C-E*+. In case no cage effect is detected, the natural test to answer the main objective of this study would be the comparison

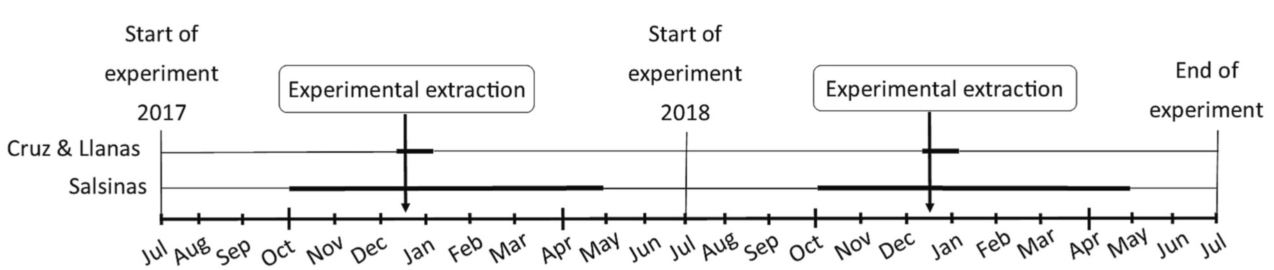

Fig. 3. *P. pollicipes* harvest schedule at the three experimental locations. Unbolded lines indicate harvest is not allowed due to the closure of the season (May until October), or due to location-specific harvest bans agreed to by the co-management of the TURFs; bolded line indicates that harvest is allowed (Only 15 days per year in *Cruz* and *Llanas*). Experimental extraction events are indicated with arrows.

between *C+E-* and *C-E-*, looking for differences in structure of the intertidal community among exploited (by the harvesters only) and unexploited (caged) areas. If the comparison between *C+E+* and *C-E+* results statistically significant, a cage effect cannot be excluded, leaving only one possible comparison between *C+E+* and *C+E-* to examine changes in the community structure among exploited and unexploited areas.

2.4. Image analysis

To document changes over time, all experimental plots were photographed at the beginning of the experiment and on a monthly basis thereafter. Before and after the experimental extraction, each plot was also photographically documented. Photographs were taken using a camera positioned as perpendicular to the surface area as possible and at waist height (approximately 70 cm from the ground) to achieve a realistic representation of the coverage of each species with minimum distortion. Organisms were identified to the lowest taxonomic level possible, and in cases where image analysis did not allow a distinction at the species level, the genus was used. In this study, *Corallina* spp. comprised *Corallina* species and *Ellisolandia elongata* (formerly known as *Corallina elongata*). All present species were recorded, and their percentage cover was quantified using the point intercept method. A 100-point grid was overlaid on the picture of each plot in Adobe Photoshop, and species present but without detectable cover were assigned an arbitrary 0.1% cover. The net coverage change (%) of *P. pollicipes* was calculated as $100 \times \frac{(\text{final coverage} - \text{initial coverage})}{\text{initial coverage}}$.

The exploitation intensity was estimated by calculating the cumulated removal throughout the entire experiment, detected with the image analysis.

2.5. Data treatment and statistical analysis

Before conducting any type of analysis the underlying assumptions were tested. Non-parametric tests were used instead of their parametric counterparts, when appropriate. A *p*-value of <0.05 was considered to indicate a significant result in all statistical tests. To assess whether the experiment resulted in significant changes in *P. pollicipes* coverage, we conducted a paired-sample Wilcoxon test to compare the initial and final coverage. Hypotheses regarding changes of the intertidal community structure were tested applying analysis of variance (ANOVA) with permutation tests for *P. pollicipes* cover and Shannon-Wiener diversity index data (using Euclidean distance matrix), and permutational multivariate analysis of variance (PERMANOVA) for the community data. For the latter, a semi-matrix of Bray Curtis dissimilarities was calculated on untransformed species coverage and a Type III sum of squares was applied. Pooling of non-significant interactions involving random factors was done where possible to increase the power of the test (Winer, 1971). The Shannon-Wiener index was applied to measure ecological diversity and similarity percentage (SIMPER) was used to determine the species, which were responsible for the differences. Non-Metric Dimensional Scaling (nMDS) was conducted with *R* computing software (R Core Team, 2022) using the Bray Curtis dissimilarities matrix calculated on untransformed species coverage. Software PRIMER 6 & PERMANOVA+ was used to perform statistical procedures of ANOVA, PERMANOVA and SIMPER (www.primer-e.com; Anderson et al., 2008). The ggplot2 package (Wickham, 2016) in the *R* computing software was used to create graphics (R Core Team, 2022).

3. Results

The species observed in the intertidal community are listed in the Appendix (Table A1) and original species coverage data of this study are available at Mendeley Data (Geiger et al., 2023). Due to storms during the first winter, two replicates of the 2-year treatment were lost (one *C+E+* and two *C+E-* plots), leading to an unbalanced design. The missing replicates were substituted with the average of the two remaining replicates of the same treatment groups and one degree of freedom for every missing replicate was subtracted from the residuals in the ANOVA, as recommended by Winer (1971).

3.1. Initial conditions

At the start of the 2-year experiment in July 2017, significant differences in *P. pollicipes* coverage were observed among locations (ANOVA, $p_{Location} = 0.001$; Table A2 Geiger et al., 2023). The initial *P. pollicipes* coverages of the plots used in the 1-year experiment (average coverage 20.2 ± 9.1%) were generally higher than in the 2-years experiment (average coverage 14.5 ± 5.2%), however, no statistically significant differences among locations were found. The intertidal community composition varied among locations (Table A3), with *La Cruz* exhibiting a denser coverage and less bare rock than the other locations. The most prevalent species in all three locations were the cirripedes *Chthamalus* spp. and *P. pollicipes*, along with the calcareous algae *Corallina* spp. in *La Cruz* and *Las Salsinas*. In *La Cruz*, in addition, *Mytilus* spp. were dominant, while in *Las Llanas* the algae *Ralfsia verrucosa* was abundant. Trigo et al. (2018) identified *Mytilus galloprovincialis* as the sole mussel species present on the north coast of Spain. Nevertheless, we refer to *Mytilus* spp. in our study, as the image analysis we employed does not allow us to distinguish between different mussel species.

3.2. Effects of exploitation on the coverage of P. pollicipes

Significant differences of net change in *P. pollicipes* coverage was found among treatments (Table 1). The detailed comparison among treatments showed no cage artefact for the observed changes in *P. pollicipes* coverage (Table 2). The differences between the non-extraction treatment (*C+E-*) and the extraction treatments were significant (Table 2). The percent cover of *P. pollicipes* in plots protected by a cage and not extracted experimentally (*C+E-*) showed an increase after both 1-year and 2-year experiment durations, despite losses due to storms and poaching (Fig. 4A). The *P. pollicipes* coverages removed through the extraction done by scientists were similar to those removed through a combination of the exploitation by harvesters and minor losses due to other predators or storms (Fig. A1). As expected, we observed a decrease in the average *P. pollicipes* coverage regardless of the type of exploitation: by scientists only (*C+E+*), by both scientists and

Table 1
Results of ANOVA comparing net change of *P. pollicipes* coverage among treatments.

	Df	Sum Sq	Mean Sq	F value	Pr(<F)
2-years Treatment					
Cage (C)	1	109.773	109.773	7.977	0.010*
Experimental Extraction (E)	1	55.872	55.872	4.060	0.057
Location (L)	2	23.502	11.751	0.854	0.440
C × E	1	17.295	17.295	1.257	0.275
C × L	2	14.010	7005	0.509	0.608
E × L	2	28.920	14.460	1.051	0.367
C × E × L	2	12.371	6185	0.449	0.644
Residuals	21	288.995	13.762		
1-year Treatment					
Cage (C)	1	33.018	33.018	8.107	0.009**
Experimental Extraction (E)	1	69.366	69.366	17.033	0.0003***
Location (L)	2	70.088	35.044	8.605	0.001**
C × E	1	12.609	12.609	3.096	0.091
C × L	2	759	379	0.093	0.911
E × L	2	25	13	0.003	0.997
C × E × L	2	6561		0.806	0.458
Residuals	24	97.741	4073		

*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Table 2
Results of Tukey-Kramer post-hoc pairwise test of *P. pollicipes* coverage net change data.

	Treatments	P-value	Interpretation
2-Years Experiment Duration	*C-E+* vs *C-E-*	0.780	No effect of experimental extraction in plots without cages
	C-E+ vs *C+E+*	0.447	No cage artefact
	C+E- vs *C+E+*	0.081	No effect of experimental extraction in cages
	C+E- vs *C-E+*	0.002**	Combined extraction effect
	C+E- vs *C-E-*	0.019*	Effect of extraction by harvesters
1- Year Experiment Duration	*C-E+* vs *C-E-*	0.360	No effect of experimental extraction in plots without cages
	C-E+ vs *C+E+*	0.760	No cage artefact
	C+E- vs *C+E+*	0.026*	Effect of experimental extraction in cages
	C+E- vs *C-E+*	0.002**	Combined extraction effect
	C+E- vs *C-E-*	0.117	No effect of extraction by harvesters

*: $p < 0.05$; **: $p < 0.01$.

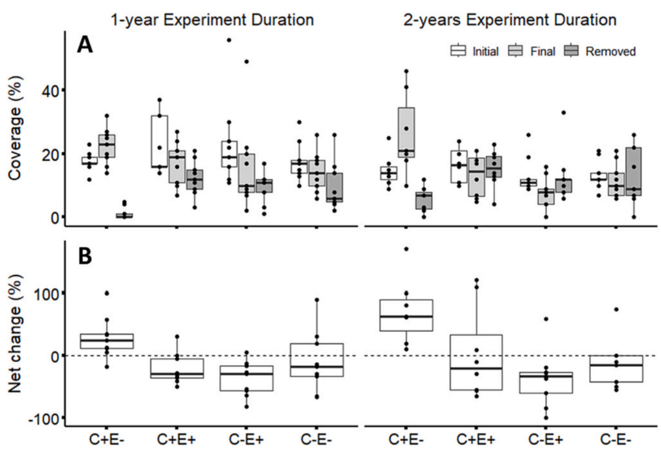

Fig. 4. A) *P. pollicipes* coverages (dots represent replicates and boxplots represent average coverages of all three locations with standard errors) at beginning (white boxplots) and end (light grey boxplots) of the experiment in the 1-year experiment duration (July 2018 to July 2019) and 2-years experiment duration (July 2017 to July 2019), and cumulated removal of *P. pollicipes* coverages throughout the study period by scientific extraction and/or harvesters, including minor losses due to predators or storms (dark grey boxplots). B) Net change of *P. pollicipes* (dots represent replicates and boxplots represent average coverages of all three locations with standard errors) from beginning to end of the experiment.

harvesters (*C-E+*), or by harvesters only (*C-E-*) (Fig. 4B). The average net change of *P. pollicipes* coverage was negative in all treatments, except for the *C+E-* treatment, where the average increase reached 80% after 2 years (Fig. 4B).

3.3. Effects of exploitation on the structure of the intertidal community

A significant interaction between the experimental extraction and the cage treatments was detected in species coverage ($P_{\text{Experimental Extraction x Cage}} = 0.031$, Table 3(A)). A post-hoc pairwise test revealed no significant differences between open plots with harvest by harvesters only (*C-E-*) and open plots exposed to both harvesters and experimental extraction (*C-E+*; $P_{\text{C-E- vs C-E+}} = 0.155$, Table 4). This suggests that the effect of the experimental extraction conducted by scientists is equivalent to the effect of harvest done by harvesters. However, a significant difference was found between caged (*C+E+*) and open (*C-E+*) plots that were experimentally extracted ($P_{\text{C-E+ vs C+E+}} = 0.031$; Table 4; see the relevant tests in methods), indicating a methodological cage artefact. Therefore, to evaluate the effect of exploitation on the intertidal community structure, it is necessary to compare the caged, experimentally extracted (*C+E+*) with the caged non-extracted (*C+E-*) treatments. This comparison revealed a significant difference ($P_{\text{C+E- vs C+E+}} = 0.047$; Table 4).

3.4. Changes in the species composition

At least 80% of the dissimilarity in the intertidal community composition between all treatments could be attributed to the coverage of *P. pollicipes*, *Mytilus* spp., *Chthamalus* spp. *Corallina* spp. and *Ralfsia* spp., as well as the amount of bare rock (Tables 5 and 6). At the species level, dissimilarities varied across treatments and duration. The coverage of *P. pollicipes* and *Mytilus* spp. decreased in harvested plots (Table 5) and increased in the caged plots, with larger and more significant differences after two years (Table 5).

In the 1-year experiment treatment, the caged plots with (*C+E+*) and without experimental extraction (*C+E-*) exhibited a significant difference in bare rock coverage, with the latter having a higher percentage due to the removal of *P. pollicipes* (21.3% dissimilarity; Table 5). However, by the end of the 2-year experiment, the dissimilarity among caged plots was mainly due to the increase in *P. pollicipes* coverage in the treatment with no experimental extraction (21.2%, Table 5). The coverage of *Mytilus* spp. was consistently higher in the plots without experimental extraction regardless of the experiment duration (14.6 to 16.1% of the dissimilarity; Table 5).

The cage effect was noticeable in the 2-years experiment duration, with both *P. pollicipes* and *Mytilus* spp. being more abundant in the caged plots, compared to the uncaged plots, despite extraction in both treatments. In contrast, *Chthamalus* spp. and *Corallina* spp. occupied more available space in the uncaged plots, with an increase in *Chthamalus* spp., which was more apparent after two years (Table 6).

3.5. Effects of the exploitation intensity

The nMDS (non-Metric Dimensional Scaling) graph provides a visual representation of the relationship between the experimental factors and the species composition. The graphs show that there are two distinct groups corresponding to the cage and open plots (Fig. 5A), and reflect an increase in exploitation intensity (Fig. 5B). The composition of the intertidal community shifts from being dominated by *P. pollicipes* and *Mytilus* spp. at lower extraction intensities (represented by plots of *C+E-*) and protected by cages to a higher coverage of bare rock, *Corallina* spp. and *Chthamalus* spp. in unprotected conditions with higher extraction intensities (represented by plots of *C-E+* and *C-E-*) (Fig. 5A&B).

3.6. Effects on the ecological diversity

ANOVA revealed differences in the Shannon-Wiener index among treatments based on a three-way interaction (Table 3(B)). Experimental extraction, cage usage and experiment duration in combination, thus have a significant impact on the ecological diversity. In the 1-year

Table 3
Results of the PERMANOVA (A) Multivariate species coverage and the ANOVA (B) Shannon index.

	Source of variance	df	Error term	MS	Pseudo-F	P (perm)	Error term	MS	Pseudo-F	P (perm)
			(A) Multivariate species coverage				(B) Shannon index			
(a)	Location (L)	2	(q)	2472.3	40.182	0.001**	(p)	0.178	5.97	0.006**
(b)	Cage (C)	1	(e)	7010.2	10.012	0.081	(e)	0.006	0.1	0.796
(c)	Experimental Extraction (E)	1	(f)	1066.7	20.028	0.185	(f)	0.007	0.26	0.601
(d)	Experiment Duration (D)	1	(g)	688.77	13.302	0.327	(g)	0.011	1.36	0.44
(e)	L × C	2	(q)	700.26	11.381	0.331	(p)	0.068	2.28	0.122
(f)	L × E	2	(q)	532.33	0.86518	0.555	(p)	0.029	0.97	0.393
(g)	L × D	2	(q)	517.66	0.84133	0.595	(p)	0.008	0.27	0.774
(*h*)	C × E	1	(q)	1699.6	27.623	0.031*	(*k*)	0.023	1.66	0.322
(i)	C × D	1	(*l*)	632.23	0.81434	0.506	(l)	0.062	6.35	0.118
(j)	E × D	1	(m)	260.02	0.76539	0.51	(m)	0.011	0.41	0.59
(k)	L × C × E	2					(p)	0.014	0.46	0.653
(l)	L × C × D	2	(q)	776.55	12.621	0.267	(p)	0.01	0.32	0.74
(m)	L × E × D	2	(q)	338.87	0.55075	0.841	(p)	0.026	0.86	0.419
(n)	C × E × D	1	(o)	299.06	0.46276	0.699	(o)	0.059	36.88	0.032*
(o)	L × C × E × D	2	(q)	646.41	10.506	0.399	(p)	0.002	0.05	0.944
(p)	Residual (Res)	45		615.57				0.03		
(q)	Pooled term (Res + L × C × E)	47		615.29						

Note that for the community data the three-way interaction Location x Cage x Experimental Extraction (non-significant: $p > 0.98$) was pooled with the residual to increase the power of the test. *: $p < 0.05$; **: $p < 0.01$.

Table 4
Post-hoc pairwise test comparing the different treatments using raw species coverage data at the end of the full experiment (1 and 2-years experiment durations).

Treatments	t	P (perm)	Interpretation
C-E+ vs *C-E-*	1.280	0.155	No effect of experimental extraction
C-E+ vs *C+E+*	3.527	0.031*	Cage artefact
C+E- vs *C+E+*	1.609	0.047*	Extraction effect
C+E- vs *C-E-*	3.527	0.001**	Not relevant (confounds cage & exploitation effects)

*: $p < 0.05$ and ** $p < 0.01$.

experiment duration the caged, non-extraction treatment (*C+E-*) showed the highest Shannon index (Fig. 5), while values among the other treatments were similar to each other (Fig. 6). For the 2-years experiment duration the Shannon index was similar among all treatments, with the caged non-extraction treatment (*C+E-*) presenting the lowest value (Fig. 6).

4. Discussion

To our knowledge this is the first study to assess the response of the intertidal community to the harvest of *P. pollicipes*, an important, highly-valued resource in Southwest Europe (Aguión et al., 2022). Stalked barnacles grow on very exposed rocky shores, making the study environment particularly challenging for experimentation, especially when cages are involved. In our experiment, the presence of cages had an influence which could not be neglected and was possibly due to a reduction in wave action (Miller and Gaylord, 2007) and predator pressure (Hayworth and Quinn, 1990; Wootton, 1993, 2001). Thus, although the cages generally withstood storms and vandalism and successfully controlled exploitation, future experiments should simulate human exclusion in no-take areas rather than using cages, to avoid artefacts. Harvesters stepping on the intertidal community can also impact the open but not the caged plots (Addessi, 1994) and there may be differences in the extraction methods used by scientists and harvesters. Scientists followed selective harvesting for market-sized individuals and avoided removing entire clusters, whereas harvesters have time limitations and extract clusters with individuals of all sizes, selecting the larger ones for sale afterwards. In spite of the cage artefact and the very small percentage of the plot area affected by the harvest (<15%), we were able to detect significant changes in community structure.

The extraction initially decreased the diversity during the first year, but as new organisms settled and covered the bare rock during the second year, diversity increased. Essentially, extraction opened space for species to settle during the course of succession. In contrast, in the absence of exploitation, diversity increased during the first year until *P. pollicipes* and *Mytilus* spp. became dominant in the second year. This led to a subsequent decrease in the diversity index of primary space occupiers. Dynamic changes in the intertidal community, as observed in our study, are commonly observed during the course of ecological succession which follows perturbations due to human exploitation (Duran and Castilla, 1989; Dye, 1992). As noted in other studies, intermediate disturbance levels can lead to greater ecological diversity within the rocky intertidal community (Levin and Paine, 1974; Paine and Levin, 1981). Throughout the Iberian Peninsula, humans are undeniably the most significant predators of *P. pollicipes*, and they can be viewed as selective keystone predators (Castilla, 1999) who promote ecological diversity through regular disturbance resulting from the stalked barnacle harvest. However, it is unclear whether this apparent higher ecological diversity is a sign of a more diverse community, as we only focused on primary space occupiers and did not include highly mobile and cryptic species. We want to point out that there is a current knowledge gap concerning the diversity of cryptic species associated with the three-dimensional structure created by *Pollicipes* and *Mytilus* reefs.

Previous studies in a comparable ecosystem on the Pacific East coast documented the entire succession process during 5–10 years in cleared gaps within established mussel beds due to storm events (Paine and Levin, 1981; Wootton, 2001). *Mytilus californianus* outcompeted *Pollicipes polymerus* and dominated the intertidal community due to its large size and ability of adult individuals to resettle once detached (Wootton, 1993, 2001). However, the duration of the current study was too short to describe a complete succession, validate whether the succession process was slow or dynamic, and determine the final stable community structure. Whether *Mytilus* spp. can outcompete *P. pollicipes* in the European and African coasts is unknown, because competition for space is not the only factor that determines the dominance of species within rocky shore

Table 5
Results of the SIMPER analysis on the contribution of the different species to the dissimilarities in community structure between caged with (*C+E+*) and without experimental extraction (*C+E-*).

Species	Coverage (%)			Contribution (%)	Cumulative Contribution (%)
	C+E-	C+E+	Average Dissimilarity		
Complete Experiment					
Rock	19.5 ± 7.0	28.6±10.9	6.4	16.9	16.9
Pollicipes pollicipes	24.1 ± 9.1	17.4 ± 11.0	6.1	16.1	33.0
Mytilus spp	15.8 ± 11.2	10.5 ± 7.7	5.9	15.5	48.5
Chthamalus spp	12.1 ± 7.7	12.5 ± 8.7	4.6	12.1	60.6
Corallina spp	6.6 ± 7.8	8.2 ± 9.1	4.4	11.6	72.2
Ralfsia verrucosa	10.4 ± 5.8	10.8 ± 5.6	3.3	8.6	80.8
1-year Experiment Duration					
Rock	19.7 ± 6	31.2 ± 12.9	7.8	21.3	21.3
Mytilus spp	14.1 ± 10.1	8.4 ± 6.4	5.4	14.6	35.9
Corallina spp	8.4 ± 8.9	9.0 ± 11.1	5.3	14.5	50.4
Chthamalus spp	13.3 ± 8.4	12.1 ± 6.2	4.4	12.0	62.4
Pollicipes pollicipes	22.4 ± 5.4	17.3 ± 6.4	4.0	10.8	73.2
Ralfsia verrucosa	9.8 ± 3.5	9.8 ± 5.9	2.8	7.6	80.8
2-years Experiment Duration					
Pollicipes pollicipes	26.3 ± 12.0	17.4 ± 14.6	8.4	21.2	21.2
Mytilus spp	17.9 ± 12.3	12.9 ± 8.3	6.4	16.1	37.3
Rock	19.3 ± 8.2	25.6 ± 7.0	5.1	13.0	50.2
Chthamalus spp	10.4 ± 6.5	13.0 ± 10.8	4.8	12.1	62.4
Ralfsia verrucosa	11.3 ± 7.7	12.0 ± 5.1	4.0	10.1	72.4
Corallina spp	4.1 ± 5.2	7.3 ± 5.9	3.3	8.3	80.8

intertidal communities. Physical factors such as the substrate inclination, height within the intertidal and wave exposure also play a determinant role in the final stable structure of the community (Paine and Levin, 1981). The coexistence and direct interaction between stalked barnacles and mussel species, however, appear to be a general pattern (Barnes and Reese, 1959; Barnes, 1996; Cruz et al., 2022; Kameya and Zeballos Flor, 1998; L. Hoffman, 1989; Paine and Levin, 1981; Wootton, 1993). While between *P. polymerus* and *M. californianus* predominantly competitive interactions have been observed (Paine and Levin, 1981; Wootton, 1993, 2001), our study results suggest a positive interaction among *P. pollicipes* and *Mytilus* spp. Our study provides evidence that reducing the exploitation intensity of *P. pollicipes*, while utilizing cages, leads to higher coverages of both *P. pollicipes* and *Mytilus* spp. We observed a cage artefact in the community analysis Table 4), which may indicate a protective effect of the cages on mussels, as this artefact did not show up in the *P. pollicipes* net change analysis (Table 2). Our

Table 6
Results of SIMPER analysis on the contribution of the different species to the dissimilarities in community structure between open plots with experimental extraction (*C-E+*) and caged plots with experimental extraction (*C+E+*).

Species	Coverage (%)			Contribution (%)	Cumulative Contribution (%)
	C-E+	C+E+	Average Dissimilarity		
Complete Experiment					
Rock	29.1 ± 10.5	28.6 ± 10.9	6.1	15.9	15.9
Chthamalus spp	18.7 ± 9.9	12.5 ± 11.0	6.0	15.6	31.6
Pollicipes pollicipes	11.9 ± 11.0	17.4 ± 7.7	5.9	15.4	47.0
Corallina spp	11.7 ± 13.6	8.2 ± 8.7	5.9	15.4	62.4
Mytilus spp	3.9 ± 2.8	10.5 ± 9.1	4.1	10.7	73.1
Ralfsia spp	10.6 ± 5.0	10.8 ± 5.6	3.0	7.9	80.9
1-year Experiment Duration					
Rock	27.7 ± 11.0	31.2 ± 12.9	6.9	17.8	17.8
Corallina spp	12.3 ± 16.4	9.0 ± 11.1	6.9	17.8	35.5
Chthamalus spp	16.6 ± 12.5	12.1 ± 6.2	6.0	15.3	50.8
Pollicipes pollicipes	16.0 ± 14.0	17.3 ± 6.4	5.6	14.4	65.2
Mytilus spp	4.5 ± 3.2	8.4 ± 6.4	3.2	8.1	73.3
Ralfsia spp	9.1 ± 4.5	9.8 ± 5.9	2.9	7.5	80.9
2-years Experiment Duration					
Chthamalus spp	20.8 ± 6.5	13.0 ± 10.8	6.4	16.9	16.9
Pollicipes pollicipes	7.8 ± 5.0	17.4 ± 14.6	6.0	15.9	32.8
Rock	30.4 ± 10.5	25.6 ± 7.0	5.4	14.4	47.2
Mytilus spp	3.3 ± 2.2	12.9 ± 8.3	5.2	13.8	61.0
Corallina spp	11.0 ± 11.2	7.3 ± 5.9	4.8	12.6	73.6
Ralfsia spp	12.0 ± 5.3	12.0 ± 5.0	2.9	7.6	81.2

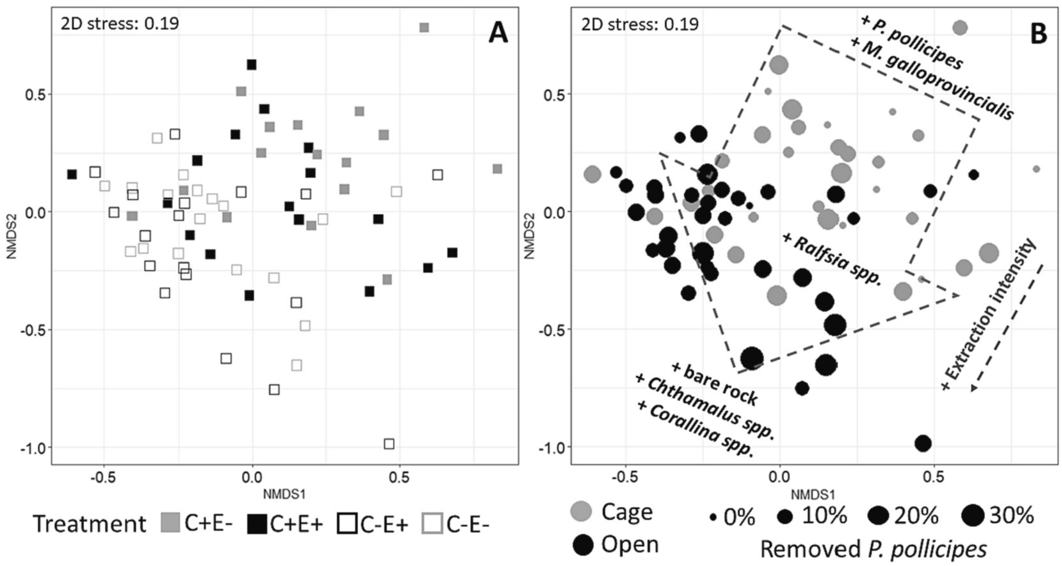

Fig. 5. nMDS of the intertidal community data, based on species coverage, with symbols indicating (A) combinations of extraction and cage treatments and (B) extraction intensity in terms of % *P. pollicipes* removal.

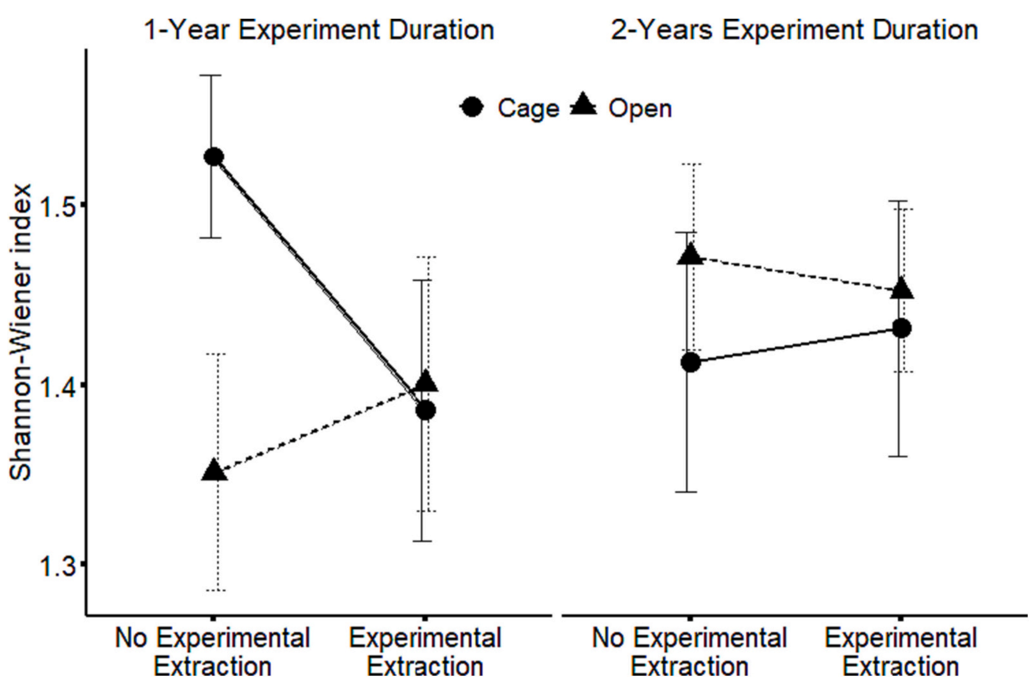

Fig. 6. Differences in community diversity. Symbols represent averages and error bars indicate standard errors.

experimental findings suggest that the presence of adult individuals from both *P. pollicipes* and *Mytilus* spp. facilitates the recruitment of both species. The favourable physical structures created by these individuals likely provide suitable environments for larval settlement, thereby contributing to a mutual enhancement of species coverages.

Throughout the 2-years experiment duration, the exploitation intensity resulted somewhat higher than in the 1-year experiment, because of the cumulated removal of all commercially sized stalked barnacles by both scientists and harvesters, spanning both years (Figs. 4 and A1). However, the overall exploitation intensity was not simply doubled in the 2-year experiment because the extraction conducted during the second year was not as extensive as in the first year. This was due to the time required for stalked barnacles to grow. Since the initial extraction, fewer barnacles had reached the minimum harvest size, resulting in a reduced extraction in the second year. Additionally, at the beginning of the experiments, the total barnacle coverage was higher in the 1-year experiment compared to the 2-years experiment. Consequently, the 1-year experimental plots allowed for a higher initial extraction due to the increased number of barnacles available.

The recovery potential of exploited *P. pollicipes* aggregations was variable (Fig. 4). A study on *P. polymerus* in British Columbia also found a high variability in the speed of recovery of stalked barnacles (Edwards, 2020). In that study *P. polymerus* were entirely cleared from plots of different sizes which were then followed during 14-months. The recovery of *P. polymerus* was generally low (12% of the initial biomass after 14 months), and varied greatly among plots, while other barnacle species and mussels recovered faster (Edwards, 2020). Despite the variability in our study, we observed an increasing trend of up to 80% of the initial *P. pollicipes* coverage in non-exploited conditions and a decreasing trend down to 30% of the initial coverage after two years in exploited conditions. Hence, *P. pollicipes* populations have the capacity to recover within two years when undisturbed, at least in terms of surface cover. This is likely due to the growth of larvae attached to adults rather than the settlement and growth of new individuals on bare rock, since *P. pollicipes* larvae recruit preferentially on the stalks of conspecific adults (Franco, 2014). Thus, the recovery of exploited *P. pollicipes* stocks will ultimately require a combination of time and availability of conspecific adults. It is likely that, below a certain threshold of *P. pollicipes* coverage, a much longer period would be required for stock recovery.

Current management of the stalked barnacle fishery in Asturias-West involves yearly harvest bans that can be extended (Gobierno del Principado de Asturias, 2022). The decision to lift or renew a harvest ban for the following season is based on the outcomes of stock assessments in the banned areas. Our results suggest that extended harvest bans can be a useful measure for the recovery of exploited stalked barnacle stocks and contribute to the sustainability of the fishery. However, further research is necessary to determine the minimum coverage percentage of *P. pollicipes* required to initiate and sustain the recovery of the stock. Long-term studies are needed to characterize the complete succession process, determine the final stable species composition of this intertidal community, and establish the time scale of the recovery process.

5. Conclusion

Our study confirms that harvesting stalked barnacles leads to changes in the species composition of the rocky intertidal ecosystem. Regular exploitation increased the proportion of *Corallina* spp. and *Chthamalus spp*, while significantly reducing the coverage of *P. pollicipes* and *Mytilus* spp. Although, ecological diversity in exploited plots initially decreased, it increased again after two years when new organisms re-colonised the bare rock. In contrast, the unexploited community showed higher dominance of *P. pollicipes* and *Mytilus* spp., resulting in a lower diversity. Despite variable recovery potential of *P. pollicipes* aggregations, an increase of up to 80% of initial coverage was observed after two years of no extraction. Therefore, prolonged harvest bans of at least two years can be an effective recovery measure for exploited stalked barnacle stocks, promoting the sustainability of the fishery. To better understand the long-term effects of this fishery on the intertidal community and acquire conclusive results regarding community succession towards a stable state, human-exclusion studies in no-take zones lasting at least 5 years are required.

Submission declaration and verification

We declare that the work described has not been published previously and is not under consideration for publication elsewhere. Its publication is approved by all authors and explicitly by the responsible authorities where the work was carried out. If accepted, it will not be published elsewhere in the same form, in English or in any other language, including electronically without the written consent of the copyright-holder.

Funding

This research was funded by the BiodivERsA3 2015- 2016, EU HORIZON 2020 ERA-NET COFUND and the Spanish State Research Agency under project PERCEBES (Tools for the transition to spatial management of coastal resources: the stalked barnacle fishery in SW Europe. Grant: PCIN-2016-120). Katja Geiger was supported through the Severo Ochoa Ph.D. program (Principado de Asturias, PA-18-PF-BP17-184). This is a contribution of the Asturias Marine Observatory.

CRediT authorship contribution statement

Katja J. Geiger: Conceptualization, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **Julio Arrontes:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – review & editing. **Antonella Rivera:** Writing – review & editing. **Consolación Fernández:** Writing – review & editing. **Jorge Álvarez:** Investigation, Resources. **José Luis Acuña:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

None.

Data availability

I have published the database. The reference is in the manuscript.

Acknowledgements

We thank the Tapia-Casariego and Cudillero-Oviñana *cofradías* for their collaboration and for facilitating locations to conduct the experiment. Special thanks go to the coastguards of these cofradías who kept a close eye on the installations throughout the project. We thank the Centro de Experimentación Pesquera (CEP) for their collaboration and support during the project and Teresa Cruz for her kind guidance on statistical procedures. We also thank technicians and students who participated in the field and laboratory work.

Appendix 1

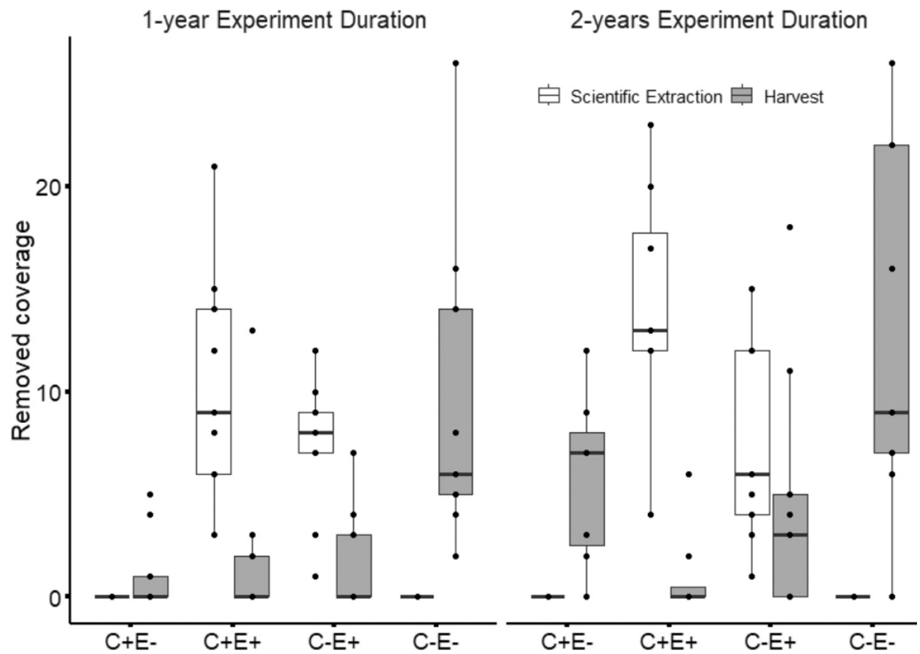

Fig. A1. Removed coverages of *P. pollicipes* (dots represent replicates and boxplots represent average coverages of all three locations with standard errors) through scientific extraction (white boxplots) and through harvesters, predators, and storms (dark grey boxplots) of the experiment in the 1-year experiment duration (July 2018 to July 2019) and 2-years experiment duration (July 2017 to July 2019).

Table A1
Species list comprising the intertidal community accompanying *P. pollicipes.*

		Average coverage (%) ± standard deviation		
		La Cruz	Las Salsinas	Las Llanas
Animals	Cnidaria, Anthozoa (Anemones):			
	Actinia equina (Linnaeus, 1758)	✓	0.09 ± 0.06	0.17 ± 0.10
	Mollusca, Gastropoda (Periwinkles, Dogwhelks, Limpets):			
	Phorcus lineatus (Da Costa, 1778)			✓
	genus *Patella* (*P. depressa* Pennant, 1777, *P. ulyssiponensis* Gmelin, 1791, *P. rustica* Linnaeus, 1758, *P. vulgata* Linnaeus, 1758)	3.42 ± 0.45	5.95 ± 0.64	5.04 ± 0.42
	Mollusca, Bivalvia (Mussels):			
	Mytilus spp.	7.13 ± 1.67	5.95 ± 0.74	6.22 ± 0.88
	Annelida, Polychaeta (Worms):			
	Eulalia viridis (Linnaeus, 1767)	✓		
	Echinodermata, Echinoidea (Urchins):			
	Paracentrotus lividus (Lamarck, 1816)	✓		✓
	Arthropoda, Cirripedia (Barnacles):			
	genus *Chthamalus* (*C. montagui* Southward, 1976, *C. stellatus* (Poli, 1791))	23.08 ± 3.51	24.41 ± 2.27	21.70 ± 2.24
	Pollicipes pollicipes (Gmelin, 1791 [in Gmelin, 1788–1792])	19.58 ± 2.21	17.18 ± 1.40	15.61 ± 1.03
Algae	Rhodophyta (Red algae):			
	Asparagopsis armata Harvey, 1855			✓
	Callithamnion spp.		✓	✓
	Ceramium spp.	0.46 ± 0.21	0.09 ± 0.09	0.04 ± 0.04
	Gelidium spp.			✓
	Laurencia obtusa (Hudson) J.V.Lamouroux, 1813	✓		✓
	Lomentaria articulata (Hudson) Lyngbye, 1819	✓		✓
	Mastocarpus stellatus (Stackhouse) Guiry, 1984	✓	0.46 ± 0.46	✓
	Nemalion helminthoides (Velley) Batters, 1902	0.63 ± 0.15	2.23 ± 0.71	0.91 ± 0.43
	Osmundea pinnatifida (Hudson) Stackhouse, 1809	0.88 ± 0.35	1.00 ± 0.46	✓
	Plocamium cartilagineum (Linnaeus) P.S.Dixon, 1967			✓
	Polysiphonia spp.		✓	✓
	Porphyra sp. (in *Conchocelis* phase)		✓	
	Rhodothamniella floridula (Dillwyn) Feldmann, 1978			✓
	Calcareous:			
	Corallina spp. and Ellisolandia elongata (J.Ellis & Solander) K.R.Hind & G.W.Saunders, 2013	12.21 ± 2.96	13.27 ± 1.77	4.00 ± 1.30
	Lithophyllum incrustans Philippi, 1837	3.42 ± 0.86	1.45 ± 0.46	1.00 ± 0.37

(*continued on next page*)

Table A1 (*continued*)

	Average coverage (%) ± standard deviation		
	La Cruz	Las Salsinas	Las Llanas
Tenarea tortuosa (Esper) Me.Lemoine, 1910	4.54 ± 0.94	1.68 ± 0.46 ±	6.22 ± 1.06
Ochrophyta (Brown algae):			
Caulacanthus ustulatus (Mertens ex Turner) Kützing, 1843	0.21 ± 0.09	0.46 ± 0.41	0.04 ± 0.04
Colpomenia peregrina Sauvageau, 1927		✓	
Ectocarpus siliculosus (Dillwyn) Lyngbye, 1819			✓
Leathesia marina (Lyngbye) Decaisne, 1842		✓	
Petrospongium berkleyi (Greville) Nägeli ex Kützing, 1858	✓	0.46 ± 0.46	0.09 ± 0.06
Ralfsia verrucosa (Areschoug) Areschoug, 1845	6.71 ± 0.70	5.73 ± 0.92	11.09 ± 1.27
Sphacelaria fusca (Hudson) S.F. Gray, 1821		✓	✓
Chlorophyta (Green algae):			
Bryopsis plumosa (Hudson) C.Agardh, 1823	✓	0.14 ± 0.14	
Chaetomorpha linum (O.F.Müller) Kützing, 1845		✓	✓
Lychaete pellucida (Hudson) M.J.Wynne, 2017			✓
Ulva spp.	✓	✓	✓
Cianobacteria			
genus *Microcoleus* Desmazières ex Gomont, 1892			✓

This is not an exhaustive list, but describes species or genus found in the experimental plots of this study in the three study locations (*La Cruz*, *Las Salsinas* and *Las Llanas*) between July 2017 and July 2019.

Table A2
ANOVA using permutation tests on initial stalked barnacle coverage data separately for 1-year and 2-years experiment durations with **$p < 0.01$.

Source	df	MS	Pseudo-F	P (perm)	df	MS	Pseudo-F	P (perm)
	Stalked barnacle coverage data							
	2-Years duration				1-Year duration			
Location (L)	2	2850.4	3.803	0.001**	2	226.08	2.691	0.074
Cage (C)	1	310.0	0.416	0.774	1	0.69	0.020	1.000
Experimental Extraction (E)	1	1019.8	1.416	0.263	1	261.36	9.325	0.164
L × C	2	744.5	0.993	0.411	2	34.36	0.409	0.656
L × E	2	694.1	0.926	0.446	2	28.03	0.334	0.715
C × E	1	109.2	0.093	0.830	1	0.69	0.034	0.832
L × C × E	2	1176	1.569	0.176	2	20.19	0.240	0.795
Residual (Res)	22	749.6			24	84.03		
Total	33				35			

Table A3
PERMANOVA of initial raw species coverage community data with **$p < 0.01$.

Source	df	MS	Pseudo-F	P (perm)
Location (L)	2	3295	4.72	0.002**
Cage (C)	1	595.71	0.618	0.577
Experimental Extraction (E)	1	604.71	1.534	0.291
Treatment Duration (D)	1	3533.4	2.695	0.168
L × C	2	964.45	1.382	0.165
L × E	2	394.13	0.565	0.795
L × D	2	1311.1	1.878	0.063
C × E	1	175.29	0.252	0.808
C × D	1	352.93	0.602	0.574
E × D	1	709.86	1.144	0.376
L × C × E	2	695.4	0.996	0.437
L × C × D	2	586.52	0.840	0.545
L × E × D	2	620.26	0.889	0.495
C × E × D	1	398.25	0.530	0.623
L × C × E × D	2	751.14	1.076	0.367
Residual (Res)	46	698.09		
Total	69			

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