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Lipophrys pholis is larger, grows faster and is in better condition in protected than in unprotected rocky shores

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Abstract

1. Intertidal fish are a key component of littoral food webs, contributing to the diets of birds and commercial fish species. Ascertaining their growth and condition can therefore help understand the health status of local communities.
2. *Lipophrys pholis* is a fish of the rocky intertidal with a wide distribution throughout the North-eastern Atlantic (NE Atlantic) that has been recommended for use as an indicator in the environmental biomonitoring of marine ecosystems. However, it is unclear yet if this species is sensitive to the reserve effect.
3. In this study, the size, growth and body condition of specimens caught at protected and unprotected rocky shores of two contrasting marine provinces of the NE Atlantic were analysed to address whether *L. pholis* is sensitive to the reserve effect.
4. *L. pholis* were larger, grew faster in weight and were in better condition in the protected shores of both provinces. A faster growth rate was observed in the populations of the warmer province.
5. Inshore waters of unprotected sites in the Northern European Seas sampled in this study have recently been incorporated into a protected area. Thus, these results can help assess the success of the marine conservation programme and the time *L. pholis* needs to improve its population's health at these shores.
6. Regulating access to shores to avoid trampling and harvesting is a protection measure that can help enhance the health and conservation of *L. pholis* populations.

KEYWORDS
Blenniidae, body condition, intertidal fish, length–weight relationship, Lusitania, NE Atlantic, Northern European Seas, shanny, tidepool

1 | INTRODUCTION

The cosmopolitan shanny *Lipophrys pholis* (Blenniidae) is a fish species with high site fidelity (Compaire et al., 2022; Martins et al., 2017) that spends its entire life within the intertidal zone. This species is commonly found in Northern European Seas (NES) and Lusitania (LU) (Barrett et al., 2016; Monteiro et al., 2005); two marine provinces of the temperate North-eastern Atlantic (NE Atlantic, Spalding et al., 2007).

L. pholis has been proposed as a sentinel species for biomonitoring programmes in marine ecosystems due to its wide latitudinal distribution in the NE Atlantic (Zander, 1986) and exposure to multiple anthropogenic stressors (Ferreira et al., 2011; Lima et al., 2008; Santos et al., 2010). Studies that evaluated the potential of *L. pholis* as a bioindicator of ecosystem health have been mainly performed using histological and biomarkers analysis that require killing the specimens (Ferreira et al., 2011; Lima et al., 2008; Santos et al., 2010). An alternative to destructive methods should be used whenever possible because removing fish from pools alters both their population and the entire ecosystem structure due to the cascade effect (Pinnegar et al., 2000). Anaesthetizing intertidal fish in pools allows specimens to be captured alive and their length and weight recorded before releasing them back into the ecosystem. Length and weight measurements are used to calculate growth and body condition; biological variables indicative of ecosystem health (Courtney et al., 2014; Maceda-Veiga et al., 2014).

On unprotected shores, trampling and harvesting of algae and macro-invertebrates, which are prey items for many intertidal fish species including *L. pholis* (Barrett et al., 2016; Mazé et al., 1999; Velasco et al., 2010), are major human activities leading to body size decrease, abundance declines and lower overall biodiversity (Pinn & Rodgers, 2005; Stevčić et al., 2018; Tydlaska & Edwards, 2022). Protected areas are biodiversity hotspots that often hold higher population densities, biomass and a larger average organism size relative to unprotected sites (Halpern & Warner, 2002; Virtanen et al., 2018). Yet, studies into the effect of protected areas on fish populations have produced contrasting results. Some studies have reported higher abundances and an increase in the size of individuals (e.g. Anticamara et al., 2010; García-Charton et al., 2008; García-Rubies & Zabala, 1990), while others found no significant differences between fish populations from protected and unprotected areas (e.g. Lipej et al., 2003; Vigliola et al., 1998). Divergent results were also reported for different fish species within the same marine reserve (Cole et al., 1990).

The 'reserve effect' (García-Rubies & Zabala, 1990) can take a long time to become apparent for some species with slow growth rates and high longevity (Muñoz et al., 2013), while short-lived, fast-growing species with restricted movements, such as resident intertidal fish appear to have a faster, positive response to protection efforts (Blyth-Skyrme et al., 2006; Halpern & Warner, 2002). Previous studies at the family level indicated that Blenniidae did not benefit from inhabiting a protected area (Mosquera et al., 2000), but at present it is not clear if *L. pholis* is sensitive to the reserve effect.

Environmental conditions such as wave exposure and temperature can also affect the health status of fish. Wave exposure drives the spatial patterns of vertical zonation in the intertidal (Harley & Helmuth, 2003) and can also rip sessile organisms (such as barnacles and limpets) from the bedrock (Blanchette et al., 2016), limit the spatial distribution of mobile organisms (Petraitis et al., 2008) and affect homing abilities of intertidal fishes (Green, 1971). Thus, although *L. pholis* is adapted to live in a productive yet ecologically challenging habitat such as the intertidal, under harsh environmental conditions this species can become less active, reduce its feeding activity and/or move temporarily to the subtidal for a more stable environment (Gibson, 1967; Qasim, 1957). Temperature regulates metabolic rates and energy expenditure (Wootton, 1998) affecting the onset of reproduction, feeding habits, body condition and growth rates (Compaire et al., 2016; Kovačić, 2001; McCormick & Molony, 1995; Pankhurst & Munday, 2011). At a broad latitudinal scale, and for an equivalent rise in temperature, blennies inhabiting warmer regions have exhibited a smaller increase in their maintenance rate of energy expenditure than their counterparts from colder ones (Pulgar et al., 2005). As *L. pholis* is a species with a wide latitudinal distribution along the NE Atlantic coast, populations inhabiting provinces with different thermal regimes could show different conditions and growth rates. Further, climate change will likely modify latitudinal gradients of temperature and the incidence and severity of extreme events on rocky shores (Bindoff et al., 2019; Trenhaile, 2014). Thus, to understand and be able to compare the future states of intertidal fish populations it is necessary to have assessed the present body condition and growth parameters of these populations.

Coastal marine environments perform important ecosystem and socio-economic services (Barbier et al., 2011; Liquete et al., 2013). These habitats act as settlement, feeding and nursery grounds for piscivorous birds (Lindström & Ranta, 1992) and fish species that recruit to coastal fisheries (Mendonça et al., 2019; Ribeiro et al., 2012). In this sense, blennies contribute to the diet of commercially important species such as cod (*Gadus morhua*), sole (*Solea solea*), mackerel (*Scomber scombrus*) and black scorpionfish (*Scorpaena porcus*) (Compaire, Casademont, Gómez-Cama & Soriguer, 2018; Pinnegar & Platts, 2011). Thus, as intertidal fish are key components of littoral food webs, it is important to understand the factors affecting their body condition and growth rate.

Comparing the sizes of a species occurring in protected versus unprotected shores can help determine the effectiveness of a protected area on the organisms within (Alexander & Gladstone, 2013; Buxton & Smale, 1989; Reis-Filho et al., 2019). The current study used *L. pholis* length and weight data from protected and unprotected shores of two contrasting marine provinces, LU and NES, of the NE Atlantic to address whether the growth and body condition of this species differed according to the protection status of shores. We hypothesized that *L. pholis*' size, body condition and growth differ between the protected and unprotected shores of both provinces.

2 | METHODS

2.1 | Ethics declarations

In LU, regional animal welfare laws, guidelines and policies were complied; these documents were approved by the Territorial Delegation of Agriculture, Fisheries and Environment of the Regional Government of Andalusia (*Law 11/2003 November 24th of Animal*

Protection) to avoid specimens' unnecessary distress. The care and use of experimental animals in NES complied with the licence held by Dr. Magnus L. Johnson, valid at the time of the study.

2.2 | Study sites and datasets

Surveys were conducted on protected and unprotected shores from two marine provinces, LU and NES. In LU, both shore types sampled were within the marine ecoregion of the South European Atlantic Shelf. While in NES, protected shores were located in the ecoregion of the Celtic Seas, and unprotected ones were situated in the ecoregion of the North Sea (Spalding et al., 2007). *L. pholis* is a species adapted to living in the intertidal where physico-chemical parameters such as temperature, oxygen and salinity range over tidal cycles. Its wide tolerance range for oscillations in those variables allows it to inhabit from Morocco to Norway. Thus, although there is a difference between the marine ecoregions of the Celtic Seas and the North Sea, such small differences in environmental conditions do not seem large enough to prevent a comparison within the same province.

Protected sites were defined as shores where public access is forbidden or regulations apply which limit human impacts at the site, such as restrictions on construction activities or banning of pesticide application within the area. Operations potentially affecting the marine life in these protected intertidal areas require the consent of the relevant authorities (in LU by the Torregorda Testing Centre, and in NES by the Welsh Government sponsored body *Natural Resources Wales*). Unprotected sites were defined as shores outside protected areas and with no access restrictions. The protection status of sites was: forbidden public access, sites protected for marine features, sites protected but not for marine aspects and sites where public access is allowed (Table 1).

Fish from LU were collected from a protected rocky shore at Torregorda (36°26′ N – 6°14′ W; https://inta.es/INTA/es/), and from an unprotected rocky shore at El Chato (36°28′ N – 6°15′ W) (Figure 1). Specimens from NES were collected from two rocky shores located in an indirectly protected area (http://angleseynature.co.uk/) at Rhosneigr (53°13′ N – 04°30′ W); where recreational fishing/angling, species collection/removal, boat moorings, pollution and sewage discharge are monitored and at Penrhos (53°18′ N – 04°36′ W); where a terrestrial designation exists to support heathland and marshland, and some of the associated restrictions (e.g. restrictions on pesticide usage) may help prevent any pesticide runoff onto Penrhos' rocky shore, and from two unprotected rocky shores at Filey Brigg (hereafter 'Filey'), (54°13' N – 0°16'W); designated for its geology and at Thornwick Bay (hereafter 'Thornwick') (54°07' N – 0°06' W); designated for its geology and also bird life (Figure 1). Torregorda has been protected from public access since 2000 (Order 371/2000 – BOE number 4, 4 January 2001), while Penrhos and Rhosneigr have been indirectly protected from human disturbances mentioned above since 1992 (Special Area of Conservation EU code: UK9013061).

The dataset from LU is a long-term record of monthly surveys for the years 2003–2004 and 2006–2016. The dataset from NES is a short-term record that includes surveys from 2010 (August, September and December) and 2011 (January and February) (Table 2). In LU, a smaller number of surveys were conducted on the protected shore because access to this site was regulated by the Ministry of Defence of Spain, thus entrance was not always possible. In NES, there was no difference in the number of surveys between protected and unprotected shores as access is not restricted.

The rocky intertidal zones in both provinces are a combination of extensive bedrock outcrops with shallow-sloping sandy beaches. *L. pholis* is a species that inhabits a wide band on the shore (tidepools at different shore heights: Faria & Almada, 2006; Compaire et al., 2022) and occupies different microhabitats (Faria & Almada, 2001; Monteiro et al., 2005). Consequently, the rocky pools sampled were located at different shore heights to encompass different pool sizes and microhabitats. Intertidal temperature can vary over small spatial scales due to several factors such as tidal dynamics, wave exposure and emersion time, topography and the presence and characteristics of pool crevices (Harley, 2008; Jackson, 2010). *In-situ* temperature measurements may be appropriate to evaluate physiological responses at short-time scales. Nonetheless, for the study of broad-scale biological patterns, satellite-derived measurements can be more representative of the overall conditions experienced by the nearshore communities than local point temperature measurements (Smale & Wernberg, 2009; Stobart et al., 2016). Sea temperature data were retrieved from the E.U. Copernicus Marine Service Information (10.48670/moi-00021) for LU, and the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) portal for NES (Morris et al., 2016). The mean significant wave height was retrieved from

TABLE 1 Site summaries according to protection status established on UK marine policy statement for Northern European Seas (SAC, special area of conservation; SSSI, site of special scientific interest; SPA, special protection area) and access restrictions to civilians for Lusitania (PAF, public access forbidden; PAA, public access allowed).

Province	Site	Designation/restriction	Protection of intertidal biological resources	Shore length (km)
Northern European Seas	Rhosneigr	SAC, SSSI	✓	~0.4
	Penrhos	SAC	-	~0.9
	Filey	SSSI, SPA	-	~1.5
	Thornwick	SAC, SSSI	-	~0.25
Lusitania	Torregorda	PAF	✓	~1.5
	El Chato	PAA	-	~1.2

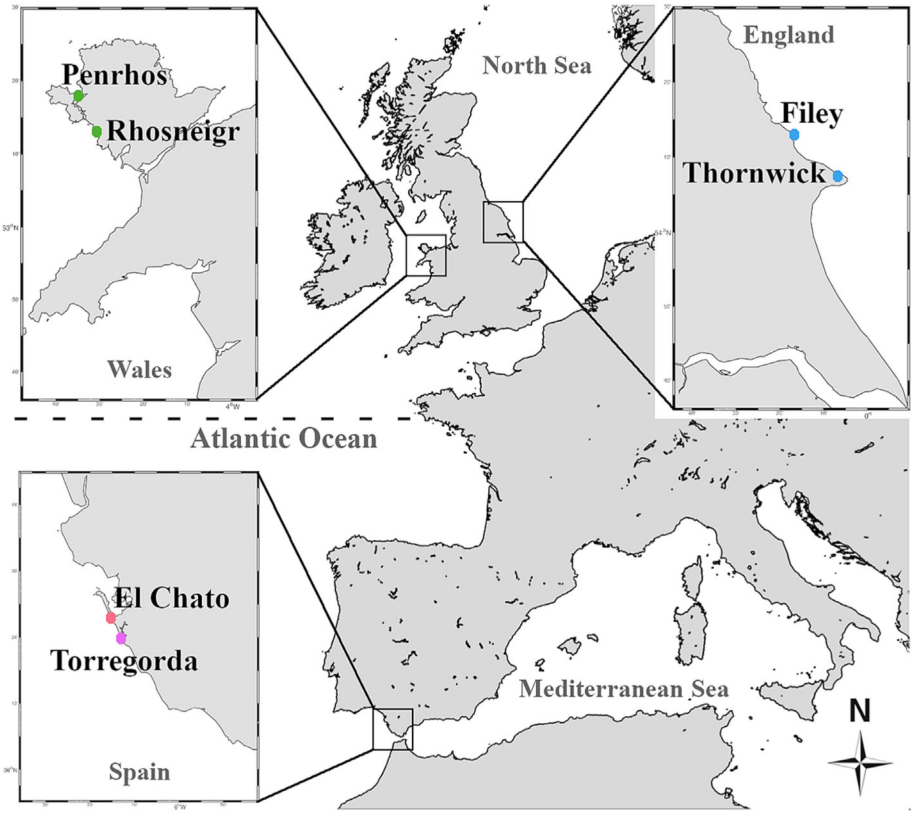

FIGURE 1 Sample locations in the Northern European Seas (NES) and Lusitania (LU). Dashed line indicates boundaries between NES and LU marine provinces according to Spalding et al. (2007). Unprotected shores of NES: Filey and Thornwick (blue dots), protected shores of NES: Rhosneigr and Penrhos (green dots). Unprotected shore of LU: El Chato (red dot), protected shore of LU: Torregorda (pink dot).

TABLE 2 Number of surveys (*N*) conducted, minimum and maximum mean values of seawater temperature (T) and mean significant wave height (Hs) at protected and unprotected shores for each marine province. Values in parenthesis are the total number of surveys carried out at Lusitania (LU) including those were *L. pholis* was not caught.

Province	Shore	*N*	T (°C)	Hs (m)
Northern European Seas	Protected	4	6.1–15.9	0.87–1.57
	Unprotected	4	5.5–14	0.87–1.48
Lusitania[a]	Protected	20 (100)	14.5–22.3	0.69–1.16
	Unprotected	34 (124)		

[a]The same values of temperature and wave height are provided for the Lusitania province due to the close proximity of both shores.

Puertos del Estado (https://www.puertos.es/es-es/oceanografia/Paginas/portus.aspx) for LU, and from the UK renewables atlas (https://www.renewables-atlas.info/explore-the-atlas/) for NES. Salinity was not recorded due to *L. pholis* being highly insensitive to a wide salinity range (Davenport & Vahl, 1979).

2.3 | Sampling design and fish collection

Different techniques can capture fish of different developmental stages, even within the same location (Barrett et al., 2020; Beja, 1995). Thus, to reduce sampling technique bias and detect differences due to local factors, studies that evaluate fish body conditions and growth parameters at different sites should ensure sampling protocols are consistent (Compaire & Soriguer, 2020). Intertidal rock pools were randomly sampled during low spring tides. Fish were sedated in a seawater solution with clove oil (40 mg·L^{-1}) (Griffiths, 2000). Sedated fish became lethargic and floated to the surface, where they were captured using hand nets (1.5 mm mesh size). The pool volume to calculate the quantity of clove oil necessary was determined by approximating the shape to a triangular prism (Compaire et al., 2019). This procedure was proven to be efficient in catching juveniles and adults of *L. pholis* in LU and NES (Barrett et al., 2020; Velasco et al., 2010). In laboratories at the University of Hull (England) and at the University of Cadiz (Spain), specimen total length (TL) was measured to the nearest millimetre and total weight (WT) to 0.01 g.

2.4 | Statistical analysis

The body condition of specimens was determined using Fulton's condition factor (K) calculated as $K = WT/TL^3 \cdot 10^5$ (Ricker, 1975). The parameters of the length–weight relationship (LWR) $WT = aTL^b$ were estimated by least-squares linear regression from the log-transformed equation, where *a* is the intercept and *b* is the slope. The 95% confidence intervals (CI) of parameters *a* and *b* were estimated. Pearson r-squared (r^2) was calculated to evaluate the fit of the growth model. The slope *b* was employed to identify growth as isometric ($b = 3$) or allometric ($b \neq 3$) (Ricker, 1975).

The differences in TL and K between protected and unprotected rocky shores for each province were analysed using a non-parametric Kruskal–Wallis test. An analysis of covariance (ANCOVA) test (with TL as a covariate) was performed on the regression coefficients to assess different growth patterns between protected and unprotected rocky shores for each province. Ontogenic development may lead to different growth rates (Ricker, 1975), thus, when the observed length–frequency distribution showed a bimodal distribution represented by a near-equal number of specimens, an ANCOVA test was performed dividing the population based on different size classes. Specimens were assigned to length bins of 5 cm TL. A threshold of 5 cm was selected as the cut-off value to separate size classes. This length was chosen based on the observed length–frequency distribution and a previous study about the relationship between the length of *L. pholis* and age in NES province that indicated that specimens shorter than 5 cm belonged to the young age class 0+ (Qasim, 1957). Environmental temperature can also influence growth rate (Mazumder et al., 2016), so an ANCOVA test was done to evaluate if growth varied according to seasons: warm versus cold. This division into warm and cold periods is supported by the temperate NE Atlantic exhibits a clear seasonal pattern in temperature. The warm season in LU encompassed months whose average water temperature exceeded 20°C (June–October), while the cold season included the remaining months (Compaire et al., 2016). In NES, August and September were considered the warm season (average water temperature exceeded 14°C), and December to February the cold season. Statistical analyses were performed with R software (R Core Team, 2021). Matplotlib (Hunter, 2007) and Seaborn (Waskom et al., 2017) Python modules were used for plots of length-frequency distribution and LWRs. Further details on sampling, dates and data per site and specimen are available at the PANGAEA digital repository (Compaire et al., 2021).

3 | RESULTS

L. pholis showed a larger average length and better condition on protected shores in both provinces (Table 3). Such differences were significant ($p < .05$) for both variables in NES, but only for conditions in LU. Specimens caught at protected shores reached larger sizes (TL and WT) in both provinces (Table 4). The peaks of the length–frequency distribution of fish from protected and unprotected shores of LU were located at the same length at approximately 3.8 cm, but the latter showed a narrower length distribution (Figure 2), implying conditions may be favourable for these small-size specimens, but not for larger adults, or, because of human pressures (larger specimens are taken by tourists and fishers as bait for capturing bigger fish). Fish populations at NES showed bimodal distributions. The length–frequency distribution for the protected shores presented peaks at approximately 4 and 8.5 cm (the proportion of specimens was: smaller ∼19% and larger

TABLE 3 Total length and body condition (mean ± SD) of *L. pholis* caught at protected and unprotected shores of each marine province.

Province	Shore	*n*	TL (cm)	K
Northern European Seas	Protected	52	8.45 ± 2.54	1.29 ± 0.23
	Unprotected	151	4.25 ± 2.00	1.06 ± 0.55
		KW	df = 1, H = 77.39, $p < .001$	df = 1, H = 58.11, $p < .001$
Lusitania	Protected	101	4.93 ± 2.38	1.05 ± 0.18
	Unprotected	143	4.27 ± 1.27	0.95 ± 0.17
		KW	df = 1, H = 1.12, $p = .289$	df = 1, H = 24.11, $p < .001$

Abbreviations: K, Fulton's condition factor; KW, Kruskal–Wallis test results; *n*, number of specimens; TL, total length.

TABLE 4 Length–weight relationships for *L. pholis* caught at protected and unprotected shores for each marine province. *a* and *b* are the intercept and slope of the length–weight relationship, respectively; 95% CI are the confidence intervals; r^2 is the coefficient of determination for the regression on logarithms.

Province	Shore	*n*	TL (cm) (min–max)	WT (g) (min–max)	a (95% CI)	b (95% CI)	r^2
Northern European Seas	Protected	52	3.3–15.3	0.37–45.30	.0101 (.0077–.0133)	3.110 (2.978–3.241)	.978*
	Unprotected	151	1.6–8.7	0.05–6.00	.0109 (.0097–.0122)	2.949 (2.870–3.029)	.973*
Lusitania	Protected	101	1.7–11.4	0.05–18.65	.0080 (.0072–.0089)	3.173 (3.104–3.241)	.988*
	Unprotected	143	1.4–7.5	0.02–4.48	.0079 (.0068–.0091)	3.125 (3.025–3.224)	.965*

Abbreviations: n, number of specimens; TL, total length; WT, total weight.
*$p < .001$.

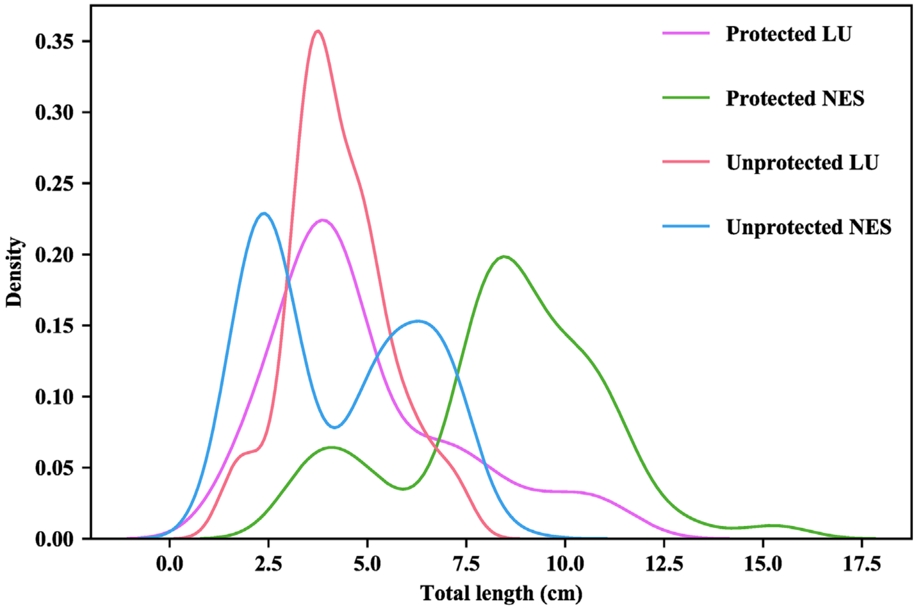

FIGURE 2 Density plot for *L. pholis* length distribution from protected and unprotected rocky shores for each marine province. LU, Lusitania; NES, Northern European Seas.

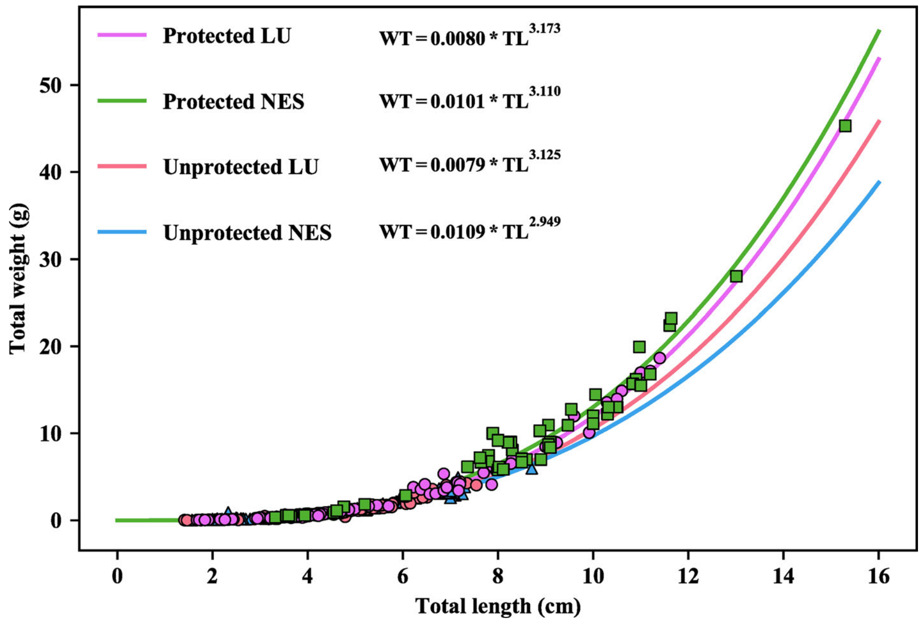

FIGURE 3 Length–weight relationships for *L. pholis* from protected and unprotected rocky shores for each marine province. LU, Lusitania; NES, Northern European Seas; TL, total length; WT, total weight.

~81%), while the unprotected shores showed peaks at approximately 2.5 and 6 cm (smaller ~57% and larger ~43%). For the latter, which showed a relatively near-equal proportion of size classes, there was no significant difference in the growth rate between both size classes (ANCOVA, $F_{(1,147)} = 1.478$, $p = .226$). It is therefore unlikely that ontogeny is responsible for LWR differences and fish from NES' unprotected shores can be treated as a single population.

A slightly negative allometric growth was evident only in NES unprotected shores. LU's populations showed higher allometric slopes in both protected and unprotected shores in comparison to NES (Table 4 and Figure 3). There were no significant differences in LWR regression slopes according to the protection status of the shore for any province (NES: ANCOVA, $F_{(1,199)} = 2.719$, $p = .101$; LU: ANCOVA, $F_{(1,240)} = 0.623$, $p = .431$). Yet, *L. pholis*' populations at protected shores from both provinces showed a faster growth in weight. There were no significant differences in growth between seasons in LU (protected: ANCOVA, $F_{(1,97)} = 1.603$, $p = .209$; unprotected: ANCOVA, $F_{(1,139)} = 1.912$, $p = .169$) or in NES (protected: ANCOVA, $F_{(1,48)} = 1.908$, $p = .174$; unprotected: ANCOVA, $F_{(1,147)} = 2.070$, $p = .152$). Details about the parameters and curves for the LWRs for each population according to protection status and province are shown in Table 4 and Figure 3.

4 | DISCUSSION

This study focused on analysing the length and weight of *L. pholis* specimens caught from protected and unprotected shores to identify whether growth and body condition differed according to the protection status of shores. However, there are biological and environmental limitations to our study that must be considered when interpreting results.

L. pholis' reproductive cycles and feeding habits could also influence body condition and growth. With the onset of the breeding period, adults can move out of rocky pools to the subtidal (Monteiro et al., 2005), which can skew the length frequency distribution of tidepools towards smaller specimens. Because fish may change their body proportions according to their life-history stage (Froese, 2006), it must be ensured that the entire fish size distribution is sampled to avoid obtaining biased results for a population. Fish were not aged in our study, but according to lengths and based on the literature, the year-classes of specimens caught in LU at the protected shore would range from 0+ to 2+ and at the unprotected shore from 0+ to 1+ (Faria et al., 1996). While in NES, year-classes would range from 0+ to 6+ in protected shores, and from 0+ to 2+ in unprotected ones (Qasim, 1957). These studies support that length–frequency distributions of fish caught in our study included juveniles to adults in all sites, so it seems unlikely that breeding season will be responsible for the observed differences. Regarding feeding habits, fish select the largest prey they can swallow to maximize energy intake relative to the energy cost of handling times (time needed to pursue, capture, retain and digest prey) (Setran & Behrens, 1993). The better condition of *L. pholis* in protected shores could be related to the presence of larger-sized specimens that possesses the aptitude to feed on larger prey, meeting the baseline energy expenditure more rapidly.

The substratum type and complexity (De Raedemaecker et al., 2010; Macpherson, 1994), biocover (Kovačić et al., 2012), rock pool size (Compaire et al., 2019) and its position with respect to tidal height (Compaire et al., 2022; Malard et al., 2016) can affect intertidal fish populations. The shore platform at the sampling sites in LU is composed of cemented deposits formed by alternating laminated sandstones and quartzitic conglomerates (Del Río et al., 2008). The protected shores in NES are comprised of schist, granite, sandstone and conglomerate with deposits of sand, silt and clay (BGS, 2020; Westley & Edwards, 2017), while unprotected ones are composed of calcareous grit, sandstone, chalk, flint, mudstone and shale (BGS, 2020; Crosby, 1995). Because rocky pools are mainly produced by abrasion of drag-boulders along the bedrock (Trenhaile, 1997), differences in the nature of these shores could promote different types of pools in terms of physiographic features and microhabitat availability both for feeding and hiding from predators.

Human exclusion from shores has been shown to promote a cascading effect on intertidal organisms affecting communities in terms of abundance, dominance and zonation of flora and fauna (Gubbay, 2006; Moreno, 2001). One of the most remarkable effects of human activities recorded on the shores of LU is the structure response of intertidal communities to harvesting. Because harvesting is not regulated on the unprotected shore, only 1% of the pools at this shore are inhabited by sea urchins (*Paracentrotus lividus*), while on the protected adjacent shore they inhabit almost 60% of pools (Compaire et al., 2019). Sea urchins are benthic herbivores (Ruitton et al., 2000) that have a leading role in structuring intertidal communities at different levels and can play a positive role in providing shelter to intertidal fishes (Hartney & Grorud, 2002). While sea urchin occupancy was not assessed in *L. pholis* pools, due to the differences in the mean physiography of the pools between shores, it seems plausible that this factor partly affects *L. pholis*' populations.

Unprotected rocky shores are more likely to have a greater number of anthropogenic stressors that could adversely impact fish populations. Recreational fishing and harvesting of larger fish species and their potential prey can impact fish populations at the behavioural level, affecting reproductive and feeding success, which in turn can alter the intertidal community structure and organization (Durán & Castilla, 1989; Moreno, 2001; Underwood, 1993). Conversely, in protected rocky shores, the absence of, or lower, human-induced disturbances can enhance habitat quality, leading to improved fish body condition and the occurrence of larger specimens, as health and welfare are less compromised (Francour, 1994; Jouvenel & Pollard, 2001; Lloret & Planes, 2003). Our results indicated that *L. pholis* populations were positively affected by the 'reserve effect' as they increased faster in weight, were larger and were in better condition inside protected than on unprotected rocky shores in both provinces.

The positive impact of the reserve effect upon a population, however, may not be reflected in all specimens because inhabiting a protected site can lead to higher rates of inter- and intraspecific co-occurrence, thus resulting in the spillover of competitively excluded specimens (Barrett et al., 2018). A higher abundance of larger predators migrating from the subtidal system to the protected area could increase mortality rates on intertidal fishes (Macpherson, 1994; Willis & Anderson, 2003), especially on smaller individuals. Larger body-sized intertidal fish could also compete for rock pools and exclude smaller fish from the best pools that offer greater opportunities for shelter and feeding (Macieira & Joyeux, 2011; Mahon & Mahon, 1994). Inter- and intraspecific relationships can act independently or synergistically, promoting a greater reduction in the abundance of smaller specimens when competition may be high, and a smaller reduction when competition is reduced (Barrett et al., 2014) which could also explain why there were larger individuals of *L. pholis* on the protected shores. Specimens on protected shores of NES were larger and may have competitively excluded smaller specimens. At unprotected shores, a length–frequency distribution skewed to smaller size classes could partly be the result of the human preference for harvesting larger specimens (Moreno, 2001).

Intertidal fish assemblages also respond to changes in environmental conditions. Pools on wave-exposed shores are often less desirable habitats for intertidal fish than in sheltered areas (Compaire et al., 2022; Griffiths, 2003). Although a lower abundance of blennies has been related to harsh physical conditions experienced in the intertidal (Compaire et al., 2019), this was not noticed in the current study, perhaps due to the negligible difference (~6%) mean wave height between sites at NES. The thermal tolerance of *L. pholis* enables it to inhabit over a broad latitudinal range in the temperate NE Atlantic (Vinagre et al., 2013). Although growth rates of populations analysed during warm and cold seasons exhibited no differences within the same shore, the growth rate of *L. pholis*' populations may be different as a result of the latitudinal temperature gradient regulating their metabolic rates (Kamler, 1992). For all sites, the values of the *b* parameter of the growth curve remained within the expected range of 2.5–3.5 (Froese, 1998). The lower values of the *b* parameter for *L. pholis* caught in NES shores may be because poikilothermous organisms grow slower in colder latitudes (Hile, 1936). This would explain why larger (and most certainly older) specimens were recorded in NES. The higher values of the *b* found for fish from LU shores could be a consequence of warmer temperatures accelerating the digestion process (He & Wurtsbaugh, 1993; Mazumder et al., 2020), allowing fish to achieve the energetic requirements faster to sustain basic functions and grow. A previous study comparing *L. pholis*' growth in LU and NES also reported a faster growth associated with a longer warm-temperature period in southern Europe (Faria et al., 1996). Thus, the faster growth in weight observed on the shores of LU than in NES (Table 4) suggests that *L. pholis* growth is likely influenced by temperature.

4.1 | Conservation implications

L. pholis' size will have an impact on the reproductive output of its populations because intertidal fish size is positively related to fecundity (Compaire, Casademont, Cabrera, et al., 2018; Delpiani et al., 2021). Thus, as *L. pholis* inhabiting protected shores were larger such populations will likely have a higher reproductive output than populations from unprotected shores. In the long-term, a higher fecundity of *L. pholis* at protected shores will be beneficial for its local populations, and to conserve or enhance those from adjacent sites. Protected ecosystems are often hotspots in terms of diversity and biomass (Halpern & Warner, 2002), hence, predators hunting intertidal fish on these shores will likely spend less time to reach their energy requirements, enhancing their populations not only because they will likely feed on more profitable preys in terms of energy but also due to having more time for other non-foraging activities as finding mates to reproduce. So, because intertidal fishes are a key component of littoral food webs contributing to the diets of both piscivorous birds and commercial fish species, *L. pholis*' larger size and better condition at protected shores, predators within those ecosystems might be advantaged by having readily available prey items which may require less energy to capture than if having to capture multiple smaller specimens for the same nutritional gain.

A main concern of conservation is how to apply research results to practical conservation because the impact of habitat management takes a long time (Boon & Baxter, 2016; Boon & Baxter, 2020). Furthermore, evaluating the impact of protective measures can be tricky if previous baseline conditions are unknown (Mosquera et al., 2000 and references therein). The lack of monitoring on *L. pholis* previous to regulating public access to shores prevented a before and after comparison of the analysed variables (size, body condition and growth rate) for the same shore. Nevertheless, results observed at both marine provinces and at distinct temporal scales (short- and long-term datasets) suggest that the protection of rocky shores diminishes the negative effect of human activities, whether directly or indirectly, upon *L. pholis*' populations. As fish samples were not collected throughout the year in the NES province, further studies sampling year-round would be necessary to corroborate these findings at a finer temporal scale.

Intertidal communities are often under pressure from rapidly growing human populations inhabiting low-lying coastal areas (Thompson et al., 2002). Even though sewage discharges, thermal effluent, nautical traffic and noise are some of the human activities becoming more common and able to downgrade habitat quality and affect intertidal fishes (Henriques et al., 2013; Popper & Hawkins, 2019; Voellmy et al., 2014), the harvesting for food or bait, along with the associated effects of trampling, are still the major direct threat for intertidal fishes; relating to the latter, removal of barnacles or seaweed via trampling can deprive *L. pholis* of important food items and shelter opportunities during high tide (Brosnan & Crumrine, 1994; Pinn & Rodgers, 2005; Stevčić et al., 2018; Tydlaska & Edwards, 2022). The protected shore at Torregorda, for example, has been regulated to prevent trampling and harvesting for more than 20 years. Several reports evaluating different ecological aspects of species inhabiting the protected shore in LU have been published because its access was regulated (Hernando Casal et al., 2002; Hernando Casal et al., 2007; Hernando Casal et al., 2009), but there are no reports that evaluated if those populations were different from their nearby unprotected counterparts. Inshore waters of unprotected sites in NES were included within the Special Protection Areas of Filey Brigg and Flamborough Head in August 2018 to provide support to seabirds during the breeding and nesting seasons (Natural England, 2018). *L. pholis* was not established as a conservation objective for this programme, yet, because this species occupies habitats subject to direct human impacts and the trend of their populations is unknown, more studies are needed to monitor the health of *L. pholis* populations (Williams & Craig, 2014). Our data and metadata are publicly available at https://doi.pangaea.de/10.1594/PANGAEA.932955.

5 | CONCLUSIONS

For decades, studies using different methodologies have analysed distinct aspects of the biology and ecology of *L. pholis* throughout the NE Atlantic shores (Almada et al., 1990; Dunne, 1977; Faria et al., 1996; Gibson, 1967; Martins et al., 2017; Qasim, 1957; South et al., 2018). Yet, this is the first study that shows that *L. pholis* may be affected by the reserve effect.

Fish body condition and growth rate are key variables for studying and managing natural fish populations (Froese et al., 2011; Nash et al., 2006). Here, the use of the same standardized non-destructive protocol allowed capturing *L. pholis* juveniles to adults to obtain valuable biological information on the body condition and growth parameters of the species populations, inhabiting protected and unprotected rocky shores, at two contrasting provinces in the NE Atlantic. The larger size, faster growth and better condition of *L. pholis* recorded at protected shores in both provinces support that inhabiting shores where anthropogenic pressure is regulated is beneficial for this species.

Intertidal ecosystems are one of the most at-risk marine environments threatened by climate change and anthropogenic activities. The modifications to the shoreline triggered by sea-level rise, along with an increase in wave action due to more frequent extreme events such as storms (heavy rainfall, strong winds and the inverse barometer effect), may increase the depth of the water over sloping and horizontal rock surfaces. This could lower rates of wave attenuation, causing breaker zones to migrate landward (Trenhaile, 2014), and will likely increase the natural vulnerability of intertidal communities, potentially leading to population depletion (Andrades et al., 2018). Shoreline hard armouring may be used as a fast response to diminishing the threat of sea-level rising and wave exposure on intertidal habitats (Morley et al., 2012). Nevertheless, it is unknown whether such a measure would be beneficial for intertidal fish because armoured seawalls can alter nearshore currents or even isolate some areas from the tidal flow. As shoreline modifications may reduce feeding resources entering the nearshore ecosystem (Sobocinski et al., 2010) and *L. pholis* is a species especially abundant in the mid- and upper intertidal (Compaire et al., 2022; Faria & Almada, 2006), using armoured structures could have an adverse effect on their populations. An alternative approach to protect the shoreline against extreme events without drastically disrupting the nearshore circulation patterns would be the use of 'living shorelines' incorporating natural elements of habitat that may help shoreline stabilization and enhance productivity and habitat quality (Polk & Eulie, 2018; Subramanian et al., 2006). Also, the protection of shores from human-induced perturbations can lead to a modification of *L. pholis*' growth pattern and its population structure encouraging a faster growth and population distribution skewed to larger individuals (this study). Thus, at present our results suggest that regulating public access to shores is an effective protection measure, to avoid trampling and harvesting, enough to enhance the health of *L. pholis*' populations. Finally, for a comprehensive understanding of mechanisms leading to the observed differences in *L. pholis*' growth and body condition, future research should consider analysing both feeding habits and tidepool features.

AUTHOR CONTRIBUTIONS

Jesus C. Compaire: Conceptualization (equal); formal analysis (lead); investigation (lead); visualization (lead); writing—original draft preparation (equal); writing—review and editing (equal). **Natalia Visintini:** Conceptualization (equal); formal analysis (supporting); writing—original draft preparation (equal); writing—review and editing (equal). **Milagrosa C. Soriguer:** Funding acquisition (lead); investigation (supporting). **Magnus L. Johnson:** Funding acquisition (equal); investigation (supporting). **Susan L. Hull:** Funding acquisition (equal); investigation (supporting). **Christopher J. Barrett:** Conceptualization (supporting); investigation (lead); writing—review and editing (equal). All the authors have accepted to be listed and have given final approval of the version to be published.

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CONFLICT OF INTEREST STATEMENT

The authors declare they are not aware of any conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in PANGAEA digital repository at https://doi.pangaea.de/10.1594/PANGAEA.932955.

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