ORIGINAL RESEARCH

Recovery after exploitation of stalked barnacles is facilitated by the presence of conspecifics: a study of post-harvest gap recolonization dynamics in SW Europe

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Abstract We have followed the recovery of gaps produced either by harvesters or by scientists in stands of stalked barnacle (*Pollicipes pollicipes*) during two years in four regions of Europe (SW Portugal, Galicia and Asturias in Spain and Brittany in France; n=423 gaps), which was extended to four years in Asturias (n=252 gaps). The presence of adult conspecifics in the margins of the gaps increased by at least four times the probability of initiation of their recovery. After two years of follow-up in the four regions, 90% of the gaps with adjacent conspecifics had initiated recolonization as opposed to only 60% in gaps with no adjacent adults. These figures remained stable after three years of follow up in Asturias, pointing to a large fraction of gaps which are recalcitrant to recolonization. Once initiated, the median rate of recovery after latency was 0.47 cm^2/month in the four regions and 0.61 cm^2/month in Asturias, increasing from 0.5 to 2.5 cm^2/month for a 0 to 25 cm increase of perimeter in contact with adults, which is consistent with heavy recruitment on the stalks of conspecifics. The median estimated time to full recovery of gaps which initiated recovery was 2.65 years, thus recolonization is a slow process. Our results point to the main recommendations that a barnacle clump should never be removed entirely, so that the remaining adults serve as recruitment nuclei for the population, and that a maximum scraper width of 3.5 cm should be set to limit accessory capture of non-target individuals.

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Introduction

Limitations in harvest effort and catches, guided by rigorous evaluations of the stock and supplemented with specific measures regarding fishing gear, minimum sizes or harvest seasons, represent the classical approach in fisheries management. Spatial management has entered the picture more recently, with the adoption of marine reserves, territorial user rights for fisheries, and other space-based management tools (Douvere 2008, 2009; Gelcich et al. 2012; Qiu and Jones 2013; Rivera et al. 2014). Spatial management units range in size from the mesoscale to just a few meters (e.g. Orensanz et al. 2013, 2016; Rivera et al 2014). However, many processes that are important for the recovery of sessile species after a disturbance—and harvest is a disturbance—happen at the smaller, spatial scales of the individual or clumps of individuals. For example, Paine and Levins (1981) characterized the succession and rate of recovery of bare rock gaps left by wooden logs in a community dominated by mussels, and found that gap size, shape and orientation, slope, wave exposure and the characteristics of the surrounding matrix influence the successional rate and the recovery time within the gap. Henceforth, disturbance and successional patterns have been explored in a variety of communities and species (Dayton 1971; Sousa 1984; Underwood 1998; Airoldi 1998, 2003; Schiel and Taylor 1999; Foster et al. 2001; Deza and Anderson 2010; Cole et al. 2012; Barrientos et al. 2019), and for different kinds of natural perturbations, such as wave action, grazing, predation, diseases or natural disasters (Benedetti-Cecchi and Cinelli 1994; Kim and DeWreede 1996; Airoldi 2003; Chapman 2013; Noda et al. 2016). More recently, some studies have been extended to small-scale perturbations due to human exploitation (Lasiak and Dye 1989; Airoldi 2003; Smith and Murray 2005; Piñeiro-Corbeira et al. 2018; Barrientos et al. 2019; Edwards 2020).

Pollicipes pollicipes is a pedunculate cirripede which inhabits the exposed coasts from southern England to Senegal, while rarely appearing in the Mediterranean (Cruz et al. 2022). It lives firmly attached to rocks from the shallow subtidal to mid-intertidal zone, where it forms dense aggregations (Cruz et al. 2022). *P. pollicipes* is heavily harvested throughout its entire distribution range (i.e. France, Spain, Portugal, and Morocco; Cruz et al. 2022). It is considered a delicacy in Spain and Portugal, where it represents the most important rocky intertidal fishery (Cruz et al. 2010; Aguión et al. 2022). The harvest is a risky activity, done at very exposed sites using scrapers which are used to remove clumps of barnacles, leaving carved gaps in the rocks (Cruz et al. 2022; Supplementary Video). These gaps may differ in size, shape, and biological conditions, i.e. whether they remain in contact with stalked or acorn barnacles, mussels, or other species. The fishery in SW Europe is managed through a range of approaches, from open access to limited entry to Territorial User Rights for Fisheries (TURF) in the regions of Galicia and Asturias (N Spain, Aguión et al. 2022). Although the management scale in TURFs at Asturias and Galicia spans from hundreds to just a few meters, this is still much larger than the size of the gaps left by the harvesters, which are in the range of tens of square centimeters.

The species presents a two-phase life cycle, with a planktonic larvae (nauplii and cyprid) (Molares et al. 1994; Kugele and Yule 1996) and a benthic adult form. Competent larvae settle on the stalks of conspecifics, bare rock, calcareous algae, acorn barnacles, mussels and even on artificial substrates (reviewed in Cruz et al. 2022; Supplementary Video). Something similar applies to its Pacific North American relative *Pollicipes polymerus*, whose larvae also settle on a variety of substrates, including conspecifics (reviewed in Cruz et al. 2022). However, recruitment happens heavily on the stalks of conspecifics, either due to active selection of settlement habitat by the planktonic, competent larvae or because of increased survival of the settled larvae and juveniles on the adults (Cruz et al. 2022). Part of these juveniles will finally become incorporated to the clump, remaining attached to the lower part of the peduncle of their conspecifics or to the rock, after a process of downward migration while growing or simply because of differential increased survival in the lower part of the stalks (reviewed in Cruz et al. 2022; Supplementary Video). Recruitment on the adults explains aggregate formation in this species and has been identified as a vulnerability of the fishery (Cruz et al. 2015). Clearly,

the harvest of adults from the population involves the removal of a key recruitment habitat, which may have a profound influence on the regeneration of the cleared surfaces.

To guide relevant management policy, there is a need for research on the processes operating at the small scales of clumps and gaps. Our interest in this work was on documenting the extent and velocity at which harvested gaps -which represent potential stalked barnacle habitat- are recolonized, and what processes may facilitate or inhibit recolonization. For this, we studied the morphological and biological characteristics of gaps produced by natural disturbances or harvester activity and of gaps created experimentally. We followed their recovery -or lack of it- for a period between two and four years and developed models to describe and predict the onset and pace of the recovery process. Among the explanatory variables in those models, we have paid special attention to the presence or absence of adult conspecifics in contact with the gaps, as this may play a key role in the recruitment of new individuals. The results provide insight into the recovery dynamics of exploited *P. pollicipes* populations and lead to potential, sound management recommendations.

## Materials and methods

Sampling design

Sampling was done at four regions, with three sites per region: Brittany, N France (Toulbroch, La Torche and Quiberon), Asturias, NW Spain (Las Llanas, Las Salsinas and La Cruz); Galicia, NW Spain (A Coruña, Cangas and Baiona) and Alentejo, SW Portugal (Sines, Sardao and Carrapateira) (Fig. 1). In July 2017, six 35×35 cm plots were selected at each site. Three of those plots were not manipulated and were used to record any gaps left by the harvesters or by other causes. To guarantee the creation of new gaps in case no harvester activity happened in the unmanipulated plots, the other three plots were harvested experimentally in a way as close as possible to that done by the harvesters. This involved the removal of individuals above 18 mm rostro-carinal length (RC) by means of a scraper from their attachment point to the rock, resulting in the removal of a median of 50.45 cm^2 [6.87–205.93] [range] in total from each

plot. This procedure was done in December 2017, December 2018 and July 2018 in Asturias and July 2017 and July 2018 in the rest of the regions (Fig. 2).

Our aim was to visit each plot at least once every three months, although this was finally conditioned by the double requirement of good weather conditions and spring tides, which is particularly stringent in this harsh environment. Finally, the median time between visits was 4.8 months, with a range between 1 and 11.4 months, with small differences between regions. Because of the difficult shooting conditions, pictures were shot by hand on each visit. To create a homogeneous flat perspective for comparison, the flattest photo, defined as the one with lowest variance in the lateral length of the sampling quadrat, was selected as reference, and a minimum of 36 points in common with each of the rest of pictures were used for photo-registration using a Thin Plate Spline transformation within Geographic Information System QGIS (QGIS 2023). This transformation matches those control points while minimizing local surface curvature (QGIS 2023). Control points were usually acorn barnacles or easily identifiable rock surface features. This registration process could not be completed for some of the plots, due to the absence of adequate control points, excessive inclination of the photography or poor photographic quality, leading to a total number of 10, 34, 18 and 16 plots in Brittany, Asturias, Galicia and Portugal, respectively.

In this context, a gap is defined by an area that had barnacles in a given date but where those barnacles have been removed. We used QGIS to create polygons around all detected or created *P. pollicipes* gaps (Fig. 3). The precise timing of gap formation was known for experimentally created gaps. However, gaps resulting from harvesting activities or other factors such as bird predation, storms, poaching, etc., could have been created anytime between the last date without gap and the date at which the gap was detected. For those gaps, we assumed that the time of creation was the time at detection of the gap. Once a gap was created or detected, the recovery process was followed by analyzing two pictures per year, during a period of 24 months (July 2017–July 2019) in Brittany, Galicia and Alentejo, and up to 50 months (October 2017–September 2021) in Asturias (Fig. 2). For each gap, at the time of creation or detection we registered the creation/detection date, the area, the perimeter in contact with *P. pollicipes*

Fig. 1 Geographical location of the study sites (white dots) at Brittany (NW France), Asturias and Galicia (N Spain), and Alentejo (SW Portugal)
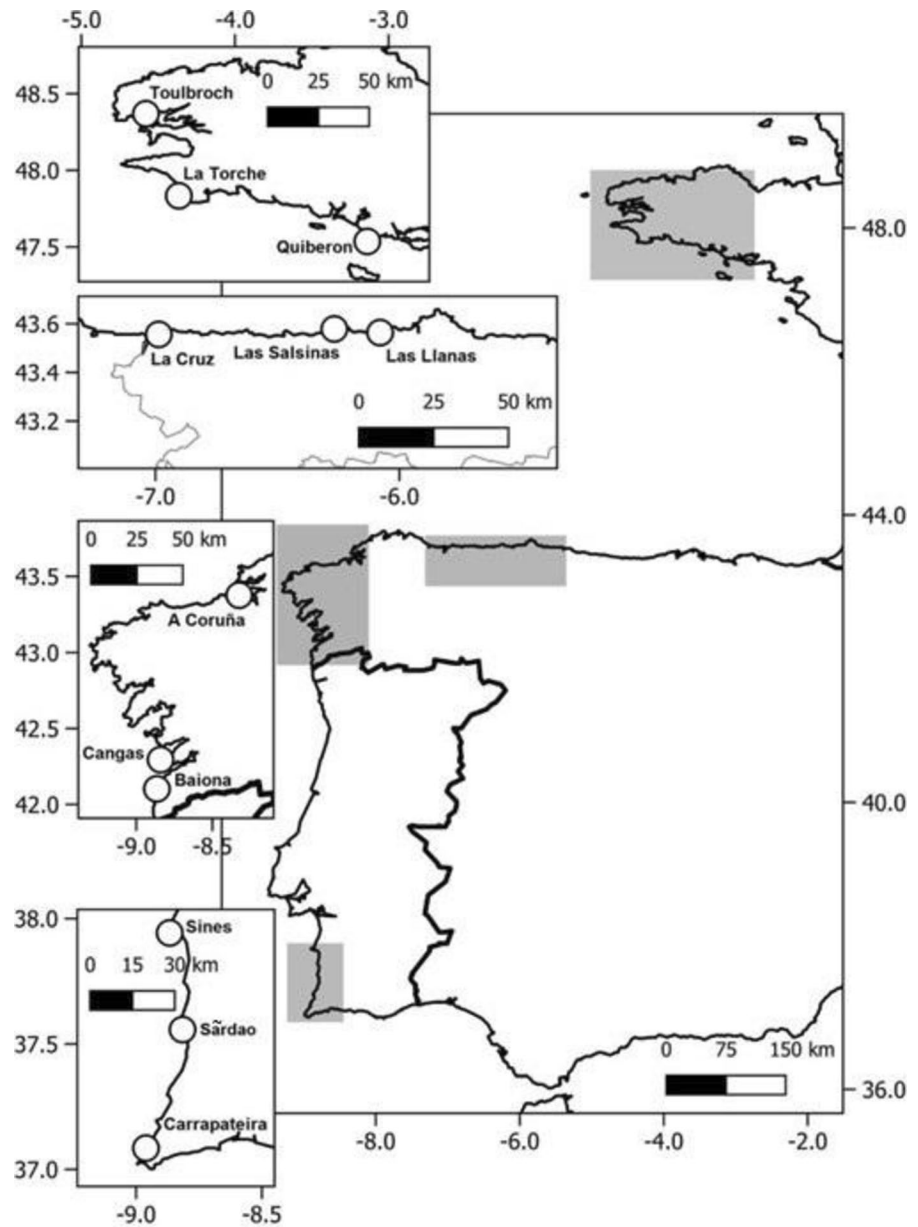
and the percentage cover of animals in the plot by the point intercept method using a 100-point grid overlaid on the picture of each plot in Adobe Photoshop®. We also calculated an area-independent shape index which indicates the degree of deviation of the gap from a round shape, varying between 0 and 1, where 1 is a perfect circle (Rosenfeld 1974).

$$Shape index = \frac{4 \times \pi \times area}{perimeter^2}$$

In subsequent dates after creation or detection of the gap, we quantified the surface recolonized by barnacles along with the date. A summary of the variables used in the models is given in Table 1.
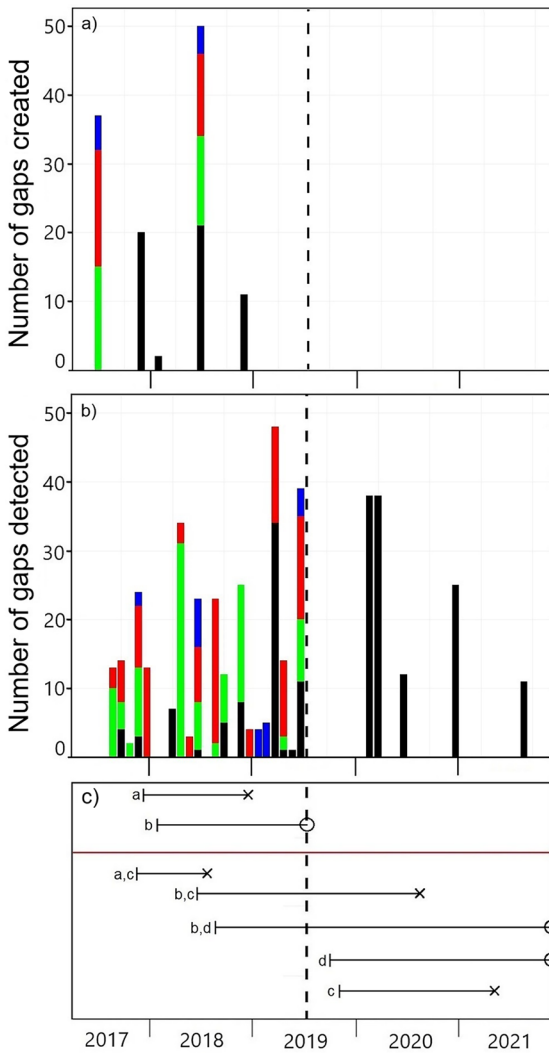
Fig. 2 Dates, locations and types of gaps utilized in the analysis. **a** Histogram of gaps created experimentally by date of creation. Colors correspond to Asturias (black), Portugal (green), Brittany (blue), Galicia (red). The vertical, black dashed line indicates the end of observations for the four region, two year dataset. **b** Same histogram, but for gaps created by fishers or other causes, in which case the date at detection is registered. **c** Classes of gaps and how they were used in the survival analysis. Horizontal lines indicate a gap lifeline. Vertical ticks indicate the creation or detection of a new gap. Crosses indicate initiation of recovery. Empty circles indicate the last available observation for a gap which did not show recovery. Gaps above the red line belong to Portugal, Galicia and Brittany. Gaps below the red line belong only to Asturias. Letters indicate how the different kinds of gaps were used in the survival analysis: a, included in the four regions, two year analysis; b, censored in the four regions, two year analysis; c, included in the Asturias, four year analysis; d, censored in the Asturias, four year analysis

Data analysis and modeling

On one hand, we analyzed all the gaps in the four regions that appeared during two years. Separately, we analyzed only those that appeared in Asturias during the four years of the study. Thus, although the two datasets are not fully independent, one provides wider spatial coverage while the other provides wider temporal coverage. For the global analysis with four regions (two years), we considered all gaps created or detected between July 2017 and July 2019 (i.e., a follow-up period of 24 months) (Fig. 2a, b). For the analysis of Asturias (four years), we considered all gaps created or detected between October 2017 and September 2021 (i.e., a follow-up period of 47 months) (Fig. 2a, b). We analyzed two different aspects of the gap recovery process: i) the onset of recovery and ii) the recovery rate, defined as the increase in recovered surface per unit time following the onset of recovery.

To model the onset of recovery, we applied survival analysis (Kleinbaum 1996; Therneau 1997; Therneau and Grambsch 2000; Moore 2016). This is akin to clinical studies where the proportion of surviving patients is followed after being submitted to some kind of clinical treatment (i.e., Alarcón-Soto et al. 2018). In our case, we followed the proportion of gaps which did not initiate recovery as a function of gap age, here defined as the time elapsed since their detection or creation. The proportion of not-recolonizing gaps as a function of gap age was represented by means of Kaplan–Meier survival curves, which allow visualization of the effect of one factor or one continuous variable (Kleinbaum 1996; Therneau and Grambsch 2000; Moore 2016).

We also applied proportional hazards mixed Cox regression to model the hazard function, which in this context is the gap age-dependent instantaneous risk of initiating recolonization for a gap which did not yet initiate recolonization at that age. Mixed Cox regression allows to determine the influence of different fixed variables and factors (Table 1) on the initiation of gap recolonization while controlling for a set of random factors. The random component for the four regions dataset consists of spatial factor *plot* nested within *site* nested within *region*. The structure of the full Cox mixed model is therefore:

Fig. 3 Representative examples of the gaps followed during the observations. **a** A whole plot where a new gap has appeared, as indicated by a red polygon. **d** Same plot, another gap appears. **g** The same plot, three years later. In **b**, **e**, **h**, the gap detected in picture A is followed through time, with three representative pictures: before gap detection, after gap detection and three years later; this gap fully recovers its *P. pollicipes* coverage at the end of the series. In **c**, **f**, **i**, the gap detected in B is also followed through time. This gap did not recover its *P. pollicipes* population after four years of observation and was initially isolated from any adjacent *P. pollicipes* patch
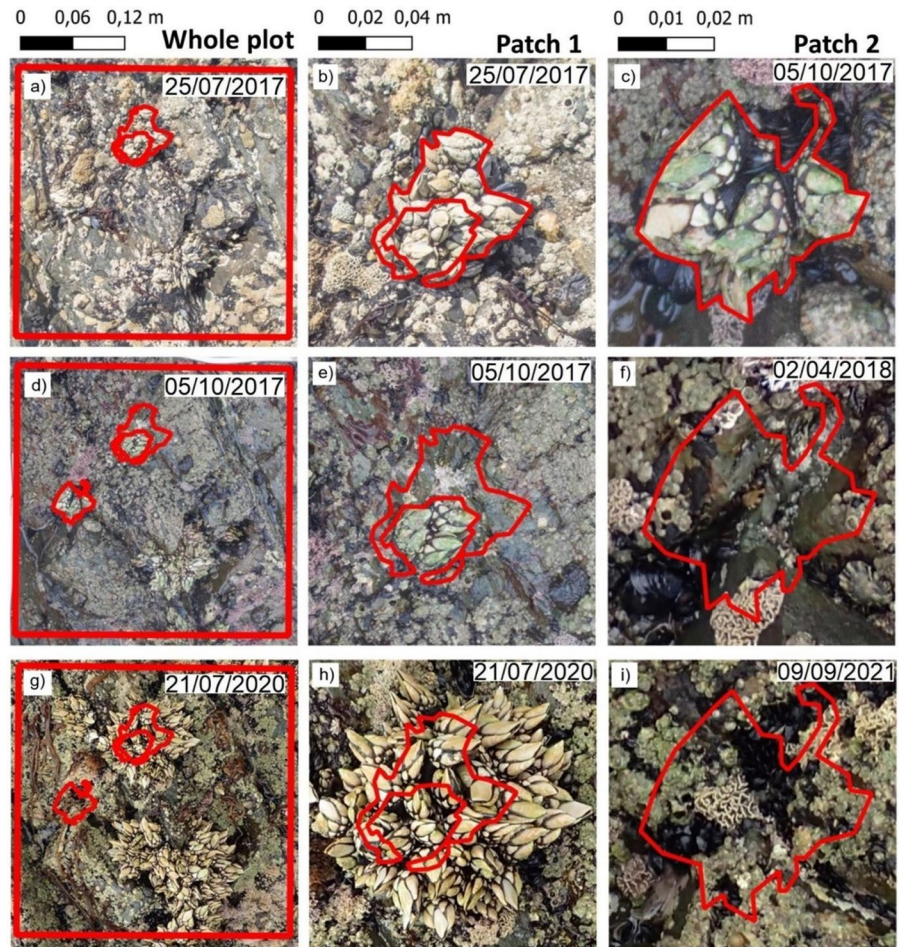
Table 1 Variables used for the models

Model explanatory variables	Acronym	Units	Range
Perimeter of the gap in contact with *P. pollicipes*	*pp*	cm	> 0
P. pollicipes in contact with the gap-dummy	*pg*	–	Yes(1)/No(0)
Area of the gap	*ar*	cm^2	–
Shape index of the gap	*si*	–	0–1
Cover of animals species in the sampling plot	*ca*	%	0–100
Season when the patch was created-dummy	*se*	–	Summer(1)/Winter(0)
Origin of the gap-dummy	*og*	–	Experimental(1)/Harvester(0)

$$h_i(t) = h_0(t) \times e^{X_i\beta + a_{ir} + b_{isr} + c_{ipsr}}$$
$$a_{ir} \sim G(0, \sigma_a), \quad b_{isr} \sim G(0, \sigma_b), \quad c_{ipsr} \sim G(0, \sigma_c)$$
$$(1)$$

where $h_i(t)$ is the hazard rate of individual i at gap age t, $h_0(t)$ is the unspecified baseline hazard function at gap age t, $\mathbf{X_i}$ is a row vector of fixed covariate values

for individual, $\boldsymbol{\beta}$ is a column vector of fixed covariate coefficients, and a_{ir}, b_{isr} and c_{ipsr} are random components for region, site within region and plot within site within region, respectively, in gap i. All these random components have a Gamma distribution, with mean 0 and a given variance. For the Asturias, four year model, the structure is similar to that in Eq. 1,

but with random components *site* and *plot* within *site* only. We did not include interactions among factors, because this would prohibitively increase the number of parameters for such a reduced dataset. Gaps where the onset of recovery could not be observed within the specified period were censored for the analysis (i.e. administrative censoring; gaps which ended with non-recolonization, Fig. 2c). These full models were fitted using R package *coxme* (Therneau 2023a). Simpler Cox regressions including only the most significant variable without any random factors were fitted with R package *survival* (Therneau 2023b).

Our survival data are interval-censored (sensu Finkelstein 1986) because time at the onset of recovery is an unknown value falling within the interval defined by the last time without and the first time with observed recovery. To our knowledge, there is no simple Cox mixed modeling approach for interval-censored data (Alarcón-Soto et al. 2018), thus we have simply assumed that the onset of recovery happened at the midpoint between the last observation without and the first observation with recovery. However, to check for the validity of parameter estimates using this simplified approach, we also applied a multiple-imputation procedure which allows precise estimates of parameters in mixed Cox regression models for comparison (Alarcón-Soto et al. 2018). All Cox models variables were tested for the proportional hazard assumption and excluded if this condition was not met.

Next, we focused on the recovery rate in those gaps which initiated recovery. For this, we collected data of total recovered surface vs gap age, starting from the first date in which any recovery was detected in a gap and in approximate intervals of half a year afterwards. Only gaps with at least two recovery observations were used for the calculation. For each gap, we fitted the surface recovered vs gap age data to a line and used the slope as a measure of recovery rate (Appendix Fig. 8). We decided that a linear regression would be the simplest and more effective approach to represent recovery, although there is a possibility of non-linear recovery dynamics in gaps which recovered a large proportion of their surface, which was not frequent.

Inspection of kurtosis vs skewness diagrams for the recovery rate using R package *fitdistrplus* (Delignette-Muller and Dutang 2015) indicated that the distribution of recovery rates was close to gamma.

Thus, we modeled the recovery rate using a gamma GLMM with a log link:

$$recov_{irsp} \sim G(\mu_{irsp}, \alpha)$$
$$E[recov_{irsp}] = \mu_{irsp} = e^{(\beta h_{irsp} + a + b_{ir} + c_{isr} + d_{ipsr})}$$
$$b_{ir} \sim N(0, \sigma_b), \quad c_{isr} \sim N(0, \sigma_c), \quad d_{ipsr} \sim N(0, \sigma_d)$$
(2)

where $recov_{irsp}$ is the recovery rate, which follows a Gamma distribution with shape parameter α and mean μ_{irsp} for gap i in plot p within site s within region r. $E[recov_{irsp}]$ is the expected value for each gap, a is the general intercept, while b_{ir}, c_{isr} and d_{ipsr} are random intercepts for region, site within region and plot within site within region, respectively. These random intercepts are normally distributed, with mean 0 and standard deviation σ_b, σ_c and σ_d, respectively. β is the column vector of regression coefficients for the covariates in the model, and h_{irsp} is the column vector of values for the t covariates in the model for i in plot p within site s within region r (See in Table 1). Gamma GLMMs were diagnosed with QQ plots and Kolmogorov–Smirnov tests on the deviations (not shown) and pseudo-R^2 (Tables 2, 3) (Massey 1951; Razali 2011).

Last, we calculated the expected total recovery time for those gaps which showed any recovery. For this, we extrapolated the surface recovered vs gap age regression line to find the gap age at which the full gap surface should be completely recovered (Appendix Fig. 8). Note that the recovery time is just an estimation since none of the gaps reached full recovery during our observation period.

Results

Characterization of the gaps

We studied a total of 551 gaps, of which 424 belonged to the four regions, two year dataset and 252 to the Asturias, four year dataset, with 125 gaps shared between the two datasets. In total, 120 gaps were experimental and 431 were created by harvesters or other causes. Median gap area was 12.43 cm^2 [1.48–182.73] [range] and shape index was 0.27 [0.01–0.83]. Experimental gaps were larger (24.11 [3.80–87.41] cm^2 vs 10.39 [1.48–182.73] cm^2, Appendix Fig. 9a, b), had a slightly smaller

Table 2 Results of the mixed Cox regression models for the initiation of recovery of harvested gaps

Source of variation	Coefficients	Variance	exp(Coeff)	p value
Global full model with region				
pg	1.514 ± 0.204		4.577	$1.1\ 10^{-13}$***
ar	0.007 ± 0.004		1.006	$1.4\ 10^{-1}$
si	-1.942 ± 0.561		0.143	$5.4\ 10^{-4}$***
ca	-0.001 ± 0.005		0.998	$8.0\ 10^{-1}$
Region/site/plot		$3.548\ 10^{-1} \pm 5.956\ 10^{-1}$		
Region/site		$1.687\ 10^{-1} \pm 4.108\ 10^{-1}$		
Region		$3.970\ 10^{-4} \pm 1.993\ 10^{-1}$		
Global only presence of adults				
pg	1.665 ± 0.171		5.284	$2\ 10^{-10}$***
Asturias full model with site				
pg	1.371 ± 0.237		3.941	$6.9\ 10^{-9}$***
ar	0.004 ± 0.004		1.004	$3.5\ 10^{-1}$
si	-3.520 ± 0.764		0.029	$4.1\ 10^{-6}$***
ca	-0.006 ± 0.007		0.994	$3.7\ 10^{-1}$
Site/plot		$8.722\ 10^{-2} \pm 2.953\ 10^{-1}$		
Site		$2.574\ 10^{-4} \pm 5.074\ 10^{-2}$		
Asturias only presence of adults				
pg	1.805 ± 0.201		6.083	$2\ 10^{-16}$***

Coefficients are summarized as estimate $\pm$ standard error. ns: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

shape index (0.26[0.09–0.83] vs 0.31, [0.01–0.77]; Appendix Fig. 9c, d) and were more frequently in contact with adult *P. pollicipes* (80% vs 60%) than non-experimental gaps. Smaller gaps were less often in contact with adult *P. pollicipes* (Appendix Fig. 9a, b).

Onset of gap recolonization

In the four regions dataset, nearly 40% of the gaps were not recovering after two years of follow up (Fig. 4a). This percentage stood steady during two more years in Asturias (Fig. 4b), which reveals an important group of gaps which are recalcitrant to recolonization. Most of those gaps did not have conspecifics in contact with their borders at the time of creation (Fig. 4c, d).

Mixed Cox regressions identified the presence of adjacent conspecifics at the gap border as the most influential variable for the onset of recolonization in the four regions (Table 2, $P < 0.001$) and in the Asturias dataset (Table 2; $P < 0.001$). The chances of onset of recolonization in the gaps increased by fourfold when they were in contact with conspecifics at the time of creation (see exponentiated regression coefficients in Table 2), which is readily apparent in

Kaplan–Meier curves split among gaps that did and gaps that did not have conspecifics in their periphery (Fig. 4c, d). The likelihood of initiation of recolonization decreased with the roundness index, although this effect was less marked (for the 4 regions, $P < 0.001$, Table 2, Fig. 5a; for Asturias, $P < 0.001$, Table 2, Fig. 5b). Gaps from Galicia showed a slightly higher resistance to initiate recolonization (Fig. 4e). These results are very similar to those obtained by a more sophisticated multiple imputation method (Appendix Table 4) although this last method only converged for the 4 regions dataset.

We did not include the origin of the gap (experimental vs harvester or other causes) as a factor in the models because it did not fulfill the proportional hazards assumption (proportional hazards test value, $P < 0.001$). This is because the experimental gaps were created only during the first two years of experiment, thus the effect is not constant through time. This effect has to do with a difference in the definition of gap creation between experimental and non-experimental gaps, which can be clearly appreciated at the start of the survival curves (see the initial part of the survival curves in Appendix Fig. 10). Its magnitude is limited and inclusion of this variable in the models yielded almost identical results (not shown).

Table 3 Results of the generalized linear model for the recovery rate

Source of variation	Coefficients	p-value	Variance	Pseudo R2
Global full model with region				0.355
pp	0.065 ± 0.018	$4.13\ 10^{-4}$ ***		
ar	0.017 ± 0.009	$5.43\ 10^{-1}$		
si	1.046 ± 0.980	$2.86\ 10^{-1}$		
ca	-0.019 ± 0.008	$1.79\ 10^{-2}$ *		
se	0.013 ± 0.247	$9.59\ 10^{-1}$		
og	0.094 ± 0.233	$6.84\ 10^{-1}$		
Region:Site:Plot			$8.997\ 10^{-2} \pm 3.000\ 10^{-1}$	
Region:Site			$1.484\ 10^{-9} \pm 3.853\ 10^{-5}$	
Region			$5.426\ 10^{-11} \pm 7.366\ 10^{-6}$	
Global only presence of adults				0.251
pp	0.062 ± 0.011	$5.81\ 10^{-8}$ ***		
Asturias full model with site				0.259
pp	0.049 ± 0.017	$4.25\ 10^{-3}$ **		
ar	0.011 ± 0.007	$1.22\ 10^{-1}$		
si	1.116 ± 1.029	$2.78\ 10^{-1}$		
ca	-0.013 ± 0.012	$2.78\ 10^{-1}$		
se	0.833 ± 0.449	$6.41\ 10^{-2}$		
og	-0.199 ± 0.271	$4.61\ 10^{-1}$		
Site:Plot			0.022 ± 0.150	
Site			0.293 ± 0.541	
Asturias only presence of adults				0.149
pp	0.045 ± 0.013	$3.39\ 10^{-4}$ ***		

ns not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

Recovery rate

We could estimate recovery rates in 93 gaps of the four regions dataset (Appendix Fig. 11A) and 70 gaps in the Asturias dataset (Appendix Fig. 11b). The median recolonization rate was 0.47 [0.05 and 6.38] cm^2/month [range] (Fig. 6a). According to these recolonization rates and to the area of the gap, the median estimated time to full recolonization of the gap was 2.65 [0.22–40] years, with 21.5% of the gaps requiring more than six years (Fig. 6b). The perimeter of the gap in contact with *P. pollicipes* (*pp*) was the main predictor for the rate of recovery in the global and Asturias datasets (Pr < 0.005, Table 3). The modeled recovery rate increased from 0.5 cm^2/month at 0 cm pp to 2.54 cm^2/month at 25 cm pp in the global model (Fig. 7a) and from 0.28 cm^2/month at 0 cm pp to 0.96 cm^2/month at

25 cm pp in the Asturias model (Fig. 7b). Only the total cover of animals seemed to have a significant, slightly inhibiting effect on the recovery rate in the four regions dataset (Table 3). Models incorporating only *pp* were almost as good as the full models, according to their pseudo-R^2 (Table 3).

Discussion

Here we provide the first quantitative account of the dynamics of recovery of harvested *Pollicipes pollicipes* gaps. The results indicate that recolonization is a very slow process which is facilitated by the presence of adult conspecifics in the rocks. Full appreciation of these data and their implications first requires careful consideration of methodological limitations. First, for gaps created by fishers or
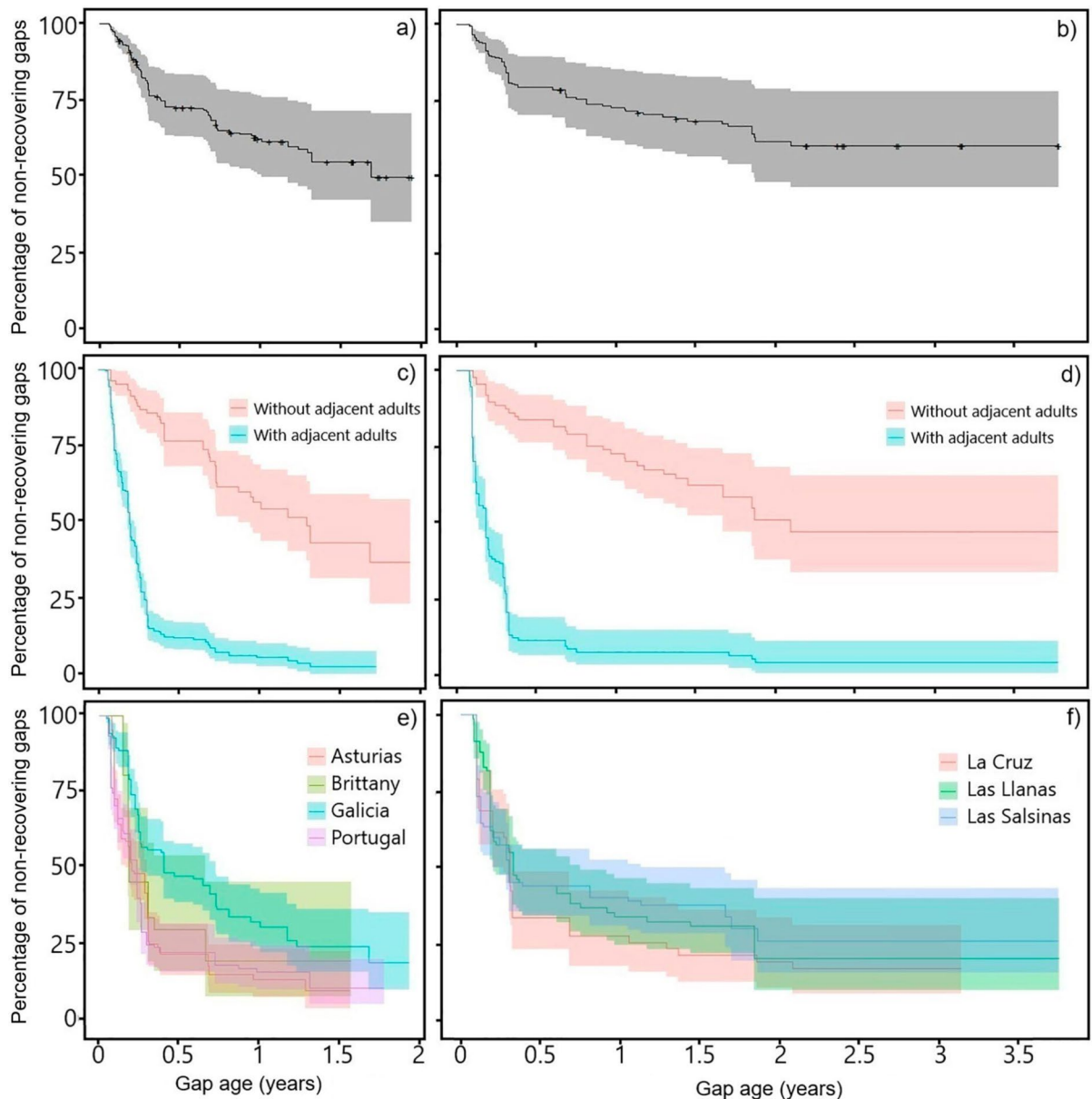
Fig. 4 Kaplan Meier survival curves for the onset of recolonization in harvested stalked barnacle gaps. Color shading indicates the confidence interval at each point in time. **a** Four regions dataset. **b** Asturias dataset. **c** Four regions dataset split into gaps with and without initial contact with conspecifics (see inset for color coding). **d** Same as c, but for the Asturias dataset. **e** Four regions dataset split into the four regions (see inset for color coding). **f** Asturias dataset split into the three sites (see inset for color coding)

other causes we assumed that the date of creation was the date of detection, resulting in an underestimation of between 0, if the gap was created when first detected, and the next visit available, if the gap was created when the previous picture was obtained. However, this has a limited effect on the recovery

initiation data, according to our results (Supplementary Fig. 3).

Note also that gap recovery does not include growth outside the gaps, by occasional recruits on bare rock or other substrates or by expansion of patches outside the gaps. To fully account for
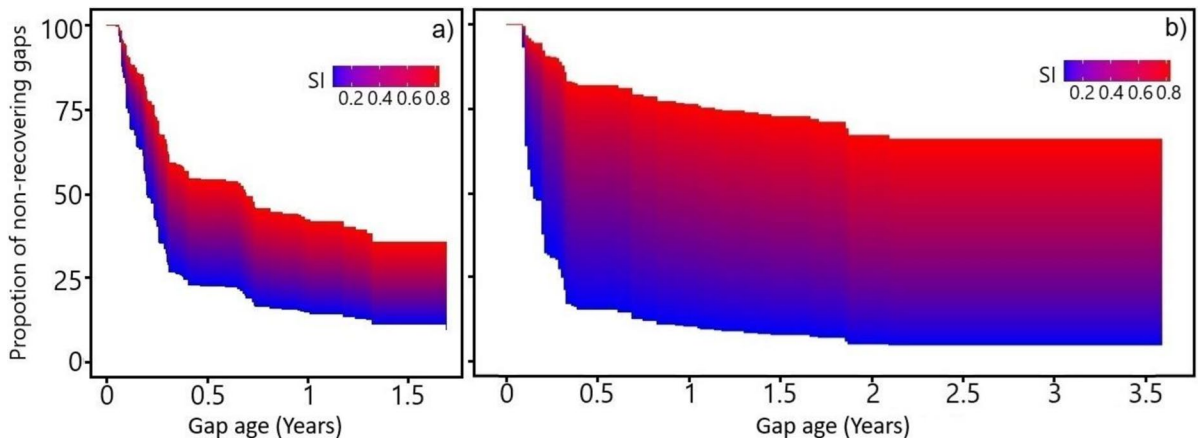
Fig. 5 Effect of the shape index on the Kaplan–Meier survival curves for the onset of recolonization. Color shading indicates the range of the continuous variable. **a** Four regions dataset. **b** Asturias dataset

surface recolonization by *P. pollicipes* populations we should have taken those processes into account, what would have required a different approach (i.e. Geiger et al. 2024). Nevertheless, for the purpose of this paper, we decided to monitor only gaps where we knew through our photographs that they were previously occupied by *P. pollicipes*.

Last, we must point out that this is not a manipulative experiment to infer causality but a correlational study. Thus, the patterns revealed can only be taken as hints of the underlying processes affecting the recovery of *P. pollicipes* gaps. Despite acknowledging these caveats and limitations, the consistency of the results across the vast scale of the EU Atlantic Arc as well as the strong significance of the analysis allow us to clearly identify patterns in the population recovery of these populations after harvesting in the exposed rocky intertidal.
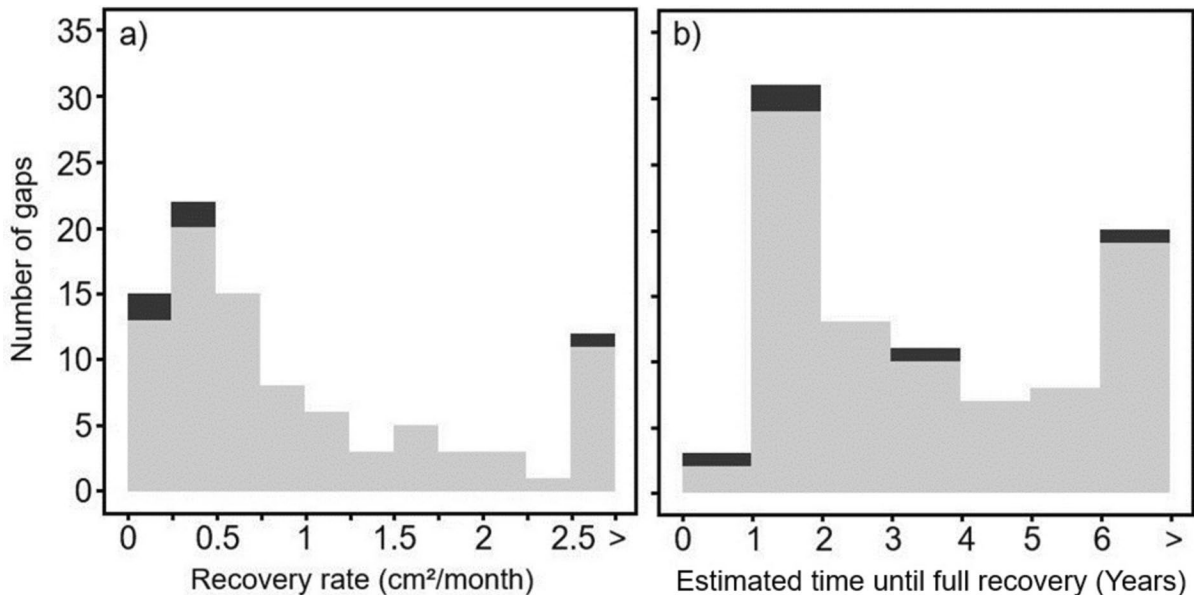
Fig. 6 Histograms of recolonization variables. **a** recovery rates. **b** Estimated recovery times. Darker shading indicates gaps that had no adult barnacles in contact with their perimeter when first detected or created
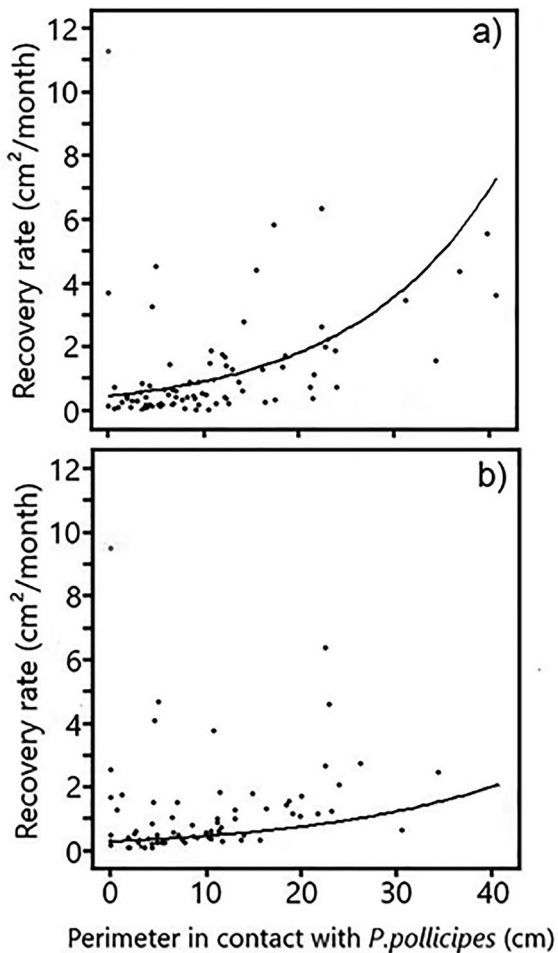
Fig. 7 GLMM fits for the recovery rate vs the perimeter of the gap in contact with *P. pollicipes* conspecifics. **a** Four regions, two year dataset. **b** Asturias, four year dataset. Points are data. Lines are model fits. The highest point in both panels represent an extreme recovery rate which we removed from the analysis

The clearest result emerging from our analysis is that the presence of adult conspecifics in the gap margin boosts gap recovery. Gaps were more likely to recover (Fig. 4c, d) and had faster recovery rates (Fig. 7) when adult conspecifics were present in their periphery. This was an expected result, since recruitment in this species is heavy on the stalks of adult conspecifics, either because of differential settlement of cyprids or because of differential mortality of the juveniles (Cruz et al. 2022). Most likely, adult stalks represent a more suitable habitat, with reduced physical and biological stress (Satchell and Farrell 1993; Cruz et al. 2022). The presence of adult conspecifics

had an overwhelming influence on recolonization, but the models also revealed that elongated gaps were more likely to recover, according to the shape index (Table 2). Frequently, elongated gaps were related to the presence of narrow crevices and cracks which may offer shelter to the stalked barnacle clumps, although the 3D structure of the substrate was not considered in our analysis.

Another outcome of major significance for the fishery is that gap recovery is slow. Nearly half of the gaps studied did not show any signs of recolonization after 3.5 years (Fig. 4b). Fifty percent of those that did show some recovery should take longer than 2.5 years to fully recolonize, and 21.5% more than six years (Fig. 6b). This aligns with findings from a recent experiment involving the exclusion of human activity, indicating that a minimum of two years is necessary for the restoration of a previously exploited surface in Asturias, one of the regions of our study (Geiger et al. 2024). Our results are also consistent with recovery times of nine years in denuded *Pollicipes polymerus* stands, where no adult conspecifics were available for recolonization (Edwards 2020). Another study with *P. polymerus* in Oregon (USA) found that a harvested area requires a minimum of three years to recover its initial density, and as long as seven years to develop established patches of multiple size classes with a significant proportion of large individuals (Bingham 2016; Bingham et al. 2017). Moreover, the succession from perturbation to full regeneration of stands of the mussel *Mytilus californianus* in the exposed shores of Washington, USA (Levin and Paine 1981) and of the South African *Perna perna* (Dye 1997) took up to four and eight years, respectively. This confirms that establishment of final animal stands in shores that are highly exposed requires significant time and special adaptations, for example the strong adhesive cement secreted by the stalked barnacles (Abbott 1990) or the firmly attached byssus in mussels (Waite 1998).

In our experiment the harvestable fraction of the population is typically determined by size (Cruz 2010). We did not measure individual sizes; thus, the results of our study cannot be directly translated into quantitative fishery management recommendations. However, our observations provide important hints for meaningful management. The first is that any harvesting practice that results in the total denudation of the rocks sets the population into a slow road of recolonization with higher chances of

generating spots recalcitrant to recovery in scales of several years (Fig. 4c, d) or by slowing regeneration when it starts (Fig. 7). One such practice is the removal of isolated individuals -those not pertaining to a clump- on the premise of their higher quality and sales price. Another is the wild harvest of *Mytilus edulis* and *Mytilus galloprovincialis* spat to supply mussel aquaculture (Kamermans and Capelle 2019). This practice depletes gooseneck barnacle populations, not only by the immediate removal of coexisting stalked barnacles but by slowing further recolonization due to the complete removal of all organisms over the rock (some of them suitable substrates for *P. pollicipes* recruitment like acorn barnacles, calcareous algae and the mussel seed itself, Cruz et al. 2022). If the removal of mussel spat is repeated over successive years, this will inevitably lead to a reset of the colonization process and the chronic reduction of the *P. pollicipes* population. In contrast to Barrientos et al. (2019), who recommended concentrating the mussel seed harvest on large patches to favor a faster reoccupation of the gaps, we contend that larger denuded areas will lead to much slower recolonization by stalked barnacles. Another relevant message is that one year bans like those applied in Asturias (Geiger et al. 2024) are excellent measures to regenerate overexploited populations, but only if there are nuclei of adult individuals to initiate the process. Otherwise, regeneration in those banned rocks would be very slow, regardless of the application of sophisticated management practices.

In conclusion, our results lead to the main management recommendation that a patch of barnacles should never be removed entirely. Instead, some individuals should be left attached to the rock to facilitate recolonization of the gap. This simple rule-of-thumb should boost the initiation of recovery and shorten recovery rates. One way to achieve this is by using narrow scrapers to remove only the largest individuals of the barnacle clump. By law, the maximum scraper width is 7 cm in Brittany and 5 cm in Galicia. In Portugal it is 3 cm for recreational harvesters, but undefined for the professionals, and in Asturias scraper width is unregulated. Informal conversations with harvesters and barefoot biologists reveal that in several Galician fishers guilds the harvesters voluntarily utilize scrapers with a 2–3 cm wide blade in one end and a spike in the other, which allows them to extract single individuals from crevices which are hard to reach. Thus, we suggest setting a maximum scraper width of 3.5 cm in Galicia, Asturias and Portugal, although it may not be necessary in Brittany, where the fishery is not fully developed and exploitation rates are moderate. A narrower scraper will minimize the bycatch of individuals which, while not reaching commercial size, do actually provide important settling habitat. Recent estimates put this bycatch in the range of 30% of the total harvest in some TURFs in Galicia (Macho et al. 2013), demonstrating the potential relevance of this practice for the population. This change to the rule in Galicia and the introduction of a new rule in Portugal and Asturias should be discussed and consensually agreed with professional harvesters.

Enforcing a conservative harvest that leaves adult barnacles on the rocks would require in situ surveillance of the harvesting activities, which is economically unfeasible for any fisheries administration. It would only be possible if the harvesters themselves adopt those measures voluntarily, which is not realistic in an open access fishery. However, this could be put into practice in co-managed, Territorial User Rights for Fisheries (TURFS) systems like those currently in place in Galicia and Western Asturias (Spain) and Berlengas (Portugal) (Molares and Freire 2003; Macho et al 2013; Rivera et al. 2014; Aguión et al. 2022; Geiger et al. 2024). These TURFs consist of swaths of coast where a group of fishers are granted exclusive access to the stalked barnacles and actively participate in the management of the fishery (Aguión et al. 2022). Co-managed TURFs usually promote a sense of ownership and cooperation among fishers, who may actively agree on the best approach to improve the health of the harvested population. Galician and Asturian TURFS have produced some salient management and organizational solutions, and some are fully prepared to adopt some of these recommendations experimentally (i.e. the Baiona TURF and the Cangas TURF, both in Galicia, Geiger et al. 2023). Alternatively, active dissemination of good harvesting practices and outreach activities may encourage recreational and professional harvesters in regions without rights-based management. Our data strongly suggest that, with adequate time, implementation of such management practices at the very small scale of the gaps would result in healthier, more productive and more profitable fisheries.
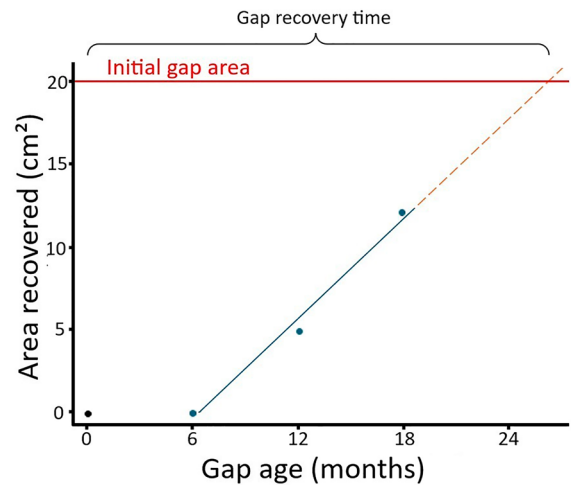
Fig. 8 Example calculation of the recovery rate and the recovery time. The recovery rate is calculated as the slope of the regression line (blue line) built using the last zero-recovery observation (6 months) and all observations with non-zero recovery (12 and 18 months; blue dots). The recovery time, or estimated time to full recolonization of the gap, is calculated by extrapolating the regression line (dashed red line) until it intercepts the initial gap surface (horizontal red line)

Appendix

See Table 4, Figs. 8, 9, 10, 11.

Table 4 Parameter estimates for fixed effects in a simplified model which assumes that the start of recolonization is the midpoint between last non-recovery and first recovery observation (same as in Table 2) as compared to a multiple imputation method allowing precise estimation of parameters (Alarcón-Soto et al. 2018)

Source of variation	Midpoint approach	Multi imp coeff
Global full model with region		
pg	1.514 ± 0.204	1.275 ± 0.039
ar	0.007 ± 0.004	0.009 ± 0.001
si	-1.942 ± 0.561	-1.155 ± 0.292
ca	-0.001 ± 0.005	-0.009 ± 0.001
Global only presence of adults		
pg	1.665 ± 0.171	1.539 ± 0.192

Both models incorporate the full random effects structure. Models have been built with the four regions, two years dataset. The multiple imputation approach did not converge for the Asturias dataset
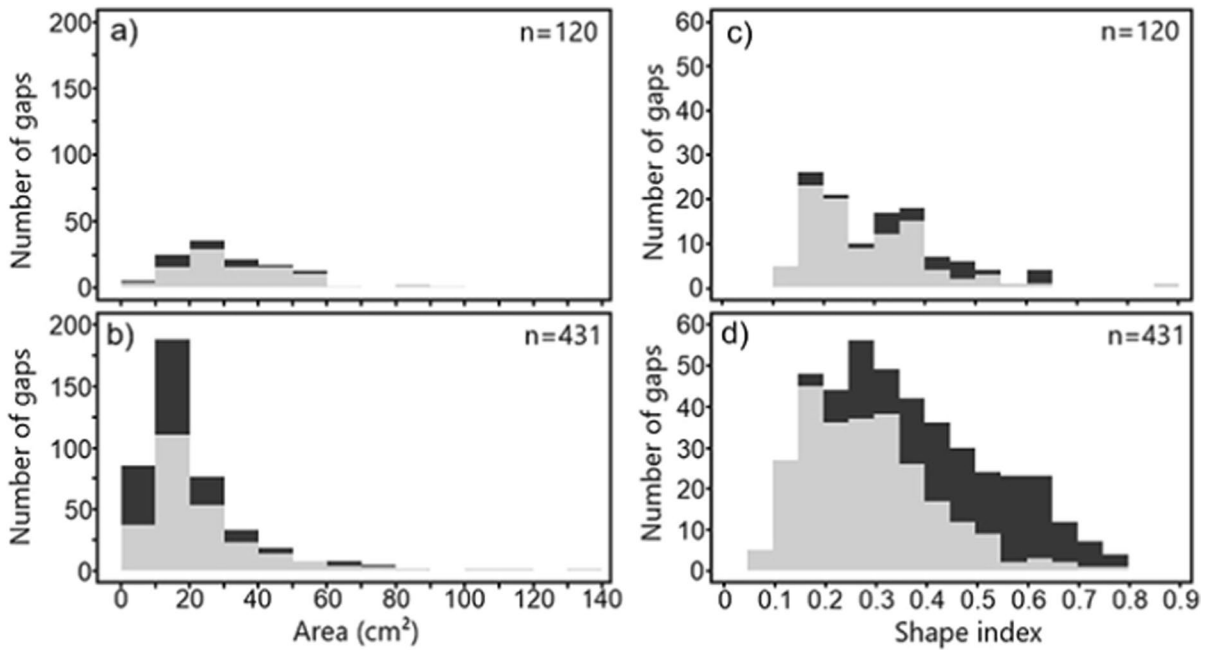
Fig. 9 Gap size and shape. **a** Histograms of the number of gaps created experimentally by gap area class. **b** Same as A, but for gaps created by fishers or other causes. **c** Histograms for the shape index for gaps created experimentally. **d** Same as C, but for gaps created by fishers or other causes. Black shading indicates gaps which had no adult barnacles in contact with their perimeter
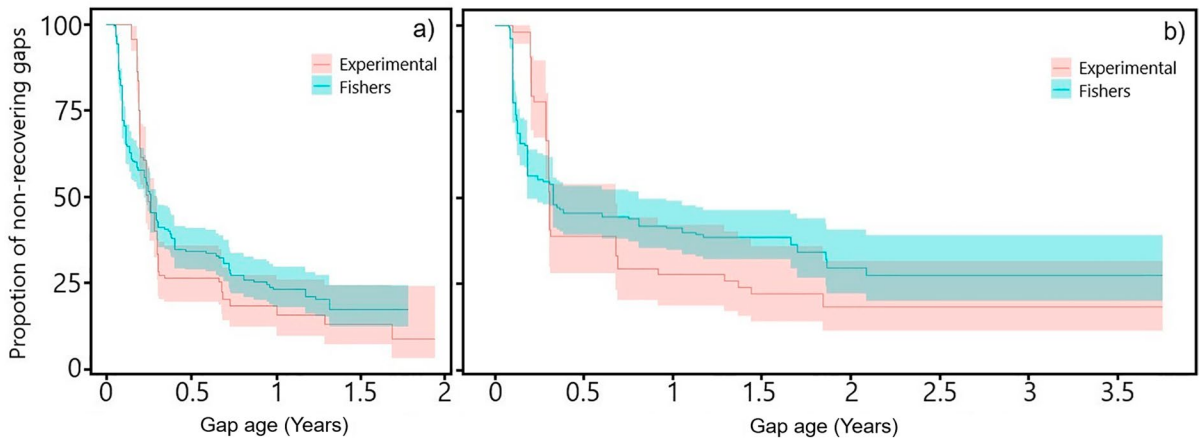

Fig. 10 Kaplan Meier survival curves for the onset of recolonization in harvested stalked barnacle gaps. Curves are split into gaps created experimentally and those created by fishers or other causes (see inset for color coding). Color shading indicates the confidence interval at each point in time. **a** Four regions dataset. **b** Asturias dataset
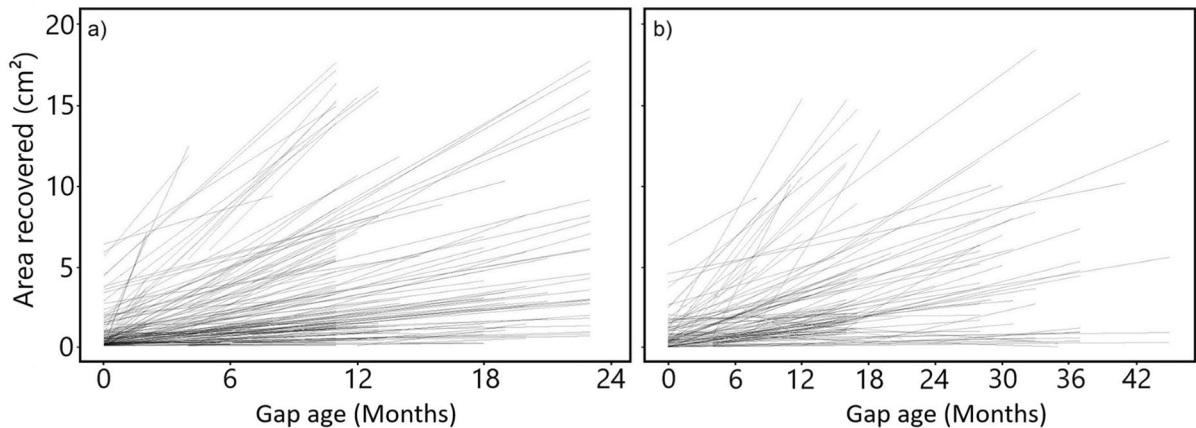
Fig. 11 Linear fits of recolonized surface vs gap age all studied gaps. **a** Global dataset. **b** Asturias dataset

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