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Predator-prey collapses at the edge of predator distribution: the case of clupeids and common guillemots (*Uria aalge*) in NW Iberia

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Summary: The spatial structuring of seabird populations makes individual colonies very dependent on regional factors. That is especially the case in small edge populations located far from large colonies. We analysed retrospectively the poorly known collapse, some 50 years ago (around 1962-1973), of a relatively small population of breeding common guillemots (*Uria aalge*) located at their southernmost limit of distribution in Europe (NW Iberia). We assumed that guillemots behaved locally as facultative specialists in small pelagic fish due to the occurrence of a strong clupeid fishery, and we studied the association between the guillemot collapse and annual regional landings of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*), used as a proxy of total stock size. The overall relationship between ln-transformed guillemot counts (May-June) and ln-transformed sardine landings (May-October) was stronger than the fit on untransformed variables (r^2=0.52 vs. 0.27), indicating an exponential relationship between the non-transformed variables. This relationship was somewhat stronger and linear after the collapse, when only a few tens of guillemots remaining (r^2=0.60). A strong regime shift in sardine landings was detected in 1968 and also in anchovy landings in 1969. The overall relationship between guillemot numbers and anchovy landings was linear and strong (r^2=0.72) but completely dependent on the large 1960s estimate of guillemots. However, no relationship was found between guillemot numbers and anchovy landings (April-June) after the guillemot collapse. The most likely period for the guillemot collapse was therefore 1968-1970, as seabird colonies are known to collapse immediately after their staple prey crashes. Local guillemot colonies were not subsequently rescued by immigration and have remained empty or almost empty until present, showing the high sensitivity of edge populations to environmental variability at the regional scale.

Keywords: common guillemot collapse; regime shift; edge of distribution; metapopulation dynamics; sardine landings; anchovy landings; retrospective analysis.

Colapsos depredador-presa en el límite de la distribución del depredador: el caso de los clupeidos y el arao común (*Uria aalge*) en Iberia

Resumen: Las poblaciones de aves marinas están espacialmente estructuradas y eso hace que las colonias individuales dependan mucho de factores regionales. Ese es especialmente el caso en pequeñas poblaciones ubicadas lejos de grandes colonias. Aquí analizamos retrospectivamente el colapso de una población relativamente pequeña de araos comunes (*Uria aalge*) reproductores, ubicada en su límite de distribución sur en Europa (NO de Iberia), sucedido hace unos 50 años (alrededor de 1962-1973). Asumimos que los araos reproductores se comportaron localmente como especialistas facultativos en el consumo de peces pelágicos pequeños debido a la existencia de una potente pesquería de clupeidos y estudiamos la asociación entre el colapso del arao y los desembarcos regionales anuales de sardina (*Sardina pilchardus*) y boquerón (*Engraulis encrasicolus*), utilizados como un proxy del tamaño total del stock. La relación general entre los conteos de araos (mayo-junio), transformados mediante el logaritmo neperiano, y los desembarcos de sardina (mayo-octubre) transformados, fue más fuerte que el ajuste de las variables no transformadas (r^2=0.52 frente a 0.27), lo que indica una relación exponencial entre las variables no transformadas. Esta relación fue algo más fuerte y lineal después del colapso, cuando solo quedaron unas pocas decenas de araos (r^2=0,60). Se detectó un fuerte cambio de régimen en los desembarcos de sardina en 1968 y también en los de boquerón en 1969. La relación entre el número de araos y los desembarcos de boquerón fue lineal y fuerte (r^2=0.72). Sin embargo, no se encontró relación entre el número de araos y los desembarcos de boquerón (abril-junio) después del colapso del arao. La fecha más probable para el colapso del arao, por lo tanto, fue el período 1968-1970, ya que las colonias de aves marinas colapsan inmediatamente después de que sus presas principales hayan colapsado. Las colonias locales de araos no fueron rescatadas posteriormente por inmigración y han permanecido vacías o casi vacías hasta el presente, lo que demuestra la alta sensibilidad a la variabilidad ambiental a escala regional de las poblaciones ubicadas en el límite de la distribución de la especie.

Palabras clave: arao común; cambio de régimen; límite de distribución; dinámica metapoblacional; desembarcos de clupeidos; análisis retrospectivo.

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INTRODUCTION

The dynamics of marine top predator colonies are complex, as they are typically structured in space, so changes over time in a given colony are often explained by the regional dispersal of individuals among patches of the same metapopulation (see e.g. Oro and Pradel 1999). Hence, colonization and extinction of individual seabird breeding sites cannot be explained by considering only local factors of individual colonies in isolation from regional conditions (see e.g. Spendelow et al. 1995, Fernández-Chacón et al. 2013, Goyert et al. 2018). A special case is that of edge populations, as they are typically small and distant from other large colonies that could buffer local population declines by immigration when environmental conditions become unfavourable at the regional scale (Fagan et al. 1998).

Common guillemots (*Uria aalge*) in the Iberian Peninsula (henceforth Iberia) collapsed during the second half of the 20th century. It has been suggested that this precipitous decline was due to local anthropogenic causes (i.e. direct human persecution and mortality in fishing gear) (Munilla et al. 2007). However, Iberian guillemots may have been involved in metapopulation dynamics (including colonization and extinction of local patches) for centuries or millennia as a result of environmental variability. An alternative hypothesis is that changes in food availability not only affected breeding success or true survival but that food scarcity could also have forced guillemots to permanently emigrate from Iberia.

The presence of guillemots in Iberia has been traced back to the upper Pleistocene rocks of Gibraltar, Málaga, Valencia, Asturias and the Basque Country (Cortés et al. 1980, Carrasquilla 1993, Elorza 2014, Fig. 1A) and to the Holocene rocks of Málaga and the Basque Country (Eastham 1986, Elorza and Marco 1993). In Brittany, France, guillemots were also present during postglacial times, 5500 to 2500 years before present (BP) (Fig. 1A) (Tresset 2005). However, fossils cannot reveal whether the species was wintering or breeding around that time.

The modern presence of breeding guillemots in NW Spain and Portugal is only known to have certainly oc-

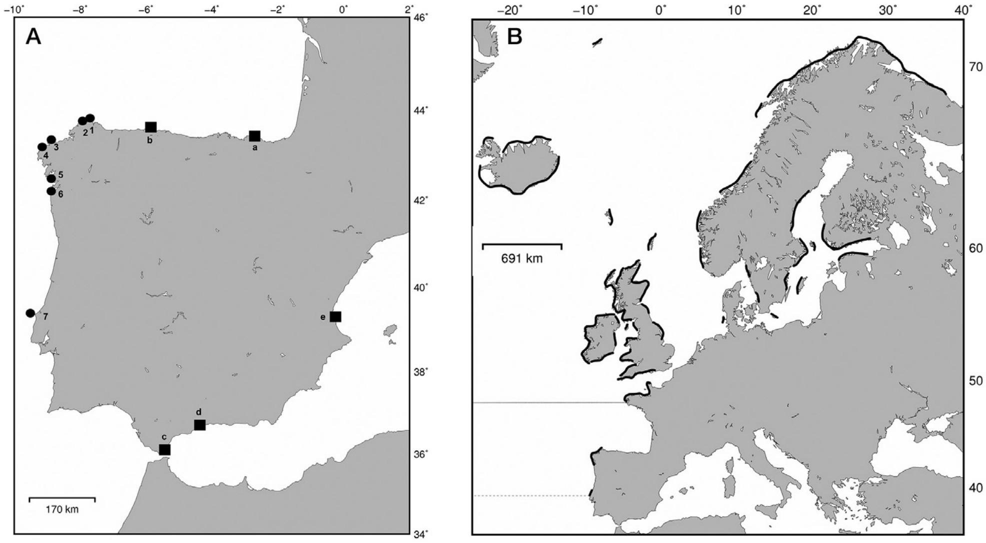

Fig. 1. – A, approximate location of the main former common guillemot colonies in Iberia (solid black circles: 1, Estaca de Bares; 2, Cape Ortegal; 3, Sisargas Islands; 4, Cape Vilán; 5, Ons Islands; 6, Cies Islands; 7, Berlengas Islands) and location of sites where fossils of the species have been found (solid black squares: a, Santa Catalina, Bizkaia; b, Cueto de la Mina, Asturias; c, Devil's Tower, Gibraltar; d, Nerja Cave, Málaga; e: Cullera, Valencia). B, general distribution of the breeding range of common guillemots in the western Palearctic, including past presence in the Iberian Peninsula. The dashed grey line depicts the past southernmost limit of distribution of the guillemots in Europe whereas the solid grey line delimits the current southernmost limit of the species. After Keller et al. 2021).

curred since the late 19th century and early 20th century (Tait 1924). One of the possible scenarios is that guillemots were present as breeders in southern Europe during the cold and productive upper Pleistocene and beginnings of the Holocene, but that they became rare or intermittent breeders in Iberia during most of the Holocene, with warmer and less productive waters (the Holocene Climate Optimum took place between 9000 and 5000 years BP, with a thermal maximum around 8000 years BP).

From this perspective the most recent of these recolonization events of Atlantic Iberia could have happened in the final decades of the 19th century and the early 20th century (when the oldest written references to breeding guillemots are dated), ending at some unknown point between the 1960s and 1970s (1962-1973 according to available counts), and this is the focus of the present study. Apparent mortality, identified as the main mechanism of the guillemot collapse in Iberia (Munilla et al. 2007), could hence reflect true mortality but also emigration/immigration to other metapopulation patches as a result of deteriorating regional environmental conditions (Martínez-Abraín 2015, but see Munilla and Velando 2015).

Because guillemots are known to feed on clupeids, and the study region supports a rich clupeid fishery, we propose as a working hypothesis that they were facultative specialists on clupeids in Iberia (i.e. they specialized locally in one prey type though it could changed from site to site), and that the crash of small pelagic fisheries likely caused a rapid collapse of guillemots. The diet of breeding guillemots in Atlantic Iberia is unknown, but the chicks and adults of the species typically consume fish from the families Ammodytidae, Clupeidae and Gadidae in European colonies (see e.g. Barrett and Krasnov 1996, Anderson et al. 2013, Budge et al. 2011). In some colonies they consume a high percentage of two Clupeidae: Atlantic herring (*Clupea arengus)* and European sprat (*Sprattus sprattus*) (99% in Wales and 96% in the Baltic Sea; Harris and Wanless 1984, Öesterblom and Olsson 2002). Moreover, a high percentage of the winter diet of guillemots in France is known to be composed of anchovies (*Engraulis encrasicolus*) and sardines (*Sardina pilchardus*) (Pasquet 1988). Direct, although anecdotal, evidence of sardine consumption by 20th-century Iberian guillemots comes from the report that out of 12 collection skins of birds captured in Galicia during the breeding seasons of 1964 and 1965 and preserved at the Doñana Biological Station, one of them contained a sardine in its stomach (Carlos Urdiales, pers. com.).

Collapses of large seabird colonies resulting from sudden crashes in its main local prey have been commonly reported (e.g. Cury et al. 2011, Erikstad et al. 2013, Sherley et al. 2013). Crashes in prey populations can cause the decline of predatory seabird populations by negatively influencing apparent survival (i.e. either true mortality or dispersal) or by heavily reducing offspring production and recruitment (e.g. Sandvik et al. 2012, Waugh et al. 2015, Fayet et al. 2021). Declines due to decreases in apparent survival happen faster than those caused by reduced fecundity and/or recruitment, which typically show a pattern of delayed effects arising from the late-maturing age of long-lived seabirds (Erikstad et al. 2013, Meade et al. 2013, Reynolds et al. 2019). Breeding dispersal is not common in guillemots, as is to be expected in long-lived species in which territorial vacancies are scarce (Harts et al. 2016). However, a catastrophic crash in staple prey species can force massive and rapid runaway dispersal of adults, as sometimes occurs in nesting colonial birds when a predator is involved (see Oro 2020). Additionally, sink seabird populations can experience fast declines if the rescue from source colonies by dispersal is discontinued (Bonnaud et al. 2009, Sanz-Aguilar et al. 2016, Seward et al. 2019).

Here we explore possible associations between the incomplete time series of breeding guillemot numbers in NW Iberia and the complete time series of sardine and anchovy landings at the regional level, used as a proxy of overall stock size. We expected to find some strong relationship between the time series of predator and likely prey species, in a similar way to that recently found by Martínez-Abraín et al. (2019) for the NW Iberian collapse of the black-legged kittiwake (*Rissa tridactyla*) population.

METHODS

We first compiled the most comprehensive time series available for common guillemot breeding numbers in Galicia (NW Spain, Fig. 1B) from 1961 to 2015 (55 years). Guillemot information available for 1961 is based on an estimate made by Bárcena (1985) from surveys of sailors and fishermen along the coast of Galicia. This estimate is consistent with the few quantitative data available before the 1960s that characterize the pre-collapse situation, showing relatively large numbers such as the 660 individuals on Sisargas Islands counted by Bernis (1948) and the *ca.* 6000 pairs in Berlengas Islands, Portugal estimated in 1939 (Lockley 1952). The next available counts after the 1961 estimate come from 1974-1976, and only provide partial information from four of the eight known breeding sites (Bermejo and Rodríguez-Silvar 1983, Bárcena 1985). Although the total number of pairs for that point in time should be somewhat larger, the data reflect unequivocally a reduction of two orders of magnitude in the number of individuals (from *ca.* 3000 to only 40). The next available counts correspond to the 1980s (Bárcena 1985). From then on, systematic censuses for the three remaining guillemot colonies became more frequent and were taken from Mouriño et al. (2004), adding our own unpublished data (Jorge Mouriño) since 2003. We provide a more detailed summary of guillemot count data in Appendix 1, indicating the period, the method used, the number of birds counted, the colony, the number of colonies and the data source. Guillemot counts in colonies were performed from May to June.

Secondly, we contrasted the guillemot time series with the information on sardine and anchovy landings for the period 1960-2015. Fish landings (May-October for sardines and April-June for anchovies) were obtained from the International Council for the Exploration of the Sea (ICES) official databases and used areas 8bc (anchovies) and 8c (sardines) (ICES 2017). In 2017 targeted anchovies were mostly Age 1 and Age 2 (around 13 cm in modal length) and all were sexually mature; targeted sardines also belonged to ages 1 and 2 and had a modal length of 16 cm (ICES 2017). These mean prey sizes are among the upper range of staple prey sizes delivered to chicks in northern latitudes (e.g. mean *Sprattus* length 11.5 cm; range 10.6-13.1 cm in Sweden; Enekvist 2003). Fish landings were assumed to be a good proxy of total clupeid stock size in the study region because fishing boats are added to the fishery when the stock size is large and removed when the stock shrinks. In addition, although the horsepower of fishing boats has increased over time, clupeid landings have shown an almost monotonic declining trend (anchovies since the 1960s and sardine since the early 1990s). Hence, if landings clearly follow a declining trend despite the increase in fishing effort or horsepower, the trend must reflect an actual decline, even stronger than that reflected by our uncorrected landings. Our approach can be considered conservative.

We fitted general linear models to ln-transformed guillemot counts and ln-transformed sardine/anchovy landings. A strong relationship (assessed by means of the coefficient of determination r^2 in comparison with models fitted to untransformed data) indicates an exponential relationship between the untransformed variables. Models were fitted using the software environment R and graphs were plotted using the ggplot2 library in R (https://www.r-project.org/).

We analysed the occurrence of regime shifts in the anchovy landings time series following Rodionov (2004), a technique based on sequential t-test analysis. To detect regime shifts, we used an add-in for an Excel spreadsheet developed by the National Oceanic and Atmospheric Administration (www.beringclimate.noaa.gov/regimes/index.html). The cut-off length was set at 10 years, following Cabrero et al. (2019) in a study of Iberian sardines. Huber's weight parameter was set at 1 (standard deviations) to account for the outliers by a weighting factor. Statistical significance was set at $\alpha=0.05$. Pre-whitening was performed before regime shift detection to prevent autocorrelation in time series that could increase the number of incorrectly identified regime shifts. Red noise was modelled with a first-order autoregressive model, and its coefficients were estimated by means of the ordinary least squares method. Since there were no counts of guillemots between 1961 and 1974, we were not able to run the regime shift tool for the common guillemot time series, as we did with both the sardine and anchovy landings time series. The use of a tool to fill in the missing values in the guillemot time series of counts was deemed unadvisable because of the large number of consecutive missing values (e.g. from a single count in 1961 to the next one in 1974). The large number of missing values in the guillemot time series also made it impossible to use more ad hoc analytical tools such as time-series analysis tools for the detrending of time series or the study of time delays.

Maps were generated using the free Maptool program available at www.seaturtle.org.

RESULTS

The abrupt collapse of guillemot numbers in an undetermined year between 1962 and 1973 can be deduced from Figure 2A. The time series of sardine and anchovy landings showed that a regime shift took place in sardines in 1968 and in anchovies in 1969 (Fig. 2B). These dates of prey crashes (1968 and 1969) might narrow down the collapse date of guillemots to the period 1968-1970 if the response of guillemots to prey scarcity was fast (i.e. the year after the sardine crash or the year after the anchovy crash, which would be two years after the sardine crash). Regime shifts in the sardine landings time series were also detected in 1980, 1988, 1998 and 2012, following the decadal-scale periodicity of sardine abundance cycles reported previously in the specialized literature (Cabrero et al. 2019). A second regime shift in anchovy landings was detected in 1979. All those regime shifts were not considered in our analyses as they happened when only a few guillemot individuals were remaining.

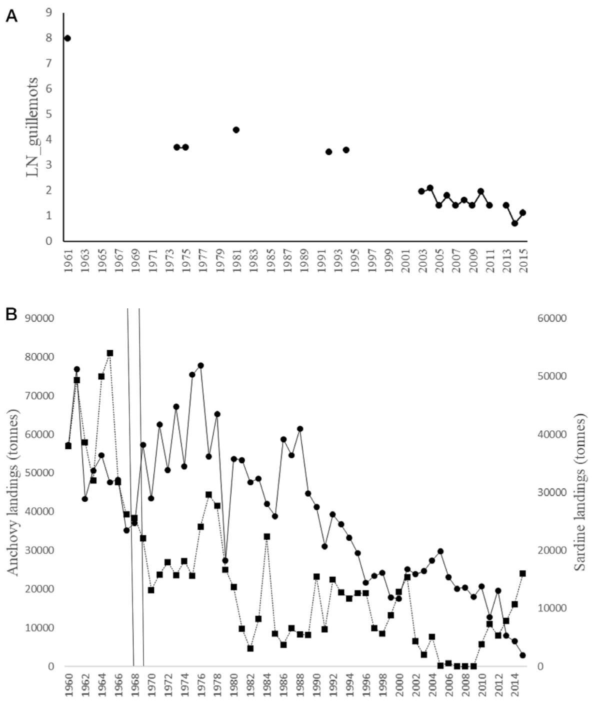

Fig. 2. – A, natural logarithm of the annual number of guillemot counts in NW Iberia from 1960 to 2015. B, time series of sardine (solid black line and black dots) and anchovy (dashed black line and black squares) landings in the study area over time for the same time period. The vertical bars depict the regime shifts detected within the time window of guillemot collapse (1968 for sardines, 1969 for anchovies).

The overall relationship between guillemot numbers and sardine landings was exponential (see Appendix 2 for the results of a linear model fitted to ln-transformed data, $r^2_{adj}=0.52$ compared with non-transformed data, $r^2_{adj}=0.27$).

The overall relationship between guillemot numbers and anchovy landings was linear, but completely dependent on the large 1960s large estimate of guillemots (see Appendix 2 for the results of a general linear model fitted to untransformed data, r^2_{adj}=0.72, compared with ln-transformed data, r^2_{adj}=0.13).

When the high 1961 pre-collapse guillemot count was excluded, general linear models fitted to both transformed (r^2_{adj}=0.61; Fig. 3) and untransformed guillemot and sardine data (r^2_{adj}=0.60) provided similar results, suggesting a linear relationship between the two variables at the scale of tens of guillemots or fewer.

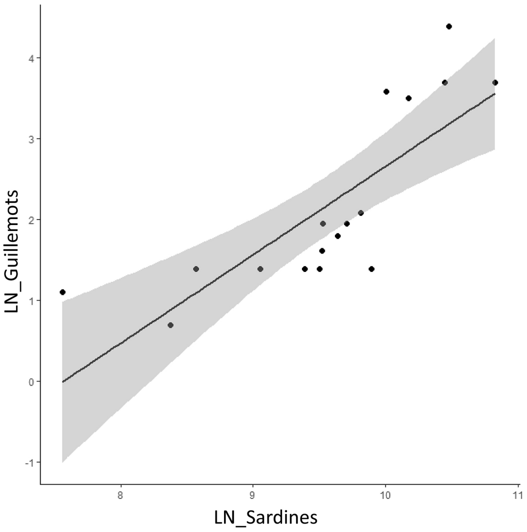

Fig. 3. – General linear model fitted to the ln-transformed data of common guillemot counts as a function of ln-transformed sardine landings in the study area for the period after the guillemot collapse (i.e. excluding the first large estimate from the early 1960s). The shaded area represents the 95% confidence interval of the model estimates (r^2_{adj}=0.61). The fit of a general linear model on untransformed variables was statistically equivalent (r^2=0.60).

However, we detected no relationship between the amount of anchovies landed and the number of guillemots after the collapse using either ln-transformed (r^2_{adj}=0.04) or untransformed data (r^2_{adj}=0.14).

As an exercise to assess the possibility of getting spurious results in our analyses, we detrended the guillemot and sardine landings time series from 2003 to 2015 (a continuous guillemot time series without missing data). The linear relationship was not statistically significant (F=1.6; 1 and 11 degrees of freedom; p-value=0.23). However, the detrended guillemot time series was shorter than the one we analysed (from 1974 on) and included guillemot abundance only at the scale of individuals, an order of magnitude smaller than the analysed time series with counts of up to 80 individuals.

Table 1. – Regime shifts (regime shift index, RSI) detected in the time series of sardine (ICES division 8c+9a) and anchovy landings (ICES divisions 8bc) between 1960 and 2015. Conf: confidence level of the difference between the mean values of the neighbouring regimes based on Student's two-tailed t-test with unequal variance and equivalent sample size. Values in bold are years with regime shifts around the reported period of guillemot collapse. Negative values of the RSI indicate declines and positive values indicate increases.

Parameter	Year	RSI	Conf
Sardine landings	**1968**	**–0.77**	**1.0×10^{-6}**
Sardine landings	1980	0.58	3.8×10^{-5}
Sardine landings	1988	–1.0	1.9×10^{-5}
Sardine landings	1998	–0.4	2.9×10^{-7}
Sardine landings	2012	–1.1	6.2×10^{-6}
Anchovy landings	**1969**	**–0.36**	**0.0012**
Anchovy landings	**1979**	**–0.62**	**0.0002**

DISCUSSION

Our results allowed us to reduce the current uncertainty about the dates of the guillemot collapse in Atlantic Iberia, suggesting that it most likely coincided with or immediately followed the crash of sardines and anchovies (1968-1970). A rapid response of guillemots to the abrupt decline of the two species of small pelagic fish seems feasible considering the colonization/extinction dynamics of the breeding population of black-legged kittiwakes that occurred two decades later in the same area. Kittiwakes colonized NW Spain and Portugal in the mid-1970s (Rodríguez-Silvar and Bermejo 1975), coinciding with a temporal recovery of the sardine stock during the 1970s and 1980s (see Fig. 3B for a peak of sardine landings in that period; Cendrero 2002, Cabrero et al. 2019). The kittiwake colonies, which were also located at the southernmost limit of their European distribution, collapsed two decades after their formation, coinciding with a severe crash of Iberian sardines in 1991 (see Martínez-Abraín et al. 2019) that has been permanent ever since. Guillemots and kittiwakes shared a similar nesting habitat along the Atlantic Iberian coast (i.e. cliffs and caves on small islets or large rock pinnacles), and even nested on the same locations at times (i.e. the Sisargas Islands, Cape Vilán; Fig. 1A). In both kittiwakes and guillemots, small pelagic fish abundance may have played a key role in regulating (bottom-up) metapopulation dynamics at the southernmost edge of European distribution.

Cases of rapid collapse of guillemot populations associated with crashes in their staple prey have been previously reported. For example, an 80% decline in a colony with 245000 guillemot pairs occurred in only one year on Bear Island, located on the Svalbard archipelago, Barents Sea (Norway). In this case, the decline was linked to low abundance indices of fish prey (Anker-Nilssen and Barrett 1991, Erikstad et al. 2013). Similarly, Gaston et al. (2009) found that long- and even short-term trends of Canadian seabirds (including guillemots) were strongly influenced by physical changes in the marine environment surrounding colonies, through food-web effects.

Local crashes of small pelagic fish can be driven by a severe primary productivity crisis arising from oceanographic changes (see e.g. Goyert et al. 2018), sometimes in interaction with overfishing. Other causes include recruitment problems after intense catches (Cendrero 2002) and mass displacements of fish due to changes in sea water temperature (Junquera 1986, 1991).

Iberian sardine stock dynamics in the second half of the 20th century were linked with changes in oceanographic conditions in interaction with overfishing (Holling 1973, Cendrero 2002). The Iberian anchovy crash in the late 1960s seemingly resulted from the shrinkage of the anchovy distribution (i.e. a permanent emigration of anchovies towards the eastern side of the Bay of Biscay) as a result of cold-water marine upwellings (see Junquera 1986, 1991, Uriarte et al. 1996, Cendrero 2002). This might well explain the strong linear relationship detected between anchovy landings and guillemot numbers when the whole time series was used versus the absence of relationship when only the guillemot time series without the first 1960s datum was considered. Simply, anchovies emigrated en masse out of the study area, and hence could not influence any further guillemot dynamics after their collapse because of the low anchovy densities. Additionally, the period in which anchovies are more abundant and hence are fished (April-June) only overlaps partially with the breeding period of guillemots (May-July), whereas the period of sardine abundance (May-October) is longer and overlaps better.

Relatively rapid recoveries can take place in large guillemot populations as a result of the exchange of individuals among colonies, making them more resilient to prey crashes than small colonies. For example, a recovery from 36000 pairs to 95000 pairs was reported in Bear Island in just two years by Anker-Nilssen and Barrett (1991). However, rapid recoveries do not always occur. For example, the guillemot population of Hornøya Island (Troms og Finnmark, Barents Sea, Norway) took 20 years to recover to the numbers reached before the collapse (Eriskstad et al. 2013).

Small edge populations are less likely to recover from abrupt environmental changes, as they experience both Allee effects (i.e. inverse density-dependence or depensation) and poor rescue by immigration (Schippers et al. 2011, Sanz-Aguilar et al. 2016). This is especially the case in populations in which the geographic range does not occur along a continuous distribution but shows a large gap in relation to the bulk of the population. This may have been the case of the common guillemot populations in Spain and Portugal, which were relatively small colonies (one recorded in Portugal and nine in Spain) and showed a considerable geographical gap between them and the French Bretagne and southern British populations (500-1000 km away; see Fig 1b). Probably owing to this marginal situation, the local Iberian guillemot populations were not rescued by immigration. Surprisingly, the guillemot time series showed a stable state of quasi-extinction during the last 13 years of study (2003-2015), even scoring 0 pairs in one year (2012) and then recovering a few pairs in subsequent years (2013-2015). This pattern was already described and discussed by Oro (2020) using the same guillemot time series and some other series.

Current sardine densities in the study area are far from the large figures of decades past (Cabrero et al. 2019). The same is true for anchovies, whose crashes in the 1960s to 1970s have been permanent until now (i.e. multi-decadal hysteresis). Only during the last few fishing seasons (2021), have anchovy catches seemingly shown some recovery along the western Bay of Biscay (according to media news on captures of anchovies in the western Cantabrian Sea). If sardine and/or anchovies were to again reach suitable densities to sustain a new recolonization of guillemots, conditions in the large northern European guillemot colonies (either as good as to provide a surplus or as bad as to cause long-distance dispersal) would be critical for the return of guillemots to southern European latitudes (see Oro 2020). However, current sea warming conditions promote reduced primary productivity by increasing the vertical stratification of the water column, which can make it difficult to recover past clupeid densities.

A word of caution finally to account for the statistically non-significant results of our exercise with detrended data from 2003 to 2015 (continuous time series without missing data). Our results would be much more reliable if performed on complete and detrended time series, but this was not feasible because of the large number of missing data in the guillemot time series. Our results make biological sense, although the possibility of getting some spurious results (cause-effect relationships) when working with poor data sets is always present.

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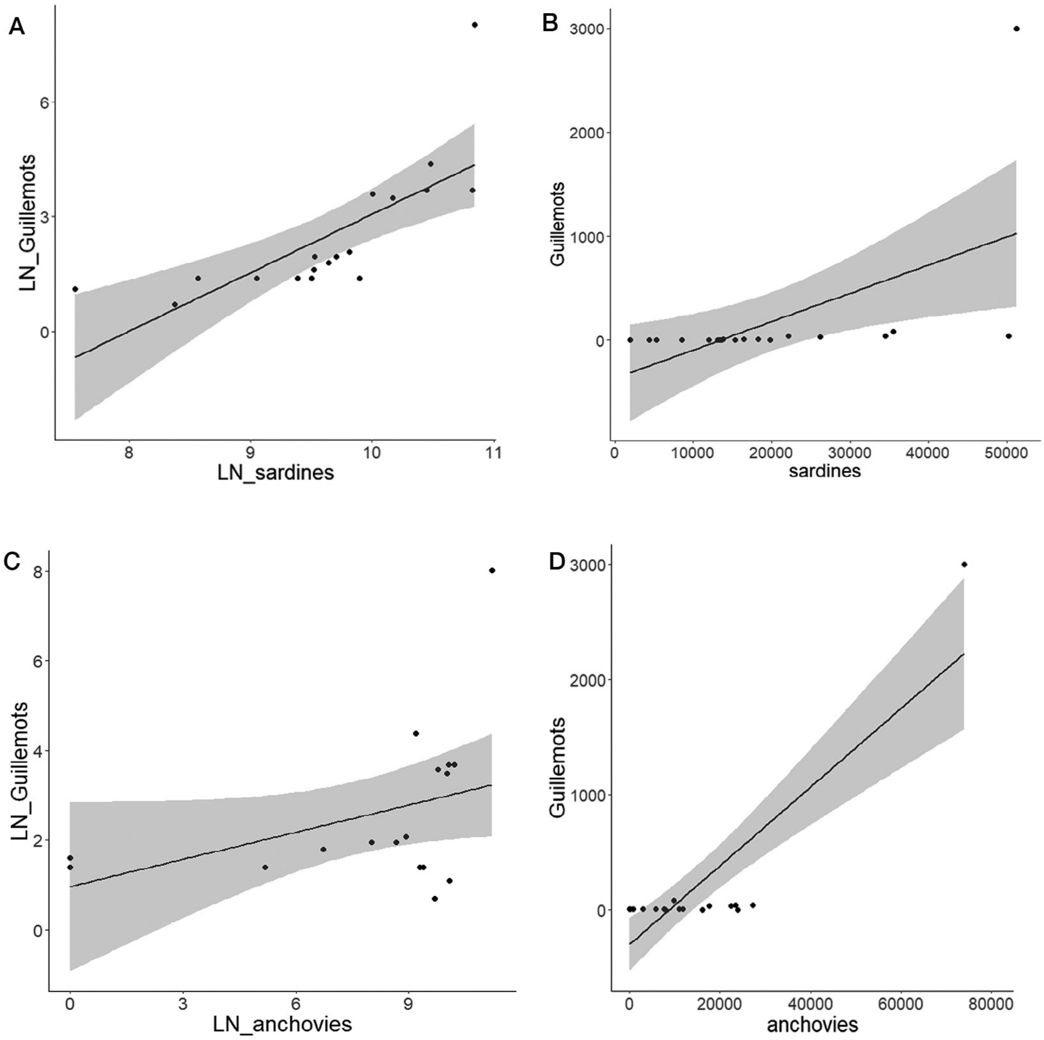
APPENDICES

Appendix 1. – Summary of the information available on common guillemot breeding numbers in Galicia, NW Spain.

Period	Method	No of birds	Colony	No of colonies	Source
1948	Counts of birds in the colony	660	Sisargas islands	1	Bernis (1948)
ca. 1960	Surveys to fishermen	ca. 3000	Galician coast	8	Bárcena (1985)
1974-75	Counts of birds in the colony	40	Sisargas islands	1	Bermejo and Rodríguez-Silvar (1983) Bárcena (1985)
1981-82	Counts of birds in colonies	80	Galician coast	3	Bárcena (1985)
1992/1994	Counts of birds in colonies	33/36	Galician coast	2	Mouriño et al. (2004)
2003-2015	Counts of birds in colonies	4-8	Galician coast	1-2	Own unpublished data (JM)
2016-2022	Counts of birds in colonies	0	Galician coast	0	Own unpublished data (JM)



Appendix 2. – Fits of general linear models to ln-transformed and non-transformed guillemot and sardine/anchovy landing data using the complete guillemot time series, including the first large early 1960s estimate. A, sardine landings and guillemot counts (ln-transformed data, exponential fit, r^2=0.52). B, sardine landings and guillemot counts (untransformed data, linear fit, r^2=0.27). C, anchovy landings and guillemot counts (ln-transformed data, exponential fit, r^2=0.13). D, anchovy landings and guillemot counts (untransformed data, linear fit, r^2=0.72)