

Research Article

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Insights obtained from a multidecadal citizen science scheme: grey seal (*Halichoerus grypus*) strandings in Cornwall and Isles of Scilly (2000–2020)

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Abstract

Changes in abundance and distribution of marine top predators can indicate environmental change or anthropogenic pressure requiring management response. Here, we used an extensive dataset (21 years) to conduct a spatial and temporal analysis of grey seal strandings in Cornwall and the Isles of Scilly, close to the southern edge of the breeding range of the species. A total of 2007 strandings were reported from 2000 to 2020, increasing by 474% from 35 to 201 individuals per year during this period. The continued rise in strandings was consistent across all life stages and timeframes (5, 10 and 20 years), underpinning the suggestion of increasing abundance in the region. The observed seasonality differed by life stage, coinciding with the increased presence of animals near the coast for key life phases such as breeding, moulting and pupping. Strandings are widely distributed across the coast of Cornwall and the Isles of Scilly; however, most strandings were recorded on the north coast of Cornwall (70%) where major pupping and haul out sites are found. Despite hosting several pupping and haul out sites, a small proportion was recorded on the Isles of Scilly (5%) where it is thought that strandings are particularly underreported. Describing baselines in magnitude of strandings and life-stage compositions across space and time allows future deviations in frequency, demographic composition or spatial distribution to be detected and investigated. We demonstrate the utility of long-term citizen science data to provide valuable and cost-effective information on the distribution and abundance of a highly mobile marine mammal.

Introduction

Monitoring marine vertebrates

Understanding trends in the abundance and distribution of species is essential for their effective conservation (Bowler *et al.*, 2022), in particular to assess response to management measures and to assess and reduce potential overlap with anthropogenic activities (Bograd *et al.*, 2010; Bianchi *et al.*, 2022). Moreover, site conservation objectives for environmental legislation such as for marine special areas of conservation (SACs) may require managers to report on trends in abundance of key species. Many marine vertebrates are widely dispersed at low densities for much of the annual cycle and, as such, obtaining reliable estimates of abundance and dispersion from direct observations is often difficult (Peltier *et al.*, 2013; Rohner *et al.*, 2022). Furthermore, monitoring demographic trends and population dynamics over timescales that are meaningful for long-lived species can be limited by the high cost of equipment and dedicated aerial surveys or marine cruises (Hammond *et al.*, 2013; Peltier *et al.*, 2014; Meager and Sumpton, 2016; Thompson *et al.*, 2019).

Utility of strandings

Strandings can serve as an ongoing surveillance tool to provide valuable and cost-effective information on highly mobile marine species which would otherwise be difficult to obtain *in-situ* (Ijsseldijk *et al.*, 2020). A long time series of strandings data can also set a comprehensive baseline which can be used to monitor deviations in mortality numbers (Prado *et al.*, 2022). The importance of stranded animals for biological information and monitoring has long been demonstrated (Peltier and Ridoux, 2015), generating important data for birds (Ortiz-Alvarez *et al.*, 2022), turtles (Tomás *et al.*, 2008; Brunson *et al.*, 2022), cetaceans (Coombs *et al.*, 2019), sharks (Wosnick *et al.*, 2022), sirenians (Adimey *et al.*, 2014), seals (Baker, 1984) and invertebrates (Sheehan *et al.*, 2017; Canepa *et al.*, 2020). Carcasses of stranded individuals present an excellent opportunity to gain knowledge and understanding of rarely observed species (Chan *et al.*, 2017), and offer insights into causes of mortality

and incidence of disease (Hart *et al.*, 2006; ten Doeschate *et al.*, 2017; Brunson *et al.*, 2022; Ortiz-Alvarez *et al.*, 2022). Strandings can also act as early indicators of environmental change by documenting species occurrence and revealing shifts in distribution due to changing oceanic conditions (Truchon *et al.*, 2013; Byrd *et al.*, 2014; Prado *et al.*, 2016; Sepúlveda *et al.*, 2020; Warlick *et al.*, 2022).

Strandings in seals

Pinnipeds are top predators living at the land–sea interface and as such are often considered sentinels of ocean health (Bossart, 2010; Warlick *et al.*, 2018). For animals that spend much of their time by the coast such as seals, strandings databases are of particular utility to help understand some of the threats they face, as well as gaining insights into their life history and behavioural responses to their natural environment and anthropogenic activities. Analysis of long-term strandings records of northern elephant seals (*Mirounga angustirostris*) and Pacific harbour seals (*Phoca vitulina*) in central California, for example, revealed annual variability in the prevalence of several diseases, which is especially relevant for the evaluation of risk factors of disease in the wild population (Colegrove *et al.*, 2005). Similarly, in Californian sea lions (*Zalophus californianus*), strandings records were used to identify regional and seasonal fisheries interaction hotspots, with fisheries interactions found to be greater under El Niño oceanographic conditions which affect prey availability (Keledjian, 2013).

Life history of grey seals

Grey seals are one of the UK's most abundant marine mammals (Leeney *et al.*, 2010; Barnett *et al.*, 2021). Although they forage across wide ranges at sea, grey seals regularly return to land to rest, gathering in large aggregations during the breeding (September–December) and moulting (December–April) seasons (Hewer, 1974). Whitecoat pups are generally born during autumn and winter with a non-waterproof, white lanugo coat, and are weaned at around 15–21 days before all maternal care ceases and they must learn to forage independently (Pomeroy *et al.*, 1999; Carter *et al.*, 2017). Following a post-weaning fast, during which they lose up to 25% of their body mass (Noren *et al.*, 2008), pups leave their natal site and move into an exploratory dispersal phase before settling, often a considerable distance from their place of birth (Carter *et al.*, 2020; Peschko *et al.*, 2020). Outside the breeding season, grey seals exhibit local redistributions and partial migration to foraging grounds – often several hundred kilometres offshore and are dispersed at much lower densities (Sayer *et al.*, 2021; Carter *et al.*, 2022).

UK grey seal populations

Historically, numbers of grey seals around British coasts were reduced by commercial and subsistence hunting and, in 1914, following concern about local extirpation, they became the first mammal in the UK to be protected by legislation (Thomas, 2019). Current legislation (The UK Conservation of Seals Act 1970) requires the Natural Environment Research Council (NERC) to provide scientific advice to UK and Scottish governments on matters related to the status and management of seal populations. In order to provide advice on assessment and management at appropriate spatial scales, the UK Statutory Nature Conservation Bodies require an understanding of the geographical range of populations and subpopulations. Fourteen small management units (SMUs) were defined on the basis of distribution of haul out sites and for reasons such as jurisdictional boundaries

and the ability to survey within one season (SCOS, 2021). However, it is important to note that SMUs do not infer discrete populations, and although often monitored independently, they are not managed as such. SMU 11 refers to the southwest England management unit, comprising mainland Cornwall, the Isles of Scilly, Lundy Island and mainland Devon. Monitoring within this SMU is primarily conducted by the Seal Research Trust (SRT) and the Lundy Company.

Despite grey seals being one of the most abundant marine mammals in the southwest of the UK, the abundance and dynamics of the species in this region is poorly understood due to the uncertainty surrounding influx and efflux of individuals from neighbouring regions. Several studies have observed seals in France, Wales and Ireland which were known to have been born in Cornwall and the Isles of Scilly (Vincent *et al.*, 2005, 2017), demonstrating that animals in this region are not geographically isolated and are an integral part of a metapopulation spanning the Celtic Sea.

Additionally, the difficulty of conducting pup counts during the first few weeks of pup production, which is considered to be the only component of grey seal populations to provide reliable population estimates (Cronin *et al.*, 2007), limits understanding of the seal abundance in this region. In Scotland and the east coast of England, most of the breeding sites are open beaches or on islands which make aerial or land-based surveys achievable; however, in southwest England and Wales seals often breed in caves and narrow coves which means aerial surveys would miss a large proportion of individuals (Stringell *et al.*, 2014). For this reason, the southwest SMU is not included in the population model currently used by Special Committee on Seals (SCOS) to estimate pup production in grey seals (SCOS, 2021) and data for this region are thought to be underrepresented in the UK total figures (Sayer *et al.*, 2020). This modelling has revealed a steady increase in numbers in the last 40 years, but the rate of growth varies regionally (Russell *et al.*, 2019; SCOS, 2020).

Grey seals in Cornwall

Cornwall and the Isles of Scilly is the southernmost point of grey seal distribution in the UK and close to the southernmost point of the breeding range for the species (Westcott, 1997). Although the numbers of breeding grey seals in southwest England likely represent less than 1% of the UK population (SCOS, 2020), monitoring in this region may be key to understanding the dynamics of grey seals across their range (Leeney *et al.*, 2010). Grey seals are also a designated feature of the Isles of Scilly SAC and much of the archipelago falls within Marine Conservation Zone protection. Here, we set out to conduct a spatial and temporal analysis of grey seal strandings around the coast of Cornwall and the Isles of Scilly spanning 21 years (2000–2020), elaborating any temporal and seasonal trends and highlighting strandings hotspots, data which may be built upon and used to inform management of the species within this region.

Methods

Study area and data collection

The study area is shown in Figure 1. Data used were compiled from records extracted from the Cornwall Wildlife Trust Marine Strandings Network (CWTMSN) database, which currently holds over 10,000 records of strandings at the Environmental Records Centre for Cornwall and the Isles of Scilly (ERCCIS). CWTMSN collects records of stranded marine organisms across all taxa in Cornwall and the Isles of Scilly and a network of volunteer recorders has provided a comprehensive reporting and

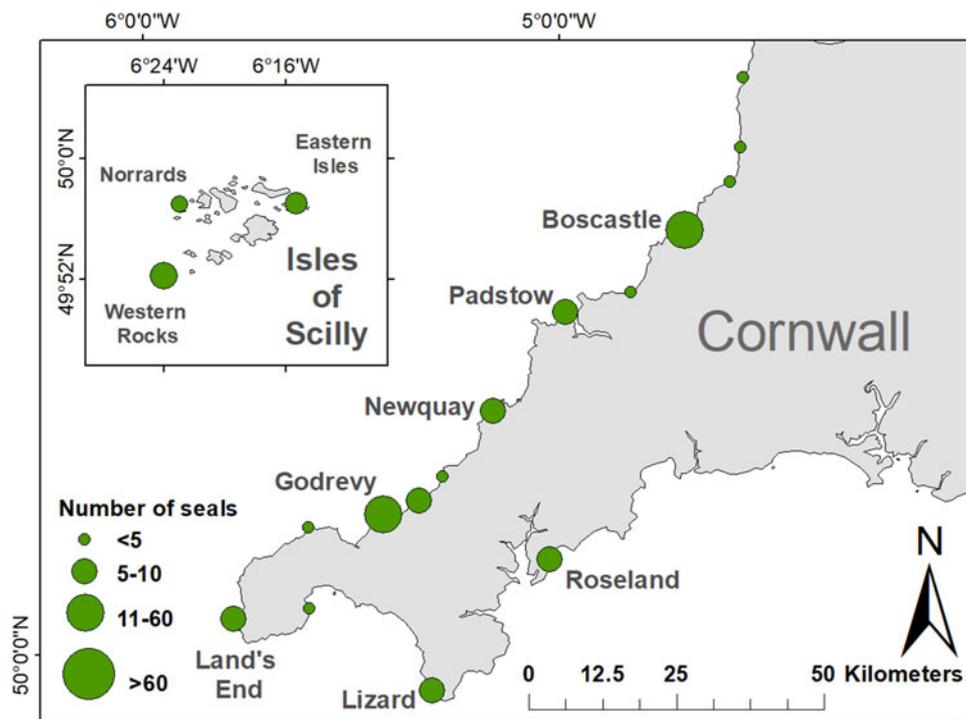


Figure 1. Study area of Cornwall and the Isles of Scilly (inset), UK illustrating key sites. Major haul out sites as defined by Leeney *et al.* (2010) are labelled with text. Main pupping sites are highlighted with relevant values for Cornwall (Sayer *et al.*, 2020) and the Isles of Scilly (Sayer *et al.*, 2012).

recording system for strandings, in particular of marine mammals for the last 27 years. Rigorous procedures for reporting and recording stranded marine animals, coupled with volunteer training in investigating carcasses, ensure accuracy of the records held. All strandings volunteers are given detailed training to ensure accurate and consistent data collection and are continually supported by ERCCIS staff. Detailed reports and photographs are obtained where possible, which are then verified and assessed by experts to avoid multiple counts of the same stranding. The CWTMSN has a dedicated Strandings Hotline for the reporting of dead stranded marine animals, which operates year-round and is staffed by a rota of dedicated volunteer Hotline Coordinators, reducing the likelihood of strandings going unreported. Carcasses reported to CWTMSN are either examined *in-situ*, or via post-mortem examination by a veterinary pathologist. Despite regular turnover, the overall number of active volunteers remains the same year on year. In 2005, there was a concerted effort to raise awareness of the strandings scheme and level of reporting, but since then it is assumed that the level of public awareness, and subsequent effort of reporting, has stabilised (Crosby, personal observation).

Records of grey seal strandings ($n = 2007$) spanning a recent 21-year period from 2000 to 2020 were extracted from the CWTMSN database. Grey seal strandings have been recorded in detail on the CWTMSN database since 2000, and data are reviewed and assessed in partnership with the Seal Research Trust (Crosby and Hawtrey-Collier, 2020). Initial screening of the data involved discarding records not suitable for spatio-temporal analysis based on the level of decomposition. Stranded animals are assigned a decomposition score between 1 and 5, with score 1 referring to an animal which is alive and scores 2–5 for dead animals. The CWTMSN database only holds records of dead stranded animals. We included all animals with scores 2 (freshly dead) and 3 (moderate decomposition). More decomposed carcasses with a score of 4 (advanced decomposition) or 5 (mummified/skeletal) were omitted to account for any temporal bias ($n = 362$), as it is not possible to determine with confidence

how recently such animals have died and an accurate life stage can be less easily established. To ensure an accurate life stage was assigned wherever possible, each record was cross-checked against descriptions, photographs and life-stage categories (HC). The latter are classified by CWTMSN based largely on body length (nose to hind flipper measurement), with animals >160 cm classified as adults, ≤ 160 cm as juveniles, ≤ 120 cm as pups in their first year of life, and pups with white neonate lanugo coat classified as pre-weaned pups, hereafter referred to as ‘white-coats’. Records where no life-stage category could be determined were excluded from the analysis ($n = 96$).

Spatial analysis

All records have an associated grid reference relating to the location of the stranding. These were cross-checked against the described location of the stranding and converted to the longitude and latitude format for use in ArcMap GIS software (version 10.8.1). Records where no location information was available, or where the animal was floating at sea, were removed from the data ($n = 15$). Kernel density estimate (KDE) analyses were used to identify spatial clusters of strandings (Worton, 1989) using a 2000 m search radius. All analyses were conducted using the OSGB_1936 coordinate system and an OSGB 1 km sampling grid.

Statistical analysis

Five negative binomial and binomial generalised linear models (GLMs) were considered for the analyses and were checked for overdispersion and temporal autocorrelation. These are discussed below, and results are shown in Table 1.

Temporal trend by life stage

The first model investigated the variation in the annual number of grey seal strandings over time for each of the four different life stages (1a). This model was replicated to investigate the variation in the relative contribution of each life stage to the annual number

Table 1. Summary results of GLMs for each key question

Key question (model number)	Model (GLM)	Response variable	Fixed effects	Intercept	df	logLik	AIC	Δ AIC	Weight
Multi-annual temporal trend by life stage (1a)	Negative binomial	Annual number of strandings	~Life stage + year	-184.3	6	-258.90	529.8	0.00	0.892
	Negative binomial		~1	2.915	2	-317.36	638.7	108.91	0.00
Temporal trend in relation contribution by life stage (1b)	Binomial	Annual proportion	~Life stage	-0.970	4	-134.29	276.6	0.00	0.696
	Binomial		~1	-1.01	1	-152.038	306.1	29.4	0.00
Multi-annual temporal trend by life stage and sex (2a)	Negative binomial	Annual number of strandings	~Life stage + sex + year + life stage: sex	-203.10	10	-345.85	711.7	0.00	0.991
	Negative binomial		~1	1.38	2	-418.72	841.4	129.75	0.00
Temporal trend in relation contribution by life stage and sex (2b)	Binomial	Annual proportion	~Life stage	-0.970	4	-136.33	280.7	0.00	0.695
	Binomial		~1	-1.0990	1	-154.36	310.7	30.07	0.00
Seasonal trend by life stage	Negative binomial	Monthly number of strandings	~Life stage + month + year + life stage: month + month:year	-249.40	61	-1328.85	2779.7	0.00	0.665
	Negative binomial		~1	0.4293	2	-1699.35	3402.7	623.01	0.00

df, degrees of freedom; logLik, log likelihood; AIC, Akaike's information criterion; Adj. weight, adjusted weight.

Top-ranked models and adjusted weights after selection for Δ AIC ≤ 2 and applying the nesting rule. Top set models are highlighted in bold.

of strandings over the time series (1b). The response variables were the annual number of strandings and the annual proportion of strandings for models 1a and 1b, respectively. For both models, the fixed effects were year, life stage and their interaction to investigate whether the number or annual proportion of strandings differed between life stages and over time.

Temporal trend by sex and life stage

Due to factors such as scavenger damage, sex was undetermined for more than half of the dataset. Therefore, a separate model was used to investigate temporal variations in grey seal strandings between sexes and life stages over the study period (model 2a).

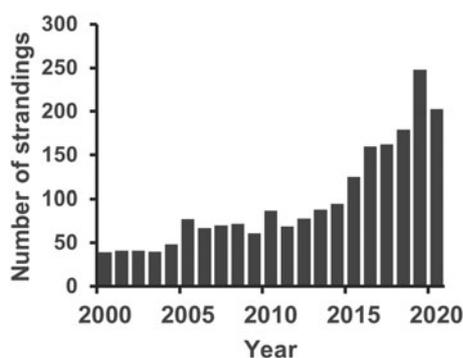


Figure 2. Temporal patterns of seal strandings Cornwall and the Isles of Scilly (2000–2020). Annual number of grey seal (*Halichoerus grypus*) strandings ($n = 2007$) in Cornwall and the Isles of Scilly (2000–2020).

This model was replicated to investigate variation in the annual proportion of each sex within each life stage and was then modelled to examine whether the relative contribution of each sex differed over the time series (model 2b). The response variables were the annual number of strandings and the annual proportion of strandings for models 2a and 2b, respectively. For model 2a, the four fixed effects were year, life stage, sex and an interaction term between year and sex to investigate any difference in strandings over time between males and females. For model 2b, the three fixed effects were year, life stage and their interaction to investigate whether the number of strandings or the annual proportion of strandings differed between life stages and over time.

Seasonal distribution

A final model examined the within-year temporal variation in grey seal strandings across life stages (model 3). The response variable was the monthly number of strandings and the fixed effects were life stage, month, year, an interaction term between life stage and month to determine if the seasonal trend differed between life stages within each life stage and an interaction term between month and year to investigate monthly variations among years.

Model selection process

All analyses were conducted in the MASS package (Venables and Ripley, 2002) in R v4.2.0 (R Core Team, 2022). All combinations of terms were examined and ranked by Akaike's information criteria (AIC) using subset selection of the maximal model using the MuMIn package v1.46.0 (Bartoń, 2022). Top-ranked models were

defined as models $\Delta\text{AIC} \leq 2$ units of the best supported model, after excluding further models where a simpler model attained stronger weighting ('nesting rule'; Richards *et al.*, 2011).

Results

Temporal trend by life stage

A total of 2007 grey seals were recorded stranded dead in Cornwall and the Isles of Scilly between 2000 and 2020 (Figure 2), 1549 of which were suitable for our detailed analyses. The total number of strandings in each life stage were as follows: adults ($n = 418$, 27%), juveniles ($n = 329$, 21%), pups ($n = 499$, 32%) and whitecoats ($n = 303$, 20%).

The annual number of strandings increased by 575% (for all life stages combined) between 2000 and 2020 (Figure 3, Table 1). The overall annual rate of increase from 2000 to 2020 was 23%. The annual rate of increase remained steady throughout the most recent part of the study period, with a mean annual rate of increase of 13.1% for 2010–2020 and of 12.1% for 2015–2020. The relative contribution of individuals by each life stage each year remained relatively constant throughout the study period, with pups representing $31.6 \pm 1.7\%$ (mean \pm SE) of strandings each year, followed by adults ($27.5 \pm 1.6\%$), juveniles ($21.3 \pm 1.5\%$) and whitecoats ($19.6 \pm 1.5\%$; Figure S1, Table 1).

Temporal trend by sex and life stage

Strandings were composed of 27% males ($n = 418$) and 16.5% females ($n = 256$), while sex remained undetermined for more than half of individuals (56.5%, $n = 875$). Sex was unknown for 44.5% of adults, 53.5% of juveniles, 59.9% of pups and 70.6% of whitecoats.

Of the individuals of known sex, the annual number of strandings was influenced by life stage, sex, year and the interaction between life stage and year (Table 1). For all life stages, consistently more males stranded over time than females (Figure S2), though the relative annual contribution of each sex within each life stage remained relatively constant over the study period (Figure S2, Table 1). On average, males represented $72.8 \pm 2.9\%$ of adults, $55.6 \pm 4.0\%$ of juveniles, $51.8 \pm 3.5\%$ of pups and $66.7 \pm 5.0\%$ of whitecoats stranding across the period (Figure S3).

Seasonal distribution

Overall, most stranding events occurred during the autumn (September–November; 42.4%, $n = 657$) and the winter (December–February; 35.1%, $n = 544$) compared to in spring (March–May; 12.1%, $n = 188$) and summer (June–August; 10.3%, $n = 160$).

The number of strandings was influenced by life stage, month, year and the interaction between life stage and month (Table 1). The seasonal pattern of strandings was different for each life stage, with monthly stranding numbers showing slight variations throughout the year for adults and juveniles, while patterns were more pronounced for the other two life stages (Figure 4). Pup strandings increased gradually from September, peaking in January and decreasing until March before remaining relatively stable (Figure 4). For whitecoats, very few strandings occurred between January and August, before increasing and peaking in October, after which they decreased (Figure 4).

Spatial distribution

The spatial distribution of grey seal strandings was widespread across the entire coast of Cornwall and the Isles of Scilly; however,

more strandings were found on the north coast of Cornwall ($n = 1099$) than the south coast of Cornwall ($n = 372$) or Isles of Scilly ($n = 78$; Figure 5). This distribution was consistent over time with a mean \pm SD of annual proportions of $71 \pm 6\%$ of strandings occurring on the north coast of Cornwall, $24 \pm 7\%$ on the south coast of Cornwall and $5 \pm 4\%$ on the Isles of Scilly.

The spatial distribution was also consistent across all life stages. Two-thirds of adults ($n = 282$, 67%), and 67% of juveniles ($n = 220$), 72% of pups ($n = 480$) and 82% of whitecoat pups ($n = 117$) were found on the north coast of Cornwall (cf. south coast of Cornwall: $n = 114$, 27% adults; $n = 101$, 30% juveniles; $n = 141$, 21% pups and $n = 16$, 11% whitecoats). Very few animals were found on the Isles of Scilly ($n = 24$, 5% adults; $n = 9$, 2% juveniles; $n = 37$, 5% pups and $n = 8$, 5% whitecoats). Hotspots of strandings, particularly for whitecoats and pups (Figure 5) occurred close to major pupping and haul out sites on the mainland as shown in Figure 1.

Discussion

In this study, we used a 21-year dataset to conduct a spatial and temporal analysis of grey seal strandings around the coast of Cornwall and the Isles of Scilly. This has led us to a number of insights into the biology and status of the one of the most abundant marine mammals in the southwest of the UK and allows us to present a baseline and life-stage breakdown of strandings across space and time. This initiative is noteworthy in its duration and highlights the importance of citizen science to obtain synthetic long-term data over a large geographical scale.

Increase in strandings

Our analysis identified a considerable increase in grey seal strandings year on year. Increased numbers of strandings may be a consequence of increased abundance, increased mortality, unusual environmental conditions or of greater observer effort (Pikesley *et al.*, 2012; ten Doeschate *et al.*, 2017). The observed increase in strandings remained relatively steady throughout the study period and the rate of increase was also consistently positive and similar across different timescales (recent 5 years, 10 years, 20 years). The fact that the rate of increase was found to be similar across life stages and sexes makes it unlikely that any single cause of increased mortality is acting on seals and lends some support to an overall increase in abundance.

Increased abundance could be resultant from an increase in breeding output in the region. Conducting pup counts during the first few weeks of pup production is considered to be the only life-history component to provide reliable grey seal population estimates (Cronin *et al.*, 2007). Elsewhere in the UK, these counts are conducted using aerial surveys; however, the topography of pupping sites in Cornwall and the Isles of Scilly precludes this method (SCOS, 2021). Suggestions have been made previously to conduct staged counts of whitecoat pups at 3-week intervals from land to produce pup production estimates, based on the assumption that all pups counted in the previous survey will have moulted by the second survey (SCOS, 2020, 2021). However, most pupping sites in the Isles of Scilly can only be surveyed by a boat, which can be expensive and dangerous to conduct, as well as being associated with high levels of disturbance. On mainland Cornwall, Sayer *et al.* (2020) found that <5% of pups were detectable only from boat-based surveys, suggesting that very few pups would be missed by conducting only land-based surveys in this region.

A boat-based census of the Cornwall and Isles of Scilly coast conducted over 4 days in 2007 by Leeney *et al.* (2010) at the end of the moulting season observed a total of 592 seals, of

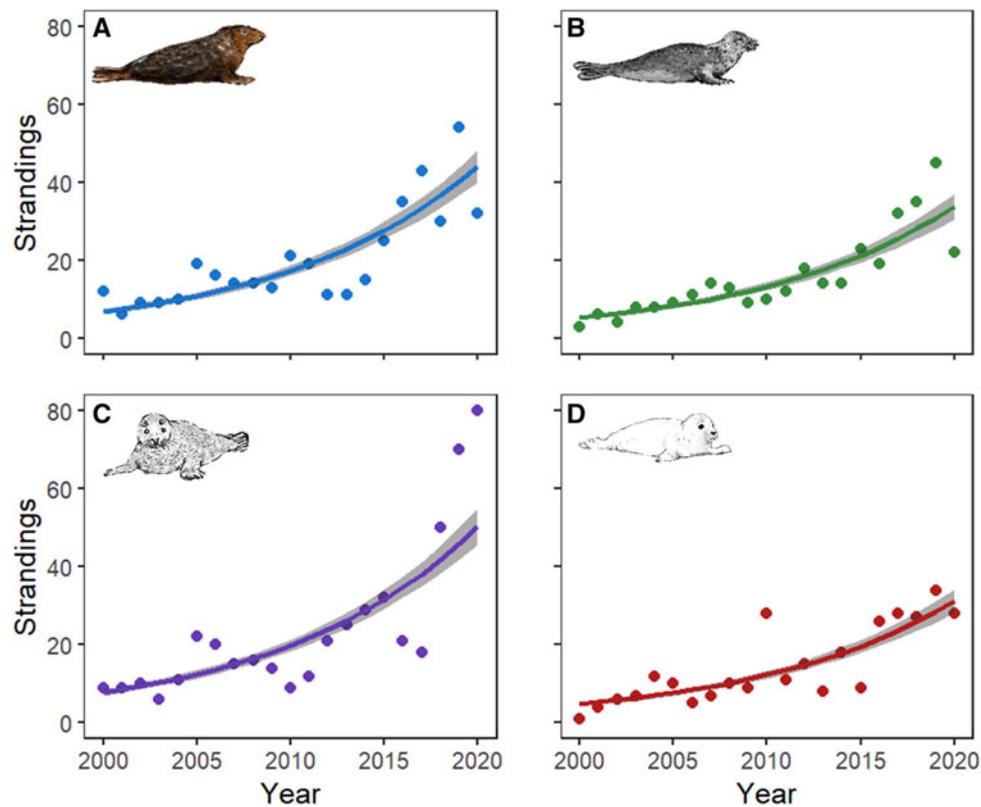


Figure 3. Temporal trends of strandings of different grey seal life stages in Cornwall and the Isles of Scilly from 2000 to 2020. Adults are shown in blue in panel (A), juveniles in green in panel (B), pups in purple in panel (C) and whitecoats in red in panel (D). Solid lines denote predictions from the top-ranked model 1a presented in Table 1. Standard errors are shown by the grey shaded area in each panel.

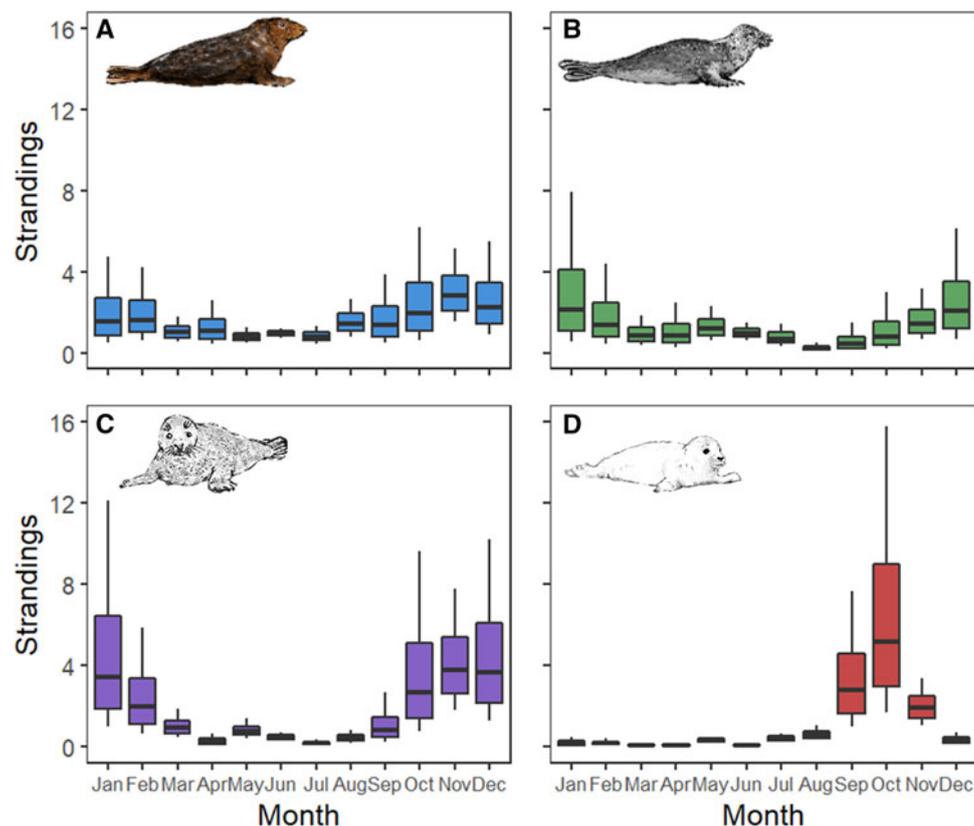


Figure 4. Seasonal distribution of grey seal strandings recorded in Cornwall and the Isles of Scilly from 2000 to 2020. Adults are shown in blue in panel (A), juveniles in green in panel (B), pups in purple in panel (C) and whitecoats in red in panel (D). Predictions from the top-ranked model 3 presented in Table 1 are shown as boxplots, indicating the median and interquartile range. Whiskers indicate minimum and maximum values for each month.

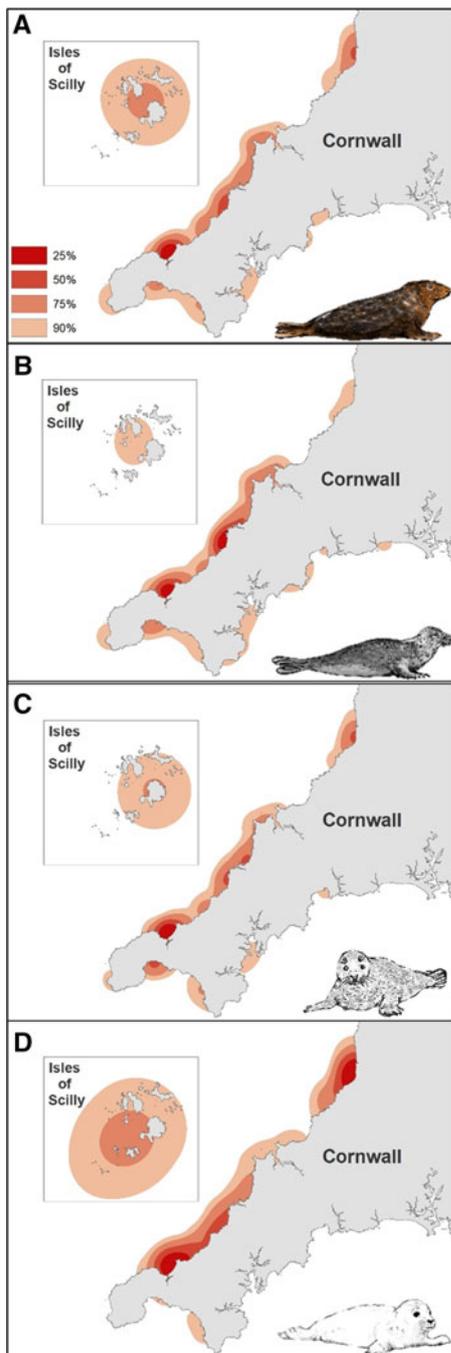


Figure 5. Spatial distribution of grey seal strandings by life stage recorded in Cornwall and the Isles of Scilly from 2000 to 2020. Panels (A)–(D) show the spatial distribution of adults, juveniles, pups and whitecoat pups, respectively. Darker shades represent a higher density of strandings per km². KDE percentile breaks set at 25, 50, 75 and 90%. Note: see Figure 1 to contextualise with main haul out and pupping sites.

which 472 were adults. Similar surveys (not including the Isles of Scilly) have been carried out annually by the Seal Research Trust (formerly Cornwall Seal Group Research Trust). While there is significant seasonal and interannual variation in numbers recorded, there has been no apparent increase in abundance of seals recorded. To address possible seasonal variation, SRT began quarterly surveys in 2018, though more data are needed to assess any interannual trend (2008–2022; Sue Sayer Seal Research Trust (SRT), personal communication).

In mainland Cornwall, pup production was estimated to be ~110 in 2016 (Sayer and Witt, 2018) and ~150 in 2019 (Sayer *et al.*, 2020). For the Isles of Scilly, pup production numbers

were estimated at 89–134 in 2010 (Sayer *et al.*, 2012) and 221–234 in 2016 (Sayer and Witt, 2018). Unless more is known about pup mortality rates, it is not known whether this reflects any overall increase in seal numbers. Relatively fewer seal pups are recorded in Devon, though 43 were recorded in a 2019 survey on Lundy Island (Jones, 2020). At this stage, with partial and limited comparable published data, any interannual variation cannot be considered as evidence of any trend. A comparison of grey seal strandings, extension of quarterly counts and long-term pup production surveys will be useful to assess pup mortality rates and reduce the uncertainty surrounding seal abundance estimates in the South West.

Increased numbers of seals could be due to immigration from elsewhere. According to SCOS reports (2021), the most likely source of immigrants to the South West would be from the Hebrides where the large breeding population has been stable and survival rates of post-weaning juveniles are estimated to be low. Movements between the UK and elsewhere are also well documented, with as much as 35% of the observed population growth of grey seals in the Dutch Wadden Sea being attributed to immigration of grey seals from the UK, that are known to visit the area temporarily (Brasseur *et al.*, 2015). It is clear that further work would be beneficial to look at movements into and out of the South West region to better understand the abundance there.

Patterns across life stages

The fact that the increasing trend in strandings was found to be consistent across life stages and that the annual rate of increase was relatively consistent despite volunteer effort remaining stable, underlines the likelihood of increasing seal abundance in Cornwall and the Isles of Scilly. Additionally, it suggests no major difference in drivers of mortality over time. In a study of 107 post-mortem examinations of grey seals in southwest England between 2013 and 2020, trauma was the most common primary pathological finding (45%) followed by infectious disease (34%; Barnett *et al.*, 2021). Fisheries-related trauma – bycatch and entanglement – was suspected to be the primary pathological condition in 14% of seals examined and rates of entanglement in marine debris as high as 5% have been observed elsewhere in live grey seals in Cornwall (Allen *et al.*, 2012). Approximately 81% of UK seal bycatch is known to occur in the southwest (SCOS, 2021). The most recent estimated bycatch of seals in UK fisheries was in 2019 and amounted to a total of 488 animals. Although this number is not large in the context of the entire UK population, most of this bycatch is known to occur around the Celtic Sea, where numbers are much smaller and effects may be less sustainable. Furthermore, these figures were based on estimates from UK-registered vessels only and as such are likely to underestimate the total bycatch in the region. Inclusion of bycatch from Irish, French and Spanish vessels working in the same region would undoubtedly increase these numbers (Luck *et al.*, 2020).

Due to challenges in reliably sexing carcasses, over half of animals subject to analysis were of unknown sex; however, of the individuals where sex was known, there appeared to be an over-representation of males. Previous studies on the demographics of stranded grey seals suggest that there may be a slightly skewed sex ratio which favours males (Sayer *et al.*, 2012; SCOS, 2021). Males make up a larger proportion of adults sighted across southwest England (Sayer *et al.*, 2019) and this sex bias is reflected in the number of male grey seal pups admitted for rehabilitation in the region (Barnett and Westcott, 2001). This male-skewed sex distribution also appears to be present in other regions of the UK. For example, in Scotland, a greater proportion of pups

reported dead and ailing on North Rona were male (Boyd and Campbell, 1971), and on the Isle of May, Hall *et al.* (2001) reported male grey seals having a lower probability of post-weaning survival in the first year of life. Although it is not fully understood why more males appear to strand, one possibility is greater risk taking in males. For example, Carter *et al.* (2017) found that male pups in the Celtic Sea travel further offshore and dive deeper than female pups. As males need to reach a large enough body size for competitive breeding, they forage in deeper water further offshore looking for larger prey and thus expose themselves to a greater risk of starvation when compared with females, which subsist on predictable but low-yield prey such as sand eels in shallow coastal bays. Additionally, a review by Northridge *et al.* (2017) found a male-skewed sex bias in grey seals bycaught in gillnet fisheries, again possibly due to increased risk taking. This is an area which would benefit from greater understanding and should be investigated further.

Seasonality

There were pronounced and consistent annual cycles in patterns of stranding, generally spanning from late summer into autumn and winter. Unsurprisingly, the temporal distribution of strandings of whitecoats closely matched the pupping season. In southwest England, this occurs from mid-August through to December, with the peak production occurring between August and October (Sayer *et al.*, 2012; Silpa *et al.*, 2015; SCOS, 2021). Seasonal peaks in strandings for the other life stages occurred around times when greater numbers of animals are on and near the coast for key events, such as breeding and moulting phases for adults and the post-weaning dispersal phase for pups.

Autumn and winter are also the time when the weather, particularly wind and waves, is harsher for coastal seals (Figures S4–S6). Previous research suggests that storms may be a cause of maternal separation in grey seals and likely cause a high proportion of fatalities in pre-weaned individuals during the pupping season (Baker, 1984; Baker and Baker, 1988; Baker *et al.*, 1998; Barnett and Westcott, 1999). Likewise, findings from Prado *et al.* (2016) demonstrated high numbers of pinniped strandings occurring immediately post-weaning. Turbidity in water during storms may make it difficult for inexperienced foraging pups to feed (Miersch *et al.*, 2011) leaving them more susceptible to injury or fatality from large waves (Anderson *et al.*, 1979; Gazo *et al.*, 2000). Furthermore, Luck *et al.* (2019) found seasonal trends in bycatch in Irish fisheries were driven by water turbidity, suggesting that bycatch-related strandings are higher following stormy weather. Much of Cornwall is characterised by high cliff-backed beaches and high-energy wave regimes (Scott *et al.*, 2016) and may present difficult terrain for young seals to navigate under rough conditions. Baker and Baker (1988) suggested that the cause of death of grey seal pups is largely influenced by the conditions and topography of the breeding colony they are born into, as pups born onto cliff-backed beaches or in caves have little opportunity to avoid storm surges.

Although there is variation among regions, the survival of grey seal pups in their first year of life is affected by their condition at weaning (Hall *et al.*, 2001). Model predictions using data from the North Sea population of grey seals have suggested that mean estimates of pup survival were around 50% (SCOS, 2021) and a large proportion of known bycaught seals were identified as being first- or second-year animals (SCOS, 2021). Regional data on survival rates of pups in southwest England would allow us to better understand trends in the abundance of seals in this region. While it would be of interest to understand how inclement weather drives the timing of stranding events (Truchon *et al.*, 2013; Vishnyakova and Gol'din, 2014; Prado *et al.*, 2016; Sepúlveda

et al., 2020; Backe *et al.*, 2021), upon initial exploration of these factors (Figures S4–S6), we found the complicated coastline with diverse aspects, presence of islands and relatively small sample sizes of each life stage per month in any given year, precluded a correlative approach, at this stage.

Geographic distribution

Although the spatial distribution of grey seal strandings covered much of the Cornwall and Isles of Scilly coastlines, the majority of strandings were recorded along the north coast of Cornwall. This distribution was consistent over time and across all life stages, though the pattern was more pronounced in pups and whitecoats, likely due to major pupping sites being situated on the north coast of Cornwall and close to accessible beaches with regular footfall. Juvenile and adult strandings were observed across all coasts, though higher numbers of strandings were concentrated around major haul out sites on the north coast of Cornwall. It is noteworthy that relatively few strandings are recorded on the Isles of Scilly, given their importance for breeding and haul out sites (Sayer *et al.*, 2012). On the Isles of Scilly, most seals are, however, found on and around the uninhabited isles and, unlike the mainland beaches of Cornwall, there is likely a much lower likelihood that carcasses will strand and/or be encountered. Detailed knowledge of the current regime around the Isles of Scilly is relatively lacking. There are two tidal jets which result from strong tidal streaming around the Isles of Scilly and these are found to propagate in a clockwise direction around the island group (Pingree and Mardell, 1986) and may cause fewer carcasses to beach. This combined with the lower human population and reporting effort on the Isles of Scilly is likely to in part explain the smaller numbers of strandings in this area.

Caveats

Because of their opportunistic nature, strandings data have innate biases driven by physical and social processes which should be considered if they are to be used to assess or interpret trends in abundance or demographics (Peltier *et al.*, 2013, 2014; Peltier and Ridoux, 2015; ten Doeschate *et al.*, 2017; Prado *et al.*, 2022). We recognise that the strandings investigated will be an underestimation of the animals dying in the coastal waters as the likelihood of a carcass reaching land depends on multiple factors including carcass buoyancy, ocean currents and wind regimes. Consequently, not all animals that die will be found, as those that strand on inaccessible stretches of coast, remain at sea, or achieve negative buoyancy, are less likely to be encountered and may therefore go unrecorded (Osinga *et al.*, 2012). Additionally, scavenging, decay and physical breakup are likely to affect detection, particularly of smaller animals.

Lastly, in 2020, 201 seal strandings were reported which is a decrease from the previous year ($n = 246$). It is important to consider the impact that COVID-19 restrictions may have had on strandings data in 2020. Undoubtedly, with fewer volunteers able to attend and record strandings, it is possible that numbers of strandings during this restricted period are underestimated. Despite this, the numbers of seal strandings in 2020 remain higher than all of those prior to 2019.

Nevertheless, the accumulation of stranding data over a long time series such as presented here has allowed the analysis of trends and patterns of considerable local and regional utility. Efforts have been made in the design of the strandings scheme and how we filtered and analysed the data with these biases in mind. CWTMSN has been collecting detailed data on stranded marine organisms for over 27 years. While we excluded data

before 2000 it is possible that increasing awareness of marine mammal conservation and associated activism, particularly related to seals, has, in part, driven an increase in grey seal strandings reported. There was likely an initial increase in public awareness of the strandings scheme in 2005 following publicity; however, since then there has been little intention to raise the profile of the scheme and it is thought that public awareness has remained relatively stable. The Marine Strandings Network consists of a team of approximately 200 trained volunteers throughout Cornwall and the Isles of Scilly who record all reported strandings of organic organisms from over 579 km of coastline. Though there is some degree of annual turnover, the number of active volunteers has remained stable throughout the study period (Crosby, personal observation). The CWTMSN has a dedicated Strandings Hotline for the reporting of dead stranded marine animals, which operates year-round and is staffed by a rota of dedicated volunteer Hotline Coordinators, reducing the likelihood of strandings going unrecorded. Carcasses reported to CWTMSN are either examined *in-situ*, or via post-mortem examination by a veterinary pathologist. Detailed reports and photographs collected by volunteers are verified and assessed by experienced experts to avoid multiple counts of the same stranding.

Further work

The Cornwall and the Isles of Scilly strandings monitoring scheme is exemplary, has yielded significant insights into the assessment of abundance and mortality of grey seals, and should be continued as a useful part of monitoring the status of seals in the region, partly as a proxy for ecosystem health. In addition to enhanced and continued pup production surveys, carried out in parallel, this work could be augmented by several complementary studies. Firstly, with additional years of data, possibly with increasing annual sample size, it is likely that additional insights will be obtained into the meteorological and sea state factors that drive stranding events. Secondly, it is not possible to say for certain how far from the stranding location an animal died (Hart *et al.*, 2006; Witt *et al.*, 2006). It may be appropriate to apply more complex modelling investigating weather conditions in the days or months prior to stranding, as well as incorporating tidal state, currents and prevailing winds which may also affect carcass recovery. Finally, through molecular profiling of stranded (dead and rehabilitated) animals, insights may be obtained into patterns of relatedness (Oremus *et al.*, 2013; Palmer *et al.*, 2022) and population connectivity across the UK and wider Celtic Sea population (Vincent *et al.*, 2005, 2017; Sayer *et al.*, 2021). A combination of tracking or re-sighting studies alongside strandings studies like this one would afford an insight on how trends in pup production detected on breeding colonies might be affected by threats at foraging areas. This in particular is a significant knowledge gap in grey seal conservation and management as highlighted by Carter *et al.* (2017). The UK is home to a globally important population of grey seals (Leeney *et al.*, 2010), and thus has a responsibility to secure effective conservation, with Cornwall and the Isles of Scilly representing part of the southern edge of the species range. It is clear that extension of this valuable dataset will be a key part of the monitoring strategy needed, going forward.

Here, we conducted a spatial and temporal analysis of grey seal strandings around the coast of Cornwall and the Isles of Scilly using a multidecadal dataset. The data, which have offered a valuable insight into the biology and status of grey seals in the region, resulted from efforts of hundreds of volunteers and highlight the importance and utility of citizen science for population monitoring and management. The UK has recently launched a Marine Natural Capital and Ecosystem Assessment Programme (mNCEA) which seeks to create a platform for a thriving marine

environment, where nature is at the heart of decision-making. Detailed datasets such as marine vertebrate strandings can form part of the required ecological, societal and economic information that needs to be brought together in a holistic way, helping better decisions to be made about the marine environment. Describing a baseline in the magnitude of strandings and their life-stage composition across space and time allows the future detection of deviations in frequency, demographic composition or spatial distribution to be detected and investigated. We demonstrate the worth of long-term citizen science data to provide valuable and cost-effective information on the distribution and abundance of a highly mobile marine mammal, providing a dimension to our knowledge which tracking data alone cannot.

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Data. Data are available in full from the Environmental Records Centre for Cornwall and the Isles of Scilly (ERCCIS).

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References

- Adimey N, Hudak C, Powell J, Bassos-Hull K, Foley A, Farmer N, White L and Minch K (2014) Fishery gear interactions from stranded bottlenose dolphins, Florida manatees and sea turtles in Florida, U.S.A. *Marine Pollution Bulletin* **81**, 103–115.
- Allen R, Jarvis D, Sayer S and Mills C (2012) Entanglement of grey seals (*Halichoerus grypus*) at a haul out site in Cornwall, UK. *Marine Pollution Bulletin* **64**, 2815–2819.
- Anderson S, Baker J, Prime J and Baird A (1979) Mortality in grey seal pups: incidence and causes. *Journal of Zoology* **189**, 407–417.
- Backe K, Hines E, Nielsen K, George D, Twohy E and Lowry M (2021) Effects of sea-level rise and storm-enhanced flooding on Pacific harbour seal habitat: a comparison of haul-out changes at the Russian and Eel river estuaries. *Aquatic Conservation: Marine and Freshwater Ecosystems* **31**, 1749–1759.
- Baker J (1984) Mortality and morbidity in grey seal pups (*Halichoerus grypus*). Studies on its causes, effects of environment, the nature and sources of infectious agents and the immunological status of pups. *Journal of Zoology* **203**, 23–48.
- Baker J and Baker R (1988) Effects of environment on grey seal (*Halichoerus grypus*) pup mortality. Studies on the Isle of May. *Journal of Zoology* **216**, 529–537.
- Baker J, Jepson P, Simpson V and Kuiken T (1998) Causes of mortality and non-fatal conditions among grey seals (*Halichoerus grypus*) found dead on

- the coasts of England, Wales and the Isle of Man. *Veterinary Record* **142**, 595–601.
- Barnett J, Allen R, Astley K, Whitehouse F and Wessels M** (2021) Pathology of grey seals (*Halichoerus grypus*) in southwest England including pups in early rehabilitation. *Diseases of Aquatic Organisms* **145**, 35–50.
- Barnett J and Westcott S** (1999) Distribution, demographics and survivorship of grey seal pups rehabilitated in southwest England. *Mammalia* **65**, 349–361.
- Barnett J and Westcott S** (2001) Distribution, demographics and survivorship of grey seal pups (*Halichoerus grypus*) rehabilitated in southwest England. *Mammalia* **65**, 349–361.
- Bartoň K** (2022) MuMIn: Multi-Model Inference. R package version 1.46.0. Available at <https://CRAN.R-project.org/package=MuMIn>.
- Bianchi C, Azzola A, Cocito S, Morri C, Oprandi A, Peirano A, Sgorbini S and Montefalcone M** (2022) Biodiversity monitoring in Mediterranean marine protected areas: scientific and methodological challenges. *Diversity* **4**, 43–65.
- Bograd S, Block B, Costa D and Godley B** (2010) Biologging technologies: new tools for conservation. *Endangered Species Research* **10**, 1–7.
- Bossart G** (2010) Marine mammals as sentinel species for oceans and human health. *Veterinary Pathology* **48**, 676–690.
- Bowler D, Callaghan C, Bhandari N, Henle K, Benjamin Barth M, Koppitz C, Klenke R, Winter M, Jansen F, Bruelheide H and Bonn A** (2022) Temporal trends in the spatial bias of species occurrence records. *Ecography* **8**, e06219.
- Boyd JM and Campbell RN** (1971) The grey seal (*Halichoerus grypus*) at North Rona, 1959 to 1968. *Journal of Zoology* **164**, 469–512.
- Brasseur SM, van Polanen Petel TD, Gerrodette T, Meesters EH, Reijnders PJ and Aarts G** (2015) Rapid recovery of Dutch grey seal colonies fueled by immigration. *Marine Mammal Science* **31**, 405–426.
- Brunson S, Gaos A, Kelly I, Van Houtan K, Swimmer Y, Hargrove S, Balazs G, Work T and Jones T** (2022) Three decades of stranding data reveal insights into endangered hawksbill sea turtles in Hawai'i. *Endangered Species Research* **47**, 109–118.
- Byrd B, Hohn A, Lovewell G, Altman K, Barco S, Friedlaender A, Harms C, McLellan W, Moore K, Rosel P and Thayer V** (2014) Strandings as indicators of marine mammal biodiversity and human interactions off the coast of North Carolina. *Fishery Bulletin* **112**, 1–23.
- Canepa A, Purcell J, Córdova P, Fernández M and Palma S** (2020) Massive strandings of pleustonic Portuguese Man-of-War (*Physalia physalis*) related to ENSO events along the southeastern Pacific Ocean. *Latin American Journal of Aquatic Research* **48**, 806–817.
- Carter M, Boehme L, Cronin M, Duck C, Grecian W, Hastie G, Jessopp M, Matthiopoulos J, McConnell B, Miller D, Morris C, Moss S, Thompson D, Thompson P and Russell D** (2022) Sympatric seals, satellite tracking and protected areas: habitat-based distribution estimates for conservation and management. *Frontiers in Marine Science* **9**, 2296–7745.
- Carter M, McClintock B, Embling C, Bennett K, Thompson D and Russell D** (2020) From pup to predator: generalized hidden Markov models reveal rapid development of movement strategies in a naïve long-lived vertebrate. *Oikos* **129**, 630–642.
- Carter M, Russell D, Embling C, Blight C, Thompson D, Hosegood P and Bennett K** (2017) Intrinsic and extrinsic factors drive ontogeny of early-life at-sea behaviour in a marine top predator. *Scientific Reports* **7**, e15505.
- Chan D, Tsui H and Kot B** (2017) Database documentation of marine mammal stranding and mortality: current status review and future prospects. *Diseases of Aquatic Organisms* **126**, 247–256.
- Colegrove K, Greig D and Gulland F** (2005) Causes of live strandings of northern elephant seals (*Mirounga angustirostris*) and Pacific harbor seals (*Phoca vitulina*) along the central California coast, 1992–2001. *Aquatic Mammals* **31**, 1–10.
- Coombs E, Deaville R, Sabin R, Allan L, O'Connell M, Berrow S, Smith B, Brownlow A, Doeschate M, Penrose R, Williams R, Perkins M, Jepson P and Cooper N** (2019) What can cetacean stranding records tell us? A study of UK and Irish cetacean diversity over the past 100 years. *Marine Mammal Science* **35**, 1527–1555.
- Cronin M, Duck C and O'Cadhla O** (2007) Aerial surveying of grey seal breeding colonies on the Basket Islands, Co. Kerry, Co. Mayo and the Donegal Coast, Ireland. *Journal for Nature Conservation* **15**, 73–83.
- Crosby A and Hawtrey-Collier A** (2020) *2020 Annual Report Marine Strandings in Cornwall and the Isles of Scilly*. Truro, United Kingdom. Cornwall Wildlife Trust. Available at <https://www.cornwallwildlifetrust.org.uk/sites/default/files/2021-12/2020%20MSN%20Summary%20Report%20V2-min.pdf>.
- Gazo M, Aparicio F, Cedenilla M, Layna J and Gonzalez L** (2000) Pup survival in the Mediterranean monk seal (*Monachus monachus*) colony at Cabo Blanco Peninsula (Western Sahara-Mauritania). *Marine Mammal Science* **16**, 158–168.
- Hall AJ, McConnell BJ and Barker RJ** (2001) Factors affecting first-year survival in grey seals and their implications for life history strategy. *Journal of Animal Ecology* **70**, 138–149.
- Hammond P, Macleod K, Berggren P, Borchers D, Burt L, Cañadas A, Desportes G, Donovan G, Gilles A, Gillespie D, Gordon J, Hiby L, Kuklik I, Leaper R, Lehnert K, Leopold M, Lovell P, Øien N, Paxton C, Ridoux V, Rogan E, Samarra F, Scheidat M, Sequeira M, Siebert U, Skov H, Swift R, Tasker M, Teilmann J, Van Canneyt O and Vázquez J** (2013) Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. *Biological Conservation* **164**, 107–122.
- Hart K, Mooreside P and Crowder L** (2006) Interpreting the spatio-temporal patterns of sea turtle strandings: going with the flow. *Biological Conservation* **129**, 283–290.
- Hewer HR** (1974) *British Seals*. The New Naturalist No. 57. London, United Kingdom: Harper Collins.
- IJsseldijk L, ten Doeschate M, Brownlow A, Davison N, Deaville R, Galatius A, Gilles A, Haelters J, Jepson P, Keijl G, Kinze C, Olsen M, Siebert U, Thøstesen C, van den Broek J, Grøne A and Heesterbeek H** (2020) Spatiotemporal mortality and demographic trends in a small cetacean: strandings to inform conservation management. *Biological Conservation* **24**, e108733.
- Jones DW** (2020) *Atlantic Grey Seal (Halichoerus grypus) Population and Productivity Studies, Lundy 2019*. United Kingdom: The Lundy Company.
- Keledjian A** (2013) The impacts of El Niño conditions on California sea lion (*Zalophus californianus*) fisheries interactions: predicting spatial and temporal hotspots along the California coast. *Aquatic Mammals* **39**, 221–232.
- Leeney R, Broderick A, Mills C, Sayer S, Witt M and Godley B** (2010) Abundance, distribution and haul-out behaviour of grey seals (*Halichoerus grypus*) in Cornwall and the Isles of Scilly, UK. *Journal of the Marine Biological Association of the United Kingdom* **90**, 1033–1040.
- Luck C, Cronin M, Gosch M, Healy K, Cosgrove R, Tully O, Rogan E and Jessopp M** (2019) Drivers of spatiotemporal variability in bycatch of a top marine predator: first evidence for the role of water turbidity in protected species bycatch. *Journal of Applied Ecology* **57**, 219–228.
- Luck C, Jessopp M, Tully O, Cosgrove R, Rogan E and Cronin M** (2020) Estimating protected species bycatch from limited observer coverage: a case study of seal bycatch in static net fisheries. *Global Ecology and Conservation* **24**, e012213.
- Meager J and Sumpton W** (2016) Bycatch and strandings programs as ecological indicators for data-limited cetaceans. *Ecological Indicators* **60**, 987–995.
- Miersch L, Hanke W, Wieskotten S, Hanke F, Oeffner J and Leder A** (2011) Flow sensing by pinniped whiskers. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 3077–3084.
- Noren S, Boness D, Iverson S, McMillan J and Bowen W** (2008) Body condition at weaning affects the duration of the postweaning fast in gray seal pups (*Halichoerus grypus*). *Physiological and Biochemical Zoology* **81**, 269–277.
- Northridge S, Coram A, Kingston A and Crawford R** (2017) Disentangling the causes of protected-species bycatch in gillnet fisheries. *Conservation Biology* **31**, 686–695.
- Oremus M, Gales R, Kettles H and Baker C** (2013) Genetic evidence of multiple matrilineal and spatial disruption of kinship bonds in mass strandings of long-finned pilot whales, (*Globicephala melas*). *Journal of Heredity* **104**, 301–311.
- Ortiz-Alvarez C, Guidino C, Verhaegen C, Alfaro-Shigueto J and Mangel J** (2022) Lessons from 12 years of marine fauna stranding data in the south of Peru. *Environmental Monitoring and Assessment* **194**, 142.
- Osinga N, Pen I, Udo de Haes H and Brakefield P** (2012) Evidence for a progressively earlier pupping season of the common seal (*Phoca vitulina*) in the Wadden Sea. *Journal of the Marine Biological Association of the United Kingdom* **92**, 1663–1668.
- Palmer E, Alexander A, Liggins L, Guerra M, Bury S, Hendriks H, Stockin K and Peters K** (2022) A piece of the puzzle: analyses of recent strandings and historical records reveal new genetic and ecological insights on New Zealand sperm whales. *Marine Ecology Progress Series* **690**, 201–217.

- Peltier H, Baagoe H, Camphuysen K, Czeck R, Dabin W, Daniel P, Deaville R, Haelters J, Jauniaux T, Jensen L, Jepson P, Keijl G, Siebert U, Van Canneyt O and Ridoux V (2013) The stranding anomaly as population indicator: the case of harbour porpoise (*Phocoena phocoena*) in north-western Europe. *PLoS ONE* **8**, e62180.
- Peltier H, Jepson P, Dabin W, Deaville R, Daniel P, Van Canneyt O and Ridoux V (2014) The contribution of stranding data to monitoring and conservation strategies for cetaceans: developing spatially explicit mortality indicators for common dolphins (*Delphinus delphis*) in the eastern North-Atlantic. *Ecological Indicators* **39**, 203–214.
- Peltier H and Ridoux V (2015) Marine megavertebrates adrift: a framework for the interpretation of stranding data in perspective of the European Marine Strategy Framework Directive and other regional agreements. *Environmental Science & Policy* **54**, 240–247.
- Peschko V, Müller S, Schwemmer P, Mercker M, Lienau P, Rosenberger T, Sundermeyer J and Garthe S (2020) Wide dispersal of recently weaned grey seal pups in the southern North Sea. *ICES Journal of Marine Science* **77**, 1762–1771.
- Pikesley S, Witt M, Hardy T, Loveridge J, Loveridge J, Williams R and Godley B (2012) Cetacean sightings and strandings: evidence for spatial and temporal trends? *Journal of the Marine Biological Association of the United Kingdom* **92**, 1809–1820.
- Pingree RD and Mardell GT (1986) Coastal tidal jets and tidal fringe development around the Isles of Scilly. *Estuarine, Coastal and Shelf Science* **25**, 518–594.
- Pomeroy P, Fedak M, Rothery P and Anderson S (1999) Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *Journal of Animal Ecology* **68**, 235–253.
- Prado J, Daudt N, Perez M, Castilho P and Monteiro D (2022) Intensive and wide-ranging beach surveys uncover temporal and spatial stranding patterns of marine megafauna. *ICES Journal of Marine Science* **80**(3), fsac119.
- Prado J, Mattos P, Silva K and Secchi E (2016) Long-term seasonal and inter-annual patterns of marine mammal strandings in subtropical western South Atlantic. *PLoS ONE* **11**, e0146339.
- R Core Team (2022) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at <https://www.R-project.org/>.
- Richards S, Whittingham M and Stephens P (2011) Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. *Behavioural Ecology and Sociobiology* **65**, 77–89.
- Rohner C, Venables S, Cochran J, Prebble C, Kuguru B, Berumen M and Pierce S (2022) The need for long-term population monitoring of the world's largest fish. *Endangered Species Research* **47**, 231–248.
- Russell D, Morris C, Duck C, Thompson D and Hiby L (2019) Monitoring long-term changes in UK grey seal pup production. *Aquatic Conservation: Marine and Freshwater Ecosystems* **29**, 24–39.
- Sayer S, Allen R, Bellman K, Beaulieu M, Cooper T, Dyer N, Hockin K, Hockley K, Jarvis D, Jones G, Oaten P, Waddington N, Witt M and Hawkes L (2021) Post release monitoring of rehabilitated grey seal pups over large temporal and spatial scales. *Marine Mammal Science* **38**, 539–556.
- Sayer S, Allen R, Hawkes L, Hockley K, Jarvis D and Witt M (2019) Pinnipeds, people and photo identification: the implications of grey seal movements for effective management of the species. *Journal of the Marine Biological Association of the United Kingdom* **99**, 1221–1230.
- Sayer S, Hockley C and Witt M (2012) Monitoring Grey Seals (*Halichoerus grypus*) in the Isles of Scilly during the 2010 Pupping Season. Natural England Commissioned Reports (NECR103). ISBN: 978-1-78354-651-0. 68pp.
- Sayer S and Witt M (2018) Special Area of Conservation Condition Monitoring: Grey seals (*Halichoerus grypus*) in the Isles of Scilly during the 2016 pupping season. Report Commissioned for Natural England (NECR261). ISBN: 978-1-78354-509-4.
- Sayer S, Millward S and Witt M (2018) Monitoring Grey Seal (*Halichoerus grypus*) Pupping Sites in Cornwall 2016. Report Commissioned for Natural England (NECR262). ISBN: 978-1-78354-508-7. 23pp.
- Sayer S, Millward S and Witt M (2020) Monitoring Grey Seal (*Halichoerus grypus*) Pupping Sites in Cornwall 2019/2020. Report Commissioned for Natural England (NECR322). ISBN: 978-1-78354-651-0. 30pp.
- Scott T, Masselink G, O'Hare T, Sautler A, Poate T and Russell P (2016) The extreme 2013/2014 winter storms: beach recovery along the southwest coast of England. *Marine Geology* **382**, 224–241.
- Sepúlveda M, Quiñones R, Esparza C, Carrasco P and Winckler P (2020) Vulnerability of a top marine predator to coastal storms: a relationship between hydrodynamic drivers and stranding rates of newborn pinnipeds. *Scientific Reports* **10**, e12807.
- Sheehan E, Rees A, Bridger D, Williams T and Hall-Spencer J (2017) Strandings of NE Atlantic gorgonians. *Biological Conservation* **209**, 482–487.
- Silpa M, Thornton S, Cooper T and Hedley J (2015) Prevalence of presenting conditions in grey seal pups (*Halichoerus grypus*) admitted for rehabilitation. *Veterinary Sciences* **2**, 1–11.
- Special Committee on Seals (SCOS) (2020) Scientific Advice on Matters Related to the Management of Seal Populations: 2020. Available at <http://www.smru.st-andrews.ac.uk/files/2021/06/SCOS-2020.pdf>. 223pp.
- Special Committee on Seals (SCOS) (2021) Scientific Advice on Matters Related to the Management of Seal Populations: 2021. Available at <http://www.smru.st-andrews.ac.uk/files/2022/08/SCOS-2021.pdf>. 266pp.
- Stringell T, Millar C, Sanderson W, Westcott S and McMath M (2014) When aerial surveys will not do: grey seal pup production in cryptic habitats of Wales. *Journal of the Marine Biological Association of the United Kingdom* **94**, 1155–1159.
- ten Doeschate M, Brownlow A, Davison N and Thompson P (2017) Dead useful; methods for quantifying baseline variability in stranding rates to improve the ecological value of the strandings record as a monitoring tool. *Journal of the Marine Biological Association of the United Kingdom* **98**, 1205–1209.
- The UK Conservation of Seals Act (1970). Chapter 30. Available at: <https://www.legislation.gov.uk/ukpga/1970/30> (Accessed: November 2022).
- Thomas L (2019) Modelling the population size and dynamics of the British grey seal. *Aquatic Conservation: Marine and Freshwater Ecosystems* **29**, 6–23.
- Thompson D, Duck C, Morris C and Russell D (2019) The status of harbour seals (*Phoca vitulina*) in the UK. *Aquatic Conservation: Marine and Freshwater Ecosystems* **29**, 40–60.
- Tomás J, Gosalbes P, Raga J and Godley B (2008) Bycatch of loggerhead sea turtles: insights from 14 years of stranding data. *Endangered Species Research* **5**, 161–169.
- Truchon M, Measures L, L'Hérault V, Brêthes J, Galbraith P, Harvey M, Lessard S, Starr M and Lecomte N (2013) Marine mammal strandings and environmental changes: a 15 year study in the St. Lawrence ecosystem. *PLoS ONE* **8**, e59311.
- Venables W and Ripley B (2002) *Modern Applied Statistics with S*, 4th Edn. New York, NY: Springer.
- Vincent C, Fedak M, McConnell B, Meynier L, Saint-Jean C and Ridoux V (2005) Status and conservation of the grey seal, (*Halichoerus grypus*), in France. *Biological Conservation* **126**, 62–73.
- Vincent C, Huon M, Caurant F, Dabin W, Deniau A, Dixneuf S, Dupuis L, Elder J, Fremau M, Moss SEW, Provost P, Spitz J, Turpin Y and Ridoux V (2017) Grey and harbour seals in France: distribution at sea, connectivity and trends in abundance at haulout sites. *Deep-Sea Research Part II* **141**, 294–305.
- Vishnyakova K and Gol'din P (2014) Seasonality of strandings and bycatch of harbour porpoises in the Sea of Azov: the effects of fisheries, weather conditions, and life history. *ICES Journal of Marine Science* **72**, 981–991.
- Warlick A, Duffield D, Lambourn D, Jeffries S, Rice J, Gaydos J, Huggins J, Calambokidis J, Lahner L, Olson J, D'Agnesse E, Souze V, Elsy A and Norman S (2018) Spatio-temporal characterization of pinniped strandings and human interaction cases in the Pacific Northwest, 1991–2016. *Aquatic Mammals* **44**, 299–318.
- Warlick A, Huggins J, Lambourn D, Duffield D, D'Alessandro D, Rice J, Calambokidis J, Hanson M, Gaydos J, Jeffries S, Olson J, Scordino J, Akmajian A, Klope M, Berta S, Dubpernell S, Carlson B, Riemer S, Hodder J, Souze V, Elsy A, King C, Wilkinson K, Boothe T and Norman S (2022) Cetacean strandings in the US Pacific Northwest 2000–2019 reveal potential linkages to oceanographic variability. *Frontiers in Marine Science* **9**, e758812.
- Westcott S (1997) *The grey seals of the West Country: And their neighbours*. Truro, United Kingdom: S. Westcott in cooperation with the Cornwall Wildlife Trust.
- Witt M, Penrose R and Godley B (2006) Spatio-temporal patterns of juvenile marine turtle occurrence in waters of the European continental shelf. *Marine Biology* **151**, 873–885.
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 64–168.
- Wosnick N, Leite R, Giaretta E, Morick D and Musyl M (2022) Global assessment of shark strandings. *Fish and Fisheries* **23**, 786–799.