Understanding the interaction between climate change and anthropogenic pressures, in relation to the demography and distribution of Caspian seals (*Pusa caspica*)

Harrison Tan

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The candidate confirms that the work submitted is their own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

- **The work in Chapter two has been prepared as a manuscript for publication as follows:**

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Thesis abstract

Many pinnipeds are threatened from anthropogenic sources of disturbance and climate change. Although ice-breeding pinnipeds face several additional threats relating to climate heating, such as the loss of ice breeding substrates. Understanding how these threats interact with the ecology of ice-breeding pinnipeds, in isolation and in combination, is an essential component of conserving ice-breeding pinnipeds. However, incorporating the ecology of a species within conservation frameworks can be challenging if complex behavioural phenomena are difficult to describe to non-experts. The application of quantitative methods can aid this process by providing an unbiased framework for interpreting ecological observations. Although, in the past, the application of these methods has been challenging due to long standing analytical challenges that emerge from practicalities associated with collecting data that describes the behaviour and distribution of free-ranging wild animals. Fortunately, several statistical innovations have provided precise frameworks that can address these challenges, and, in this thesis, I apply these methods in spatial and temporal contexts using Bayesian modelling frameworks to study the ecology of the Caspian seal (*Pusa caspica*), an Endangered ice-breeding pinniped.

In this thesis, I use these methods to investigate how the distribution and behaviour of Caspian seals is associated with environmental factors and demonstrate how these associations relate to temporal variability and change over time. **Chapter one** is a general introduction to the field where I introduce pinniped ecology and the Caspian study system, discuss the knowledge gaps and overarching concepts relevant to the thesis, and discuss research objectives and aims. **Chapter two** is a research chapter, where I investigate the distribution of Caspian seal pups concerning the spatiotemporal history and stability of the ice they breed on. In this chapter, I integrate an ice visual tracking algorithm within a multivariate hierarchical model to investigate associations between ice characteristics, breeding sites, and pups at breeding sites. Using these methods, I provide evidence that breeding seals depend upon stable ice conditions and are currently breeding on ice that remains stable for marginally longer than that is required for pups to finish weaning. **Chapter three** is a research chapter, where I investigate the temporal change in the use of different habitats by Caspian seals and use these inferences to develop spatially and temporally flexible marine protected area plans. In this chapter, I use spatial and temporal models to investigate how spatial associations between environmental factors change over time, provide evidence that foraging seals may utilise specific habitats during periods associated with fish migrations, and show how these insights can be applied to inform the design of protection schemes. **Chapter four** is a research chapter, where I use inferences gained in Chapter 1, alongside other research on Caspian seals to

develop population projections that incorporate how threats that impact Caspian seals may change over time. Within this chapter, I constructed a mechanistic population simulation to investigate how the quasi-extinction risk of Caspian seals may change over time and in response to a variety of temporally structured threat scenarios. Finally, chapter five concludes the thesis, discusses the combined contribution of each research chapter to the field of pinniped research, as well as future advances and applications.

A Note on Style

Chapters two-four of this thesis have been written in a manuscript format and intended for publication. I am lead author on all these chapters, but I acknowledge contributions of co-authors by using terms ‘we’ and ‘our’ throughout. The General Introduction and the General discussion represent my sole work, and I therefore use the terms ‘I’ and ‘my’ throughout. Chapters two-four follow a classic manuscript format with introduction, methods, results, and discussion.

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1. Chapter one – General Introduction

Effective conservation planning requires understanding how species respond to the combined pressures of climate change and anthropogenic impacts, and among marine vertebrates, pinnipeds are particularly impacted by these combined threats (Kovacs et al., 2012; Albouy et al., 2020). Historically, pinnipeds were harvested for their fur, meat, and blubber. However, organised hunts are now comparatively rare, and contemporary sources of anthropogenic mortality are mostly related to fisheries and mortality from bycatch (Kovacs et al., 2012; Svolkinas, 2021). Pinnipeds are also sensitive to climate heating due to physiological adaptations to living in cold water, although those that breed on ice are particularly threatened due to their dependence on sea ice which is declining due to rising temperatures (Albouy et al., 2020). These anthropogenic and climate change threats make pinnipeds, particularly ice-breeding pinnipeds, vulnerable to population to decline. One way to improve the conservation of ice-breeding pinniped populations is to incorporate the aspects of their ecology that make them vulnerable in the design of conservation and mitigation strategies. However, to achieve these goals we must fill gaps in our understanding of unresolved threats, how habitat use relates to life history, explore how environmental factors may influence behaviour, and develop frameworks that can incorporate these insights into conservation policy.

1.1. Pinniped ecology

Pinnipeds (*Pinnipedia*) are a diverse clade of marine mammals with three monophyletic lineages: *Phocidae* (true seals), Otariidae (fur seals and sea lions), and Odobenidae (Walruses) (Berta et al., 2018). Phocids (*Phocidae* spp.) are commonly referred to as the "true" or "earless" seals and possess numerous adaptations to aid locomotion in water. They are generally unable to traverse far on land or ice and do not possess external ear flaps. Otariids (*Otariidae spp.)* have large fore flippers and dextrous hind limbs that enable better manoeuvrability on land, and they do possess external ear flaps. Walruses (*Odobenus sp.)* are well recognised for their large tusks and possess similar fore flipper and hind limb physiology to otariids, although, they do not possess an external ear flaps. In general, pinnipeds are cold water specialists with diving capabilities and insulative blubber layers. They can be found in every major ocean, although most are found within polar and sub-polar habitats. One of the key aspects of pinniped ecology is their need to partition foraging, which occurs within aquatic environments, with the nursing of young, which requires a solid terrestrial or ice substrate (Van Bonn, 2015; Berta et al., 2018).

The main ecological division of pinnipeds when nursing is into income and capital breeders, where phocids are predominantly capital breeders with shorter lactation periods (typically less than a month), and otariids are mainly income breeders with longer lactation periods (typically between 3 and 18 months) (Riet-Sapriza, 2020). Capital breeders deplete extensive energy reserves that are accumulated during the foraging season, and income-breeders intermittently return to the water to feed in between nursing bouts, with individual species falling on a spectrum between the two strategies. Compared to nursing strategies, foraging behaviours are much more variable within and among more closely related species. During the foraging season, species such as elephant seals (*Mirounga* spp.) and fur seals (*Arctocephalinae* spp.) are central place foragers that periodically re-visit a selection of terrestrial sites in between foraging trips, although others such as Caspian seals (*Pusa caspica*) spend much longer periods at-sea (Lowry, 2014; Van Bonn, 2015; Dmitrieva et al., 2016; Berta et al., 2018). Harbour seals (*Phoca vitulina*) are known to forage close to river estuaries at a higher rate during salmon migrations (Allegue, 2017), and the grey seal (*Halichoerus grypus*) often forages further from shore and is a sea-shelf specialist (Nowak et al., 2020). This variability in habitat use impacts the diets of pinnipeds, however, overall, pinnipeds typically feed on a diverse array of aquatic animals, such as crustaceans and fish (Dehn et al., 2007; Tucker et al., 2009; Van Bonn, 2015).

At the end of the foraging season and before the breeding season adult seals typically travel to familiar regions for breeding and nursing. Although whilst nursing, the breeding behaviour of pinnipeds varies with the substrate that is used for nursing and the density of their breeding aggregations. All pinnipeds are born upon floating pack ice, fast ice, sandy beaches, or rocky beaches (Riet-Sapriza, 2020) and the density of breeding colonies is typically higher on land compared to ice. Some pinnipeds breed within dense colonies at isolated terrestrial sites, such as elephant seals and fur seals which both breed in large aggregations on land and on isolated rocky beaches (Lowry, 2014; Geeson et al., 2022). Compared to land breeders, most ice breeding seals breed in lower densities, such as Caspian seals which breed in sparse aggregations (Wilson et al., 2017a), and Leopard seals which breed in isolation (Southwell et al., 2008). The precise nursing conditions of ice-breeding seals can vary, for example, ringed seals (*Pusa hispida*) construct nesting lairs made of snow and ice (Kelly and Quakenbush, 1990; Lindsay et al., 2021), and Caspian seals (*Pusa caspica*) are nursed directly on the ice sheet (Wilson et al., 2017a).

1.2. Pinniped conservation

During the last century, the Japanese sea lion (*Zalophus japonicas*) and the Caribbean monk seal (*Monachus tropicals*) were driven to extinction. Overhunting has been cited as the major threat that led to the extinction of the Japanese sea lion (Lee et al., 2022), and overhunting and intense overfishing of prey has been cited as the major threat that led to the extinction of the Caribbean monk seal (McClenachan and Cooper, 2008; Baisre, 2013). Several other species were also driven to the brink of extinction by hunting, such as the Northern elephant seal (*Mirounga angustirostris*) (Stewart, 1992) and the Antarctic fur seal (*Arctocephalus gazella*) (Hucke-Gaete et al., 2004). Although hunting pressures have since stopped, and these two species have since recovered and demonstrate the resilience of pinnipeds to recover (Stewart, 1992; Hucke-Gaete et al., 2004). When sufficiently intense or over a sufficiently long period of time, these historical case studies demonstrate the potential for human threats to cause extinction, however, direct anthropogenic drivers of decline continue to impact the survival of extant pinnipeds. In the contemporary setting, organised hunts are comparatively rare, however, accidently mortality because of bycatch within fishing nets is an increasing threat to global pinnipeds (Kovacs et al., 2012; Svolkinas, 2021).

In addition to direct threats from hunting, additional threats can emerge from an accumulation of nonlethal effects of anthropogenic disturbance (Lima, 1998; Frid and Dill, 2002; Pirotta et al., 2018). The accumulation of these nonlethal threats is formalised under the research banner of population consequences of disturbance (PCOD), which marks an important shift in the perspective of how threats are recognised and evaluated, and conceptually describes how disturbance can lead to changes in population dynamics. One of the main challenges of conducting a PCOD analyses is deciding how researchers should parametrise the demographic impact of non-lethal events, which are difficult to quantify. Most studies have utilised an approximate approach, for example, by assuming a reduction in foraging time (New et al., 2014; King et al., 2015), or nursing durations (Ruiz-Mar et al., 2022), are associated with negative demographic impacts. However, PCODs have been recognised as requiring greater statistical knowledge and a solid understanding of the biology and ecology of the species under consideration (New et al., 2015). Indirect anthropogenic threats can affect individual fitness in pinnipeds. Addressing these threats, comprehending their demographic impact, and enhancing our statistical knowledge of species biology and ecology are crucial for future conservation efforts.

In the future, climate change is likely to be one of the primary threats to ice-breeding pinnipeds, which are highly sensitive to warming due to their dependence on sea ice whilst hauled out and nursing (Kelly, 2001; Albouy et al., 2020). Recent decades have seen a remarkable decline in sea ice within polar and sub-polar seas, with the ice becoming younger, thinner, and less abundant (Tschudi et al., 2016; Kwok, 2018). This decline is particularly concerning in sub-polar regions because many may be ice-free by the end of the century and are currently essential habitats for ice-breeding pinniped species. For example, the Baltic sea is expected to see a decrease of 50-80% in its annual maximum ice extent by 2100 and is inhabited by the ice-breeding Ringed seal (*Pusa hispida*) (Meier, 2006; Andersson et al., 2015); the neighbouring freshwater lake systems, Lake Saimaa and Lake Ladoga are habitats for the vulnerable and endemic Ladoga seal (*Pusa hispida ladogensis*) (Sipilä, 2016) and the endangered and endemic Saimaa seal (*Pusa hispida saimensis*) (Sipilä, 2016) respectively; the Caspian sea is inhabited by the endangered and endemic ice-breeding Caspian seal (*Pusa caspica*) (Goodman and Dmitrieva, 2016) and is projected to have minimal ice cover by the end of the century (Tamura-Wicks et al., 2015); and the Sea of Okhotsk is an important breeding habitat for four ice-associated seal species, the ringed (*Pusa hispida*), ribbon (*Histriophoca fasciata*), bearded (*Erignathus barbatus*), and spotted (*Phoca largha*) seals (Trukhanova et al., 2017), and will potentially reach ice-free conditions by 2100 (Paik et al., 2017).

Although a complete loss of sea ice would force a switch from ice breeding to terrestrial breeding, the long-term demographic impacts of that switch are unknown. Some inferences about the effects of terrestrial breeding may be gained through studies that have investigated breeding success across years with poor breeding conditions. For example, in the Gulf of St Lawrence and off the coast of northeast Newfoundland, harp seals (*Pagophilus groenlandicus*) that are born on ice that is too thin to support pups throughout the nursing period experience pup mortality of approximately 10% (Stenson and Hammill, 2014), whereas pups that are born on stable ice have a much lower mortality rate between 1.1–1.4% (Kovacs et al. 1985). In addition, although most grey seals (*Halichoerus gryphus*) breed on land, the Baltic subpopulations are one of the only pinnipeds known to vary between land and ice breeding, depending on ice availability. In the Baltic, the pre-weaning mortality rate of terrestrial born grey seal pups is higher on land at ~21.1% and much lower on ice at ~1.5% (Jussi et al. 2008). Although variation in pup mortality rates when breeding on land or ice provides some information about the impacts of ice loss, it does not provide information about the spatial dependency between breeding seals and local ice characteristics. This is important because without improving our understanding of breeding seal distributions and ice characteristics, we cannot know what spatial and temporal characteristics of ice may result in reduced pup survival and decreased population viability. By understanding how breeding distributions relate to spatial and temporal ice characteristics, we can better understand how climate forecasts integrate with contemporary assessments of breeding distributions and better understand the risk status of modern ice-breeding seals to climate conditions and better forecast the risk status of ice-breeding pinnipeds under climate change.

1.3. Quantitative methods in pinniped conservation

Linking complex biological data with dynamic datasets that describe environmental change to describe and forecast ecological responses is a complex task. Monitoring wild animals over space and time is essential to understanding their ecology. However, tracking animals over large areas is complicated by logistical barriers that limit ground-based surveys (Bagley, 1917; Stamp, 1925; Lonergan et al., 2011; Morris et al., 2021). More recent data collection innovations have increased the ability of ecologists to gather data on an animal's location. However, the practicalities of data collection often result in datasets that break assumptions and reduce the statistical power of classical statistical methods such as ANOVA and simple linear regression (Bolker et al., 2009; Hector et al., 2010). Fortunately, statistical innovations, such as the popularization of mixed models and advances within Bayesian statistical methods (Bolker et al., 2009; Lindgren et al., 2015; Bachl et al., 2019; Tikhonov et al., 2020) have greatly increased the range of tools researchers can use to understand natural systems data and by combining data collection innovations with the latest statistical innovations, modern ecological research is well-equipped to reduce subjectivity in research and conservation by informing conclusions through robust statistical relationships. Regarding pinniped research, two of the most significant data collection innovations include aerial population surveys (Hunter and Yeager, 1949; Lonergan et al., 2011; Morris et al., 2021) and animal-borne sensors (Costa et al., 2010; Dmitrieva et al., 2016; Katzner and Arlettaz, 2020).

1.3.1. Aerial survey data

The invention of the earliest manned and powered aircraft began a technological revolution that greatly increased the capacity of people to travel (Wright, 1989). With the ability to cover distances much faster than other modes of transport, surveyors quickly adopted aviation (Bagley, 1917). Some of the earliest ecological applications include surveying inaccessible mangrove forests (Stamp, 1925). Although, the earliest aerial surveys for counting wild animals did not begin until the 1940s (Hunter and Yeager, 1949). In the modern era, aerial surveys are widely adopted when collecting data on animals over large and less accessible areas. This method of data collection is advantageous when surveying pinnipeds, for example, during their annual moult, when individuals haul out in remote locations (Lonergan et al., 2011; Morris et al., 2021), and when surveying ice-associated pinnipeds, due to the inaccessibility of remote sea-ice (Moreland et al., 2013; Young et al., 2015; Dmitrieva et al., 2015; Trukhanova et al., 2017; Lindsay et al., 2021). Aerial surveys are conducted along flight transects to count animals, where individuals are counted along a transect line or strip (Jolly, 1969; Caughley, 1977). These counts are often used to estimate population abundance after accounting for biases such as survey design (Kenyon and Rice, 1961; Jolly, 1969; Caughley, 1977). To reconstruct abundance, numerous methods have been deployed, such as combining observation counts with life tables that describe vital rates (Lowry, 2014) and applying post-hoc corrections to observed counts as a function of survey coverage (Borchers et al., 2002; Lonergan et al., 2011; Dmitrieva et al., 2015). Additionally, one further application of aerial survey data is the analysis of relationships between observations and environmental covariates.

Associating observations with covariates is often conducted using a range of regression-based tools. Although, it is becoming increasingly common to extend the utility of these tools by incorporating a combination of spatial covariates and predictive capabilities, which generally refers to the process of "species distribution modelling". Species distribution models (SDM) are increasingly used to test ecological hypotheses, investigate the impact of climate and anthropogenic impacts upon species distributions (Guisan and Thuiller, 2005), and support conservation management decisions (Farmer et al., 2022). SDMs have been used to evaluate habitat use in global pinniped populations (Kaschner et al., 2006; Briscoe et al., 2018) and to recommend management solutions for marine species (Marshall et al., 2014; McClellan et al., 2014). The application of SDMs to pinniped ecology has recently lead to a number of innovative insights, such as the preference of Ross seals (*Ommatophoca rossii*) to forage within shallow waters in the summer and deeper waters in the winter, which were used to inform the species climate change vulnerability (Wege et al., 2021). These applications highlight the potential of SDMs to inform ecology and policy. However, when applied to aerial survey data, SDMs encounter several complex statistical challenges, such as an imprecise knowledge of species absence (Warton and Shepherd, 2010) and combining data of varying types (Miller et al. 2019).

One way to overcome challenges associated with analysing aerial survey data using SDMs is to utilise modelling frameworks that account for some of these challenges. One notable framework is the point-process model, which in the context of SDMs, can be adopted as a presence-only method for modelling occurrence data (Diggle, 2006; Warton and Shepherd, 2010; Renner et al., 2015; Y. Yuan et al., 2017). This is because aerial survey data is often presented as a list of locations without information about where a species is absent. This type of data, known as "presence-only" data (Pearce and Boyce, 2006; Renner et al., 2015), is formed from binary point events that indicate if an event occurred, where a set of point events is referred to as a point process (Diggle, 2006; Renner et al., 2015). Point-process models are specifically designed to analyse point processes and the density of point events across space. By directly modelling the quantity that most SDMs are attempting to describe, point-process models avoid a deterministic categorisation of occurrences into spatial bins and they do not use "pseudo-absences", and, therefore, mitigate many issues surrounding their selection (Warton and Shepherd, 2010). However, it was not until recently that they became more frequently adopted by ecologists (Warton and Shepherd, 2010; Chakraborty et al., 2011; Y. Yuan et al., 2017).

Another analytical challenge when deploying SDMs from photographic aerial survey data is combining datasets with different data generation processes. For example, in the case of photographic surveys, a single geo-reference may record the location of an observation, with an additional variable counting the number of individuals at that location. One way of combining related datasets within a single unified model is the joint species distribution model (jSDM), which refers to a multivariate modelling framework where different but correlated outcomes can be modelled so that the effect of some covariates are jointly estimated, and the effect of other covariates are estimated separately. jSDMs have recently gained popularity through packages such as sjSDM (Pichler and Hartig, 2021), HMSC (Tikhonov et al., 2020), and INLA (Martino and Rue, 2010; Lindgren et al., 2015; Sadykova et al., 2017; Sadykova et al., 2020), and are frequently used to model the co-occurrence of multiple species, although, similar methods can be deployed upon datasets with varying data types (Jaffa and Jaffa, 2019). Furthermore, this type of analysis is an excellent example of the utility of Bayesian statistics because it highlights the inherent flexibility of defining data generation processes through data likelihoods. For instance, in a photographic dataset, two separate data likelihoods could be specified, a point process likelihood for the observation data generation process and a Poisson likelihood for the count data generation process. This type of model can be referred to as a marked point process model, which has been used to estimate killer whale space use (Watson et al., 2019).

1.3.2. Animal tracking data

One further advancement in data collection technologies has been in the implementation and development of animal-borne sensors (Katzner and Arlettaz, 2020), which refers to any device that records data and can be attached to an animal. During the 1950s, the first radio telemetry sensors were developed and deployed on humans to monitor vital rates (Barr, 1954; Mackay and Jacobson, 1957). However, ecologists quickly adopted similar technologies (LeMunyan et al., 1959; Lord et al., 1962). The earliest animal tracking applications involved using mobile receivers to locate animals within a range of less than 46 metres (LeMunyan et al., 1959). However, the field advanced quickly and by the mid-1960s (Southern, 1964) was able to track wild free-ranging Bald eagles (*Haliaeetus leucocephalus*) within a range of 2 to 3 miles, and F.C. (Craighead and Craighead, 1965) were able to track grizzly bears (*Ursus arctos horribilis*) within a range of 15 to 20 miles. These early applications made broad associations between behaviour and positioning, however, early investigations of wide-ranging species were hampered by the low resolution of positioning at range from earthbound receivers. The first truly remote tracking system was deployed upon adult elk (*Cervus canadensis*) using the Nimbus 3 and 4 satellite systems in combination with a transponder attached to an electric collar, although the resolution and performance of these early satellite trackers varied widely (Craighead et al., 1972).

In the modern era, satellite animal-borne sensors are often used to understand animal movements (Katzner and Arlettaz, 2020; Hertel et al., 2020). These technologies are beneficial when studying animals that are difficult to see, such as foraging pinnipeds (Costa et al., 2010; Dmitrieva et al., 2016; Briscoe et al., 2018; Wege et al., 2021) (Figure 1). Modern animal trackers can provide spatial positioning data that when processed returns a range of metrics, such as speed, turning angles, and more. However, previous research has condensed individual metrics into unified summary metrics. One common unified approach involves identifying sections of a data timeline that corresponds with "area restricted search" (ARS), which refers to a behavioural state where movement track topologies have higher turning angles and lower or more rapidly changing speeds (Jonsen et al., 2005; Jonsen et al., 2019; Jonsen et al., 2020). In many cases, ARS is likely to indicate foraging behaviour, which contrasts with transiting behaviour, where track topologies have lower turning angles and higher or more consistent speeds. The relationship between ARS and foraging has theoretical support from optimal foraging theory, which generally states an expectation for predators to behave in a way that maximises their time spent within regions of higher prey density (Kareiva and Odell, 1987) and minimises their time spent transiting between prey patches (MacArthur & Pianka, 1966).

Many methods can identify ARS behaviour, and both discrete (Jonsen et al. 2005) and continuous (Jonsen et al. 2019) methods exist. Discrete methods classify behaviours into a finite number of behaviours, such as "foraging" and "transiting". Compared to discrete methods, continuous approaches have a much higher numerical resolution, and this enhanced resolution may be especially useful for understanding complex behaviours. For example, when investigating behaviours that have a high degree of individual variation, higher numerical resolution may allow researchers to identify these differences more reliably. The ability to measure individual variation more precisely is particularly beneficial when analysing pinniped movements, where the magnitude or "personality" of foraging behaviours can vary widely (Dmitrieva et al., 2016). Individuals frequently exhibit different propensities for movement states (Spiegel et al., 2017), and higher numerical precision may allow researchers to detect these patterns with greater reliability. To utilise the enhanced precision of continuous metrics for ARS, researchers must maximise the accuracy of their models, although the presence of individual variability infers a data structure with several dependencies and hierarchies and these structures can present a series of challenges at during analytical stages.

When specifically analysing animal tracking data, there are three analytical challenges to consider. Firstly, the individual based dataset naturally forms a time series dataset that is temporally autocorrelated. Temporal autocorrelation refers to a statistical phenomenon where data records at one point in time are more closely related to recent datapoints than they are to distant datapoints (Yuan X.W. et al., 2017) and this phenomenon breaks the non-independence assumption of traditional regression methods such as General Linear Models and ANOVA. The second challenge refers to individual variability. Individual variability infers a nested data structure where records from a single individual are more related to themselves that other individuals and this also breaks the non-independence assumption. Finally, the response life of tracking tags can vary greatly and result in highly imbalanced datasets (Dmitrieva et al., 2016), and an imbalanced dataset typically reduces the statistical power of traditional statistical methods. Fortunately, modern statistical methods have expanded the scope of traditional statistical tests, with modern methods capable of addressing analytical challenges that a specific to tracking based data, as well as challenges associated with analysing ecological data more generally.

Figure 1 A Caspian seal about to be released after tagging with a Wildlife Computers SPOT satellite tag. Credit: Simon Goodman University of Leeds

1.3.3. Frameworks for analysing ecological data

The practicalities of ecological data collection often result in datasets that break the assumptions of, and reduce the statistical power of, traditional statistical methods such as General Linear Models and ANOVA. For example, occurrence data is typically derived from a Poisson process which is inherently heteroscedastic as its key property relates to its mean equalling its variance, and ARS movement metrics are typically bounded within a fixed interval such as 0 and 1 (Jonsen et al., 2020). Furthermore, the response of animals to environmental covariates is frequently non-linear (Miksis-Olds and Madden, 2014; Gurarie et al., 2017). Finally, it is common for data collection practicalities to result in unbalanced datasets, and for natural systems datasets to exhibit a wide range of independence breaking phenomena such as autocorrelation and hierarchies. Although traditional statistical methods are less capable when analysing data that presents these phenomena, modern statistical innovations are well-equipped to deal with this lack of functionality.

Generalised linear models (GLMs), generalised additive models (GAMs), and mixed-effects models are a series of useful advances that enable researchers to separate 'true-signals' that are useful for estimating the relationship between a species and its environment, from 'false-signals' and noise that would otherwise impact useful analyses. Firstly, the emergence of GLMs has enabled researchers to account for the wide array of the mean variance relationships that exist within ecological data. By associating model-based estimates of a mean to the linear predictor via a link function, GLMs can model phenomena that would otherwise fail to pass some of the fundamental assumptions of statistical tests due to heteroskedasticity. Secondly, GAMs, as an extension of the generalised modelling framework, do not assume linearity in the specific form of the relationship between the variables being modelled. GAMs can therefore reveal non-linear effects of the covariate on the dependent variable, and this structure is highly useful when applying smoothers that may describe, for example, non-linear covariates, time series trends, and temporal autocorrelation, and analogous solutions can be applied to account for spatial autocorrelation (Y. Yuan et al., 2017). Finally, mixed-effects models can be used by researchers to parametrise a much wider range of phenomena than traditional methods, by more accurately describing the hierarchical structure that drives the data being modelled. This structure is useful for addressing issues such as unbalanced survey designs, as well as defining model effects that impact multiple layers of the data hierarchy. For example, in a time series dataset, temporal smoothers such as a random walk effects model could be set on a discrete number of parameters so that each subset of entries at individual points in time may be autocorrelated to subsets of entries at previous points in time, and in a spatial dataset, spatial smoothers such as the besag, bsm, or SPDE effect models can be used to describe spatially dependent autocorrelations.

In this thesis, I use a combination of these statistical innovations to analyse two datasets collected whilst surveying the ice-breeding Caspian seal. From these datasets, I conducted three distinct studies that aim to address gaps in our understanding of how the environment can impact Caspian seal habitat use and behaviour and present frameworks for understanding what conservation measures may be effective at ensuring Caspian seal survival. Firstly, I conducted an evaluation of contemporary Caspian seal breeding distributions using an aerial survey dataset. In this study, the primary investigation used a Bayesian Generalized Additive Mixed Model (BGAMM) to describe non-linearities in the effect of spatial and temporal ice-continuity on seal pup densities. Secondly, I conducted an evaluation of contemporary Caspian seal foraging conditions using a satellite animal-borne sensor dataset. In this study, the primary investigation used a BGAMM to describe seasonal variability in the associations between foraging activity and habitat use. Finally, I combined knowledge gained from the first study along with previous research on bycatch rates in Caspian seals to parametrise mortality-based impacts within future population projections and evaluated how different scenarios may impact the quasi-extinction risk of Caspian seals over time. In this study, the primary investigation used a temporally structured Leftkovich model to project the future Caspian seal population structure over time regarding a series of scenarios that describe how impacts associated with threats from climate change and bycatch may evolve over time. The following sections outline the background to the Caspian seal study system and the advances that my work provides.

1.4. Caspian seals

The Caspian seal (*Pusa caspica*) is listed as endangered within the IUCN red list and may be one of the most threatened ice-breeding pinnipeds (Goodman and Dmitrieva, 2016). Caspian seals are small-bodied, ice-breeding pinnipeds that are endemic to the Caspian Sea in Central Asia, which is likely to be one of the most extreme environments inhabited by any pinniped. The Caspian Sea ranges between 47 degrees latitude in the north to 36.5 degrees latitude in the south and experiences a variable continental climate (Figures 2 and 3). During the winter, sea ice forms over the shallow north basin, although warmer temperatures occur in the south. In summer, the sea surface temperature typically exceeds averages of 23°C across most of the Caspian, although, in the shallow north basin, sea surface temperature can reach 35°C. In addition to a variable climate, there are various habitats within the Caspian. Deep regions that exceed 700 and 1000 meters can be found in the central and southern basins, and the Caspian Sea is fed by approximately 130 rivers, with the Volga, Ural, Terek, Sulak, and Kura, forming large river deltas (Kravtsova et al., 2004). The extensive reed beds, sandy islets, and muddy shallows are a unique aspect of the northern basin that provides essential habitat for foraging and resting during the spring and autumn. Furthermore, the Caspian Sea is a major centre for industry within Central Asia, with five countries bordering its 4800km of coastline. Industry-related activities generally target the wide variety of natural resources, including offshore oil and gas ventures, shipping industries, and major fisheries operations (Kosarev, 2005; Goodman et al., 2007; Strukova et al., 2016; Goodman and Dmitrieva, 2016). The Caspian Sea has also seen a large increase in illegal fishing activity since the early 1990s (Dmitrieva et al., 2013; Strukova et al., 2016; Svolkinas, 2021), which is driven by the high economic value of sturgeon fish of the *Acipenseridae family.* Six sturgeon species are present within the Caspian, with the Beluga sturgeon (*Huso huso*) being the most valuable (Dmitrieva et al., 2013).

Figure 2 Orthographic map of Earth centred at 42 degrees latitude and 51 degrees longitude. The Arctic circle, at 2600 kilometres from the North Pole, is highlighted in white. The Caspian Sea is highlighted in Yellow.

Figure 3 The Caspian Sea and bordering countries

1.4.1. Biology and ecology of Caspian seals

Caspian seals form a single panmictic population that range throughout the Caspian Sea but show a seasonal pattern of migration related to their annual life history. Breeding behaviour takes place on the single winter ice field that typically forms at the end of December and melts at the beginning of March (Dmitrieva et al., 2016). Their life cycle follows an annual pattern where the birth of pups and breeding occurs between late January to mid-March, after which they nurse for approximately 3-4 weeks. Between late March and early May, individuals haul out in large aggregations during the spring moult (Wilson et al., 2014) and begin to disperse widely throughout the Caspian sea (Dmitrieva et al., 2016). From mid-August onwards, individuals start returning to the north Caspian, where most individuals congregate amongst the north easterly regions, although some individuals may take longer foraging trips to the mid and southern regions (Krylov VI, 1972; Dmitrieva et al., 2016). From December, individuals start to track the ice edge as it forms prior to the upcoming breeding season. Throughout their seasonal movements, Caspian seals are exposed to a wide variety of habitats and threats that influence their ecology. In general, the foraging ecology of Caspian seals appears to cluster within at least 3 discrete diving groups, where some individuals spend most of their time within shallower regions in the North and others spend most of their time within deeper waters in the middle and South Caspian (Dmitrieva et al., 2016). When occupying these different habitats, Caspian seals are likely to eat different species, and their diet contains several migratory fish, as well as fish that occupy a variety of different habitats (Pochtoeva-Zakharova and Huraski 1999; Ismagambetov 2014; Wilson and Goodman 2018). Furthermore, the Caspian Sea is host to various fishing and shipping industries that occur heterogeneously across the Caspian, and the exposure of Caspian seals to anthropogenic threats is likely to vary throughout their migrations and during an annual cycle. The combination of climate threats, anthropogenic threats, and other threats make the Caspian seal particularly vulnerable.

1.4.2. Conservation threats to Caspian seals

1.4.2.1. Climate change

Current climate projections expect higher air temperatures to reduce the cover, duration, and stability of the winter ice sheet (Shahgedanova et al., 2009; Koenigk et al., 2013; Tamura-Wicks et al., 2015), in addition to increasing evaporation and freshwater inflow that may result in the land stranding of the shallow sea-ice forming areas that range between 3 to 5 meters deep (Elguindi and Giorgi, 2007; Renssen et al., 2007; Nandini-Weiss et al., 2020). Future declines in sea ice cover and sea level will impact Caspian seals because 99% of pups are born upon single-year pack ice that forms over the shallow northern basin, and in related species, breeding within poor ice conditions is associated with decreased pup survival (Stenson and Hammill, 2014), and an increase in wetting before weaning may negatively impact survival (Frisch and Øritsland, 1968; Erdsack et al., 2013; Wilson et al., 2017a). In addition, when compared to ice breeding conditions, the increased breeding densities upon land have been associated with decreased pup survival in grey seals seal (*Halichoerus grypus*) (Jüssi et al., 2008). In Furthermore, the Caspian Sea is landlocked, and sea-ice forms over shallow regions (<5 meters), with recent projections predicting the Caspian Sea level to decrease by 4.5 to 18 meters by 2100 (Elguindi and Giorgi, 2007; Renssen et al., 2007; Nandini-Weiss et al., 2020). Future water level declines may therefore force a transition to terrestrial breeding, which is associated with higher breeding densities and an increased pre-wean pup mortality in grey seals (Kovacs et al., 1985; Jüssi et al., 2008; Stenson and Hammill, 2014).

1.4.2.2. Historical commercial hunting

Industrial activity and development within the Caspian Sea have threatened the survival of Caspian seals over the last century. From the mid-19th century to the 1990s, Caspian seals were harvested extensively for furs, blubber, and meat, and as a result, the population was estimated to have collapsed from more than 1 million individuals to approximately 168,000 individuals over the last

100 years (Harkonen et al., 2008; Harkonen et al., 2012; Dmitrieva et al., 2015; Goodman and Dmitrieva, 2016). In 2008, Caspian seals were designated as Endangered in the International Union for Conservation of Nature (IUCN) Red List under the criterion of a population decline exceeding 70% in the last three generations, and because of additional multiple unresolved threats (Goodman and Dmitrieva, 2016).

1.4.2.3. Contemporary fisheries bycatch and poaching

The accidental mortality of animals in fishing operations is called bycatch and is associated with disturbance and mortality in at least 66% of extant pinniped species (Kovacs et al., 2012; Reeves et al., 2013). Bycatch can cause immediate mortality due to severe injury or drowning, although bycaught animals can be released alive and die later from sublethal injuries they sustained when bycaught (Wilson et al., 2014). In the Caspian Sea, ~96% of bycatch events are fatal, and 14%-20% of contemporary populations may die from bycatch within illegal fisheries each year (Svolkinas, 2021), and approximately 93% of bycatch events occur within illegal fisheries primarily targeting the commercially valuable sturgeon fish in the Acipenseridae family (Dmitrieva et al., 2013). Due to the high rates of mortality within bycatch, decreasing bycatch mortality within illegal fisheries is a significant objective of Caspian seal conservation within the next century.

1.4.2.4. Habitat loss and degradation

Caspian seals are at risk of habitat loss due to climate change threats that will reduce the coverage of sea ice that they depend on for breeding (Shahgedanova et al., 2009; Koenigk et al., 2013; Tamura-Wicks et al., 2015). However, additional threats include disturbance from the ice breaker vessels that traverse breeding areas to service nearby oil fields (Wilson et al., 2017b), and increasing development nearby coastal areas (Nadim et al., 2006), which may be used for seals as haul out sites when resting and during the annual moult (Dmitrieva et al., 2016). In addition, previous studies on Caspian seal movements have shown that individuals use a broad range of coastal areas, including Caspian river deltas (Dmitrieva et al., 2016), and similar habitats are known to be important foraging habitats in other pinnipeds (Allegue, 2017). Development within these river inlets may therefore degrade important foraging areas in Caspian seals and these impacts may be further compounded by erosion due to climate change (Loucks, 2019).

1.4.2.5. Disease

Many harmful diseases have been associated with population declines in marine mammals, however, morbilliviruses are notable due to their close association with several mass mortality events. Morbilliviruses like Canine distemper virus (CDV) are believed to have caused mass mortality events in several pinnipeds, including Caspian seals. To better understand the impacts of disease, several papers have investigated the prevalence of CDV and other pathogens within Caspian seals (Kennedy et al., 2000; Kuiken et al., 2006; Wilson et al., 2014; Namroodi et al., 2018). Retrospective analysis suggests that CDV outbreaks occurred during the 1970s and 1980s 1980s (Wilson et al., 2014), and thousands of seals died during epidemics between the late 1990s and early 2000s (Kennedy et al., 2000; Kuiken et al., 2006). However, several of these studies have been limited due to small sample sizes and biases relating to sample selection and, therefore, reported rates of infection may not be representative of the population.

1.4.2.6. Pollution

Persistent organic pollutants (POPs) are known to accumulate within pinnipeds and in severe cases have been associated with immunotoxicity (Bergman et al. 1992; Mortensen et al. 1992; Sormo et al. 2009) and reproductive failure (Hutchinson and Simmonds 1994). The Caspian Sea is a major oil producing region and several POPs are present. However, research suggests that hydrocarbon pollution may not significantly threaten Caspian seal survival (Wilson et al. 2014), because levels appear to be low (Allchin et al. 1997), and the species may be adapted to an environment with natural oil contamination (Kosarev and Yablonskaya 1994; Watanabe et al. 1999). Hydrocarbon exposure was not associated with CDV outbreaks during 2000, which may imply it was not resulting in immunosuppression (Kuiken et al., 2006). Polychlorinated biphenyl (PCB) and dichlorodiphenyltrichloroethane's (DDT) were associated with CDV outbreaks between 1997 and 2001, however, samples were limited to dead and stranded seals and may not be representative of contaminant levels within healthy seals (Wilson et al. 2014). Providing levels were sufficiently high, pollutants could compromise the immune system and/or fertility of Caspian seals (Kajiwara et al. 2008) and accumulative effects over time may increase their impact on older age classes over time (Wilson et al. 2014). However, this is less likely to result in major demographic impacts if most individuals successfully reproduce as younger seals.

1.4.2.7. Invasive species and other drivers of ecosystem change

The Caspian Sea hosts several non-native species, however, the most prominent invasive species is a comb jelly fish *Mnemiopsis leidiy*. Although native to the western Atlantic, *M leidiy* is believed to have colonised European waters through transportation in the ballast water of ships (Harbison and Volovik, 1994). It was subsequently introduced into the Black Sea in 1982 (Pereladov, 1983) and then into the Caspian Sea through the Volga-Don Canal by 1998 (Ivanov et al., 2000). Within 1 year of its first observation, *M. leidiy* had colonised most of the Caspian Sea, and it appears to have dramatically influenced the relative biomass of Caspian fauna. Prior to the invasion of *M. leidiy, Eurytemora* sp. copepods were one of most abundant zooplankton species in the southern Caspian Sea (Pourang et al., 2016). However, after the invasion of *M. leidiy, Eurytemora* sp. copepods are one of the rarer zooplankton species (Pourang et al., 2016). *Eurytemora* sp. are an important prey species for anchovy kilka and *M. leidiy* competes with kilka by consuming zooplankton resources and kilka larvae (Ivanov et al., 2000). Therefore, the invasion of *M. leidiy* may impact Caspian seals by competing with anchovy kilka, which are believed to be an important high energy prey species for Caspian seals (Pochtoeva-Zakharova N, 1999).

1.4.3. Caspian seal conservation

Attempts to protect Caspian seals go back to the mid-20th century when hunting quotas restricted the number of seals that could be hunted to approximately 100,000, later reduced to 40,000, and then 20,000 seals per year, and by the mid-1990s hunting pressures were substantially reduced (Harkonen et al., 2012). However, contemporary threats have since emerged that continue to threaten the survival of Caspian seals. In 2007 the Caspian seal conservation plan was produced by the Caspian Environment Programme, which generated several key recommendations to protect Caspian seals (Goodman et al., 2007). To protect Caspian seals against the emergence of higher pup mortality due to climate change and anthropogenic threats, there is an urgent need for conservation action, although, at present, there are few practices or regulations that protect Caspian seals. Speed limits have been proposed within the core-breeding area (Wilson et al., 2017b), and Important Marine Mammal Areas (IMMA's) have been defined (Marine Mammal Protected Areas Task Force, 2021). Although these existing recommendations do not have legislative enforcement and IMMA's are not explicitly designed as protected areas that could be enforced (Hoyt, 2018). Furthermore, although protection is needed, there are notable gaps in our understanding of what habitats and locations are important for Caspian seals. Filling the gaps in our understanding of where Caspian seals go and what conditions are like at these locations is an essential step towards identifying the region’s most important for Caspian seal ecology and understanding how their risk status may be change following climate change.

1.5. Knowledge gaps and aims of this thesis

1.5.1. Chapter 2 – Caspian seal (Pusa caspica) pup distributions are reliant on the spatial and temporal stability of mobile pack ice

Over the last two decades, several key papers have improved our understanding of Caspian seal breeding ecology (Harkonen et al., 2008; Dmitrieva et al., 2015; Wilson et al., 2017a). Visual surveys of Caspian seals were conducted between 2005 and 2012 and tested for a link between annual pup production and freezing degree days, number of ice days, net primary productivity, and total and fast ice cover (Dmitrieva et al., 2015). Although the study did not identify any statistically significant relationships between total pup production and environmental covariates, further investigation may examine how covariates relate to the distribution of pups, instead of the total number produced in a year. This could help reveal potential relationships between environmental factors and the spatial distribution of pup populations. Understanding the relationship between environmental factors and pup distribution is important because without that knowledge we cannot; (i) produce statistically robust predictions of space use, which can inform and reduce bias in the identification of breeding hotspots, or (ii) understand how the ice requirements of Caspian seals relate to future ice loss due to climate heating, which can inform an assessment of the vulnerability of Caspian seals to climate change. To address these research gaps this chapter seeks to answer the question: What ice characteristics influence the breeding distribution of Caspian seals?

1.5.2. Chapter 3 – Seasonally flexible Marine Protected Areas (MPA) derived from the spatial and temporal variability of animal movements in Caspian Seals (Pusa caspica)

Previous work by Dmitrieva et al. (2016) used satellite-tag tracker-derived area-restricted-search as a proxy to investigate how Caspian seals use different areas for foraging and transiting. They found foraging-like behaviours occurred within clusters in the north, middle, and southern sections of the Caspian Sea. The prevalence of behavioural clusters suggests that these regions are important. However, a research gap is present in our understanding of the environmental factors that may implicate the spatial associations. In general, the north Caspian is shallow and Caspian seal activity clusters nearby the Volga delta, which provides over 80% of the Caspian freshwater inflow (Arpe et al., 2000; Ozyavas et al., 2010) and is designated as wetland of international importance under the Ramsar Convention (Leummens, 2018). Similarly, clusters in the middle Caspian are located near to Samur and Sabrancay river inlets (Kravtsova et al., 2004), and clusters within the middle and southern Caspian are nearby areas with a highly varied physical oceanographic features (GEBCO Bathymetric Compilation Group, 2019) and are superficially similar to the shelf edge habitats that other pinnipeds use for foraging (Nowak et al., 2020). The ecological significance of these areas may explain an association with these areas and foraging, however, a systematic and quantitative investigation into when these areas are important, and how their use relates to metrics associated with foraging activity is an essential step towards progressing our scientific understanding of Caspian seal ecology. Identifying where and when these regions are important for understanding Caspian seal foraging because without that knowledge we cannot; (i) produce data-driven insights about how foraging relates to environmental factors, which can inform the spatial planning of conservation recommendations, and (ii) identify where and when the regions that are important for foraging are most important, which is essential for understanding the ecology of Caspian seals and their exposure and vulnerability to anthropogenic activities. To address these research gaps this chapter seeks to answer the question: What are spatial and temporal covariates are associated with the regions where Caspian seals forage?

1.5.3. Chapter 4 – Estimating quasi-extinction risk for the Caspian seal (Pusa caspica) with respect to climate change and direct anthropogenic threats

Previous work by Harkonen et al. (2012) used annual hunting records dating back to the mid-19th century to construct a hind-cast population model that showed human impacts were a major contributor to the collapse of the Caspian seal population over the last century. Their results were a key component of a subsequent threat status evaluation for Caspian seals and informed the updated Endangered IUCN red list status by demonstrating the population had reduced by over 70% in the last three generations (Harkonen et al., 2012; Goodman and Dmitrieva, 2016). Although commercial hunting is no longer common, official hunting is conducted under a quota system administered by the Caspian Bioresources Commission. Typical annual quotas are for 18,000 Seals, with 8,000 allocated to Russia, with the rest divided among the other Caspian states (Goodman and Dmitrieva, 2016). Despite a decline in official hunting by humans, Caspian seals are highly vulnerable to anthropogenically derived mortality by bycatch within commercial sturgeon fisheries.

Dmitrieva et al. (2013) documented a minimum bycatch of 1215 seals between September 2008 and September 2009, of which 93% occurred within illegal sturgeon fisheries, and may account for 5-19% of annual pup production. More recently, Svolkinas et al. (2022) precisely investigated bycatch rates within illegal sturgeon fisheries and found that bycatch within illegal sturgeon may result in the death of 14-20% of the Caspian seal population annually. These reported rates are high and clearly a threat to Caspian seal survival. However, a research gap is apparent in how these rates of mortality interact with the demographic life history of Caspian seals, other threats such as climate change, and how they impact the future extinction risk of Caspian seals. Identifying how bycatch mortality rates interact with the other vital rates that describe the demography of Caspian seals is important because without that knowledge we cannot; (i) evaluate the impact of extra mortality from bycatch upon the extinction risk of Caspian seals, and (ii) understand how the impact of extra mortality from bycatch compares with demographic impacts relating to climate change threats. To address these research gaps this chapter seeks to answer the question: How do different combinations of conservation threats, such as bycatch morality and reduced sea ice cover, impact the quasi-extinction risk of future Caspian seals?

1.6. Contributions of this thesis

This thesis consists of five chapters:

Chapter one is a general introduction where I briefly introduce pinniped ecology and the study system, discuss the knowledge gaps and overarching concepts relevant to the thesis, and discuss research objectives and aims.

Chapter two is presented in a paper style, where I investigate the distribution of Caspian seal pups concerning the spatiotemporal history and stability of the ice they breed on.

Chapter three is presented in a paper style, where I investigate the temporal change in the use of different habitats by Caspian seals and use these inferences to develop spatially and temporally flexible marine protected area plans.

Chapter four is a chapter presented in a paper style. I use inferences gained in Chapter 1, alongside other research on Caspian seals to develop population projections that incorporate how threats that impact Caspian seals may change over time.

Chapter five concludes the thesis.

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2. Chapter two – Caspian seal (Pusa caspica) pup distributions are reliant on the spatial and temporal stability of mobile pack ice

Harrison Tan, Lilia Dmitrieva, Chris Hassall, and Simon J. Goodman

2.1. Abstract

Ice dependent marine mammals are potentially vulnerable to climate change impacts in the 21st Century. Understanding the consequences of climate change is important if we are to meet conservation objectives and better assess population viability. The ice-breeding Caspian seal (*Pusa caspica*) is endemic to the land-locked Caspian Sea, which lies at the southern limit for sea ice formation in sub-Arctic seas. In this study, we use aerial survey data for Caspian seal pupping distributions, remote sensing data sets, and a visual feature tracking algorithm to construct hierarchical Bayesian models which investigate spatial and temporal dynamics in breeding site use and pup density. We report a novel protocol that incorporates an ice tracking algorithm (IMCORR) alongside a modelling approach that combines spatial environmental data and point process data in a spatial framework (INLA-SPDE). Our results illustrate that the stability of ice through time is the most informative ice-characteristic for predicting high pup densities, and we show that most of the pups we detected are born on mobile pack ice that has remained stable for marginally longer than the 3-5 weeks that Caspian seal pups need to complete the weaning period. These results suggest that Caspian seals may be operating at the limit of breeding ice stability, and that further reductions in ice stability may lead to significantly higher pre-weaning pup mortality. These results are likely to be indicative of future climate change impacts upon other pack-ice breeding pinnipeds in the Arctic and highlight the vulnerability of these species to increasing environmental stochasticity.

2.2. Introduction

Sea ice in polar and sub-polar seas is getting younger, thinner (Tschudi et al., 2016), less abundant, and more sensitive to seasonal variability in climate forcing (Kwok, 2018; Allan and Allan, 2019). Multi-year ice in the Arctic is become scarcer (Kwok, 2018), and many Arctic and sub-Arctic regions that were previously covered by seasonally forming ice are now 'ice-free' during the summer (Stroeve and Notz, 2018; Allan and Allan, 2019). The loss of sea-ice is likely to have a major impact on ice-dependent species, and some of the most vulnerable taxa may be ice breeding pinnipeds, which rely on ice for behaviours integral to their life-history (Kovacs et al., 2012; Albouy et al., 2020). Studies have shown that sea ice decline is associated with a decrease in the reproductive output, survival, and overall abundance of ice breeding pinnipeds (Ferguson et al., 2005; Johnston et al., 2012; Ferguson et al., 2017). However, so far, no studies have considered how seasonal variability in ice sheet dynamics may impact ice-breeding seal pup survival.

2.2.1. Climate change impacts upon ice-breeding pinniped pups

There is an urgent need to improve our understanding of how climate change can impact pinniped population dynamics and ecosystem function, and to inform conservation strategies for vulnerable species (Kovacs et al., 2012). One way of approaching this research gap is to improve our understanding of how a species distribution correlates with the surrounding environment. For example, the distribution of a species can be associated with environmental variables that are related to a species life-history (Ribic et al., 1991; Mordecai et al., 2011). By improving our understanding of the correlations between a species distribution and their environment, we can better inform predictions about the potential impacts of climate change on a species ecology and demography, and address research gaps relating to how climate change can impact pinniped populations.

One of the most impactful climate threats that impacts ice-breeding seals is the loss of sea ice due to climate heating (Albouy et al., 2020). Pups of ice breeding species, including Caspian (*Pusa caspica*), Baikal (*Pusa sibirica*), ringed (*Pusa hispida*), harp (*Pagophilus groenlandicus*), spotted (*Phoca largha*) and Baltic grey (*Halichoerus grypus*) seals, are particularly vulnerable to the premature melting of ice before moulting through mortality due to hypothermia or drowning. Pups of these species are born with white lanugo coats that persist for several weeks until pups moult after weaning. Lanugo fur provides insulation in air for young pups while they build up a blubber layer through the lactation period (Frisch and Øritsland, 1968; King, 1983; Erdsack et al., 2013). However, young pups cannot survive immersion for extend periods, and their lanugo fur is non-insulating when wet so young pups that are wetted prematurely risk hypothermia if they do not dry out quickly (Frisch and Øritsland, 1968; Erdsack et al., 2013; Wilson et al., 2017).

The potential for intermittent immersion to threaten young seal pups is somewhat dependent upon an individual species ecology. For example, following intermittent immersion, ringed seal pups *(Pusa hispida)* avoid hypothermia by drying themselves within the warm insulating snow lairs that ringed seal mothers construct (Smith and Stirling, 1975), however, early snowmelts can prematurely destroy subnivean lairs (Stirling and Smith, 2004), and reduce pup survival (Iacozza and Ferguson, 2014). Similarly, Saimaa ringed seals (*Pusa hispida saimensis)* are also dependent on snow lairs, and reduced snow cover due to climate change is considered a major threat to this species (Niemi et al., 2019; Kunnasranta et al., 2021). During warmer winters with reduced snow cover, Saimaa ringed seal pups are exposed to thermoregulatory stress, human-caused disturbance, and predation, with perinatal mortality increasing from approximately 10% to 30% (Sipilä, 2003; Auttila et al., 2014; Auttila, 2015). In addition, high pup mortality due to the early breakup of ice and drowning was noted as a major contributor to the very low harp seal pup counts in the in the Gulf of St Lawrence during 2010 (Stenson and Hammill, 2014). Furthermore, most ice-breeding pinnipeds do not construct lairs and, therefore, the age-structured vulnerability of ice-breeding pinnipeds to hypothermia and drowning suggest two physical mechanisms that could impact pup survival if current or future climate conditions increase thermoregulatory stress.

In general, ice breeding pinnipeds are broadly categorised as fast ice breeders or pack ice breeders. Fast ice breeders breed upon ice that is fixed to land and generally close to the seashore, whereas pack ice breeders breed upon floating ice floes that continually drift in response to wind and ocean currents. Due to the spatial mobility of pack ice and its susceptibility to meteorological conditions, ice sheet variability may be especially impactful for species that predominantly breed on floating pack ice such as harp (*Pagophilus groenlandica*), hooded (*Cystophora cristata*) (Davis et al., 2008), and Caspian (*Pusa caspica*) seals (Wilson et al., 2017). Pack-ice breeders may therefore be at heightened risk of climate change impacts, but no studies have considered how spatial and temporal variability in ice sheet characteristics may impact pack ice-breeding seal pup survival. To improve projections of how future climate change may increase the quasi-extinction risk of ice-breeding pinnipeds, there is an urgent need to understand how climate variability and ice conditions influence seal breeding distributions and pup survival. However, to properly assess the climate related vulnerability and the breeding requirements of pack-ice breeders we must begin to incorporate these spatial and temporal ice dynamics in our estimates of pup distribution.

2.2.2. The Caspian seal as a case study for understanding spatial-temporal ice breeding requirements.

The Caspian seal is a small-bodied ice-dependent phocid that exhibits little sexual dimorphism with adults measuring approximately 1.4 m and weighing 80kg (Goodman and Dmitrieva, 2016; Dmitrieva et al., 2016). They are endemic to the Caspian Sea in Central Asia (Figures 2 and 3), which is the world's largest landlocked waterbody, spanning approximately 1150km north to south, and around

440km at its widest point (Lebedev, 2018). Caspian seals have declined from over 1 million individuals at the start of the 20th Century to around 168,000 in 2005, with historic declines associated with unsustainable commercial hunting through the 20th Century (Harkonen et al., 2012). The species has been listed as Endangered by the IUCN since 2008 (Goodman and Dmitrieva, 2016), and key contemporary threats are high rates of fisheries-related mortality and habitat loss (Dmitrieva et al., 2013; Svolkinas, 2021). Climate related impacts are of concern and based upon life history and habitat properties the Caspian seal has been rated as one of the most vulnerable marine mammals to climate change globally (Albouy et al., 2020). However, climate impacts have not been systematically evaluated in a statistically robust framework.

At approximately 46°N, the northern basin of the Caspian Sea is currently close to the southern limit for sea ice formation in the northern hemisphere, and the stability of annual ice conditions is extremely variable (Tamura-Wicks et al., 2015). Pack ice forms within the northern basin during the winter months (typically between late December and mid-March) (Dmitrieva, 2013; Dmitrieva et al., 2015), upon which more than 99% of Caspian seal pups are born. The peak birth period occurs towards the end of January (Wilson et al., 2017) and the nursing period lasts between 3 to 5 weeks (Wilson et al., 2017). Caspian seals do not construct snow lairs, but preferentially pup in small groups beside ice ridges or ice-slab piles that can provide shelter to pups (Dmitrieva et al., 2015; Wilson et al., 2017). Most pups are born upon pack-ice that forms in the central regions of the North Caspian basin, upon ice than is at least 20cm thick and overlying water 3 to 5 meters deep (Wilson et al., 2017). Nursing pups are mostly sedentary throughout much of the nursing period (Dmitrieva et al., 2015; Wilson et al., 2017), which increases the dependence of white lanugo-coated pups upon stable ice conditions at their birth site. Finally, exceptionally poor ice conditions, defined as years when total ice melt has occurred before the end of the lactation period, have been observed in the Caspian Sea at least three times since 2005 (Lavrova et al., 2022).

Under current climate change projections, the extent, duration and stability of the ice sheet is expected to decline during the 21st Century (Shahgedanova et al., 2009; Koenigk et al., 2013; Tamura-Wicks et al., 2015). Therefore, it is necessary to improve understanding of how ice conditions impact the distribution and survival of Caspian seal pups, so we can begin to evaluate the demographic resilience of the population to changing ice conditions and other threats. One way of systematically evaluating climate related threats is to utilize the latest statistical frameworks for analysing spatial data. These frameworks can allow researchers to parametrize relationships between distribution and environmental variables that can more accurately reflect the ecological theories that may explain our observations.

Figure 4 Orthographic map of Earth centred at 42 degrees latitude and 51 degrees longitude. The Arctic circle, at 2600 kilometres from the North Pole, is highlighted in white. The Caspian Sea is highlighted in Yellow.

Figure 5 The Caspian Sea and bordering countries

2.2.3. Models for assessing a species distribution

Variation in resource availability, such as the availability of sea ice for pinnipeds, is a key determinant of the distribution of ice breeding Caspian seals and links between species distributions and the environment can be analysed within the context of species distribution models (SDMs). SDMs have been used to evaluate habitat use in global pinniped populations (Kaschner et al., 2006; Briscoe et al., 2018), and have been used to recommend management solutions in marine species (Marshall et al., 2014; McClellan et al., 2014). However, the modelling of a species distribution proposes several complex statistical challenges such as an imprecise knowledge of species absence (Warton and Shepherd, 2010), combining data of varying types (Miller et al. 2019), observer and sampling biases (Chauvier et al., 2021), and spatial and temporal auto-correlation (Yuan et al., 2017). One modelling technique that has some potential to remedy issues relating to an imprecise knowledge of species absences with SDMs is the “point process model”, which analyses the density of point events across space (Renner et al., 2015). By explicitly modelling the quantity of interest, point process models have benefits in interpretation and implementation, and avoid the issues surrounding their selection of ‘pseudo-absences’ that are common in other presence/absence modelling frameworks (Warton and Shepherd, 2010). Another analytical challenge when deploying SDM’s, is using datasets that contain more than one type of data, or different data generation processes. For example, more than one species may be recorded, or in the case of photographic surveys, a single geo-reference may record the location of an observation with an additional variable counting the number of individuals at a location. One way of combining related datasets within a single unified model is the joint species distribution model (jSDM), which refers to a multivariate modelling framework where different outcomes can be modelled in such a way that a subset of effects can be jointly estimated (Sadykova et al., 2017; Jaffa and Jaffa, 2019; Tikhonov et al., 2020; Pichler and Hartig, 2021). For example, in a photographic dataset, two separate data likelihood could be specified, a point process likelihood for the observation data generation process, and a Poisson likelihood for the count data generation process. This type of model can be referred to as a marked point process model, which has been used to estimate killer whale space use (Watson et al., 2019), but is not commonly applied within pinniped research.

2.2.4. Feature tracking

In addition to the standard set of challenges facing distribution modelling, a unique aspect of modelling the distributions of pack ice-dependent species is the fact that the pack ice itself is not a static resource. Caspian seals typically nurse their pups on drifting pack ice (Dmitrieva et al., 2015; Wilson et al., 2017), however, pack ice moves in accordance with wind and water currents (Bindschadler and Scambos, 1991; Scambos et al., 1992).. In the Caspian sea, pack ice can drift by over 1.5 km per hour during high winds (Kadranov et al., 2017), and its movement results in the geolocation of the immobile nursing site, which is fixed upon any given ice floe, to chang through time. The movement of pack-ice is a notable problem collecting data during an aerial surveys. For example, photographic aerial surveys of ice-breeding pinnipeds follow predefined flight paths over the ice sheet, with the number of individuals in each photo counted later (Harkonen et al., 2008; Moreland et al., 2013; Dmitrieva et al., 2015; Gurarie et al., 2017; Morris et al., 2021). Researchers can then associate observations with environmental data, which is usually obtained using remote-sensing satellites (Lonergan et al., 2011; Johnston et al., 2012; Iacozza and Ferguson, 2014; Gurarie et al., 2017; Briscoe et al., 2018). However, due to pack-ice mobility, the geo-reference of each photo may not match the seal's actual location prior to the survey. This issue is critical when studying pack-ice breeding pinnipeds in climate-sensitive habitats, as environmental changes before the survey could affect the location or number of seal observations. Fortunately, advances in visual-image tracking can provide a methodology to evaluate change in the position of features within a remote-sensing image (Bindschadler and Scambos, 1991; Wuite, 2006; Wuite and Jezek, 2009; Li et al., 2018). These technologies can then be used to reconstruct an approximate geo-reference of seal pups when the individuals are themselves immobile on the otherwise mobile surface (Wilson et al., 2017).

2.2.5. Hypotheses

In this study, we use a novel protocol that incorporates a joint species distribution model and a visual tracking algorithm to investigate the drivers of high pup densities across multiple years. We evaluate how variability in ice conditions throughout a breeding season may lead to reduced pup densities and use these inferences to address current gaps in the literature on Caspian seal ecology. More specifically, we address gaps in our understanding of how contemporary breeding seals are spatially associated with habitat conditions, which is a necessary step towards understanding how climate derived changes in habitat may impact their future survival (Dmitrieva et al., 2015; Goodman and Dmitrieva, 2016; Wilson et al., 2017).. This research is important because there is currently a gap in our understanding of how future increases in climate variability may impact future ice-breeding pinnipeds. Improving our quantitative understanding of how spatial-temporal variability in ice conditions impacts contemporary ice-breeding pinnipeds is an essential step toward generating more robust population projections and assessing extinction risk.

2.3. Methods

2.3.1. Seal population data

Caspian seal pup survey data for the years between 2005 and 2012 were obtained from the Caspian Seal Research Programme archive. The dataset consists of GPS-referenced photos of lone seals, pups, and mother pup pairs on the Caspian ice sheet. The data was collected during eight aerial surveys carried out annually between 2005 and 2012, between 4th February and 2nd March, when most pups were likely to have been born (Harkonen et al., 2008; Dmitrieva, 2013; Dmitrieva et al., 2015). Briefly, survey flights were conducted over the winter ice sheet in the northern section of the Caspian Sea from the airports in Atyrau (Kazakhstan) and Astrakhan (Russian Federation). Flights ran along north to south transects with an inter-transect spacing of approximately 8 km (Figure 4). GPS-linked digital photographs were taken when surveyors identified seals on the ice sheet. In general, photographs captured clusters of multiple adults and nursing pups or more isolated individual seal pups, which we will hereafter refer to as a “birth site”. Birth sites are geo-referenced by a single GPS-linked photograph which is associated with a number that represents the number of seal pups counted within each photograph.

Different numbers of observers were present on each survey flight, therefore, when multiple observers were present on the same side of the aircraft, we applied a spatially determined repeated counting bias protocol. To implement our bias protocol, prior to our analysis we standardised our observation points at 100-meter intervals along our survey transects. Within each standardised point we registered the total number of seal pups counted by each observer within a 50m radius. If multiple observers recorded seal pups on the same side of the aircraft and within the same 100 metres interval, we removed records made by the observer who recorded the least seal pups within that specific interval. These steps were taken to minimise the chance of repeated counting and result in the most conservative estimates of pup densities. In addition, we chose not to include two years of survey data where the locations of counts were derived by linking the time stamp of photographs to the flight GPS track (2005 and 2006), rather than from camera linked GPS units, and the year that followed decommissioning of the Advanced Microwave Scanning Radiometer - Earth Observing System sensor (AMSRE) sensor (2012), which we relied on for the highest resolution Caspian Sea ice data.

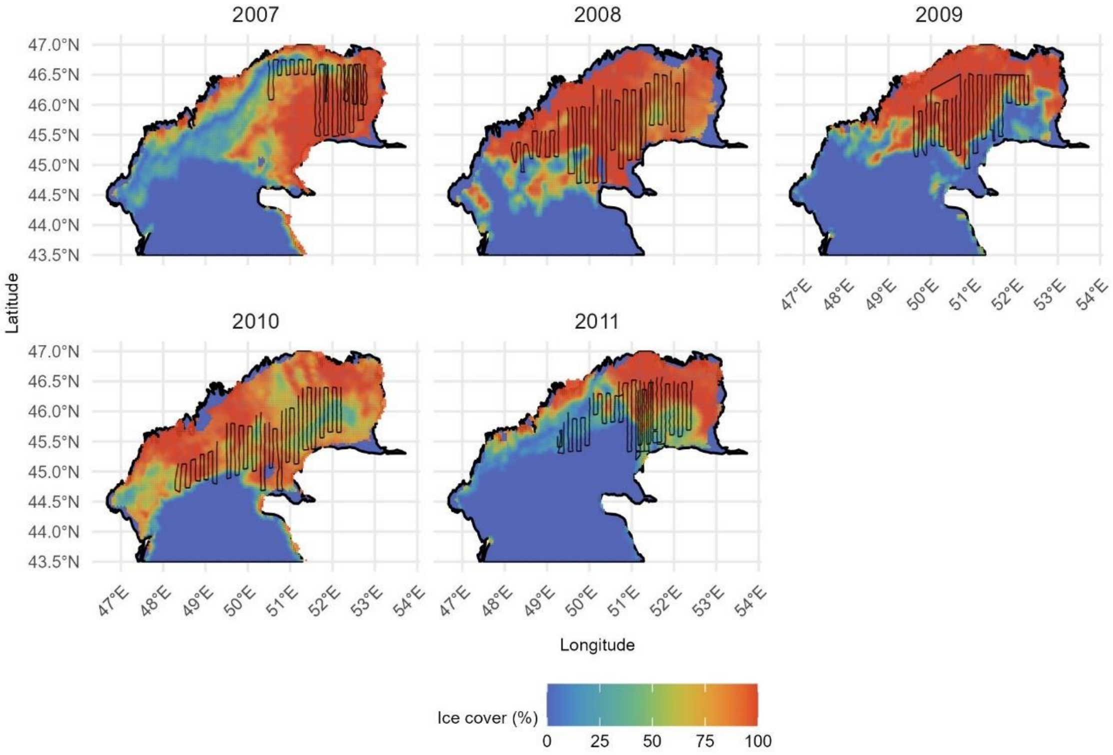

Figure 6 Ice cover on the median day of survey overlain by the aerial transects flown for each year

2.3.2. Environmental datasets

The highest resolution daily ice cover dataset for the Caspian Sea was identified as the ASI AMSR 3.125km ice concentration product (Heygster et al., 2009). Daily ice cover raster's were retrieved for each day of a period beginning on the 1st of January and ending on the median survey date of the survey year (Figure 5). The 1st January was chosen as it would represent a conservative estimate as the earliest possible start of the breeding season in Caspian seals (Wilson et al., 2017). Due to signalling faults or cloud cover, daily ASI AMSR data was not available for 2 days in 2007, 4 days in 2008, and 2 days in 2010. For 2009 and 2011 the maximum number of daily readings was available. Similarly, there was 1 incomplete daily AMSR scan in 2007, 6 in 2008, 3 in 2009, 4 in 2010, and 11 in 2011. When daily ASI AMSR data was not available or had limited coverage, ice cover values for the missing cells were interpolated by calculating the mean cellular value of the previous day and the following day. Finally, we interpolated "land" cells that were inconsistently registered as land and added additional random Gaussian noise on all grid cells which were consistently registered as "land". The two final steps were necessary to stabilize the visual tracking algorithm and prevent the tracking of static features. Data processing and modelling were conducted on a Linux HPC server running R version 4.1.0 using the packages SP, SF, RASTER, NCDF4, RGEOS, MAPTOOLS, R-INLA, and

INLABRU (Renard, 2011; Pierce, 2012; Bivand and Rundel, 2013; Lindgren et al., 2015; Hijmans and van Etten, 2016; Pebesma, 2018; Bachl et al., 2019; Bivand et al., 2020).

2.3.3. Ice motion

The motion of pack ice can result in the geolocation of nursing sites changing over time (Dmitrieva et al., 2015; Kadranov et al., 2017). This movement can occur despite the position of ice-breeding pups remaining fixed upon any given ice floe (Wilson et al., 2017). To evaluate the impact of spatial and temporal change in breeding conditions, feature tracking can be applied to detect and monitor change in ice conditions at given breeding site or ice floe, whilst accounting for its movement in space and over time. Feature tracking on imagery can be accomplished manually or automatically by using a visual feature tracking algorithm. A variety of algorithms exist which can track visual features within spatial datasets, and one algorithm is the IMCORR algorithm (Bindschadler and Scambos, 1991) which was designed to track ice sheet movement (Bindschadler and Scambos, 1991; Wuite and Jezek, 2009). To account for seasonal variability in ice conditions we implemented the visual tracking/feature displacement algorithm IMCORR using the SAGA GIS utilities available within the RSAGACMD package in R. IMCORR estimates ice motion by tracking visual features between consecutive remote sensing images, where a visual feature is defined by the spatial and numerical composition of each image. IMCORR works by first specifying a grid spacing which defines the centre point of a reference window and the placement of correlated points, a larger search window is then centred on each point, within which it attempts to pair the reference window in the first image with a visually similar uncentered window in the next image. We used IMCORR to track changes in the coordinate reference of mobile pack ice fragments across our study region, using the ASI AMSR 3.125km ice concentration product (Heygster et al., 2009). This process involved evaluating arbitrary grid cells during our survey period and tracking change in their spatial reference within consecutive daily ASI AMSR images whilst maintain a fixed reference that we could use to monitor change in conditions over time. We set our grid spacing as 10km, and to encapsulate the wide range of daily changes in ice sheet velocity we ran IMCORR twice with two alternate search/reference window size pairings, 64 and 32 cells, and 32 and 16 cells (Wuite and Jezek, 2009). For each window size pair, outlying displacement estimates were removed using a modified version of a previously published inverse distance weighted standard deviation filter (Wuite, 2006). The filter is first run for each correlated point to identify points with velocity estimates which are greater or less than the mean plus 1 standard deviation of itself and its 8 immediately adjacent neighbours. Inverse distance weighted interpolation was then used to estimate new velocities for the outlying points (Figure 6).

After tracking the pre-survey motion of each grid cell across our survey region and over the period between 1st January and the median survey date of the survey period within each year, we defined a series of competing hypotheses for mechanisms that may drive the relationship between pup density and ice characteristics. We compared four different parametrizations of ice cover and compared the performance of models which used either parametrization: (1) Observed ice cover, this model tested the hypothesis that ice cover during our survey period is associated with greater seal pup survival and/or pup densities; (2) Mean Ice cover, this model tested the hypothesis that spatial-temporal averages of ice conditions during the breeding season are associated with seal pup densities; (3) Ice continuity, these models tested hypotheses that ice that has remained continually stable prior to our survey period is associated with seal pup densities and (4) Ice accumulation, these models tested hypotheses that ice that has had stable for a sufficiently long period of time, without remaining continually stable is associated with seal pup densities.

Observed ice cover was extracted on the median survey date of each given year from the ASI AMSR 3.125km ice concentration product (Heygster et al., 2009) using the GPS coordinates associated with each birth site observation. Mean ice cover was extracted by using our visual tracking procedure to estimate spatial change in ice where each birth site was located, then calculating the average sea ice cover between the 1st of January and the median survey date of each year. To account for ice continuity and ice accumulation, we developed procedural scripts that summarise how ice cover had changed prior to our survey period in accordance with 3 different thresholds. These metrics were (i) the number of days ice cover continuously exceeded thresholds of 25%, 50%, and 75% cover (Continual Days Above - CDA), and (ii) the total number of days ice cover exceeded thresholds of 25%, 50%, and 75% cover (Total Days Above - TDA). To clarify, these metrics track how the percentage cover of ice within each grid cell has changed prior to our survey. Each of the 25%, 50%, and 75% thresholds define how high ice cover must be before the procedural scripts begin tracking the number of days ice was above a given threshold. CDA was designed to assess the importance of continuous stability in the ice sheet and may provide a better explanation for pup densities if seal pups are vulnerable to intra-seasonal variability in local habitat conditions. TDA was designed to assess the importance of accumulative stability in the ice sheet and may provide a better explanation for pup densities if pups are at least partially resilient to intra-seasonal variability in local habitat conditions. The maximum value of 58 CDA indicates that, for a specific mobile on-ice location, ice had been continually above the specified threshold since the 1st of January up until the latest survey window. In the 58 CDA example, if ice cover had fallen below, for example, 50% ice cover 29 days prior to our survey, the CDA would be 29 and the TDA would be 57.

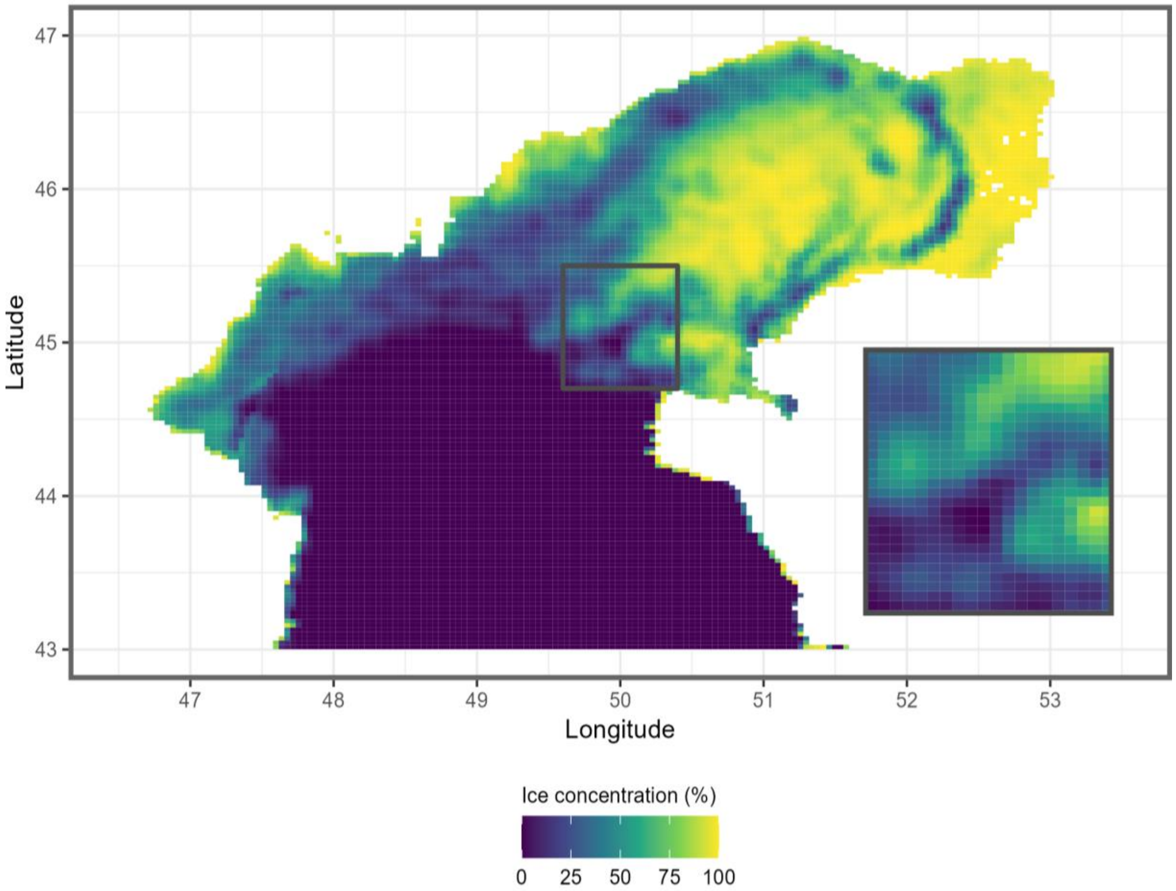

Figure 7 Daily ice conditions in the north Caspian basin on 2007-02-27 from the ASI AMSR 3.125km ice concentration product (Heygster et al., 2009). Highlighted is a central section of the ice sheet for reference in figure 6.

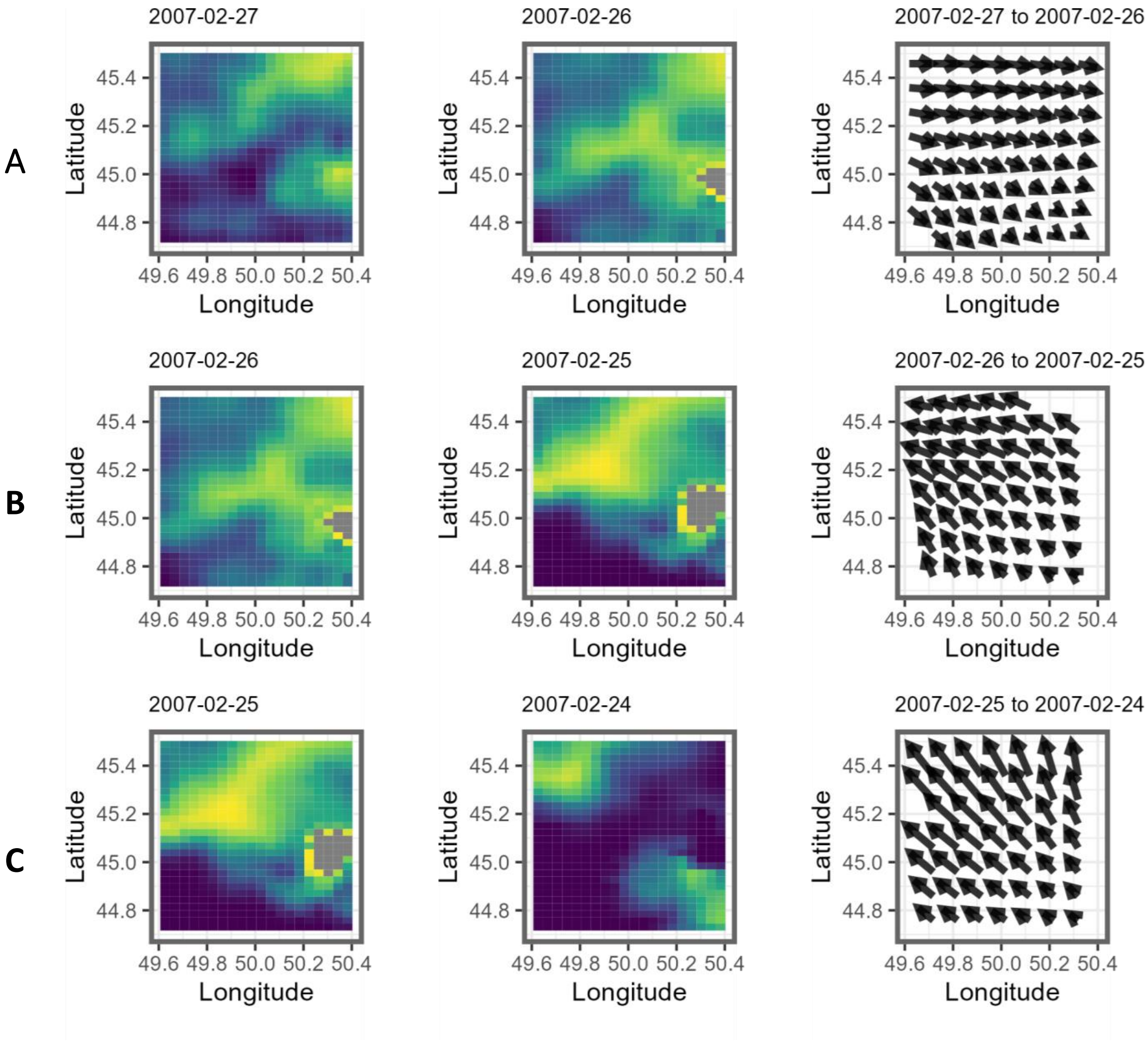

Figure 8 Rows A, B, and C show a single georeferenced window with ice conditions on a single day. The plots are ordered from A-C to highlight ice conditions on a given day and followed by the preceding day. IMCORR's trajectory estimates are visualised using arrows in the right most plot. The arrows summarise the start and endpoint of ice fragments that the algorithm detected.

2.3.4. Point process model

To analyse the effect of ice on seal distributions (Figure 7), we implemented a marked point process model using a joint likelihood approach (Illian et al., 2012). The marked quality refers to our model's discretisation of two data generation processes or data likelihoods. The first likelihood explicitly accounts for the density of birth sites, which we define by the location of individual GPS-linked photographs. The second likelihood explicitly accounts for the number of seal pups observed at any given birth site. Together, the two likelihoods describe how the aerial survey was collected and the number of seal pups expected to occur over space. Furthermore, by using a joint likelihood structure, we account for differences in the variance associated with the birth site likelihood and the variance associated with the number of pups likelihood, as well as potential differences in the relationship between the density of birth sites and the number of pups at birth sites across any given year. We developed our model within the R package INLABRU, which provides a framework to fit a variety of Bayesian models using INLA (Bachl et al., 2019). INLABRU and its parent package R-INLA utilize integrated nested Laplace approximation (INLA) within a Bayesian model. INLA is a method of approximating the posterior distribution of a parameter and is an alternative to Markov chain Monte Carlo (MCMC). Compared to MCMC, INLA is faster and can produce accurate results for models which can be cast in the form of latent Gaussian models (Martino and Rue, 2010; Lindgren et al., 2015).

Prior to model fitting, to minimize the impact of the different numerical scaling between the density of observations and the number of pups counted, we re-scaled the number of pups at each birth site by multiplying the number of pups at each location by the total number of birth sites (2827 photographs) divided by the total number of pups surveyed across every year (8210 pups). For each survey year, we specified log Gaussian Cox process likelihoods to account for the pup observation process, and log-normal likelihoods to account for the pup count process. Two random intercepts were estimated using an independent identically distributed random effect indexed by survey year, one from the Cox process likelihoods and one from the log-normal likelihoods. A random spatial effect was estimated from each observation likelihood and included within each survey year's corresponding count process likelihood after being multiplied by separate estimated scaling constants β**.** The random spatial effect was implemented using the stochastic partial differential equation (SPDE) approach (Krainski et al., 2020). To define the spatial SPDE we created a 2-dimensional mesh across our study area. The structure of our mesh was defined by a nonconvex hull which buffered the extent of our observations.

The original data collection transects were designed to not survey regions close to the coastline, in the open sea, or regions with very low ice coverage that were unsuitable for breeding seals. To account for this design, and accurately reconstruct the smooth spatial surface across the study area using the point process model, we generated integration points, using two polygons for each year. The first polygon was our survey transects buffered by the survey window on either side of the flown transect (~400m). The second polygon covered regions which were not surveyed but could not host breeding seals, such as open water. The second polygon was restricted to include regions between

20 kilometres and 40 kilometres from our survey transects. However, in 2009, we were unable to survey the southwestern section of the ice sheet, therefore, its second polygon was designed not to include regions which were not surveyed and may have had breeding seals. The integration points and their corresponding weights were then projected to the vertices of our mesh and generated independently for each year.

The effects of our ice metrics were estimated from every year and across both sets of likelihoods. Each metric was normalized prior to modelling and was defined as either linear, or non-linear using a 1-dimensional spline-like SPDE. The 1-dimensional spline was defined using a spline degree of 2 and 7 mesh vertices placed along the range of the covariate. To stabilise the estimates of the effect of each temporal metrics (CDA and TDA) at the extremities of the covariates, we specified a Dirichlet boundary condition at zero and the maximum number of days ice exceeded each threshold. This decision was supported by the rarity in which we observed pups at these extents. However, for the nonlinear effect of observed ice cover and seasonal mean ice cover we specified a Dirichlet boundary condition at zero and a free boundary condition at 1, which indicates a 100% cover of ice. Finally, we used Widely Applicable Information Criterion (WAIC) (Watanabe, 2010) scores to compare the fit of models with difference ice parametrisations and made estimates for the distribution of birth sites and pups in each year from our most parsimonious model. WAIC scores are analogous to other model selection criterion such as AIC and DIC, but compared to alternatives they are a more fully Bayesian approach and have the desirable property of averaging over the posterior distribution rather than conditioning on a point estimate (Gelman et al., 2014).

2.3.5. Prior distributions

Within INLA, priors are set on the internal scale of the model, which is the log scale for our chosen likelihoods. Following software guidance, random intercepts were assigned penalized complexity priors (pc priors) (Fuglstad et al., 2019) on the log precision of 5 and a probability of the log precision being greater than 5 of 1%. Scaling constants to account for scaling differences between the observational likelihood and the count likelihood were assigned Gaussian priors with a mean of 1 and a log precision of 2. Linear environmental effects were assigned Gaussian priors with a log precision of 0.001 and mean of 0. The non-linear 1-dimensional SPDE effects were assigned pc priors on the range of the serial correlation being 0.1 with a 1% probability of the range being less than 0.1, and on the standard deviation being 2, with a 1% probability of it being greater than 1. This prior reflects an assumption that sequential values of each environmental metric are likely to be correlated even towards more extreme ends of the data, and broadly, that the spline should behave more similarly to a global spline than a local spline. The random spatial effect was assigned a pc prior on the range of the spatial correlation being 150 km with a 1% probability of the range being less than 150km, and on the standard deviation of the spatial field being 1, with a 1% probability of it being greater than 1.

2.4. Results

2.4.1. Ice motion

For each of the daily velocity estimates generated by IMCORR, approximately 15% of the velocity estimates were discarded as outliers when implementing the modified inverse distance weighted standard deviation filter (Wuite, 2006).

2.4.2. Point process model

To evaluate the distribution of pups with respect to environmental covariates we used a joint point process model. Models describing variation in pup numbers based on environmental variables had WAIC scores ranging between 19174.09 and 19955.49. However, two models had notably lower WAIC scores compared to the other candidate models, which indicates better model performance. The top two scoring models parametrised ice cover as (i) a nonlinear effect for the number of days ice cover continually exceed 75% (WAIC 19174.09), and (ii) a linear effect for ice cover on the day and location of pup observations (WAIC 19295.75) (Figure 8). As a result of the good performance of the linear observed ice cover model, we reassessed whether there may be some effect associated with a linear relationship with ice cover on the day of observation in addition to the temporal metrics. Therefore, we refitted every nonlinear CDA and TDA model with an additional linear effect for the ice cover on the day of observation, however, this did not improve the WAIC score for our best candidate model (Figure 8 and 9).

Our model analyses indicated that breeding Caspian seals exhibit a high degree of spatial dependence, some of which is associated with environmental conditions, however, a significant amount remains due to unexplained spatial correlations. The mean correlation range quantifies spatial dependence or correlation in the data and can be understood as the distance beyond which two observations no longer exhibit spatial dependence. In our model, the mean correlation range for the random spatial effect of our best model was 317 km in 2007, 325 km in 2008, 321 km in 2009, 287 km in 2010, and 320 km in 2011. The correlation ranges between 287 km and 325 km are relatively high compared to the extent of the north Caspian, and in our context indicate lower clustering, and high spatial dependence, where the breeding distribution is generally concentrated around a single central region of the north Caspian (Figure 7 and 10). The scaling constant for the spatial effect within the count process was 0.25 in 2007, 0.20 in 2008, 0.16 in 2009, 0.15 in 2010, and 0.27 in 2011 (Table 1). Scaling constants other than 1 indicate that the detected spatial effect operates on different scales on the internal log scales of each likelihood. Within our best candidate model the correlation range of the smooth nonlinear effect was 0.429 (SD 0.122).

Our best performing candidate model parametrised ice conditions using a nonlinear effect for CDA 0.75. To determine the statistical significance of this effect, we evaluated the nonlinear effect of CDA 0.75 on the log-link scale (Figure 9). Assessing this effect on the internal link scale allows us to determine the statistical significance of the effect of CDA 0.75 across different levels relative to its extremes. In a Bayesian context, we determine the statistical significance of the effect by evaluating the degree to which the coefficient(s) of the effect of overlap with zero which would indicate a probability of no effect. We find that birth site densities and pup counts are significantly higher at levels greater than zero and less than the maximum CDA of 58 days, this effect is most certain at levels between 10 and 15 days, less certain between 30 and 40 days, and a secondary peak is notable at approximately 52 days. Subplot B illustrates the nonlinear effect of CDA 0.75 on the exponent-response. Assessing this effect on the response scale allows us to gain insights such as the multiplicative increase in the rate of birth site and pup detections across different levels of CDA 0.75 relative to its extremes. Compared with extreme levels of CDA 0.75, we find that birth site densities and pup counts are on average ~1.9 times higher upon ice that has been continually frozen for between 10 and 15 days, ~1.3 times higher upon ice that has been continually frozen for between 30 and 40 days, and ~ 1.6times higher upon ice that has been continually frozen around 58 days. Finally, we assessed the number of days ice was continually frozen above 75% ice cover at pupping sites after our survey period and found that, across each year, ice was continually stable for a further 5.48 (SD 5.74) days. This value varied slightly between years and was 5.06 (SD 5.03) days in 2007, 5.55 (SD 3.24) days in 2008, 4.62 (SD 3.86) in days 2009, 8.33 (SD 5.92) in days 2010, and 5.34 (SD 6.85) in days 2011. After evaluating our best performing model, we generated predictive maps to evaluate the continuous distribution of seal pups across the entire ice sheet (Figure 10).

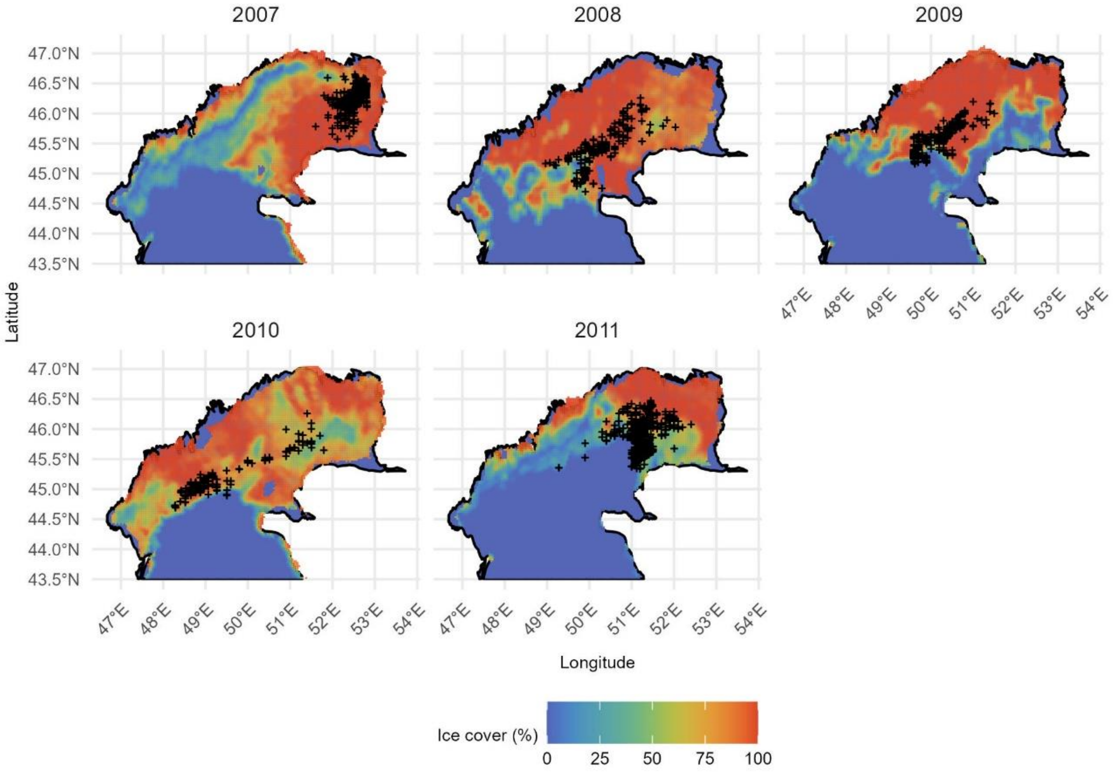

Figure 9 Ice cover on the median day of survey overlain by the locations of breeding sites (crosses) for each year. Breeding sites refer the to location where seal pup(s) were identified but not how many pups were observed at these sites.

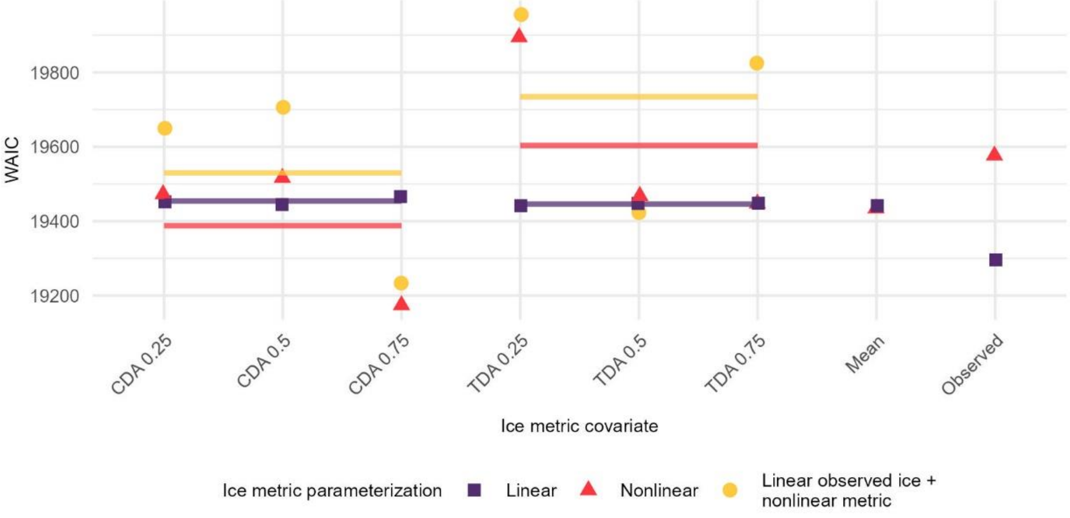

Figure 10 WAIC scores for each candidate model. Models which incorporate a single ice metric are displayed as purple squares if structured as linear and red triangles if structured as nonlinear. Models which incorporate both a linear effect for ice cover as well as a non-linear effect for either the TDA or CDA temporal metric are displayed as yellow circles. Mean WAIC scores across either the CDA metric or TDA metric models are displayed as horizontal lines and coloured according to the structure of their corresponding ice metric(s). The “Mean” model includes parametrized ice as the feature tracking

derived average ice cover and the "Observed" model includes the ice cover observed on the median date of survey.

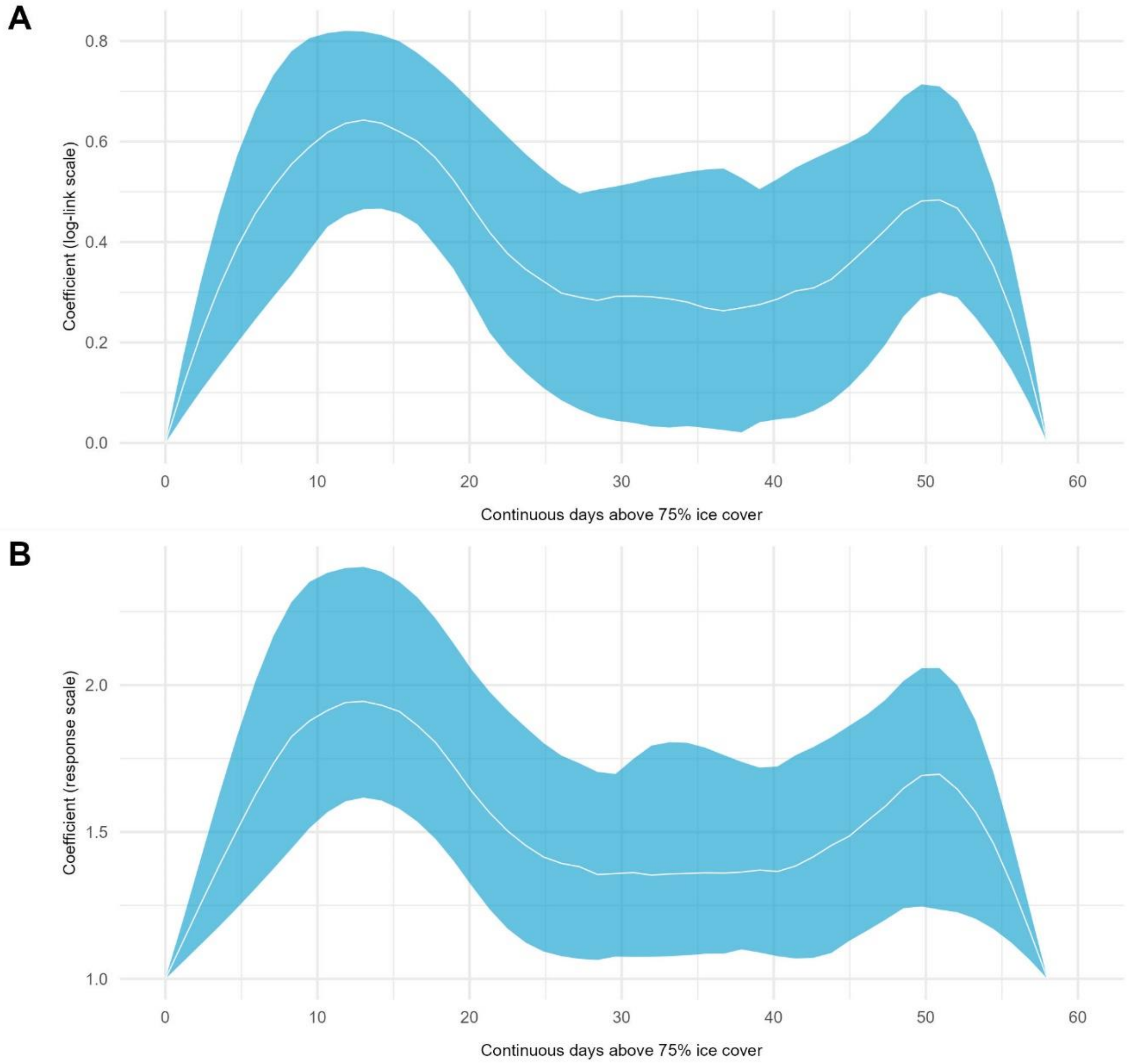

Figure 11 Non-linear effect plots from the best performing candidate model, which parametrized ice according to the number of continuous days above 75% ice cover (CDA 0.75). The plots show the effect of CDA 0.75 upon breeding site densities and the number of pups at each breeding site. Subplot A illustrates the nonlinear effect of CDA 0.75 on the log-link scale. Assessing this effect on the internal link scale allows us to determine the strength of the effect of different durations of high (75%) ice cover on pup breeding. Statistical significance of the effect is determined by the degree of overlap with zero. Subplot B illustrates the nonlinear effect of CDA 0.75 on the exponent-response. The effect on the response scale indicates the multiplicative increase in birth site densities and pup counts across different durations of high (75%) ice cover.

Table 1 Summaries of the marginal posterior distribution for the hyperparameters of the random spatial effects for model CDA 0.75

Parameter	Year	Mean	SD	2.5% Quantile	50% Quantile	97.5 % Quantile
Precision for the lognormal observations	2007	1.50	0.11	1.29	1.49	1.72
	2008	1.90	0.15	1.62	1.89	2.21
	2009	2.15	0.13	1.90	2.14	2.41
	2010	2.13	0.18	1.80	2.13	2.51
	2011	1.79	0.07	1.65	1.78	1.93
Range for the spatial field (km)	2007	316.52	44.55	237.16	313.66	412.59
	2008	324.88	44.44	245.69	322.03	420.71
	2009	321.21	42.60	245.20	318.53	412.78
	2010	287.25	39.63	216.70	284.69	372.74
	2011	320.46	36.33	255.52	318.19	398.32
SD for the spatial field	2007	4.92	0.58	3.88	4.89	6.18
	2008	4.54	0.54	3.56	4.51	5.68
	2009	4.58	0.51	3.65	4.55	5.66
	2010	4.99	0.60	3.91	4.96	6.26
	2011	4.70	0.53	3.75	4.67	5.84
Scaling for the spatial field	2007	0.25	0.05	0.15	0.25	0.35
	2008	0.20	0.04	0.12	0.20	0.28
	2009	0.16	0.04	0.08	0.16	0.23
	2010	0.15	0.03	0.08	0.15	0.22
	2011	0.27	0.03	0.22	0.27	0.32

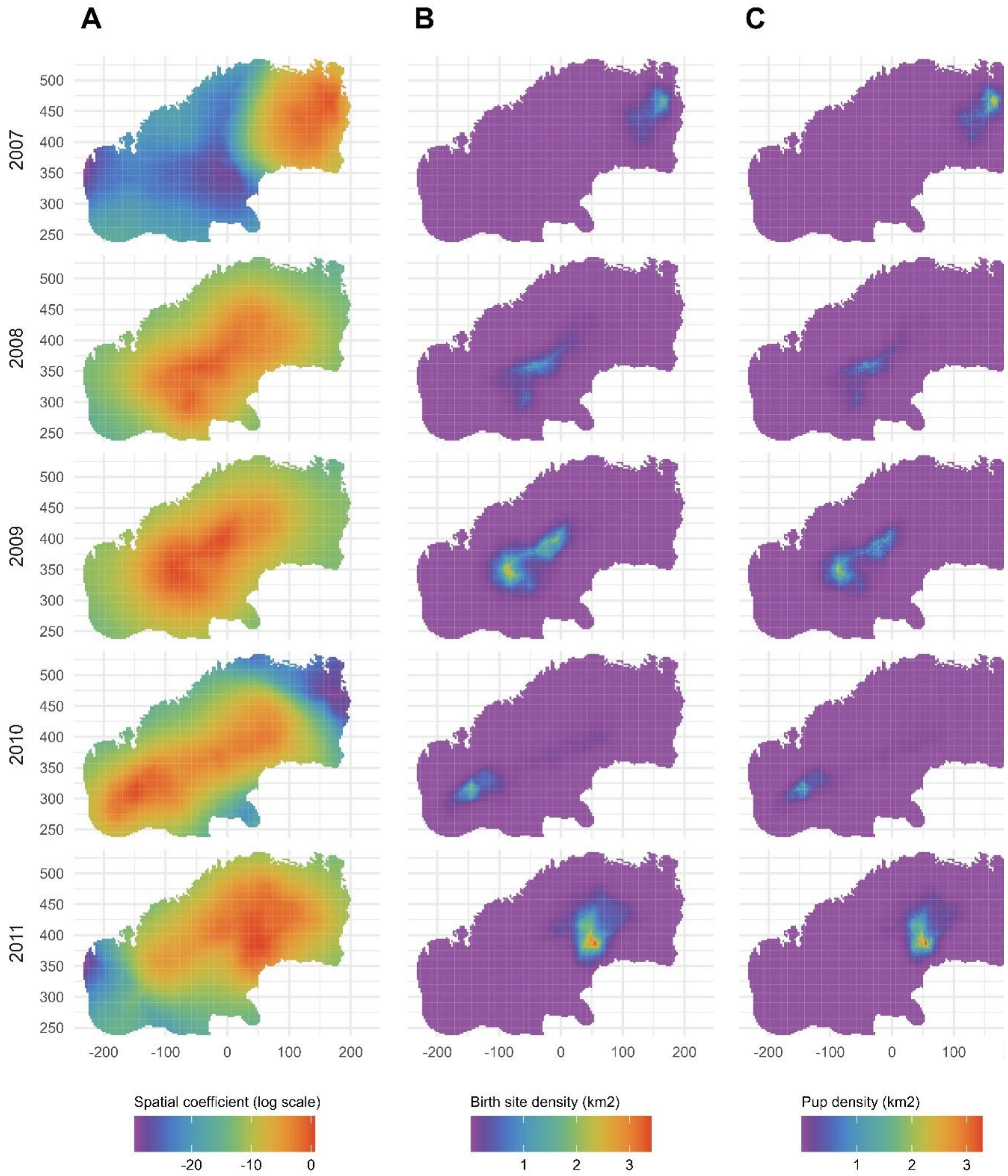

Figure 12. Spatial predictions in the North Caspian basin. Column A shows the mean spatial effect for each year on the internal log scale. Column B shows the models predictions for the density of birth sites per km^2, this represents an expected number of sites where a cluster of multiple adults and nursing seal pups may be observed. Column C shows the model predictions for the density of seal pups, this represents an expected number of individual seal pups per km2 and is estimated as a function of the birth site density, and relationships between the number pups and environmental covariates at birth sites during any given year. Predictions for each year are ordered from 2007 to 2011 by row.

2.5. Discussion

In this study, we implement a single model-based protocol to incorporate an assessment of how spatial and temporal variability in breeding ice conditions influence the distribution of Caspian seal pups. These results are important because they address gaps in our understanding of how contemporary Caspian seals are associated with habitat conditions during the breeding season (Dmitrieva et al., 2015; Goodman and Dmitrieva, 2016; Wilson et al., 2017). Our results suggest that continual ice stability over 75% ice cover (CDA 0.75) provides the best explanation of pup densities, and that the highest density of pupping sites and the highest number of pups at pupping sites were observed towards the middle of the range of conditions available across the entire breeding area. This effect was most evident upon ice that has been continually frozen for between 10 and 15 days, where birth site densities and pup counts were on average ~1.9 times higher than at extreme levels of CDA 0.75. As more pups were observed away from the least stable or most stable ice conditions, a non-linear effect for CDA has strong support and may be analogous to previous studies that have found a nonlinear relationship between ice and seal pup density (Miksis-Olds and Madden, 2014; Gurarie et al., 2017). Our estimates for the non-linear effect of CDA 0.75 imply that seal mothers preferentially nurse and/or pups survive better within birth site conditions that are away from the extremes.

These results could be interpreted in the context of habitat selection, assuming seal pup mothers actively select breeding habitats which are more likely to result in the survival of their pup. One possible explanation for this result may be due to both habitat selection and dispersal limiting conditions. For example, areas with a high CDA have been continually frozen since near the start of the breeding season and may offer the greatest stability which may promote higher seal pup survival. However, high CDA regions may also have a lower probability for mothers to initially haul out upon prior to labour if sections of ice which are further from the sea-ice interface have reduced accessibility, as they have remained frozen since before the peak birth period (Dmitrieva et al., 2016; Wilson et al., 2017). For example, in some cases natural leads deep into the ice field, or artificial leads arising from icebreaker channels, are quickly colonised by pupping seals (Harkonen et al., 2008; Wilson et al., 2017). These observations may support access limitations as a mechanism to reduce the colonisation of older section of the ice sheet. Another interpretation of these results could be in the context of survivor biases, whereby seal pups that were born upon lower CDA 0.75 regions may not have been observed during our surveys because they did not survive past the early periods of the breeding due to drowning or hypothermia. Systematically evaluating either interpretation is beyond the scope of this analysis. However, future research may improve our understanding of how survivor biases may impact seal pup densities and would likely have to incorporate longitudinal surveys through an ice season which can track the survival rate of seal pups.

In this study, our surveys were conducted towards the middle of the nursing season and when most seal mothers were likely to be hauled out for the 3-to-4-week post pupping lactation period (Wilson et al., 2017). Therefore, a high density of pups on ice which had been continually stable for 11 to 15 days may indicate that pregnant mothers haul out upon ice which is beginning the ice formation process shortly before parturition. However, after our survey period, we assessed the stability of the ice fragments where seal pups were observed and found that they remained continually frozen above 75% ice cover for, on average, 5.48 days (SD 5.74) beyond the median survey date of each year. Although there was a lot of variability within the mean, this did not vary a lot between years other than in 2010 when the ice remained stable for 8.33 (SD 5.92) days. Alongside data at sites where we observed seal pups results, these results imply that the number of days where ice was over 75% cover was just over 20 days, which is less than the 21-28 days required for pups to finish nursing and presumably maximise their survival chances (Wilson et al., 2017). However, when interpreting these results, it is important to consider that lanugo coated pups are most vulnerable to premature water contact at the start of the nursing period, whereby they later develop thicker blubber and can tolerate increasingly higher levels of ice instability or water contact (Frisch and Øritsland, 1968).

Our results suggest that contemporary Caspian seals are breeding on ice that does not remain stable for much longer than they require to complete the nursing period. This shows that they appear to be operating at their limit regarding the relationship between the duration of ice stability and the length of the weaning period and supports the conclusion that future reductions in ice stability and duration could exacerbate risks of pre-weaning mortality. These concerns are most apparent within the context of climate heating scenarios which predict the stability and duration of the Caspian ice sheet to decline during the 21st Century (Shahgedanova et al., 2009; Koenigk et al., 2013; Tamura-Wicks et al., 2015). Following climate heating, ice conditions are likely to be increasingly less suitable for successful nursing, however, since conducting these surveys, multiple premature ice melt events have been observed in the Caspian, most notably during 2016 and 2020 (Lavrova et al., 2022), and during these years, pup survival is likely to have been exceptionally low. In addition, the Caspian sea-level is predicted to decline due to increased evaporation and reduced fresh water inflow, and this may result in the disappearance of sea ice altogether (Nandini-Weiss et al., 2020; Prange et al., 2020). The complete loss of ice due to climate heating or sea level declines will force a switch to terrestrial breeding, which is known to negatively impact normally ice-breeding seals (Kovacs et al., 1985; Jüssi et al., 2008; Stenson and Hammill, 2014), and these observations highlight the importance of regular Caspian seal pup counts, so we can more accurately evaluate the threat status of Caspian seals when faced with changing climate conditions.

In addition to a statistical evaluation of environmental drivers that may influence birth site density and pup density, we used our model to predict the spatial distribution of both birth sites and pups separately (Figure 10). The ability to predict the densities of birth sites or pup densities is key property of using this joint likelihood approach, which allows us to compare the birth site density and pup density across space and within each year. Using this approach, we can illustrate differences between regional aggregations that may occur at a spatial scale of kilometres, and more localized aggregations that may occur at a spatial scale of several meters. For example, within a given year and for any given grid cell, a higher birth site density relative to pup density may indicate that a lower number of pups were identified within each birth site. This pattern appears to be most evident during 2009 and 2011, and somewhat during 2008 and 2010, which we suggest may indicate that spatial associations during these years may be driven by larger scale environmental drivers, such as broad habitat associations that may be detectable using remote sensing data (Guisan and Thuiller, 2005; Wege et al., 2021; Farmer et al., 2022). In contrast, during 2007, pup density was higher relative to birth site density. This may indicate that a higher number of pups were born within each birth site and that nursing seals were spatially aggregated within meters of each other. We suggest that spatial aggregations at this scale may be driven by a behavioural preference for breeding Caspian seals to nurse in proximity with each other (Wilson et al., 2017). Alternatively, the local proximity of nursing seals could also be driven by a preference for nursing seals to select ice-ridges or other fine scale habitats. We note that a more thorough investigation of aggregations at this scale is highly dependent upon the availability of very high-resolution spatial data, such as future the advancement of very high-resolution remote sensing data.

In the future, significant technological advances are expected to vastly increase the resolution of satellite derived based datasets. One of these advances includes the upcoming Copernicus Polar Ice and Snow Topography Altimeter (CRISTAL) satellite mission, which is expected to launch in 2027 and will provide ice extent, concentration, thickness, type, and drift, at resolution of at least 80 m (Kern et al., 2020). These advances will vastly improve the reliability of remotely sensed ice datasets, which is currently a limit factor regarding the spatial resolution of environmental data and aerial survey counts. Improved satellite technology would then increase the utility of increasing the spatial precision of visual counts so that the precise locations of individual pups are recorded. For example, increasing the spatial precision of counts could allow researchers to model the locations of individuals explicitly using an unmarked point process structure, instead of aggregating multiple counts within a single observation photograph. One method of increasing the spatial precision of counts would be to use multi-spectral imagery from belly-mounted cameras in aircraft/drones (e.g. (Morris et al., 2021; Heyer et al., 2021). In addition, thermal images provide a more easily quantified image of the survey area which eases the implementation of automated thermal image counts, and have been deployed to count grey and ringed seals (Seymour et al., 2017; Lindsay et al., 2021). Furthermore, ship-based unoccupied aircraft systems (UAS) are used within seal counts by NOAA in the Chukkchi and Bering Sea, and compared to traditional aerial surveys have increased fuel efficiency (Moreland et al., 2013; Lindsay et al., 2021). Additionally, the field of computer vision is in rapid development and improved ice tracking may be possible by harnessing state-of-the-art tracking methods based on deep learning (Li et al., 2018). Soon, the above-mentioned advances will increase the availability of data which can inform the parameter estimates within the model protocol we define here. However, at its present stage, we show that careful consideration of ice mobility and stability is essential when considering the associations between birth site observation densities and pup counts. In addition, our protocol could be applied and be useful for any of the Arctic seal surveys that breed upon ice, especially those that breed upon unstable ice, to increase the statistical insights that may be derived when associating count distributions to transient environmental variables such as ice.

In this study, we demonstrate that incorporating ice-related temporal metrics can improve model performance and parsimony and show that continual ice stability at ice cover over 75% provides a better explanation of pup densities than accumulative ice stability, seasonal average ice cover, and observed ice cover. These results imply that pups are likely to be negatively impacted by future increases in intra-seasonal variability in habitat conditions. We provide evidence that contemporary Caspian seals appear to be operating at their limit regarding the relationship between the typical duration of ice stability and the length of the weaning period, and future deterioration of ice conditions in the Caspian are likely to be detrimental to Caspian seal pup survival. Furthermore, contemporary conditions in the Caspian are likely to be indicative of future conditions in polar regions under extreme climate change scenarios, and therefore this study provides an important case-study for research into the future viability of Arctic ice-breeding pinnipeds which breed on mobile pack ice.

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3. Chapter three - Seasonally flexible Marine Protected Areas (MPA) derived from spatial and temporal variability in animal movements in Caspian Seals (Pusa caspica)

Harrison Tan, Lilia Dmitrieva, Chris Hassall, and Simon J. Goodman

3.1. Abstract

Advances in quantitative methods in ecology provide researchers with a wide array of tools which can be used to evaluate ecological phenomena that can inform conservation planning. In this study, we construct a Bayesian mixed-effects model to examine spatial and temporal structures in animal movements in Caspian Seals *(Pusa caspica)* and investigate seasonal variability in the relationship between movement persistence and environmental covariates. These insights are applied to generate plans for seasonally flexible Marine Protected Areas (MPAs) that account for trade-offs between conservation and maritime industries. Our model findings show strong evidence for a seasonally structured relationship between specific patterns of animal movement, which are likely to be indicative of foraging behaviour, and the use of habitats nearby river outlets and shelf life habitats at the 50m isobath coincides with time periods that may align with the ecology of migratory fish. We then generate model-based spatial predictions of animal movement patterns throughout an annual cycle and use these predictions to inform the design of seasonally flexible MPAs. To develop plans for MPAs we use prioritization algorithms that prioritise areas where seals are likely to forage, and be highly vulnerable to vessel-based disturbance, and deprioritise areas where vessel density is highest and protective legislation would result in costly financial trade-offs with maritime industries. Our results demonstrate that there are areas in the Caspian Sea that, if protected, would meet conservation targets for protected area coverage and result in minimal trade-offs with maritime industries within specific area limits, when compared with equivalently sized plans that do not account for trade-offs.

3.2. Introduction

3.2.1. Understanding animal movements using bio loggers

Improving our understanding of habitat use, foraging theory, and species response to environmental change is a vital component of conservation decisions (Nathan et al., 2008; Bestley et al., 2013). Within marine mammal research, the primary approach for addressing this requirement is the collection of data on animal movements using GPS biologging devices, that can retrieve data remotely (Costa et al., 2010; Katzner and Arlettaz, 2020; Nathan et al., 2022). One common approach when analysing movement data involves identifying sections of a data timeline that correspond to "area restricted search" (hereafter "ARS"), which refers to a behavioural state where movement track topologies have higher turning angles and lower or more rapidly changing speeds. In many cases, ARS can indicate foraging behaviour, as opposed to transiting behaviour, where track topologies have lower turning angles and higher or more consistent speeds (Jonsen et al., 2005; Jonsen et al., 2020). The relationship between ARS and foraging has theoretical support from optimal foraging theory, which generally states an expectation that predators maximize their time spent within regions of higher prey density (Kareiva and Odell, 1987) and minimize their time spent transiting between prey patches (MacArthur & Pianka, 1966). Many methods have been adopted to identify ARS-like behaviour, and both discrete (Jonsen et al., 2005) and continuous (Jonsen et al., 2020) approaches have been used within pinniped research. Compared to continuous approaches, discrete approaches classify behaviours into a finite number of behaviours such as "foraging" and "transiting" (Jonsen et al., 2005). Continuous approaches have a much higher numerical resolution (Jonsen et al., 2020), and this may be a useful attribute when researchers find hierarchical structures during their analysis of movement data, such as individual variability in movement patterns. For example, individual variation is common amongst marine predators, such as those which frequently display different propensities for movement states (Spiegel et al., 2017). This phenomenon may be easier to detect when using metrics with a higher numerical resolution, because it can provide researchers with an increase capacity to identify differences in behavioural patterns. However, the presence of individual based patterns infers a data structure with several dependencies and biases, and these structures can present a series of challenges at later analytical stages.

There are two major hurdles to consider when analysing movement behaviour using biologging data. First, biologging data has three characteristics that break the assumptions of general or generalised linear models: (1) the data is hierarchical, as data points that are returned from a single individual are non-independent, (2) the data is serially or temporally autocorrelated, as an individual's behavioural state at a given time step are more highly correlated to its state at an adjacent time point than it is to a distant one, and (3) the data is spatially autocorrelated, as resource distribution in nature is often clustered, and foraging typically occurs within hotspots. Second, predators often exhibit a variety of foraging modes and a high degree of individual-level variation in response. For example, age-structured foraging strategies are known to exist within a wide range of taxa, including Grey seals *(Halichoerus grypus)* (Kaspersson et al. 2010; Elbroch and Quigley 2019; Breed et al.

2011), and individual variability in behaviour is prevalent in Caspian seals (*Pusa caspica*) (Dmitrieva et al., 2016) and Southern elephant seals (*Mirounga leonine*) (Jonsen et al., 2019). Individual variations are generally thought to emerge from two main sources. For example, foraging specialisations can emerge when individuals specialise upon a small proportion of the population niche breadth (Bolnick et al., 2003; Araújo et al., 2011). In addition, foraging personalities can emerge, such as fast foragers that forage at a consistent intensity and slow foragers that are more methodical in their search for foraging habitats and forage within high intensity bursts when resources are identified (Spiegel et al. 2017). The presence of these phenomena is problematic, because, in general, the most widely applicable ecological insights can be gained from population level inferences. However, these non-independent data structures can bias inferences at the population level because the direction and magnitude of the relationships between, for example, environmental conditions and behaviour will be influenced by some datapoints more so than others.

Hierarchical models are an increasingly popular approach within pinniped movement research and have been used to evaluate variation in response across different individuals (Schwarz et al., 2021), different ages (Votier et al., 2017), between sexes (Hindell et al., 2016), and through space (Harcourt et al., 2021). However, no study to date have used these specific methods to investigate continuous spatial and temporal variation in habitat use in pinnipeds. This is an important research gap to focus on because temporal variation in habitat use may be evident in species with diets that include migratory prey, and because pinnipeds are highly mobile and have a wide dietary breadth (Dehn et al., 2007; Van Bonn, 2015). For example, Killer whales (*Orcinus Orca*) follow herring (*Clupea harengus*) migrations from inshore overwintering areas to offshore spawning grounds (Vogel et al., 2021), Red-throated divers (*Gavia stellata*) forage within different sections of the water column at different rates throughout the season (Duckworth et al., 2021), and harbour seals (*Phoca vitulina*) appear to forage close to river estuaries at higher rates during salmon migrations (Allegue, 2017). This makes pinnipeds an important study species to investigate continuous temporal variation in habitat use because their diverse use of different habitats and food items can influence their exposure to various sources of climate change impacts, ecosystem change, and anthropogenic threats (Kovacs et al., 2012; Albouy et al., 2020). Understanding variation in how they use space over time is therefore an important component of evaluating how these threats interact with their ecology and should be an important component of how we design conservation strategies.

Hierarchical models, or mixed-effects models, can incorporate a wide array of non-independent structures into model design and allow researchers to partition the variance of their data which is explained by these structures more accurately. This process has seen a series of notable advances, particular within Bayesian statistical methods, including Integrated Nested Laplace Approximation (INLA) (Martino and Rue, 2010; Lindgren et al., 2015). INLA has provided a framework for researchers to construct hierarchical models using Bayesian methods within much shorter run times and using methods that appropriately account for uncertainty within data and the models we derive from it. In addition, one attribute of INLA is the wide variety of 'random' and non-linear effects that are implemented within this framework (Illian et al., 2012; Lindgren et al., 2015; Bachl et al., 2019). Of note are the implementation of Stochastic Partial Differential Equation (SPDE) based methods, which provide a highly flexible approach for approximating 'random' spatial and temporal effects that can approximate non-linearities over continuous space (Lindgren et al., 2022). By more accurately defining effects that are associated with, for example, data collection, hierarchical structures, temporal effects, and spatial effects, we may make more precise investigations of, for example, the effect of environmental variables on movement behaviour.

3.2.2. Marine protected areas

One of the most important applications of improving our understanding of spatiotemporal patterns in animal movement and habitat use comes in the designation of protected areas. Knowledge about where animals are and what areas they use for different aspects of their biology (feeding, breeding, dispersal) can be fed into policy decisions about the prioritisation of spaces for biodiversity. Marine protected areas (MPAs) are a useful conservation measure to reduce threats to marine life by limiting human activities within important habitats (Hoyt, 2018) and they are increasingly used within conservation actions globally (Boonzaier and Pauly, 2016). MPAs are typically established as immobile and permanently closed areas (Game et al., 2009), although marine systems are known to be both spatially and temporally variable (Fisher et al., 2015; Kroeker et al., 2020). There is an increasing number of examples of spatial variability impacting species ecology, for example, many studies have observed range shifts toward deeper waters and more poleward latitudes (Nye et al., 2009; Engelhard et al., 2014; Deutsch et al., 2015; Lancaster et al., 2015). However, the interaction between seasonal variation and changes in environmental conditions has received less attention from ecologists (Godbold and Solan, 2013; Kroeker et al., 2020), despite its ability to impact species that contribute to fundamental biological processes such as food web dynamics, nutrient cycling and primary productivity (Tilman, 1999; Baggini et al., 2014). Developing methodological protocols that can account for temporal variability in habitat use is, therefore, an essential component of developing conservation measures that meet conservation objectives such as climate change resilience.

Protected areas are often expected to achieve a diverse range of objectives and are often presented regarding universal benefits that they may offer (Watson et al., 2014). However, practical conservation planning often involves trade-offs where positive impacts for one objective can result in a negative impact on another (Davies et al., 2018). Trade-offs are particularly important to consider when developing new protected areas in the marine environment as their establishment requires management and can impact local economies by overlapping historical fishing grounds, existing resource extraction sites, and shipping lanes. Maritime vessel traffic is often a proxy for numerous human impacts such as fishing and industrial development, and has long been recognised as a threat to pinnipeds whilst hauled out upon ice (Stirling and Calvert, 1983) through displacement, the separation of mother and pups, and vessel-seal collisions (Wilson et al., 2017b; Hauser et al., 2018). However, far less is known regarding the impacts of vessels upon pinnipeds whilst foraging at sea. There are likely to be harmful impacts through vessel strikes (Schoeman et al., 2020) and auditory disturbance (Mikkelsen et al., 2019) as vessel-related noise can interfere with the retrieval of acoustic signals in marine mammals (Erbe et al., 2016) and foraging behaviour can distract animals from risk detection (Dukas, 2002). These impacts could result in negative demographic consequences, for example, decreasing foraging efficiency may impact an individual’s energy balance and body condition (2015; Pirotta et al., 2018), and therefore, limiting maritime industries within foraging hotspots may be a necessary component of conservation strategies for some pinniped species. However, this is likely to result in trade-offs with maritime economies which may be mitigated, although further research is needed on how this may work in practice.

3.2.3. Caspian seals

The Caspian seal (*Pusa caspica*) is a small-bodied ice-dependent phocid that exhibits little sexual dimorphism, with adults typically reaching 1.4 meters body length and weighing 80kg. Caspian seals have declined from over 1 million individuals at the start of the 20th Century to around 168,000 in 2005 (Harkonen et al., 2012; Goodman and Dmitrieva, 2016). Historic declines are associated with unsustainable commercial hunting through the 20th Century (Harkonen et al., 2012) while contemporary threats include high rates of fisheries-related mortality and habitat loss (Dmitrieva et al., 2013; Goodman and Dmitrieva, 2016; Ermolin and Svolkinas, 2018; Svolkinas, 2021). The species has been listed as Endangered by the IUCN since 2008 (Goodman and Dmitrieva, 2016), and recommendations for the establishment of seal special protected areas were first made in 2007 (Goodman et al., 2007). However, at present, there are no coastal or marine protected areas in the region that prohibit all human economic activity or development.

Caspian seals are endemic to the Caspian Sea in Central Asia (Goodman and Dmitrieva, 2016), which is the world's largest landlocked waterbody, spanning approximately 1150km north to south, and around 440km at its widest point (Lebedev, 2018). The Caspian Sea sits between approx. 36.5 and 47.0 N latitude and experiences a continental climate, with winter sea ice cover in the northern portion, and sub-tropical conditions through the rest of the year. The Caspian can be broadly split into 3 basins, the shallow northern basin with an average depth of less than 8m, and the deep middle and southern basins exceeding 700m and 1000m respectively (Figure 11). The Caspian Sea hosts a wide variety of habitats, ranging from shallow coastal zones to deep offshore waters, that are similar to many of the habitat's pinnipeds inhabit globally, so Caspian seals may share some of the foraging strategies seen in other phocid species. For example, harbour seals (*Phoca vitulina*) are known to forage close to river estuaries at a higher rate during salmon migrations (Allegue, 2017), and the Atlantic grey seal (*Halichoerus grypus*) is a sea-shelf specialist (Nowak et al., 2020). The Caspian Sea is fed by approximately 130 rivers, many of which host migratory fish. For example, Northern Caspian zander (*Sander* spp.) spawn amongst northern river inflows between April and May (Kottelat and Freyhof, 2007), and Caspian shad (*Alosa braschnikowi*) migrate towards river deltas during the summer (Bandpei et al., 2012). In addition, the bathymetry of the Caspian Sea can vary over short distances creating 'sea-shelf' regions. Shelf-like regions off the coast of Azerbaijan and Dagestan are inhabited by oil-rich Kilka (*Clupeonella spp.*), which have historically been reported as an important component of Caspian sea diet and are targeted by commercial fisheries (Mamedov, 2006; British Petroleum, 2015; Dmitrieva et al., 2016).

Caspian seals exhibit seasonal migrations throughout the Caspian Sea (Dmitrieva et al., 2016). After breeding on the winter ice sheet between January and early March, as the ice melts, seals move to the sand islands and reed beds in the northern Caspian to moult. Moulted individuals begin to disperse and forage throughout whole of the Caspian from early April, with the moulting period concluding by early May. Individuals then return to the north Caspian over an extended period from late summer to December in advance of the next breeding season (Dmitrieva et al., 2016). Previous telemetry studies of Caspian seal migration and foraging behaviour has identified at least three foraging modes amongst individuals. Generally, individuals cluster into one of three groups, (i) individuals that forage in shallow regions in the north of the Caspian (dives typically less than 10m); (ii) individuals that foraged around the boundary for the northern and middle Caspian basins (dives less than 20m); and (iii) individuals that make longer foraging trips into deeper waters of the middle and southern basins, with typical dives depths of 50-100m, and maximum dives exceeding 200m

(Dmitrieva et al., 2016). However, the environmental drivers of habitat use and specialisation into these foraging modes are yet to be evaluated. In this paper, we analyse Caspian seal foraging behaviour in space and time using a continuous movement persistence index (Jonsen et al., 2020) and hierarchical models using the Bayesian mixed-effects package INLABRU (Bachl et al., 2019). We go on to make spatial-temporal predictions of foraging hotspots and develop spatial-temporal protected area plans that minimise negative trade-offs with maritime industries in relation to vessel transiting routes.

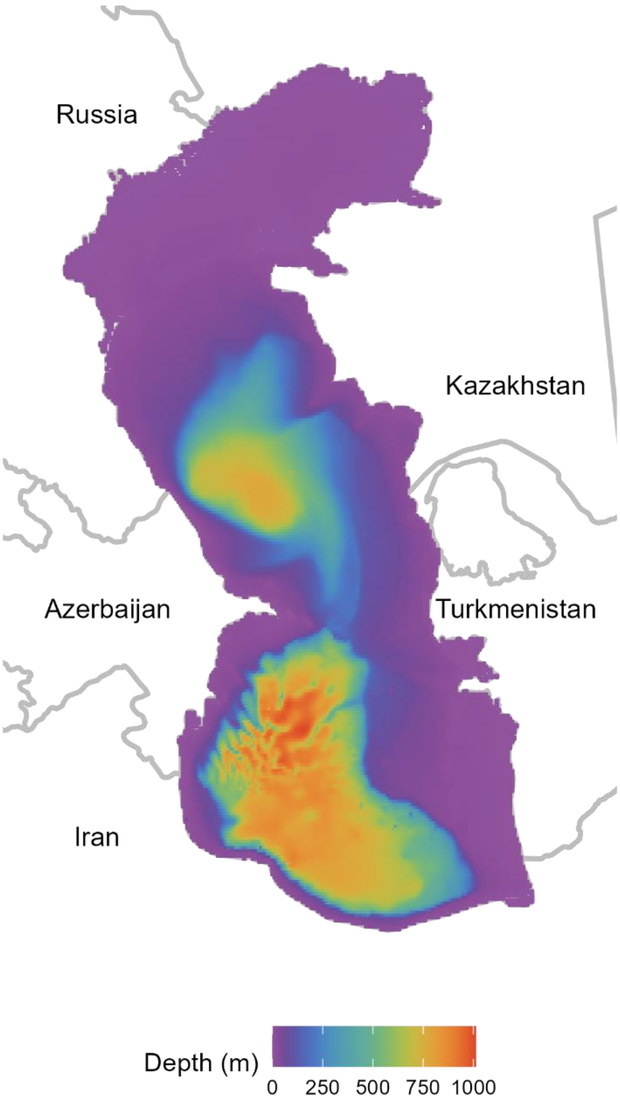

Figure 13. The Caspian Sea and its five neighbouring countries. Depth below the Caspian sea level is indicated using the global bathymetry dataset GEBCO (2019) after adjusting for the Caspian sea level, which is approximately 28 meters below the global sea level.

3.3. Methods

3.3.1. Satellite telemetry data

Post-moult Caspian seals (n = 118) were captured and tagged with Argos-capable satellite tags between 2008 and 2017 across 3 sites in Kazakhstan, across Kendirli sand bank (42.75° N, 52.55° E) and in Komsomolets Bay (45.51° N, 52.63° E). The tags were deployed over two seasons, 46 tags were deployed shortly after the post-breeding moult between April and May, and 72 tags were deployed during the pre-breeding haul out between October and November. In total, 7 tags were deployed in 2008, 5 in 2009, 22 in 2010, 33 in 2011, 15 in 2012, 28 in 2016, and 8 in 2017. A full description of the data collection protocol has been published for 75 of the tags which were analysed as part of a previous study (Dmitrieva et al. 2016). However, this study includes 43 additional Argos-Fastloc tags. Three types of satellite tags were used in this study, Smart Position-Only Tags (Wildlife Computers, 2013), SPLASH Mk10 tags (Wildlife Computers, 2011), and SPLASH10-F-297 Fast-loc tags (Wildlife Computers, 2016a). Tags were deployed with a transmission budget of 250 to 300 transmissions per day with no duty cycling. Data from tags were returned via the Argos satellite system (ArgosWeb, 2023) and were decoded using the tag manufacturer’s software (Wildlife Computers, 2016b). All animal handling and the use of instrumentation was conducted in accordance with the law of Kazakhstan, where the work was performed, and was carried out under permits issued by the Ural-Caspian Interregional Inspectorate of the Fisheries Committee of the Ministry of Agriculture of the Republic of Kazakhstan. The work was also reviewed and approved by the Research Ethics committee of the Faculty of Biological Sciences, University of Leeds.

To pre-process the tracking data, we applied a series of filters in succession to remove unreliable entries. First, we removed tags that had less than 10 Argos positions throughout their lifespan. Second, we removed tags that were deployed for less than 10 days. Third, we removed tags with more than 30 days between consecutive position retrievals. Finally, we removed tags with clearly erroneous track topologies that would not be consistent with ordinary seal movements. This final step was undertaken by manually inspecting the track topologies of each seal. After pre-processing the data, we fit a state space model to correct for uncertainty in the returned coordinate positions as a function of Argos location class error and Caspian seal physiology using function available within the R package FOIEGRAS (Jonsen et al., 2020; Jonsen and Patterson, 2021). First, we filtered the raw GPS telemetry data using the fit_ssm function to fit a continuous-time random walk state-space model to each individual animal track separately. For a detailed explanation of how fit_ssm functions please see the package documentation and publication (Jonsen et al., 2020; Jonsen and Patterson, 2021). Briefly, model fitting consists of two steps. In the first step, the SDA filter (Speed-Distance-

Angle filter) (Freitas et al., 2008) is applied to identify extreme outliers. The SDA filter considers a species maximum swim speed, distance between consecutive points, and turning angle in order to filter our extreme locations. Outliers are processed by removing locations classified as invalid by ARGOS (*ARGOS location class Z*), excluding locations that would require a swim speed greater than 8 ms, unless positions were located less than 5 km from the previous position. The SDA filter then removes locations requiring highly acute turning angles. In this study, we applied the SDA filter by removing all locations requiring turning angles less than 50◦ if the track leading to them was longer than 2500 m and all locations requiring turning angles less than 90◦ if the track leading to them was longer than 7500 m. In general, this filter provides a framework for isolating the most extreme outliers prior to fitting a state space model. For a more detailed explanation of how the SDA filter functions, see the original publication (Freitas et al., 2008) and the documentation associated with the implementation used within FOIEGRAS (Sumner et al., 2009; Sumner, 2011). After pre-filtering extreme outliers, a random walk state-space model (SSM) was fit and regularised predictions were made on a 6-hour time step.

After all initial processing and filtering stages, we used the SSM-fitted tracks to calculate the movement persistence behavioural index *g* along SSM-fitted tracks using the *fit_mpm* function (Jonsen and Patterson, 2021). Movement persistence (*g*) is a continuous measurement of the autocorrelation between consecutive animal movements. Values range continuously between 0 and 1, where lower values are associated with frequent changes in direction and/or speed, and higher values are associated with consistent speeds and more directed movements (Jonsen et al., 2019). We selected this movement metric because it provides a continuous scale of movement behaviour, which is useful when parametrizing individual-based behavioural structures. After calculating the behavioural index, we identified numerous examples of tagged seals returning ARS-like movements whilst positioned within areas with high ice cover (Heygster et al., 2009). These movements are likely to have been returned from stationary seals that are hauled out upon mobile floating pack ice, or from adult seals navigating breathing holes or leads through the ice sheet. In either context, these positions are not informative of foraging activity because the ice forming areas of the Caspian are not suitable for foraging when frozen over. To correct for these, we isolated location entries with greater than or equal to 50% ice cover and standardized their value for *g* independently across each tagged individual and as their mean value for *g* across locations with less than 50% ice cover. This step was taken instead of a direct modification of the value to the non-ARS extreme so that later inference upon the behavioural metric could still be made in relation to transiting and ARS-like behaviour. Finally, prior to analyses we calculated daily averages for each individual's position and behavioural metric, and to aid our interpretation we chose to conduct our later model-based analyses on 1-*g* so that higher ARS corresponded with a higher value in the behavioural metric.

3.3.2. Environmental variables

3.3.2.1. Initial evaluation of environmental variables

We chose the environmental variables used as covariates within our analysis by carefully considering the ecology of Caspian seals and the ecological hypotheses that our model would test. Initially we considered distance from river inflows, distance from shore, distance from the 50m isobath, bathymetric depth, slope, and sea surface temperature. Distance from river inflows was evaluated because Caspian seals are believed to eat fish that migrate through or spawn nearby rivers inflows (Pochtoeva-Zakharova N, 1999; Bandpei et al., 2012; Dmitrieva et al., 2016). However, distance from shore was subsequently removed from the analysis due to collinearity with distance from river inflows. Distance from river inflows was preferred over distance from shore because the ecology of Caspian seals indicates that it has a clearer functional ecological hypothesis associated with it. For example, Caspian seals eat fish that inhabit rivers (Pochtoeva-Zakharova N, 1999; Bandpei et al., 2012; Dmitrieva et al., 2016), and unlike many other pinnipeds, Caspian seals do not need to regularly rest onshore and can remain at sea for over 6 months (Dmitrieva et al., 2016). Distance from the 50 meter isobath was considered because it is the typical depth of deep dives by Caspian seals (Dmitrieva et al., 2016) and it approximated the location of sea shelf edge habitats in the Caspian, which are superficially similar to habitats used by foraging Atlantic grey seals (Nowak et al., 2020). Bathymetric depth and slope were subsequently dropped due to collinearity with distance from the 50m isobath. The 50m isobath was preferred over Bathymetry to minimize non-linearities or spatially inconsistent relationships between our covariates and foraging intensity. To clarify, while Caspian seals frequently dive to access food resources at depth, they also transit over depths beyond their diving capabilities (Dmitrieva et al., 2016). This inconsistency could support a highly non-linear relationship between depth and foraging, because Caspian seal physiology limits their ability to access depths that their distribution may be associated with in remote sensing bathymetric datasets. Therefore, we preferred a covariate that could support a more easily linearized relationship with ARS over a complex non-linear one that may require the implementation of polynomials or splines. This was because we intended to investigate non-linear changes to this relationship over time, and due to the higher computational demands of modelling change in a non-linear relationship over time. Finally, sea surface temperature was chosen as it is frequently used within ecological literature when describing patterns in marine animal behaviour and distribution, and its association with primary productivity (Chavez et al., 2011; Robinson et al., 2017).

3.3.2.2. Distance from river inflows

The Caspian Sea is fed by around 130 rivers, few of which form river deltas (Kosarev 2005). The extents of river deltas were mapped by identifying key features such as sediment build-up within visual spectrum satellite imagery using Google Earth Pro. Major river inflows were mapped by carefully examining the Caspian shoreline. During this process, we found that many adjacent river inflows converge at a common source less than a few kilometres inland. As a result, we spatially summarised adjacent river inflows that shared a common source according to the two most distant inflows along the shoreline (Figure 12 A), hereafter referred to as a “river complex”. After spatially summarising the major river inflows, we evaluated two river deltas, the Volga and the Ural, and four river complexes, defined by the areas between the rivers Terek and Sulak, the Samur and Sabrancay, the Kura and Astrachay, and the Safarud and Haraz. We then generated a raster describing the distance of each 3km grid cell to the intersection between either (i) the Caspian coastline with the maximal extent of a river delta, or (ii) the Caspian coastline with the two most distant river inflows in a complex (Figure 12 B).

3.3.2.3. Distance from the 50m isobath

The Caspian Sea has a complex bathymetric profile that can vary over a relatively small distance. The northern basin and most of the eastern coastal margins have a shallow and flat profile, however, steep shelving transitions occur towards the much deeper middle and southern basins. Shelf-like areas, where shallower regions are nearby steep gradients that descend into much deeper regions (Figure 11 and 12 A) are present within the areas that border the deep middle and southern (Figure 12 B). We found that these sea shelf-like habitats are approximately isolated using a 1km grid raster, with values calculated as their distance from the 50m isobath, which we identified using the global bathymetry dataset GEBCO (2019) after adjusting for the Caspian sea level, which is approximately 28 meters below the global sea level.

3.3.2.4. Sea surface temperature

Sea surface temperature data was retrieved from the Multi-scale Ultra-high Resolution Sea Surface Temperature (MUR SST) dataset. The MUR dataset combines multiple satellite sensors and in situ observation and is produced by the NASA Jet Propulsion Laboratory (https://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1). We retrieved 1km resolution raster images for each day during our study period.

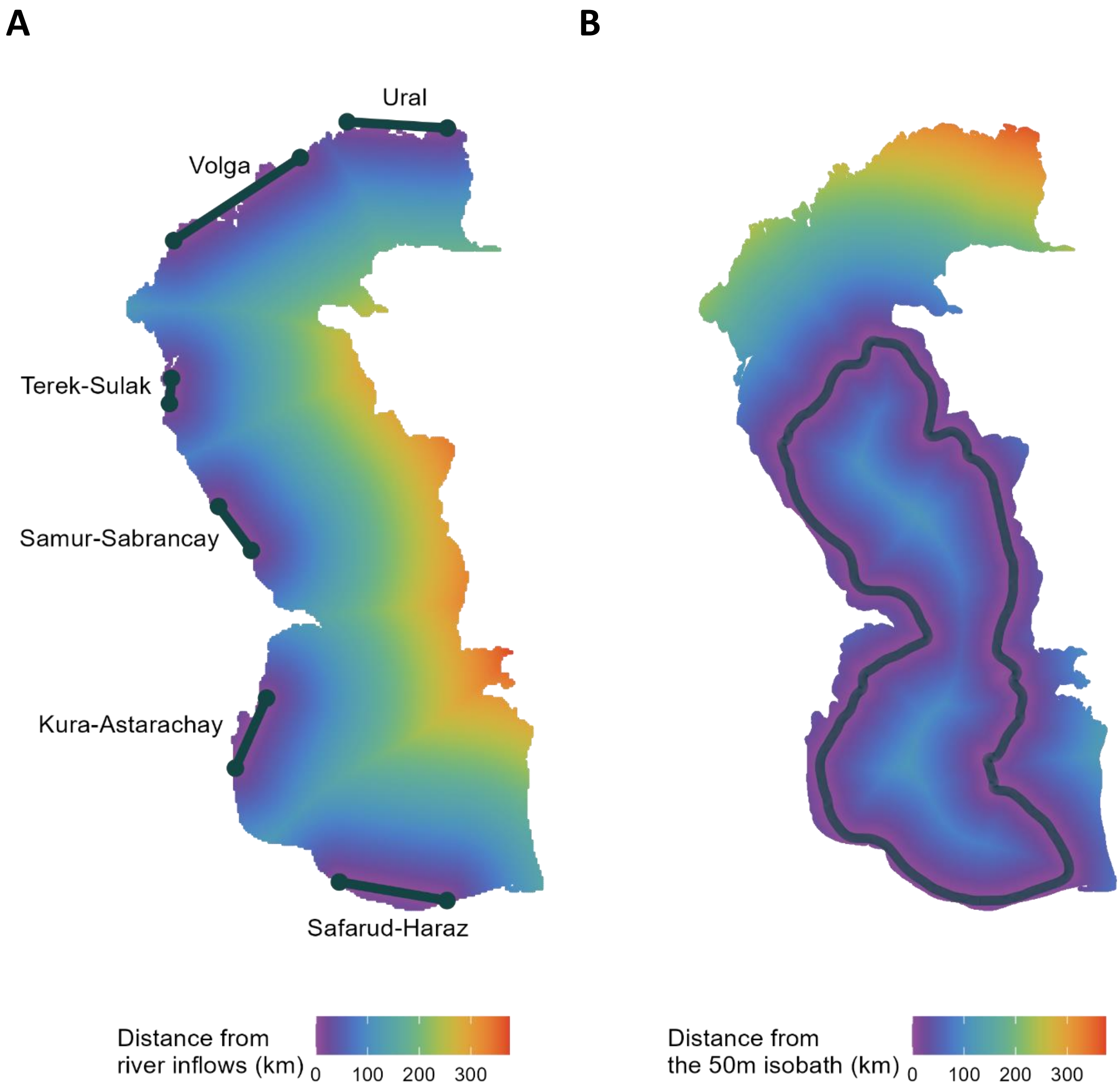

Figure 14. **A** Distance from river inflows in kilometres. River inflows and complexes are shown as line features intersecting two points which illustrate the maximum extent of their range. **B** Distance from the 50m isobath in kilometres. The 50m isobath is highlighted as a grey line feature.

3.3.2.5. Vessel AIS Data

Maritime vessel traffic is often a proxy for numerous human impacts such as fishing and industrial development. To evaluate the distribution of these impacts, vessel AIS data was purchased from www.marinetraffic.com. Data was retrieved at an hourly resolution, and, in total, we retrieved 5.57 million marine traffic AIS locations between 1st January 2015 and 31st December 2016. We used data from these two years as an approximation of vessel traffic across all years due to a high degree of track similarity between years. Raw AIS data was filtered by first removing data points more than 20km inland from the Caspian Sea shoreline, defined here by the -28 m contour relative to global sea level. These records are likely to be a result of either erroneous GPS records or vessels travelling upriver, which is particularly common in the Volga Delta which vessels use to travel between central Russia and the Caspian sea. Next, we removed records from stationary vessels. To filter these records, we identified periods when vessels remained stationary by identifying series of consecutive daily GPS records where the distance between subsequent records was less than 1 km and the pairwise distance between every record averaged less than 1 km. We then implement a modified version of a speed-based truncation protocol reported by (Greig et al., 2020).

Our speed-based truncation protocol was implemented in three stages. First, we generalised the vessel types reported in the raw data retrievals into 16 categories which represented the least specific vessel categories whilst maintaining key differences regarding vessel function, speed, and size. First, all stationary structures, such as offshore structures, pontoons, floating storage, and drilling rigs were filtered out. Different varieties of accommodation serving vessels, cargo ships, tankers, carriers, fishing vessels, freighters, passenger ships, supply vessels, dredgers, pipe laying ships, emergency service or rescue vessels, were each pooled together within separate classifications. All remaining vessels that could not be pooled together, were pooled together within a single remaining class. Each of the generalised categories were themselves vessel types reported in the raw data and were chosen as they represented the least specific type of classification. Second, we calculated a maximum speed over ground threshold for each category as the mean + 6 standard deviations of vessels' self-reported speed over ground. Finally, we estimated each vessel's course speed based on a vessel's GPS records. GPS records were removed when a time-ordered GPS record would have resulted in a travel speed from the previous GPS record which exceeded the threshold determined by the formula reported in Greig et al. (2020). After the removal of a GPS record, vessel speeds were re-estimated and re-evaluated. This process was repeated indefinitely until either no records could have resulted from unrealistic speeds, or a vessel was completely removed from the dataset. After the speed-based filtering step, we identified and removed every GPS record, both inland and otherwise, from vessels where the estimated trajectories intersected land more than 20 kilometres inland. Vessels that were filtered at this stage were a result of large spatiotemporal gaps between consecutive records from the raw GPS data retrievals. This final step was necessary due to the complex geometry of the Caspian Sea shoreline and a desire to result in the most reliable vessel trajectories.

3.3.3. Generalized additive mixed-effects model

To evaluate the influence of environmental covariates on Caspian seal movement and inferred foraging behaviour, we used a hierarchical generalized additive mixed-effects model framework. This was implemented within the Bayesian mixed effects modelling package INLABRU (Bachl et al., 2019). We chose to specify a beta likelihood family with logit link as the behavioural metric *g* is limited to an interval between 0 and 1 (Smithson and Verkuilen 2006).

3.3.3.1. Spatial-temporal effect

We defined a seasonally dependent spatio-temporal effect to account for random spatial-temporal processes using the SPDE method and the grouped random effect kronecker product syntax available within the INLA framework (Krainski et al., 2020). To implement the spatial SPDE, we defined a 2-dimensional mesh covering the Caspian Sea plus a 500m buffer, specifying a minimum knot distance of 50 km, where the knots indicate points on a mesh where weights that are used to approximate the smooth spatial correlative surface are calculated. Temporal characteristics were implemented by specifying 12 evenly spaced temporal bins covering a calendar year and assigned each data point into a its closest temporal bin. The temporal bins were then used to define a within group level SPDE model, and to account for temporal correlations, we used an autoregressive model of order 1 (ar1) as the between temporal bin group level model.

3.3.3.2. Temporal effects

We explicitly parameterised individual based temporal autocorrelation in the behavioural metric 1-*g* using a b-spline smoother, implementing a SPDE model on a 1-dimensional mesh using the grouped random effect kronecker product syntax in INLA (Krainski et al., 2020). To implement the temporal smoother, we defined a 1-dimensional mesh covering a calendar year with 12 evenly spaced knots, an integrate to zero constraint, and a free boundary condition as few of our tags lasted close to a full 365-day cycle. From the mesh, we built a 1-dimensional Matern SPDE model using a penalised complexity (PC) prior (Fuglstad et al., 2019), with a prior on the range of the temporal correlation as 10 days with a 1% probability of the range being less than 10 days and on the standard deviation of the temporal effect of 1 with a 1% probability of it being greater than 1. The temporal smoother was defined to account for individual-based deviations from an average effect by using individual tag-id to differentiate the smoothers of each individual using an independent identically distributed (iid) model.

3.3.3.3. Environmental effects

To define the effect of our environmental covariates, distance from river inflows, distance from the 50m isobath, and sea surface temperature, linear “fixed” effects were implemented to account for the temporally independent average effect of each covariate. For the fixed effects we specified

Gaussian priors with a prior mean of 0 and prior on the precision of 1. To evaluate temporal deviations from the average effect of each covariate, we estimated a random slope with temporal correlations using a similar model specification as the explicit temporal effect. We defined a 1-dimensional mesh covering the full daily 365-day calendar with 12 evenly spaced temporal knots, an integrate to zero constraint, and a cyclic boundary condition to introduce correlations between the first and last knot of an annual cycle. From the mesh, we built a 1-dimensional Matern SPDE model with PC prior (Fuglstad et al., 2019), with a prior on the range of the temporal correlation as 50 days with a 1% probability of the range being less than 50 days and on the standard deviation of the temporal effect of 1 with a 1% probability of it being greater than 1. Therefore, the full effect of either distance from rivers or distance from the 50m isobath on any given day is equal to the sum of the temporally independent average effect and the temporal deviation. Finally, we deployed square root transformations prior to standardising both distance from rivers and distance from the 50m isobath.

3.3.4. Marine spatial planning

Using the full model minus the individual-based temporal deviation components, we then made spatial predictions for an average individual to identify areas where high ARS is predicted to occur. Spatial predictions were used to develop potential spatially and temporally flexible marine protected area designs using the R package PRIORITIZR (Hanson et al., 2021) with the Gurobi Optimizer version 9.5.1 (Gurobi Optimization, 2022). PRIORITIZR uses integer linear programming (ILP) techniques to find optimal solutions for spatial planning problems. We ran PRIORITZR using the minimum set primary objective to identify regions with the highest predicted ARS and the lowest vessel density and compared these regions to an unpenalized scenario where vessel density was spatially constant at its seasonal mean. In addition, we utilised PRIORITZR's Relative target, Boundary penalty, and Linear penalty functions to impose additional criteria for our protected areas to satisfy. These additional criteria were: (i) our protected area should cover either 10% or 30% of the cumulative spatial prediction for ARS (Relative target), (ii) penalise solutions that select planning units with higher values for an additional data source according to a penalty factor (Linear penalties), and (iii) penalise solutions that are excessively fragmented according to a penalty factor and an edge factor (Boundary penalties). By applying these additional criteria, we can clearly describe a process for select spatially continuous areas that satisfy clear conservation goals and these utilities are a key attribute of using the PRIORITZR method.

We then compared vessel penalized MPAs with unpenalized MPAs within the 10% and 30% protection scenarios according to the proportion of total vessel travel and average vessel speed which occurs within each MPA in any given season. This process was implemented to evaluate if there were areas within the Caspian sea that could be protected and align with the Aichi target of a 10% protection of marine habitats (CBD 2010) and more recent targets of 30% (Baillie and Zhang 2018; Dinerstein et al. 2019). This process used maritime vessel traffic because this is often a proxy for numerous human impacts such as fishing and industrial development. To implement penalties, a penalty factor is used to penalise the selection of planning units with a high value of an additional data source compared to the main objective. We defined three separate penalties, each of the linear penalties was implemented according to an inverse of a binary presence/absence raster for (i) observation level seal data in the respective season with a penalty factor of 5, (ii) observation level seal data in any season with a penalty factor of 2.5, and (iii) vessel densities greater than the mean in any season with a penalty factor of 5. To clarify, by including observation level data and vessel data we are able to favour solutions that contain larger amounts of non-predictive ARGOS tag-based records of seal habitation and penalise solutions that have larger amounts of non-predictive vessel AIS records. To implement boundary penalties, where higher penalty factors prefer solutions with less fragmentation, we constructed (Equation 1) to account for seasonal variability in spatial clustering. Where b_i equals the boundary penalty factor a given season *i*. a_i equals the average distance (km) between each individual seal during season *i* plus one standard deviation (Equation 2), where m_{xy} is a Euclidean distance matrix calculated from the coordinate reference of individual seal positions (Equation 5), and *k* equals the maximum value for *a*, or rather the maximum average distance between individual seals during a given season (Equation 6). This penalty factor was defined so that the design of an MPA could be more fragmented when the distribution of seals was more spread out and less fragmented when the distribution of seals was more clustered.

$$b_i = 0.5\left(\frac{a_i}{k}\right) \qquad \text{(Equation 1)}$$

$$a_i = u_i + s_i \qquad \text{(Equation 2)}$$

$$u_i = \frac{\sum_{i=1}^{N} m_{xy}}{N} \qquad \text{(Equation 3)}$$

$$s_i = \sqrt{\frac{\sum (m_{xy} - u_i)^2}{N}} \qquad \text{(Equation 4)}$$

$$m_{xy} = \sqrt{\sum_{e=1}^{m} (x_e - y_e)^2} \qquad \text{(Equation 5)}$$

$$k = \max(s_1, s_2, \dots, s_n) \qquad \text{(Equation 6)}$$

3.4. Results

3.4.1. Tag performance

When pre-processing the tracking data, we applied a series of filters in succession to remove unreliable entries. The tags filtered at this stage produced anomalous track topologies that would not provide useful information or consistent with seal movements. During this process we removed two tags that had less than 10 GPS positions throughout their lifespan. We removed four tags that were deployed for less than 10 days. We removed one tag that did not return a GPS position for over 30 days, this tag also had multiple shorter but significant gaps along with large changes in position during those periods. Finally, we removed three tags with clearly erroneous track topologies that would not be consistent with ordinary seal movements, these tags also had shorter than average deployment lifespans of 18, 28, and 40 days. During pre-processing, 10 tags were excluded, and we proceeded to analyse data from 108 Caspian seals. On average, each tag had a lifespan of 146.16 days (SD 73.14). Tags that were deployed during autumn had an average lifespan of 116.55 days (SD 39.93) and tags that were deployed during summer had an average lifespan of 186.07 days (SD 87.87). Overall, 46% of the filtered locations were returned from autumn deployments and 54% were returned from summer deployments. There was a slight bias towards male tag locations, where 51.45% of tag locations were returned from male seals and 48.55% from female seals. For a description of basic movement patterns and diving behaviour see Dmitrieva et al. (2016).

3.4.2. Environmental effects

The posterior marginal distributions are summarized with error bars indicating the 50% credible interval and 95% credible interval are shown in figure 13 A. These plots show the posterior marginal distribution for the temporally independent coefficient of each covariate upon the behavioural metric *1-g* on the internal logit scale of the model. Broadly, these coefficients describe the average impact of each covariate upon ARS behaviour over a calendar year. The mean temporally independent coefficient for distance from river inflows was -0.034 with the 95% credible intervals ranging between -0.161 and 0.093. The mean temporally independent coefficient for distance from the 50m isobath was 0.086 with the 95% credible intervals ranging between -0.005 and 0.178. The mean coefficient for sea surface temperature was 0.064 with the 95% credible intervals ranging between -0.003 and 0.131. In a Bayesian context, we evaluated the statistical significance of each of these effects by assessing the degree to which the 95% credible intervals overlap with zero, which would indicate a probability of the covariates having no effect upon ARS behaviour. These results indicate that on average, the evidence of ARS occurring near river inflows is not very strong. On the other hand, the probability of ARS occurring far from the 50m isobath is higher, and there is marginally stronger evidence to support this. Additionally, the probability of ARS occurring in warmer waters is also higher.

3.4.3. Temporal effects

The posterior marginal distributions for the full temporal effect are shown in figure 13 B, with a mean line and error ribbons that correspond to the 95% credible interval. These plots represent the full marginal probability distribution for the full coefficient (fixed effect + temporal deviation) of each covariate through time. Between January and late May, ARS occurs far from the 50m isobath, and the relationship is significant. On average, between June and November ARS occurs closer to the 50m isobath, although the 95% credible intervals partly overlap with zero during June, July, and November. The relationship between ARS and the 50m isobath is most significant from August until October when there are lower odds of ARS occurring far from the 50m isobath. The relationship between ARS and distance to the 50m isobath trends toward positive during December.

Between January and April, the relationship between ARS and distance from river inflows is positive, indicating higher odds of ARS occurring far from river inflows. Between May and August, there is an increase in ARS nearby rivers and the relationship between ARS and distance from rivers remains similar until September when there is a further increase in ARS nearby rivers before a decrease in ARS nearby rivers between October and December.

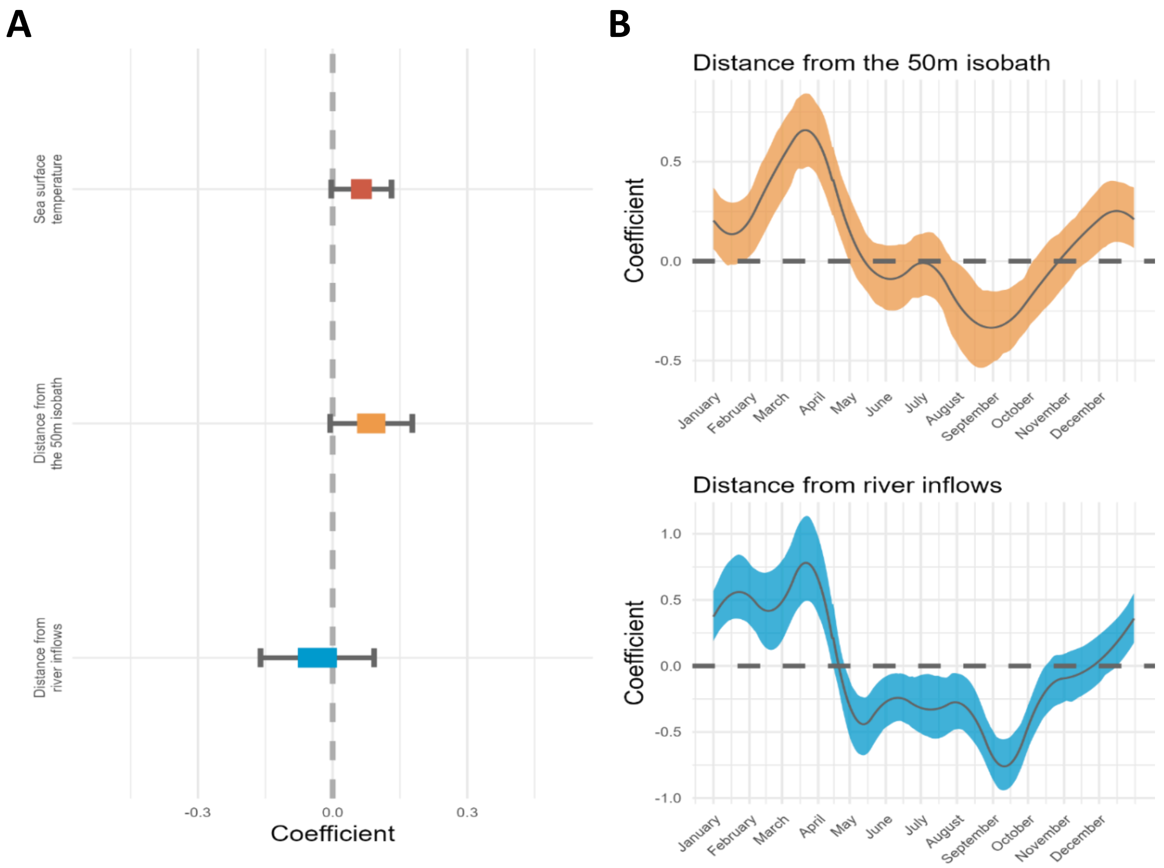

Figure 15. A: Posterior marginal distributions for the fixed effect of the covariates (i) sea surface temperature, (ii) distance from 50m isobath, and (iii) distance from river mouths. Each distribution is summarised using a boxplot. The box corresponds to the 50% credible interval and the error bars correspond to the 95% credible interval. **B**: Posterior marginal distributions for the full effect of the covariates, (i) distance from 50m isobath, and (ii) distance from river mouths, through time (fixed effect + temporal deviations).

3.4.4. Spatial-temporal effect

The spatial-temporal effect has a mean spatial correlation range of 152.21 kilometres with 95% credible intervals ranging between 127.97 and 178.32. This result indicates a moderate to high degree of spatial clustering in ARS-like behaviour, as the maximal extent of the Caspian Sea is approximately 440 km on the longitudinal gradient and 1150 km on the latitudinal gradient (Lebedev, 2018). The ar1 group-level correlation parameter has a mean of 0.096 with 95% credible intervals ranging between -0.054 and 0.227, this indicates that on average the spatial intensity of ARS changes quickly between each of the 6 successive knots.

3.4.5. Vessel AIS data

Established shipping lanes were used relatively consistently throughout the year and there was little variability in the spatial density of vessels. However, the northern winter ice sheet typically forms between December and March and restricts winter vessel traffic to icebreaker routes. Most icebreaker traffic services offshore oil and gas installations, and the icebreaker routes represent the most efficient route from logistics supply ports accounting for navigational constraints such as bathymetry (Wilson et al., 2017b). The total distance travelled by vessels varied widely between months, ranging from 1,004,092 km in November to 1,538,251 km in July (Mean 1,333,218 SD 198,896).

3.4.6. Marine spatial planning

After fitting our model, we used the generalized additive mixed-effects model to predict foraging hotspots for an average individual by not including the individual based components or coefficients when generating predictions over space. These outputs were then used within a prioritization algorithm to identify important foraging areas (Figure 14). The PRIORTIZR algorithm was able to identify solutions that exceeded the relative targets for identifying regions of higher ARS behaviour across each season (Figure 14). Overall, unpenalized MPAs had a higher proportion of vessel travel occurring within their boundaries, and vessel density penalised MPAs had a lower proportion of vessel travel occurring within their boundaries. MPAs which were designed to cover 10% of the cumulative spatial ARS prediction contained, on average, 6.57% (SD 2.42) in unpenalized plans and 2.16% (SD 0.74) in vessel penalised plans, of the total distance travelled by vessels within any given season. MPAs which were designed to cover 30% of the cumulative spatial ARS prediction contained, on average, 20.36% (SD 3.16) in unpenalized plans and 10.50% (SD 2.09) in vessel penalised plans, of the total distance travelled by vessels within any given season.

Overall, the average travel speed of vessels did not vary widely between seasons (Mean 6.87 SD 0.35), ranging between 6.03 km/h (SD 6.57) in October to 7.33 (SD 6.96) km/h in August (Figure 15). However, the average travel speed of vessels within MPA plans did vary between seasons and was on average higher than overall vessel speeds, and there was little difference between the temporal history of vessel speeds between each MPA category. Vessel speeds (km/h) within MPAs were highest in July (Mean 12.91 SD 1.54) and lowest in October (Mean 6.16 SD 1.78).

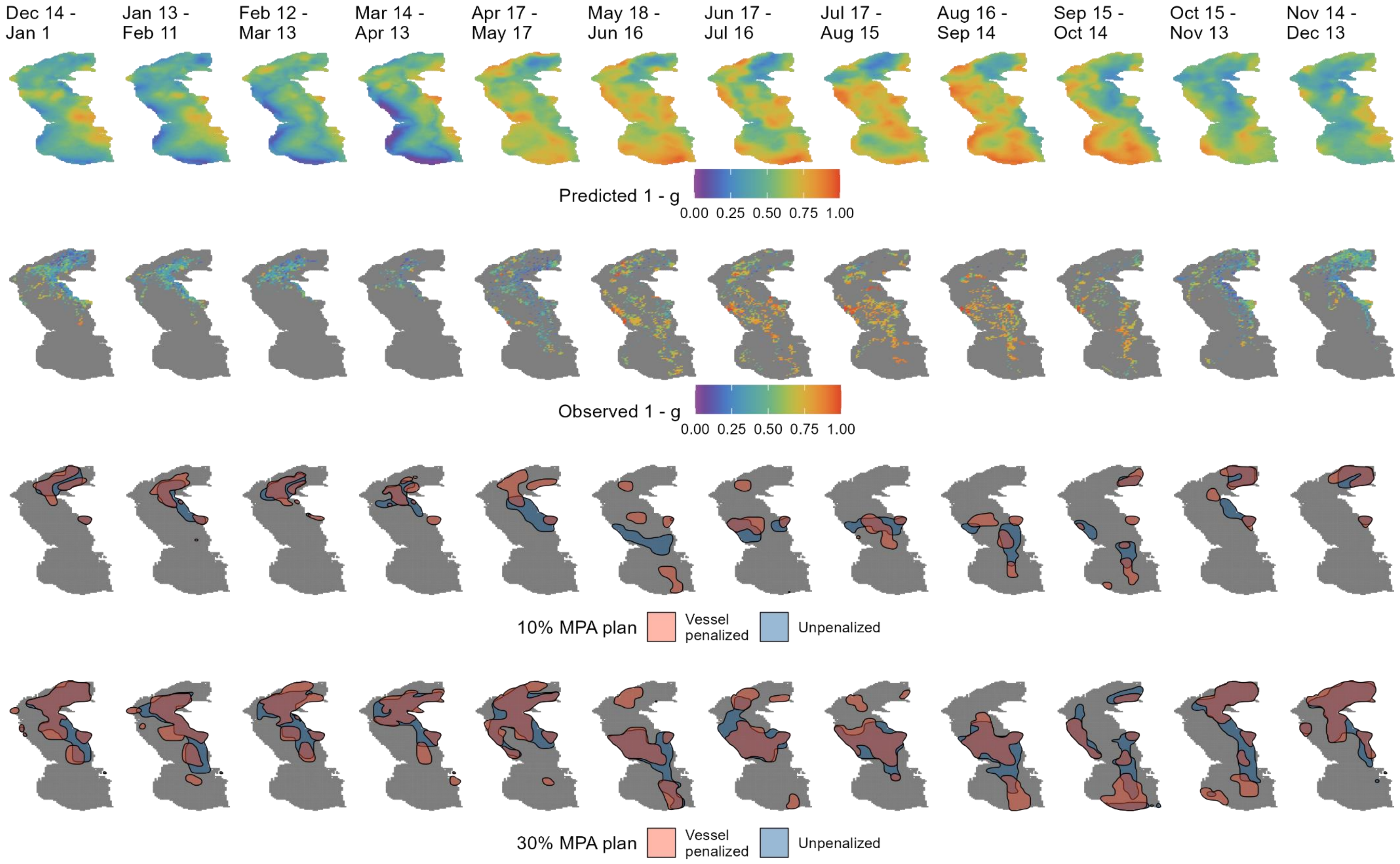

Figure 16. (First row) Spatio-temporal predictions for ARS 1-g across the entire Caspian Sea. Predictions were made using the full model minus the individual temporal component. (Second row) Heat map for the average cellular value of 1-g for the raw observation level dataset. (Third row) MPA planning solutions for 10% cover. Vessel density penalised solutions are shown in red and unpenalized solutions are shown in blue. (Fourth row) MPA planning solutions for 30% cover. Each map represents the average predictions or observations for time periods equal to approximately 30.42 days. Maps are ordered left to right by date.

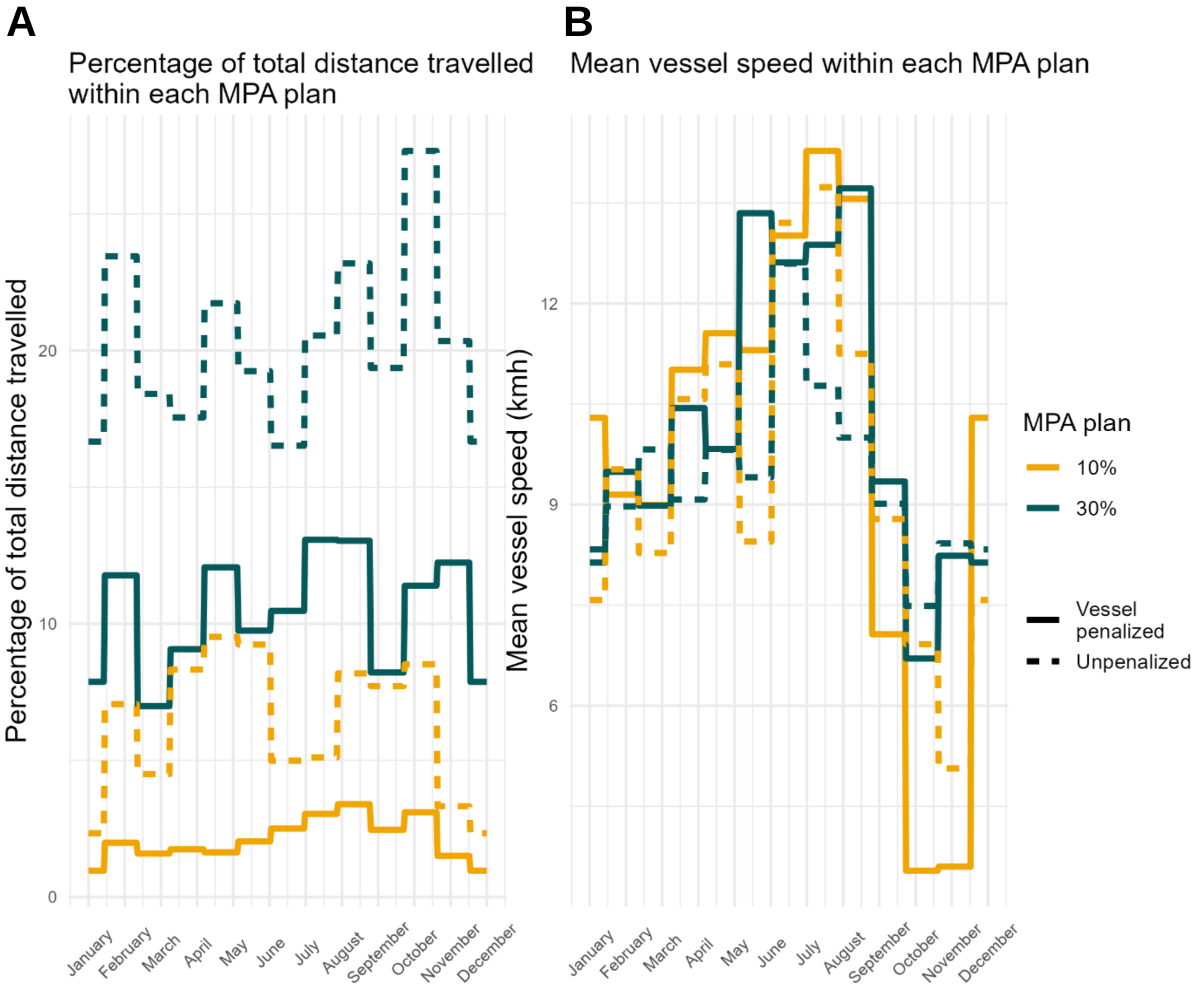

Figure 17. **A**: The proportion of the total distance travelled by vessels that occurs within each of the 4 MPA plans through a calendar year. 10% cover MPA plans are shown in yellow and 30% cover MPA plans are shown in dark green. Vessel penalised MPA plans are shown as a solid line and unpenalized MPA plans are shown as a dashed line. **B**: The average speed of vessels (km/h) that occurs within each of the 4 MPA plans through a calendar year. 10% cover MPA plans are shown in yellow and 30% cover MPA plans are shown in dark green. Vessel penalised MPA plans are shown as a solid line and unpenalized MPA plans are shown as a dashed line.

3.5. Discussion

The results of our analyses show strong evidence for Caspian seals using habitats nearby river inflows and the 50m isobath during certain times of the year much more than other times of the year. Specifically, our findings suggest that proximity to these habitats strongly influence the likelihood of individuals displaying area restricted search (ARS) movements, which are often indicative of foraging behaviour. The inferences gained during this analysis are applied to generate spatial predictions of animal movement patterns throughout an annual cycle and we used these predictions to design seasonally flexible potential MPA solutions. To develop these MPA plans we used a prioritization algorithm that prioritised areas with a high predictive foraging quality as well as a high occurrence of non-predictive tag based records, and deprioritise areas where vessel density is highest and protective legislation would result in costly financial trade-offs with maritime industries. Our results demonstrate that areas exist in the Caspian Sea that, if protected, would meet marine habitat protection targets in the context of preserving habitats that are important for foraging. We identify areas which meet both the Aichi target of a 10% protection of marine habitats (CBD, 2010) and more recent targets of 30% (Baillie and Zhang, 2018; Dinerstein et al., 2019) and result in minimal trade-offs with maritime industries within specific area limits when compared with equivalently sized plans that do not account for trade-offs.

3.5.1. Marine spatial planning

The Convention on Biological Diversity (CBD) legally commits governments to conserve biodiversity. The Aichi targets are a key component of the CBD, where Target 11 was designed to protect 10% of marine areas by 2020 (CBD, 2010). However, more recent targets have proposed a protection level of at least 30% by 2030 (Baillie and Zhang, 2018; Dinerstein et al., 2019). Conservation targets are an important component of conservation action, however, regarding foraging ecology, it is important to consider the relationship between productivity and space. One of the foundations of spatial ecology is the relationship between home ranges and forage densities. Generally, home ranges increase as forage densities decrease or energy requirements increase (van Beest et al., 2011; Tucker et al., 2014). In this context, protecting 10% or 30% of an area might not protect 10% or 30% of a species if behaviour is not considered. In this study, we have considered specific aspects of Caspian seal foraging behaviour to demonstrate a framework for protecting seals in a spatial context so that the most important foraging areas can be identified and protected. Furthermore, we implement this framework by considering interactions and trade-offs between the management of protected areas and human activity.

When protecting species, it is important to recognise when conservation action can interact with human behaviour. This is important because, for example, the relationship between environmental productivity and industry productivity can be highly correlated and in effect difficult to manage. The shared use of habitats is common in the Caspian sea, where interactions between seals and fishing vessels are believed to be one of the major drivers of recent population decline due to accidental bycatch within illegal sturgeon fishing nets (Ermolin and Svolkinas, 2018; Svolkinas, 2021). This is in addition to other conflicts such as the most productive breeding habitats intersecting with the routes used by icebreaker vessels that service offshore energy developments (Wilson et al., 2017b). However, in other areas, logistical practicalities may make certain regions important for seals but unimportant for human use, such as areas that are inaccessible to shipping vessels or where resource extraction is not commercially viable. Developing procedures that can identify these areas is an important component of pragmatic spatial conservation planning as it explicitly accounts for trade-offs between conservation and regional human objectives. In this study, we have used a comprehensive dataset to combine the outputs of spatial-temporal models, that investigate animal movement, with prioritization algorithms to demonstrate that conservation objectives can be met in the Caspian whilst minimizing their impact upon vessel-based. When comparing vessel penalised plans with unpenalized plans the PRIORITZR algorithm successfully identifies regions that both (i) meet conservation objectives and (ii) would have a lower impact upon maritime industries. Furthermore, we utilize specific features of the PRIORITZR algorithm to penalise against solutions, and identify optimum solutions that weight towards regions where we have non-extrapolated tag based records of seal habitation. However, future research may seek to investigate the direct relationships between different types of vessel related metrics, such as speed and vessel type, and how and when these metrics are associated with Caspian seal ecology.

In 2021, three Important Marine Mammal Areas (IMMA) were recognised within the Caspian Sea (Marine Mammal Protected Areas Task Force, 2021). The designation of IMMAs in the Caspian Sea marks an important milestone for Caspian seal conservation, however, IMMAs are not MPAs and do not have legal or regulatory status. IMMAs are defined as 'discrete portions of habitat, important to marine mammal species that have the potential to be delineated and managed for conservation' (Hoyt, 2018). IMMA’s are purposefully maximalist and there is not necessarily an expectation that the entire areas are protected in the future. We propose that our methodology could be used to guide the refinement IMMAs in the Caspian sea. For example, one of the Caspian IMMAs was designed to target important “transitory migration and feeding areas”. If the proposed IMMA for feeding areas was enforced year-round, through regulations such as speed limits or use restrictions, it would result in costly impacts upon legal maritime industries such as fisheries and offshore energy extraction, in addition to associated management costs. The designs we present can be considered a first step towards designing cost-effective and seasonally flexible protected areas in the Caspian Sea. Future studies may seek to utilize a wider range of data sources to incorporate a more complete understanding of environmental dynamics and pinniped ecology within the MPA designs. For example, future-proof MPA planning may need to account for rapid sea level declines (Prange et al., 2020), and compared to telemetry-based tags, more individuals could be observed during the breeding and haul-out seasons by conducting aerial surveys. Including aerial survey counts could be possible within a joint and multivariate analysis that includes different types of occurrence data and different types of behaviour, because ARS may not be a major indicator of Caspian seal ecology during the breeding season when mothers are nursing new-born pups (Wilson et al., 2017a; Wilson et al., 2017b). In addition, future studies may also seek to conduct an explicit cost analysis of implementing these MPA designs. For example, in this study we produced MPA designs on a monthly time scale. Future studies may seek to refine this procedure and evaluate how different time scales impact management costs or ease of implementation. For example, it may be more practical to define fewer changes to the protected areas within an annual calendar. In summary, we designed potential plans for MPA's to illustrate a statistically driven methodology that explicitly incorporates the behaviour of Caspian seals and trade-offs with maritime industries. In the future, actual MPA designs that may inform policy would have to careful consider variation in pinniped behaviour throughout the year, areas where seals may be more or less vulnerable to threats such as bycatch, and the cost or feasibility of implementing seasonally changing MPAs.

3.5.2. Environmental covariates

During this study, we carefully selected the environmental covariates that we used during our analysis by explicitly considering how Caspian seal foraging ecology is likely to interact with habitat qualities. The main goal of this study was to test specific ecological hypotheses related to the foraging ecology of Caspian seals over time, rather than finding the best fitting model. Therefore, to avoid favouring a covariate that improved the numerical performance of our model over one associated with a functional or mechanistic ecological hypothesis, we deliberately avoided using an extensive model selection protocol when selecting our covariates. This decision was made to improve the transferability of our ecological model and was inspired by a series of recent discussions on the application of species distribution like models (Yates et al., 2018; Bouchet et al., 2019), whereby we selected our covariates by explicitly considering the mechanistic relationship they may describe within the ecology and behaviour of Caspian seals. Initially we considered distance from river inflows, distance from shore, distance from the 50m isobath, bathymetric depth, slope, and sea surface temperature. However, distance from shore, bathymetric depth, and slope were subsequently dropped due to issues relating to collinearity, and we chose to include distance from river inflows and distance from the 50m isobath for reasons that relate to the ecology of Caspian seals. Distance from river inflows was preferred over distance from shore because Caspian seals eat fish that inhabit rivers (Pochtoeva-Zakharova N, 1999; Bandpei et al., 2012; Dmitrieva et al., 2016), and because, unlike many other pinnipeds, Caspian seals do not need to regularly return onshore and can remain at sea for over 6 months (Dmitrieva et al., 2016). The 50m isobath was preferred over Bathymetry because it broadly aligned with a notable shelf-like gradient in the middle and southern Caspian sea, which are known to be important habitats for other related pinnipeds such as the larger and deeper diving Grey seal (*Halichoerus grypus*) (Nowak et al., 2020). In addition, we preferred the 50-m isobath over bathymetry to minimize non-linearities or spatially inconsistent relationships between our covariates and foraging intensity. To clarify, while Caspian seals frequently dive to access food resources at depth, they also transit over depths beyond their diving capabilities (Dmitrieva et al., 2016) although their distribution may be associated with these depths in remote sensing bathymetric datasets. This inconsistency could support a highly non-linear relationship between depth and foraging, because Caspian seal physiology limits their ability to access the deepest regions of the Caspian. In summary, we preferred a distance to the 50m isobath over bathymetry because it would have a more easily linearized relationship with ARS, as opposed to a complex non-linear relationship that may require the implementation of polynomials or splines. This was because we intended to investigate non-linear changes to this relationship over time, and due to the higher computational demands of modelling change in a non-linear relationship over time. Finally, sea surface temperature was chosen as it is frequently used within ecological literature when describing patterns in animal behaviour and distribution, and its association with primary productivity.

3.5.3. Distance from rivers

Pinnipeds are known to target seasonally available prey (Beck et al. 2007; Allegue 2017; Leach et al 2022), and therefore, we may expect Caspian seals to also adjust their prey selection according to their with seasonal availability. The diet of Caspian seals is believed to be mostly comprised of several species of kilka (*Clupeonella* spp.*)*, silversides (Atherinidae), gobies (Benthophilinae)*,* zander (*Sander* spp.), roach (*Rutilus caspicus*), and fresh-water bream (*Abramis brama*) (Pochtoeva-Zakharova N, 1999; Mamedov, 2006; Goodman et al., 2007; British Petroleum, 2015). Northern Caspian zander (*Sander* spp.) spawn amongst the Volga and Ural river inflows between April and May (Kottelat and Freyhof 2007). In Iran, the Caspian roach (*Rutilus caspicus*) migrates through rivers along the coastline during the spawning season which begins in February and ends in April (Golpour et al. 2013). Caspian bream (*Abramis brama*) spawn and winter amongst the deltas of larger Caspian rivers but forage further at sea, first migrating upstream during April when they travel to spawn before returning to the Caspian, and then migrating back upstream during August prior to winter (Berg et al., 1949; Dement'eva, 1952). The temporally structured life cycles of these fish may explain a temporal association between foraging and the use of habitats nearby river inflows. Between May and June there is a prominent increase in ARS near rivers (Figure 13 B), most notably the Volga delta in the northwest (Figure 14), which coincides with the initial increase in the negative association between distance from rivers and ARS, and the end of the Zander (*Sander* spp.) spawning season in the river Volga. There is another prominent increase in ARS near rivers between September and October (Figure 13 B) when there are low rates of habitat use amongst the Volga and high rates of ARS and habitat use amongst the Samur-Sabrancay river complex in the west (Figure 14), which generally coincides with the autumn migration of Caspian bream (*Abramis brama*). These results may be indicative of seals utilising rivers during fish migrations. However, fish migrations are known to be influenced by environmental qualities, such as water temperature, which can vary between years and regions. Temporal variability in fish migrations makes generalisations between rivers and migration seasons difficult. Further analysis could investigate this relationship more precisely if pinniped foraging data could be paired with data on fish migrations within specific rivers, for example, by using eDNA data to monitor temporal fluctuation in the occurrence of fish (Zou et al., 2020; Milhau et al., 2021).

The temporal pattern in the effect of river inflows through time indicates that between January and April high ARS occurs far from river inflows or low ARS occurs close to river inflows. Between January and March, most Caspian seals are located away from river inflows and close to the centre of the north Caspian basin, where the highest concentration of ice forms (Heygster et al., 2009)and where the highest density of Caspian seal pups are born (Harkonen et al., 2008; Dmitrieva et al., 2015; Wilson et al., 2017a). When cross-referencing daily satellite images of ice with the locations of tagged seals, it is apparent that some of the tagged seals are likely to have been hauled out upon mobile pack ice. We took steps to minimise the impact of ice-movement-related pseudo-ARS upon our data by correcting estimates for ARS after fitting the state space model, however, it is possible that some remain. In addition, ARS occurring further from rivers during the breeding season may be a result of the legitimate non-foraging ARS behaviours of male Caspian seals, which frequently visit multiple breeding hotspots throughout this period (Goodman 2022, personal communication). Although, some foraging-related ARS does take place during this period in males and income-breeding females. Without more precise data regarding metabolic or dive profiles, the highly multifaceted nature of ARS analysis during this period makes more specific conclusions difficult.

3.5.4. Distance from 50m isobath

In general, an association between ARS behaviour and distance to the 50m isobath broadly aligns with the deep diving behavioural clusters previously identified in the central and southern Caspian (Dmitrieva et al., 2016). In the Caspian sea, the 50m isobath broadly aligns with a notable shelf like gradient and these results align with results from other pinnipeds, which use shelf-like habitats as foraging areas, such as the larger and deeper diving grey seal (*Halichoerus grypus*) (Nowak et al., 2020). During this study, we explained these behavioural clusters using relationships between ARS movements and environmental covariates. Compared to ARS nearby rivers, relationships with the 50m isobath may be explained by the occurrence of fish that are found in the pelagic zone. Caspian kilkas (*Clupeonella*) are likely to be an especially important dietary resource due to their high energy and oil content. There are three more commonly caught species of Kilka in the Caspian Sea, Anchovy kilka (*Clupeonella engrauliformis*), the Common kilka (*Clupeonella cultriventris*), and the Big-eye kilka (*Clupeonella grimmi*) (Mamedov, 2006). Kilka mostly inhabit the entire shelf region off the coast of Azerbaijan and spawn throughout the year. They do not generally have as close of an association with river inflows as other Caspian seal prey, although spawning can occur within both the sea and in rivers (Whitehead, 1985). In the summer, kilka occur at depths between 40-80 metres, in the autumn up to 60-100 metres, and in the winter up to 100-450 metres (Mamedov, 2006; British Petroleum, 2015). These depths make kilka most accessible to Caspian seals during the summer, because, although dives up to and exceeding 200m have been recorded, most Caspian seal dives are less than ~50 metres (Dmitrieva et al., 2016). If kilka are more accessible during the summer, the depth shifts of kilka may explain a summer association between ARS and the 50 metre isobath. This may be concerning in the context of climate change, as fish have been observed adapting to increases in sea temperatures by tracking thermal gradients and shifting their bathymetric range into deeper waters (Dulvy et al., 2008; Engelhard et al., 2014; Morley et al., 2018). If kilka occupy deeper waters during the crucial pre-breeding foraging season, the energetic demands of reaching kilka may increase, which could have an unknown impact upon Caspian seal fitness. Furthermore, kilka have been overexploited for many decades, became commercially extinct in the early 2000s, and fishing operations were subsequently halted (Strukova et al., 2016), although commercial kilka trawls restarted in 2019 after a 15 year hiatus (Federal Agency for Fisheries, 2021). Due to the past vulnerability of kilka to overfishing, careful consideration must be applied when managing the exploitation of future stocks, and therefore, protecting Caspian seals within kilka habitats may have the added benefit of increasing the sustainability of Kilka stocks for future Caspian fishing communities.

3.5.5. Sea surface temperature

Although sea surface temperature (SST) is often used within species distribution models (Robinson et al., 2017), a high degree of uncertainty in this coefficient during our analysis may be explained by our explicit parametrization of a spatio-temporal effect. During preliminary investigations, we found that a peak in the overall foraging rate during the summer months coincided with a peak in average temperatures. We also found that the coefficient for SST was much more positive and certain if we did not include a temporal or spatio-temporal component. We therefore suspect that variance that could be explained by a relationship between SST and ARS behaviour may be better explained by an overall peak in foraging activity during the summer months when individuals are accumulating resources before the breeding season (Dmitrieva et al., 2016). Another reason for the uncertainty of this relationship may also be because of the wide range of sea temperatures present within the Caspian Sea at all times of the year. During the winter, southern sections of the Caspian remain warm, and during the summer, some of the warmest areas are in the north where the water is shallowest. These relationships are likely to result in a correlation between SST and ARS behaviour, however, defining the ecological phenomena that may drive that correlation is complex. One hypothesis for a positive association between ARS and SST could be due to a well-defined correlation between temperature and several other environmental metrics which can directly influence environmental productivity (Chavez et al., 2011). However, a hypothesis for a negative association could be due to physiological constraints as a result of the thick insulating blubber layers of pinnipeds which may result in and extreme temperatures inducing thermal stress (Khamas et al., 2012). To explicitly investigate the thermal tolerance of Caspian seals, temperature-related data would have to account for changes in temperature at a variety of depths due to the amount of time these species can spend underwater where water is far cooler than at the surface.

3.6. Conclusions

Through a structured design utilising a spatial-temporal effect, independent individual temporal smoothers, fixed effects, and correlated random slopes, we investigated the average response of the Caspian seal population to three environmental covariates: distance from rivers, distance from the continental shelf, and sea surface temperature, alongside temporal deviations in the effects of distance from rivers, and distance from the continental shelf. This structure allows us to account for a wide variety of ecological mechanisms that are likely to drive patterns in foraging related area restricted search (ARS) behaviours most notably, temporal, and spatial-temporal mechanisms. We show that the relationship between environmental covariates and ARS behaviour can have significant temporal structure and reveal that habitats that are associated with foraging are not used consistently throughout a calendar year. Our results align well with previous research on Caspian seal migration and foraging behaviour which identified at least three foraging modes amongst individuals. It was previously identified that individuals can broadly cluster into one of three groups, (i) individuals that forage in shallow regions, (ii) individuals that forage in medium depth water, and (iii) individuals that make longer foraging trips toward deeper regions in the middle and south of the

Caspian (Dmitrieva et al., 2016). We expand upon these findings and discover that alongside individual variation, there are broader within community shifts towards using specific regions during specific periods of the year. We find that Caspian seals forage nearby to both river inflows and the 50m isobath at specific points in time, which may be associated with life cycle stages, migrations, and vertical depth changes of fish species that are likely to be an important part of Caspian seal diets. These insights provide key additions to the literature on Caspian seals foraging requirements, however, outstanding questions remain on how the use of these habitats may interact with climate change threats. For example, with a projected decline in the Caspian sea level we may expect the geographical position of river inlets to move to areas which are presently below the water level, or vanish entirely (Elguindi and Giorgi, 2007; Prange et al., 2020).

The final contribution of this paper was to use model-based spatial predictions alongside observed level data to develop spatially and temporally flexible marine protected area (MPA) plans that account for individual-level differences, random temporal and spatial processes, the impact of environmental covariates, as well as potential trade-offs between Caspian seal conservation and distribution with legal maritime industries. We found that there are regions in the Caspian that, if protected, would satisfy current global conservation targets, and protect Caspian seals when they are foraging and most at risk of vessel-based impacts. Two notable limitations of our protocol is that by only focusing on ARS behaviours, we may not appropriately identify regions during periods of the year when ARS behaviour may not be indicative of the most important regions to protect, and by only focusing on vessel density we may under account for specific types of human activities which may have the most harmful impacts. Future efforts to expand upon this protocol should seek to combine different sources of data, such as movement and aerial survey data, to prioritize the most vulnerable ecological phases of an animal's lifecycle and evaluate how those phases interact with different types of anthropogenic disturbance and evaluate how this protocol may translate to other ecological systems.

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4. Chapter four - Estimating quasi-extinction risk for the Caspian seal (Pusa caspica) with respect to climate change and direct anthropogenic threats

Harrison Tan, Linas Svolkinas, Chris Hassall, and Simon J. Goodman

4.1. Abstract

The Caspian seal (*Pusa caspica*) is proposed to face demographic impacts from at least three notable sources, very high bycatch mortality within illegal sturgeon fisheries, periodic loss of pup cohorts due to premature melting of breeding ice before lactation is completed, and mass mortalities due to disease outbreaks. However, the individual and combined effects of these threats in relation to population demography, and quasi-extinction risk for Caspian seals has not been evaluated. Here we use population projection models that account for dynamic changes in threats over time to explore the potential demography of the Caspian seal population over the next century. We evaluate how different threat scenarios influence the quasi-extinction risk of Caspian seals over the next 100 years and discuss the implications for prioritisation of conservation actions. The results of our analysis show that reducing the rate at which Caspian seals die within illegal fisheries must be a high priority for conserving this Endangered species and show that if bycatch rates bycatch rates do not decline quickly or within 40 years, the species will most likely become quasi-extinct within the next century. We provide evidence to suggest that, in most scenarios, bycatch threats far outweigh future risks associated with climate change. However, the increase in poor ice cover can have a significant impact upon the population viability in the future, especially if bycatch rates take more than 40 years to decline to negligible levels.

4.2. Introduction

Pinnipeds are a diverse clade of marine mammals composed of three monophyletic lineages: Phocidae (true seals), Otariidae (fur seals and sea lions), and Odobenidae (Walruses *Odobenus*). Compared to other mammals, pinnipeds have a high risk of population decline (Kovacs et al., 2012) and 2 out of 36 species have gone extinct within the last century (Rice, 1998). The Japanese sea lion (*Zalophus kaponicus*) and the Caribbean monk seal (*Monachus tropicals*) were heavily impacted by humans, and key threats that lead to their decline were over-hunting (Lee et al., 2022) and indirect impacts from the overfishing of their prey by humans (McClenachan and Cooper, 2008; Baisre, 2013). These anthropogenic threats continue to cause declines in extant pinnipeds, particularly those that are closely associated with fisheries (Kovacs et al., 2012). In addition, future climate change is increasingly recognised as a major threat, with ice-dependent species being vulnerable due to climate projections associated with a loss of sea ice for breeding (Stirling and Calvert, 1983; Kelly, 2001; Kovacs et al., 2012; Stenson and Hammill, 2014; Albouy et al., 2020).

4.2.1. Climate change

Pinnipeds are dependent on solid substrates as a birth and nursing ground, although various specializations have emerged over evolutionary time. For example, all otariids are born above land and phocids are generally born on either land, fast ice which is attached to land, or pack ice which floats on moves on the water surface (Riet-Sapriza, 2020). In general, the mobility of pack ice makes it more sensitive to climate conditions and the varying stability of breeding substrates may have influenced the evolution of varying lactation times. For example, the lactation period of otariids varies between 3.5-24 months (mean=11.17, SD=4.94). Whereas the lactation period of phocids can vary between 23-90 days in land breeders (mean=40.56, SD=21.32), 38.5-67.5 days in fast ice breeders (mean=48.17, SD=16.74), and 4-30 days in pack ice breeders (mean=19.11, SD=7.98) (Riet-Sapriza, 2020). The trade-off between shorter lactation periods and breeding in less stable environments may have arisen from historical disadvantages of breeding on land or fast-ice closer to land. For example, breeding upon land may increase vulnerability to terrestrial predators (Krylov, 1990; Harkonen et al., 2012). However, there is a research gap in understanding how specializing on land, fast ice, or pack ice may impact future demography and interact with emerging threats. Understanding how breeding behaviour interacts with emerging climate threats such as ice loss is important because future declines in ice cover are expected, and several normally ice-breeding species will be forced to breed on land. Grey seals in the Baltic sea (*Halichoerus grypus*) are one of few phocids that currently breeds on both land and ice. However, land breeders breed at higher densities and have higher rates of infection and also experience higher rates of predation from terrestrial predators, and as a result, the pre-weaning mortality rate of land born pups is higher and approximately 21.1% compared to 1.5% on ice (Jüssi et al., 2008). Similarly, grey seals breed exclusively on land in Scotland, and in highly dense colonies it's estimated that the mortality rate of their pups is over 14% (Baker, 1984; Twiss et al., 2003). In addition, in the Gulf of St Lawrence and off the coast of northeast Newfoundland, harp seals Harp seals (*Pagophilus groenlandicus*) preferentially breed within traditional breeding areas, which results in a higher overall pup mortality of 10% during poor ice years (Stenson and Hammill, 2014) compared to 1.1–1.4% when born on stable ice (Kovacs et al., 1985). In contrast, juvenile Bearded seals (*Erignathus barbatus*) show an apparent difference in habitat selection in poor ice years compared to stable ice years (Olnes et al., 2020). However, in general, we know little about how most ice breeding pinnipeds behave under varying ice conditions and how impacts associated with breeding under varying conditions impacts future population demography.

4.2.2. Bycatch

Another major threat that impacts most pinnipeds is the accidental mortality of animals in fishing operations, commonly referred to as bycatch (Kovacs et al., 2012). At least 66% of all pinniped species have been recorded as bycatch within gillnets since 1990 (Reeves et al., 2013), although there are major gaps in our understanding of pinniped bycatch rates. The accurate recording of bycatch data is essential as it can provide information to estimate demographic impacts, project future population sizes, estimate extinction risk, and inform policy decisions. However, there are a wide range of difficulties that are encountered when recording bycatch events. For example, records are often only available from a small fraction of the representative population, spatial and/or temporal biases can lead to biased and imprecise estimates (Martin and Crawford, 2015; Punt et al., 2021), and some bycaught animals can be released alive and die later from sublethal injuries they sustained when bycaught (Wilson et al., 2014). Recent work has highlighted how impactful bycatch related mortality may be, for example, in the Caspian Sea (Dmitrieva et al., 2013; Ermolin and Svolkinas, 2018; Svolkinas, 2021), however understanding how these rates relate to other threats remains an existing challenge.

4.2.3. Caspian seals

The Caspian seal (*Pusa caspica*) is an endangered ice-breeding pinniped that has experienced population declines of more than 90% since the start of the 20th century which exceeds 70% over the previous three generations. Alongside several other unresolved threats, these population declines were a key reason the species was listed as Endangered under the IUCN Red List in 2008 (Harkonen et al., 2012; Goodman and Dmitrieva, 2016). Caspian seals have a single panmictic population and are endemic to the Caspian Sea in Central Asia (Dmitrieva et al., 2016). Adult seals range throughout the whole Caspian Sea, although over 99% of adults breed on a winter icefield that forms in the shallow northern Caspian basin during December and melts in early to mid-March (Tamura-Wicks et al., 2015; Dmitrieva et al., 2016; Wilson et al., 2017). Caspian seal pups are nursed directly on the ice sheet with lactation lasting approximately 3-5 weeks (Wilson et al., 2017). At present, Caspian seal pups are born almost exclusively on ice, with some historical reports observing a low numbers of pup births on Orgurchinsky island in Turkmenistan, in total amounting to much less than 1% of total pup production (Krylov, 1990). In the future, widespread land breeding will be common if Caspian seals survive beyond an expected loss of suitable breeding ice (Tamura-Wicks et al., 2015), but the demographic impacts of land breeding relative to ice breeding in Caspian seals is unknown, and it is unknown to what extent a loss of breeding ice may impact Caspian seal behaviour.

4.2.3.1. Climate threats in the Caspian

The Caspian Sea sits at the southern limit for sea-ice formation in the northern hemisphere, and climate projections predict future declines in the extent, duration, and stability of the ice sheet (Shahgedanova et al., 2009; Koenigk et al., 2013; Tamura-Wicks et al., 2015). Caspian seals are threatened by these changes because they can directly impact Caspian seal demography. Young seal pups cannot survive in water for extend periods, and their white lanugo fur is non-insulating when wet so young pups that enter the water prematurely risk hypothermia if they do not dry out quickly (Frisch and Øritsland, 1968; Erdsack et al., 2013; Wilson et al., 2017). Like other pinnipeds (Stenson and Hammill, 2014), breeding on unstable ice is likely to increase pup mortality. However, in addition to losing sea ice due to climate heating, Caspian sea-ice forms over shallow regions (<5 meters) and recent projections predict increased evaporation to coincide with a sea level decline of at least 4.5, 5, 9, or 18 meters by 2100 (Elguindi and Giorgi, 2007; Renssen et al., 2007; Nandini-Weiss et al., 2020). These declines in sea level are likely to result in the land stranding of the shallow sea-ice forming areas (<5 meters deep) (Elguindi and Giorgi, 2007; Renssen et al., 2007; Nandini-Weiss et al., 2020) and will force a transition to terrestrial breeding, which is also known to increase pre-wean pup mortality in other normally ice-breeding pinnipeds (Kovacs et al., 1985; Jüssi et al., 2008; Stenson and Hammill, 2014), however, Caspian seals have an unknown ability to adapt to land breeding. An assumption that Caspian seals may breed upon land successfully may be made based upon changes in the historical Caspian Sea level. The Caspian sea-level has ranged widely between the global sea level and ~-50 meters below sea level over the last 100 thousand years (Mamedov, 1997; Dolukhanov et al., 2010). Assuming past sea level fluctuations are indicative of the conditions Caspian seals have evolved within, Caspian seals may have some adaptability to breeding upon land, if at some point in their history breeding upon ice was irregular because the current ice forming region of the Caspian is ~28 meters below sea level.

4.2.3.2. Bycatch threats in the Caspian

Recent work has used a structured interview-based approach to assess the extent of Caspian seal bycatch (Svolkinas, 2021). In the Caspian, 93% of bycatch events occur within illegal fisheries (Dmitrieva et al., 2013), approximately 96% of bycatch events are fatal, and current estimates suggest that between 14%-20% of the current population may die from bycatch within illegal fisheries each year (Svolkinas, 2021). This bycatch is mostly a result of an increase in illegal fishing activity since the early 1990s which has targeted sturgeon fish *Acipenseridae*. Due to the exceptionally high rates of bycatch, decreasing bycatch mortality is clearly a conservation priority. However, for conservation or policy actions to be effective it is vital that stakeholders address the socio-economic issues that contribute to high rates of illegal fishing. Case studies on poaching in Africa have shown that the numbers of Elephants (*Loxodonta africana*) killed by poaching activity is falling, however, the rates of poaching decline are slow (Hauenstein et al., 2019). In addition, positive correlations between poverty and poaching rates (Hauenstein et al., 2019) may suggest that the availability of gainful employment could be a key contributor to reducing poaching rates, and in cases where poaching has been reduced, there is clearly a timeline over which a transition from poaching activity occurs (Acharya et al., 2020). Therefore, although the demographic impact of bycatch on Caspian seals has not been tested within a population level framework, studies that investigate the impact of bycatch should consider how reducing bycatch may work in practice because a transition away from illegal fisheries is unlikely to be immediate.

4.2.3.3. Disease in the Caspian

Many harmful diseases have been associated with population declines in marine mammals, however, Morbilliviruses are of note due to their close association with several mass mortality events. Canine distemper virus (CDV) is a morbillivirus known to impact several pinnipeds. Several thousands of Caspian seals are likely to have died due to canine distemper virus (CDV) epidemics in the late 1990s and early 2000s, and over 10000 Caspian seal death strandings were reported during the spring of 2000, along the Kazakhstan coast (Kuiken et al., 2006) and between the Apsheron peninsula of Azerbaijan and the Turkmenistan coast (Kennedy et al., 2000). In addition, retrospective analysis of Caspian seal strandings between 1971-2008 may indicate a series of previously undocumented CDV outbreaks during the 1970s and 1980s (Wilson et al., 2014).

A few studies have investigated the prevalence of pathogens within Caspian seals. However, various practical limitations have restricted investigations to small samples, and samples restricted to stranded seals which may be potentially biased. During the 2000 CDV epidemic, 11 out of 18 (61 %) dead stranded Caspian seals tested positive for CDV (Kuiken et al., 2006) and between 2015 and 2017, 12 of 36 (33%) Caspian seals which were by-caught in fishing nets tested positive for CDV antibodies (Namroodi et al., 2018). Although the rates of infection reported in these studies are not likely to be representative of the overall population. Overestimation is likely as the probability of an animal being diseased is not independent of the probability of an animal being dead or by-caught. For example, Morbilliviruses that infect pinnipeds are associated with a variety of negative clinical symptoms which increase the risk of mortality, such as subcutaneous emphysema which in severe cases can impede normal swimming and diving, and lead to death (Duignan et al., 2014). However, in general, there is little clarity regarding the impact of morbilliviruses upon Caspian seals.

4.3. Methods

To address research gaps on how threats that impact Caspian seals may change over time, in this study, we developed a mechanistic stage structured population model to forecast the structure and size of the Caspian seal population over the next 100 years. This model was designed to specifically address sensitivity and temporal change in the demographic impacts of ice conditions and bycatch, which we implemented using a scenario-based approach. We go on to evaluate this model by comparing how our projections compare to the IUCN Critically endangered classification, which we use as a broad threshold to evaluate quasi-extinction.

4.3.1. Defining threat scenarios

To incorporate sensitivity and temporal change in the demographic impacts of ice conditions and bycatch we used a scenario-based approach. Each scenario was defined by their values for 4 scenario parameters that relate to change in the availability of ice habitat suitable for breeding and change in bycatch mortality. Two of these parameters are directly related to temporal trends: (i) *Ice trend,* which refers to change in the proportion of sea ice within breeding areas that remains stable for the duration of the weaning period and was defined to directly modulate the mortality rate of pups (hereafter referred to as *poor ice*), and (ii) *Bycatch trend,* which refers to change in the extra mortality caused by bycatch over time and was defined to modulate the mortality rate of each stage class independently. The other two parameters were: (i) *Land adaptation,* which refers to different rates at which Caspian seals may adapt to breeding on land, and (ii) *Bycatch magnitude*, which refers to different magnitudes of bycatch mortality. In total, we considered 5 different values for each of the 4 scenario parameters and considered every combination of values across each parameter which in total resulted in 625 different scenarios. In addition to these scenarios, we incorporated two other sources of stochasticity with relation to extremely poor ice years and disease outbreaks.

4.3.1.1. Breeding ice scenarios

Breeding ice scenarios were defined to directly modulate the mortality rate of pups. In total, 5 scenarios were considered to approximate the range of scenarios that may occur. The 5 values for the *Ice trend* parameter were: (i) *None*, which represents a hypothetical baseline where the threat of poor ice is absent and the proportion of unsuitable ice is held constant at 0%; (ii) *Fixed*, a scenario where further climate change is absent and the proportion of poor ice within breeding areas is constant and equal to the current proportion of poor ice within a normal year of approximately 5%; and three ice trend scenarios (iii to v) *Slow, Medium, and Fast*, which represent lower (80 years), median (40 years), and upper (20 years) estimates for the number of years until there is no suitable ice because temperatures are either too warm for any sea ice to form during the lactation period (Tamura-Wicks et al., 2015), or water levels decline and result in the drying of the sea-ice forming regions of the Caspian Sea (Prange et al., 2020). The temporal trends for the ice trend scenarios (iii to v) were included by introducing an additional increase in the mortality rates of seal pups as a function of changing ice conditions d (Equations 1, 2, 3, and 4); where Caspian seals are assumed to breed on land when there is no suitable ice and pups are subjected to an additional increase in their mortality rate of approximately 19.6%, which was based upon the difference between the reported pre-weaning mortality rates of 21.1% on land and 1.5% on ice in the closely related grey seal (Jüssi et al., 2008) (Equation 1). If the proportion of unstable ice does not equal 100%, extra mortality from breeding on unstable ice w_i is calculated by multiplying the proportion of pups that are likely to die due to breeding on unsuitable ice (75%) by the proportion of unsuitable ice within breeding areas during a given year p_i (Equation 2). Where p_i is calculated as a function of x_i held between the bounds of 0 and 1 (Equation 3), where x_i is the number of simulation years y_i multiplied by 1 minus the proportion of unsuitable ice within breeding areas during a typical year of approximately 5% divided by the number of years until there is no suitable breeding ice as defined by a given scenario t (80, 40, or 20 years).

$$d_i = f(w_i) = \begin{cases} 0.196, & \text{if } w_i \geq 0.75 \\ w_i, & \text{if } w_i < 0.75 \end{cases} \qquad \text{(Equation 1)}$$

$$w_i = 0.75 \times p_i \qquad \text{(Equation 2)}$$

$$p_i = f(x_i) = \begin{cases} 1, & \text{if } x_i \geq 1 \\ x_i, & \text{if } x_i < 1 \end{cases} \qquad \text{(Equation 3)}$$

$$x_i = y_i \left(\frac{1 - 0.05}{t} \right) \qquad \text{(Equation 4)}$$

$$i = \{1, 2, \ldots, 100\} \qquad \text{(Equation 5)}$$

$$t = \{80, 40, 20\} \qquad \text{(Equation 6)}$$

4.3.1.2. Adaptation to terrestrial breeding

The 5 scenarios for the *Land adaptation parameter* were: (i) *Just ice,* a scenario where Caspian seals remain as obligate ice-breeders and do not breed on land until there is no ice remaining in the Caspian; (ii) *Instant land,* a scenario where Caspian seals switch to land breeding when the proportion of poor ice within breeding areas is high enough to result in higher mortality than the extra mortality from land breeding of approximately 19.6% (Jüssi et al., 2008); and three land adaptation scenarios (iii to v) *Delay land 5, 15, and 25*, which represent different scenarios where Caspian seals can adapt to breeding on land when the proportion of poor ice is high enough to make land breeding more favourable, however, this adaptation takes 5, 15, or 25 years to occur. We chose 5, 15, and 25 years as broad generalizations about how long poor conditions must persist or how poor conditions must become before Caspian seals start breeding on land. The values 5, 15, and 25 were chosen as they represent 1, 3, and 5 times the age of adult maturity.

4.3.1.3. Bycatch mortality scenarios

The 5 scenarios for the *Bycatch* parameter were: (i) *None*, this represents a hypothetical baseline where mortality from bycatch is absent; (ii) *Fixed,* a scenario where the extra mortality due to bycatch remains at current levels; and three bycatch trend scenarios (iii to v) *Slow*, *Medium*, and *Fast*, which represent lower (80 years), medium (40 years), and upper (20 years) estimates for the number of years until bycatch mortality is reduced to a minimal acceptable level, for example, due to economic transitions, conservation action, or increased law enforcement. The bycatch trend scenarios were incorporated by decreasing the rate of mortality from bycatch over successive simulation years (Equations 7-13). Where B_{syt} is the extra mortality from bycatch for a specific stage s, during a specific simulation year y, and for a specific trend scenario t, and calculated as the sum of S_{rate} and R_{syt} (Equation 7). Where S_{rate} is a list containing the contemporary mortality rates due to bycatch for each stage and estimated as the conditional probability of mortality from bycatch given a specific stage class, which we estimated as approximately 28% of pups, 33% of juveniles, and 2.4% of adults (Svolkinas, 2021). To estimate this conditional probability, we first estimated the probability that a bycatch event was fatal from the proportion of fatal bycatch events in the Caspian, approximately 97% (Svolkinas, 2021). Second, we estimated the probability of a specific stage class given bycatch as the proportion of each stage class within Caspian bycatch data, of which approximately 24% are pups, 66% are juveniles, and 11% are adults (Svolkinas, 2021). Third, we estimated an overall probability of seals being bycaught as approximately 14%, from the number of bycatch events during a calendar year (Svolkinas, 2021), relative to the median contemporary population estimate of 136000 (Harkonen et al., 2008; Dmitrieva et al., 2015; Goodman and

Dmitrieva, 2016). Finally, we estimated the probability of a specific stage class as the emergent stage structure within a baseline projection with no threats (Figure 16). In addition, R_{syt} is a negative number that defines the reduction in mortality for a specific stage s during a specific simulation year y and a specific scenario t.

R_{syt} is calculated as a function of r_{syt} held between the bounds of the stage specific mortality rate due to bycatch during a specific simulation year and scenario, and a minimal acceptable bycatch rate PBR_{rate} which we approximated from the threshold of Potential Biological Removal (PBR) (Equation 9). PBR is part of the Marine Mammal Protection Act of the USA, which requires mitigation when human caused mortality or injuries exceed the PBR (Wade, 1998; Taylor et al., 2000). PBR is calculated as a product of the minimum population estimate N_{min} , which we defined as the lower contemporary population estimates of 104000 (Harkonen et al., 2008; Dmitrieva et al., 2015; Goodman and Dmitrieva, 2016), the intrinsic growth potential for the population R_{max} , which we defined as the mean growth rate of a baseline population with no threats (Figure 16 C), and a recovery parameter F_r , which we defined using the default recommended value of 0.5 (Taylor et al., 2000). Although our implementation adapted the PBR formulation to calculate it as a fraction of the minimum population estimate, which we used as a crude approximation of the minimal acceptable rate of bycatch in Caspian seals (Equation 9). r_{syt} was calculated by generating a linear function that describes the annual reduction from the contemporary stage specific mortality rates S_{rate} to the minimal acceptable bycatch rate PBR_{rate} and for each bycatch trend scenario Y_{trend}, such that the reduction to the minimal viable rate occurred over the course of 80 (*Slow*), 40 (*Medium*), or 20 (Fast) years (Equation 10).

$$B_{syt} = S_{rate} + R_{syt} \qquad \text{(Equation 7)}$$

$$R_{syt} = f(r_{syt}) = \begin{cases} r_{syt}, & \text{if } r_{syt} \geq PBR_{rate} - S_{rate} \\ PBR_{rate} - S_{rate}, & \text{if } r_{syt} < PBR_{rate} - S_{rate} \end{cases} \qquad \text{(Equation 8)}$$

$$PBR_{rate} = \frac{N_{min} \times \frac{R_{max}}{2} \times F_r}{N_{min}} \qquad \text{(Equation 9)}$$

$$r_{syt} = Y_{sim} \left(\frac{PBR_{rate} - S_{rate}}{Y_{trend}} \right) \qquad \text{(Equation 10)}$$

$$Y_{sim} = \{1, 2, \ldots, 100\} \qquad \text{(Equation 11)}$$

$$S_{rate} = \{0.29, 0.34, 0.025\} \qquad \text{(Equation 12)}$$

$$Y_{trend} = \{80, 40, 20\} \qquad \text{(Equation 13)}$$

In addition to accounting for variation in the rates at which bycatch could decline, we addressed uncertainty in the estimates of the stage specific extra mortality rates by adjusting the *Bycatch* *magnitude parameter* which was defined as the estimated rate and -10%, -20%, +10%, and +20% below or above the estimated rates.

4.3.1.4. Other random events

In addition to the four variables of interest, we incorporated two additional sources of stochasticity within each of the 625 model projection scenarios. To account for the sporadic impact of extremely poor ice years, we subjected population simulations to a 10% probability of an extremely poor ice year within any given year, which broadly corresponds with the frequency of early ice-melt events in the Caspian Sea when very little ice forms within traditional breeding areas. If an extremely poor ice year occurred during a simulation year, in the absence of data, we assumed the extra mortality rate of pups due to poor ice was equal to a rough approximation of the percentage of pups to die as a result of complete removal of ice during the core breeding period (75%). In addition to extreme ice events, to account for the impact of disease outbreaks, we included a 14.3% probability of a disease event occurring within any given year. This was chosen as it is an upper estimate for the periodicity of CDV viruses and was based upon suggestive evidence from a study that investigated the periodicity of CDV in Caspian seals (Wilson et al., 2014), and reportedly consistent with the epidemiology of morbilliviruses (Swinton et al., 1998; Mariner and Roeder, 2003; Wilson et al., 2014). If a disease event occurred during a simulation year, we increased the mortality rate of every stage class by 9.2%. We calculated the extra mortality rate due to a disease outbreak as the conditional probability of an individual dying given that they were infected by CDV. In the absence of stage specific mortality rates due to CDV infection, this conditional probability was calculated using an overall mortality rate of Caspian's seals of 5%, an overall probability of CDV infection given a seal is dead during a disease outbreak of 61% (Kuiken et al., 2006), and an overall proportion of the population that hosts CDV during a disease outbreak of 33% (Namroodi et al., 2018).

4.3.2. Model structure

To incorporate the ice trend, bycatch trend, and other random scenarios within a population projection we used the Leftkovich stage-structured population model structure (Lefkovitch, 1965). We included 4 stages within our projections. Pups were defined as individuals less than 1 year old, Juveniles were defined as individuals over 1 and less than 5 years old, Adults were the only reproductive stage and were defined as individuals over 5 and less than 23 years old, Senescence adults were defined as post-reproductive adults over 23 years old. Baseline mortality rates and fertility rates were adapted from previous research on Caspian seal demographics, where the annual baseline mortality rate of adults was set to 3% of individuals, 5% of juveniles, and 20% of pups, and the annual fertility rate was ~45% of the adult population (Harkonen et al., 2012). To clarify, whilst pup mortality has been estimated at a higher rate than this, we opted to select for a lower end mortality rate as our model explicitly parametrised several other causes of mortality that are likely to be encapsulated within previously reported rates of mortality.

We defined the starting population as 136,000 individuals, which is the median of contemporary estimates of between 104,000–168,000 animals (Harkonen et al., 2008; Dmitrieva et al., 2015; Goodman and Dmitrieva, 2016), and estimated the theoretical carrying capacity of the population as 272000 individuals which is twice the contemporary population estimates. We included annual density dependence, using an adaptation of the formulation presented in a study investigating population growth in grey seals (Svensson et al., 2011). This method involves multiplying the density independent pup survival rates (p_p) with the density-dependent factor ($1 - (N/K)$) from the logistic equation, whereby the density dependent survival rates of pups in a given year ($dp_{p(t)}$) can be estimated by from the equation: $dp_{p(t)} = p_{p(t)}(1-(N_{tot(t)}/K_e)^{\vartheta})$, where $N_{tot(t)}$ is equal to the total population size in a given year, K_e is equal to the theoretical carrying capacity of 272000 individuals, and theta θ regulates the shape of the curve, where theta = 1 refers to a linear decrease in growth as a function of density and theta = 4 refers to an initially weaker response to density. For our simulations we chose theta = 2 as an approximate midpoint between two extremes. Finally, to introduce an additional source of stochasticity, when incorporating probabilistic outcomes such as mortality rates, fertility rates, and other random events, we introduced additional random gaussian errors with a standard deviation of 5%.

To establish the stage structure at the start of our projections, before each individual model run, we ran a 100-year burn-in phase which began with a uniform distribution of individuals across each of the juvenile, adult, and senescent stages. During the burn-in phase the population was subjected to the full model specification minus the extra-mortality contributions relating to the 4 scenario parameters *Ice trend, Bycatch trend, Land adaptation, and Bycatch magnitude,* and the total population size was controlled and fixed at the starting population size of 136000. To clarify, this procedure resulted in the stage structure forming as a function of the baseline model structure, including density dependence, the baseline stage lengths, mortality rates, and fertility rates. After the burn in phase, projections were run for 100 years, and we included the extra-mortality rates associated with each of the 4 scenario parameters.

Each of the 625 scenarios that we evaluated were run for 1000 iterations and we assessed the quasi-extinction risk of each scenario as the proportion of iterations where the total population size fell below two thresholds. The first threshold was defined according to Criteria A from the IUCN Red List Critically Endangered status criteria which is assigned to species that have undergone a population decline of over 80% within 10 years or 3 generations, whichever is longer (IUCN, 2012). This threshold was defined as the proportion of model iterations that resulted in a total population size of less than 27,200 within 3 generations or 56 years, which corresponds to an 80% decline from contemporary population estimates of 136,000. Where the generation length of Caspian seals is approximately 18.8 years (Pacifici et al., 2014). Similarly, to evaluate population change over the full projection, a second threshold was defined as whether the population fell below 27,200 individuals after 100 years.

4.4. Results

Under the baseline scenario the population is not subjected to density dependence and the bycatch and ice scenarios are parametrised so there is no extra mortality from these impacts (Figure 16). The emergent stage structure of the population was 11.62% pups, 27.12 % juveniles, and 61.25% adults. The mean growth rate (λ) for the total population under the baseline scenario without density dependence was 8.14% (SD 16.74). These estimates for the growth rate of the population are broadly in line with empirical evidence from the literature. For example, the generation time for seals is typically ~10–15 years, and female fertility begins between the ages of 4–6 year, with one pup born annually. These biological constraints limit the long-term maximum population growth rate to 10–12% in fully healthy seal populations (Härkönen et al. 2002). Although, the annual growth of recovering grey seal populations in the northern Baltic Sea has typically ranged between 5-9% since 1990 (Harding et al. 2007; Kauhala et al. 2019). Recovering populations are not likely to be subjected to density dependent effects and the average growth rate for the total population in our baseline scenario was broadly in line with these field-based estimates (Figure 16).

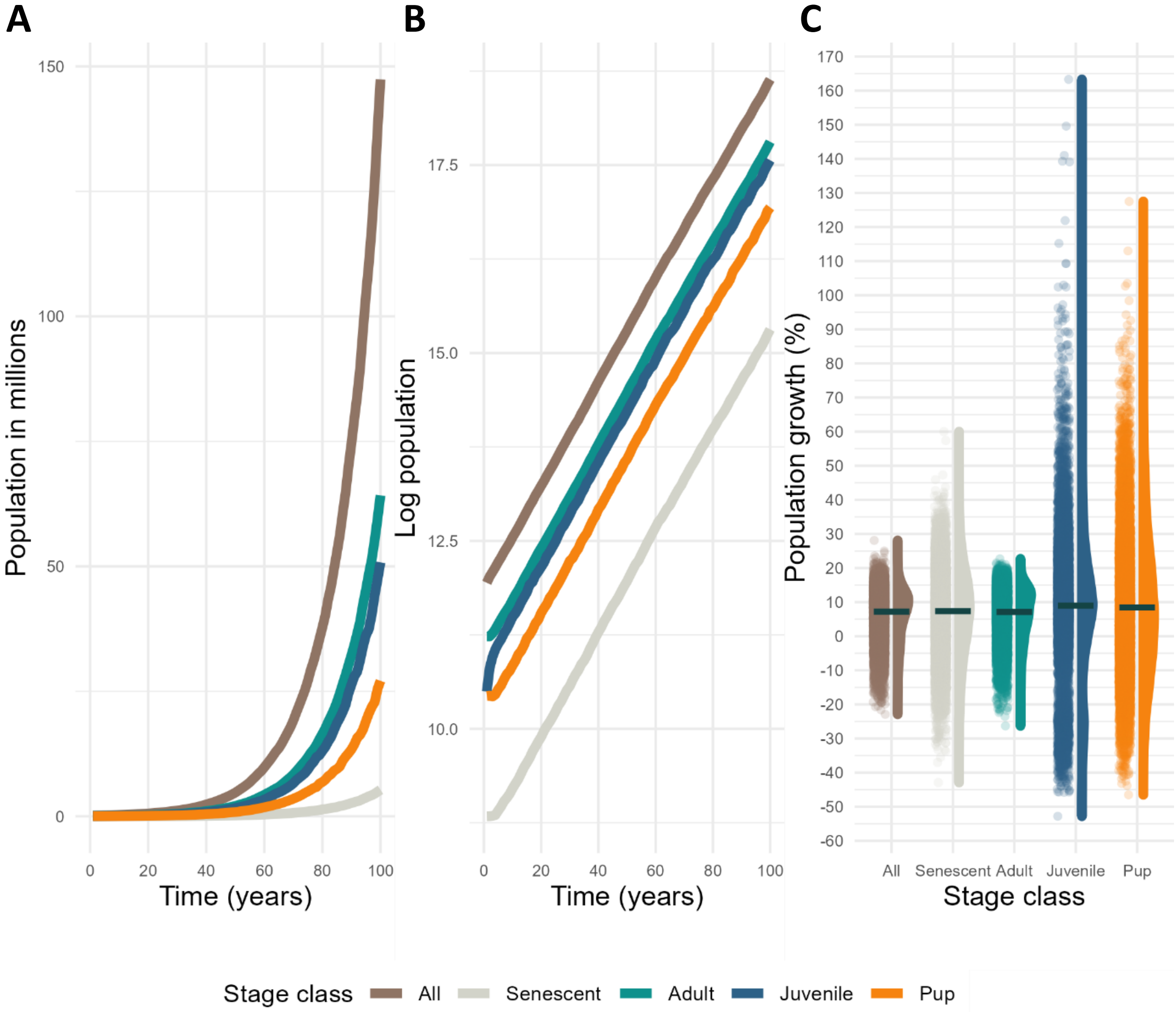

Figure 18. Population projections and growth rates for simulations under the baseline scenario without density dependence. Each stage class is highlighted separately, with the total population shown in dark grey, senescent in light grey, adults in green, juveniles in blue, and pups in orange. **Subplot A** shows time in years on the x-axis and the population size of each stage class on the y-axis. **Subplot B** shows time in years on the x-axis and the log population size of each stage class on the y-axis. **Subplot C** shows stage class on the x axis and the annual population growth of each stage class on the y-axis, with the distribution of annual values highlighted as a dot plot and half-violin plot, and the average population growth of each stage class is shown as a black horizontal bar.

Our first investigations into our models simulations were targeted at projections where the bycatch magnitude parameter was set to its mean value (Figure 17). When bycatch rates remain fixed at contemporary levels (Figure 17, *Bycatch decline trend* = “Fixed”), our projections suggests that mortality from bycatch is high enough that neither a potential adaptability of Caspian seals to breeding on land or the rate of ice sheet loss due to climate change has any substantial impact upon quasi-extinction risk. In all cases, predicted populations may become quasi-extinct within 3 generations. When bycatch rates decline slowly (Figure 17, *Bycatch decline trend* = “Slow”), reducing the rates of extra-mortality from bycatch to negligible levels over 80 years may be sufficient to prevent Caspian seal extinction. However, the predicted population may reach levels below the quasi-extinction threshold and any increase in poor ice cover increases the risk of quasi-extinction (Figure 17, *Bycatch decline trend* = “Slow”; *Ice decline trend* = “Slow”, or “Medium”, or “Fast”). The simulated populations are less likely to reach the quasi-extinction threshold when mortality due to bycatch reaches minimal levels within 40 to 80 years (Figure 17, *Bycatch decline trend* = “Medium” or “Fast”). Furthermore, if bycatch rates reduce slowly and Caspian seals are not capable of adapting to land breeding, then any future increase in poor ice cover may lead to a higher probability of quasi-extinction (Figure 17, *Bycatch decline trend* = “Slow”; *Land adaptation* = “Just ice”; *Ice decline trend* = “Slow”, or “Medium”, or “Fast”). However, if Caspian seals possess any capacity to adapt to land breeding, then the population may have the potential to recover slowly after facing severe declines (Figure 17, *Bycatch decline trend* = “Slow”; *Land adaptation* = “Delay land 25”, or “Delay land 15”, or “Delay land 5”, or “Instant Land”; *Ice decline trend* = “Slow”, or “Medium”, or “Fast). Additional graphs that summarize the average temporal history of projections where the bycatch magnitude parameters were set to -20% (Figure S1), -10% (Figure S2), +10% (Figure S3), and +20% (Figure S4) of the values estimated from the work by (Svolkinas, 2021) can be found in the supplementary materials.

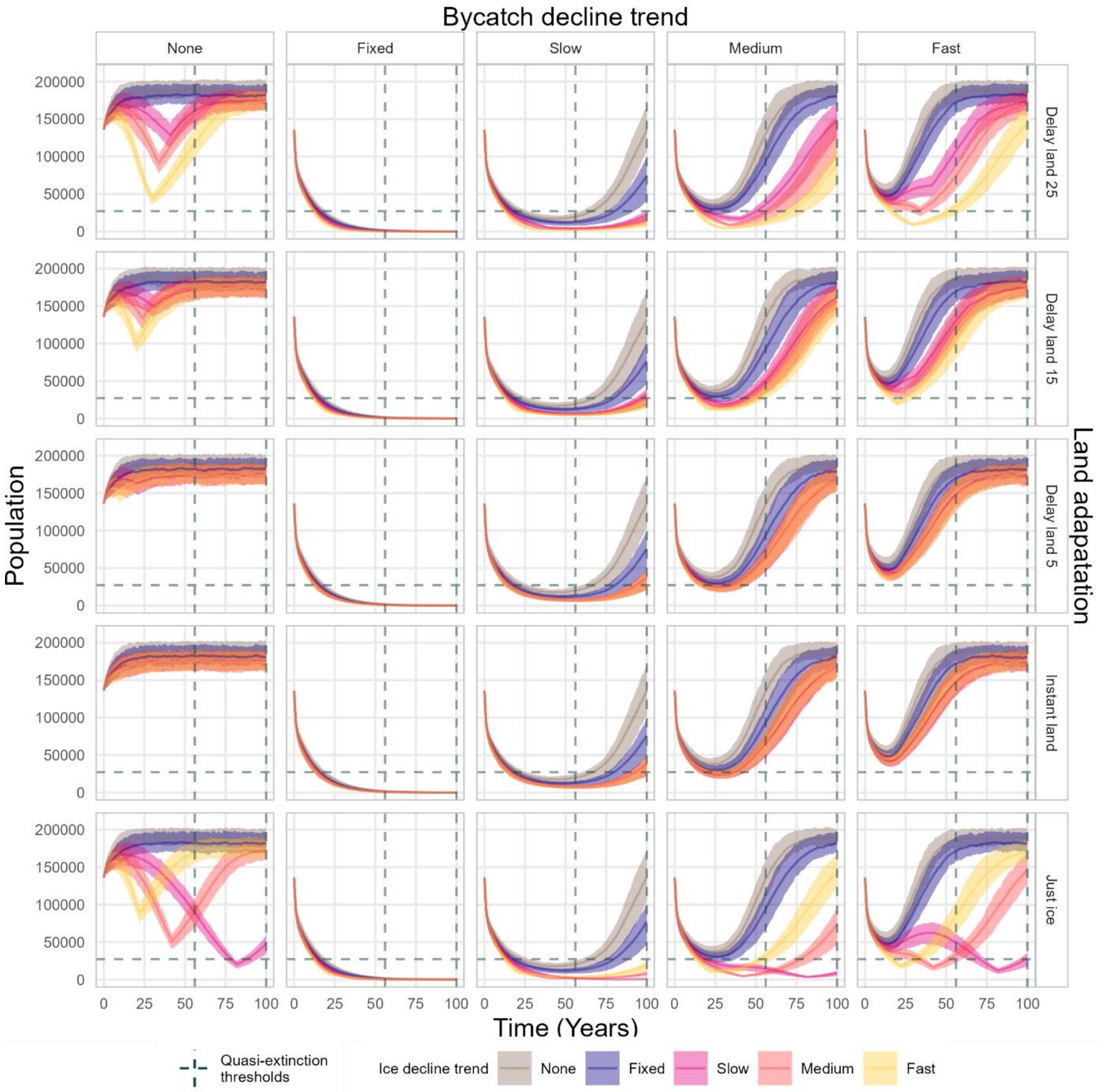

Figure 19. Temporal summaries for the total population of all scenarios where the bycatch magnitude parameters were set to the values estimates from (Svolkinas, 2021), and therefore, represents 1/5 of the 625 scenarios. The parameters shown to vary are (i) *Bycatch decline trend* on the secondary x-axis (top), (ii) *Land adaptation* on the secondary y-axis (right), and (iii) *Ice decline trend* within each graph and coloured according to their value, none (grey), fixed (blue), slow (purple), medium (pink), and fast (yellow). The mean population for each unique combination of the 4 modelled parameters is shown by mean lines along with error ribbons that indicate the sample interquartile. Thresholds relating to quasi-extinction are shown by a horizontal dashed line and two vertical dashed lines highlighting 3 generations and 100 years. The horizontal line represents an 80% decrease from the current population size of 136000. The first column "None" indicates that these summaries have no extra-mortality contribution due to bycatch. The second column "Fixed" indicates that these summaries have an extra-mortality contribution due to bycatch that is equal to contemporary levels. The third, fourth, and fifth columns "Slow" (80 years), "Medium" (40 years), and "Fast" (20 years) indicate the varying speeds that bycatch mortality may decreases from contemporary levels.

When evaluating quasi-extinction within 3 generations, and when bycatch rates are zero (Figure 18, *Bycatch decline trend* = “None”), we estimate a very low probability of quasi-extinction within 3 generations and across all other parameter combination. However, if bycatch rates remain fixed at contemporary levels (Figure 18, *Bycatch decline trend* = “Fixed”), we estimate a very high probability of quasi-extinction within 3 generations and across all other parameter combinations. If bycatch rates decline slowly, we project a high probability of quasi-extinction occurs within 3 generations, unless ice conditions do not decline from contemporary conditions and our bycatch estimates are overestimated by at least 20% (Figure 18, *Bycatch decline trend* = “Slow”, and *Ice decline trend* = “None” or “Fixed”). If ice conditions do decline, bycatch rates decline slowly, bycatch estimates are overestimated by at least 20%, and Caspian seals are able to adapt to land breeding within 5 years of a high proportion of poor ice resulting in land breeding having a lower overall mortality impact, the probability of quasi-extinction within 3 generations is lower, but still occurred within 70% of iterations (Figure 18, *Bycatch decline trend* = “Slow”, and *Ice decline trend* = “Slow”, “Medium”, or “Fast”, and *Bycatch magnitude* = “Mean -20%”, and *Land adaptation* = “Instant land” or “Delay land 5”). In general, if bycatch rates decline to minimal levels within 40 years, there is a much lower probability of quasi-extinction within 3 generations (Figure 18, *Bycatch decline trend* = “Medium” or “Fast”). However, if bycatch rates decline within 40 years but do not adapt to land breeding until ice completely disappears then there is a higher probability of extinction, which is more pronounced if ice conditions decline quickly, and more apparent if bycatch rates decline within 40 years compared to 20 years (Figure 18, *Bycatch decline trend* = “Medium” or “Fast”, *Ice decline trend* = “Slow”, “Medium”, or “Fast”, *Land adaptation* = “Just ice”, “Delay land 15”, or “Delay land 25”).

The probability of quasi-extinction within 100 years is broadly similar across parameter values to the quasi-extinction risk within 3 generations, with a few notable exceptions (Figure 19). Firstly, the results are more sensitive to uncertainty in our estimates of bycatch rates when bycatch rates decline within 80 years (Figure 19, *Bycatch decline trend* = “Slow”), but compared to the probability of quasi-extinction within 3 generations, less so when bycatch rates decline within 40 years (Figure 19, *Bycatch decline trend* = “Medium”). Secondly, there is notable interference arising between the *Ice decline trend* and *Land adaptation* parameters when ice is declining slowly, and seals are only breeding on ice (Figure 19, *Ice decline trend* = “Slow”; *Land adaptation* = “Just ice”). Compared to the probability of quasi-extinction risk within 3 generations, the quasi-extinction risk is higher for the aforementioned parameter combinations and is close to 100% when bycatch rates take more than 40 years to decline (Figure 19, *Bycatch decline* = “Fixed”, or “Slow”, or “Medium”). However, if bycatch rates decline quickly (Figure 19, *Bycatch decline* = “Fast”), the probability of quasi-extinction within 100 years is below 50% if our estimates for bycatch rates are overestimated, but above 50% if our estimates for bycatch rates are underestimated.

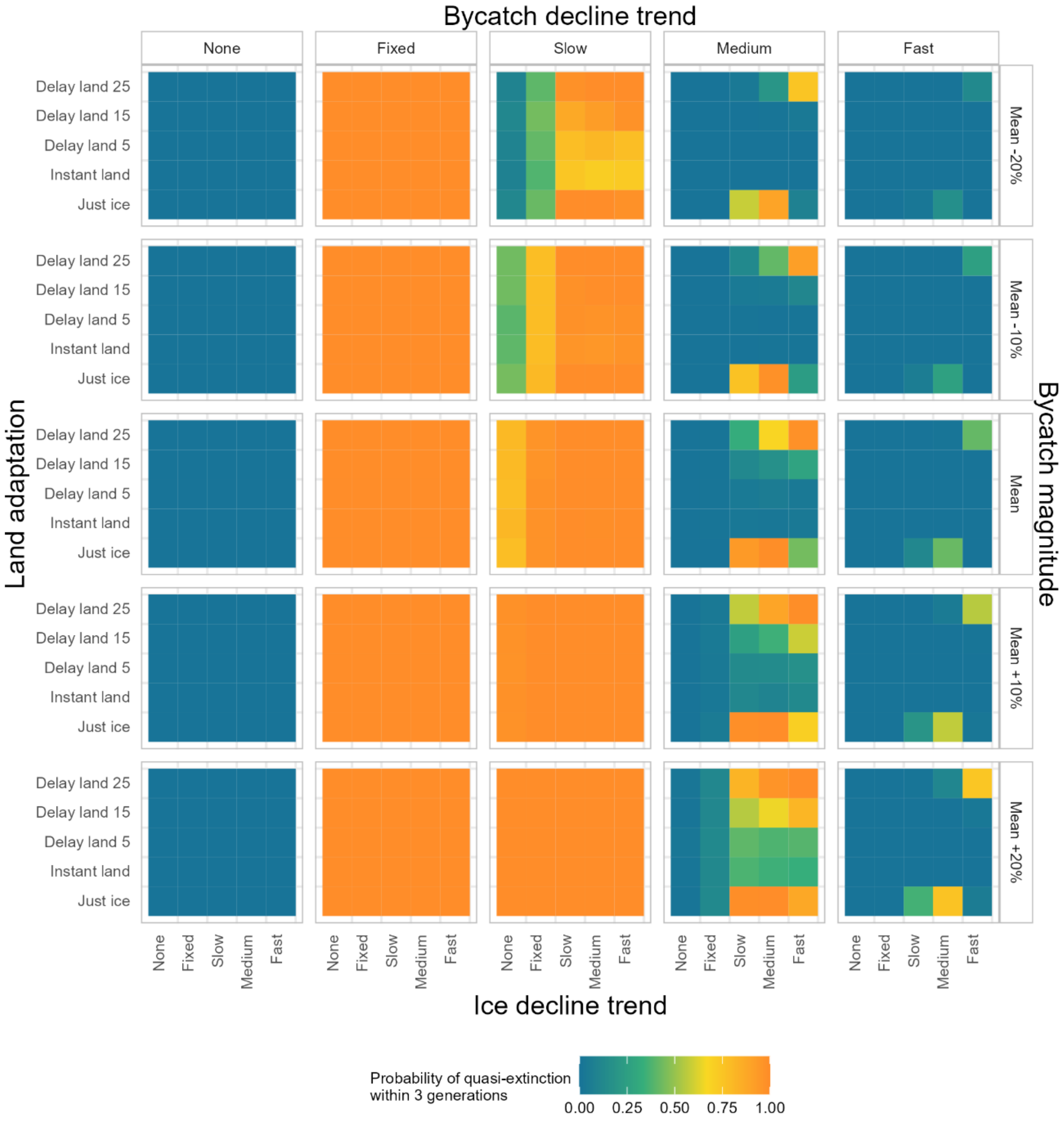

Figure 20. Quasi extinction risk heatmap which illustrates the average probability of quasi-extinction within 3 generations. Each cell represents a unique combination of values for the 4 variable parameter classes and is coloured according to the proportion of iterations where the simulated population fell below 27200 individuals within 3 generations, which would qualify the Caspian seal for Critically Endangered status if observed. The ice decline trend parameter is shown on the x-axis, the land adaptation parameter on the y axis, the bycatch magnitude parameter on the secondary y axis (right), and the bycatch decline trend parameter on the secondary x axis (top).

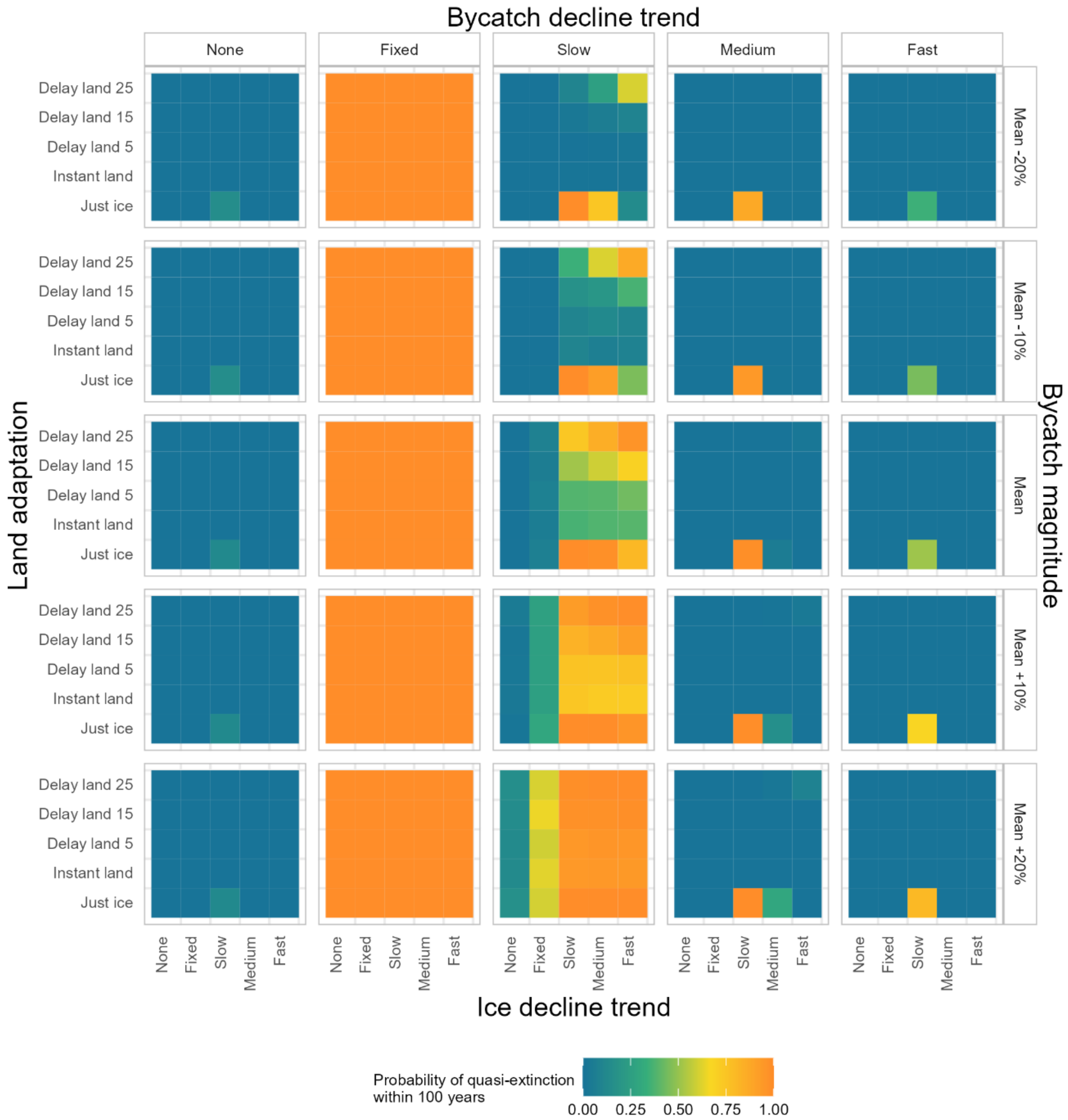

Figure 21. Quasi extinction risk heatmap which illustrates the average probability of quasi-extinction within 100 years. Each cell represents a unique combination of values for the 4 variable parameter classes and is coloured according to the proportion of iterations where the simulated population fell below 27200 individuals within 100 years. The ice decline trend parameter is shown on the x-axis, the land adaptation parameter on the y axis, the bycatch magnitude parameter on the secondary y axis (right), and the bycatch decline trend parameter on the secondary x axis (top).

To evaluate the effect of an individual parameter, we investigated the effect of a single parameter whilst averaging across all other parameter combinations upon the probability of quasi-extinction within 3 generations (Figure 20). During this process we observed several patterns. First, variation in the *Ice decline trend* (Figure 20, Ice decline trend), *Land adaptation* (Figure 20, Land adaptation), and the *Bycatch magnitude* parameters have little impact upon the average probability of quasi-extinction within 3 generations (Figure 20, Bycatch magnitude). Although, in general, the probability of quasi-extinction is higher if ice declines quickly, if seals are less able to adapt to land breeding, and if our estimates for bycatch mortality are underestimated. Second, when there is no impact of bycatch the probability of quasi-extinction within 3 generations is close to 0%, however, it is close to 100% if bycatch remains at contemporary levels, 88% if it decreases over 80 years, 24% if it decreases over 40 years, and 4% If it decreases over 20 years (Figure 20, Bycatch decline trend).

When assessing the effect of individual parameters on the average probability of quasi-extinction within 100 years (Figure 21), there were a few differences when compared with the 3-generation threshold. First, for the parameter *Ice decline trend* (Figure 21, Ice decline trend) the average probability of quasi-extinction within 100 years is highest when the parameter value is “Slow” which contrasts with the pattern observed with the 3-generation threshold (Figure 21, Ice decline trend). Next, if bycatch declines from contemporary levels, there is a much lower chance of quasi-extinction within 100 years (Figure 21, Bycatch decline trend) compared to 3 generations (Figure 21, Bycatch decline trend). Finally, overall, there is a lower probability of quasi-extinction across most parameters when compared to the 3-generation threshold.

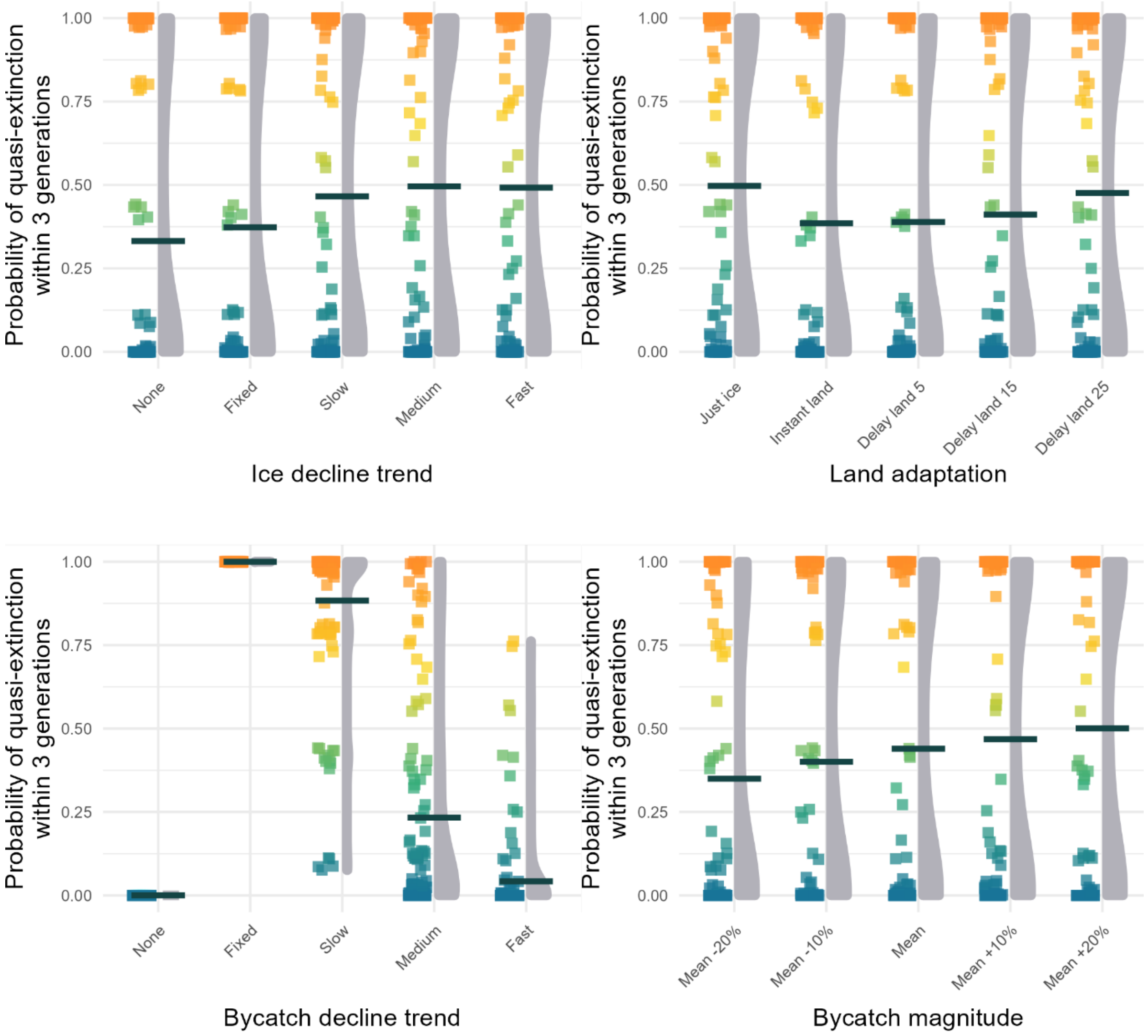

Figure 22. Four graphs which describe the quasi-extinction probability within 3 generations for each the 625 different parameter combinations we evaluated. Within each graph, the x-axis indicates a specific parameter value within one of the 4 parameter classes, (i) ice decline trend (top left), (ii) land adaptation (top right), (iii) bycatch decline trend (bottom left), and (iv) bycatch magnitude (bottom right). The data is illustrated using a square point dot plot with the square dot plot points coloured according to their value on the y-axis. The distribution of the data points across model runs with a specific value within a parameter class is shown alongside each square point dot plot and illustrated using a half-violin plot with equal scaling. The average probability of quasi-extinction across model runs with a specific value within a parameter class is shown as a horizontal black line.

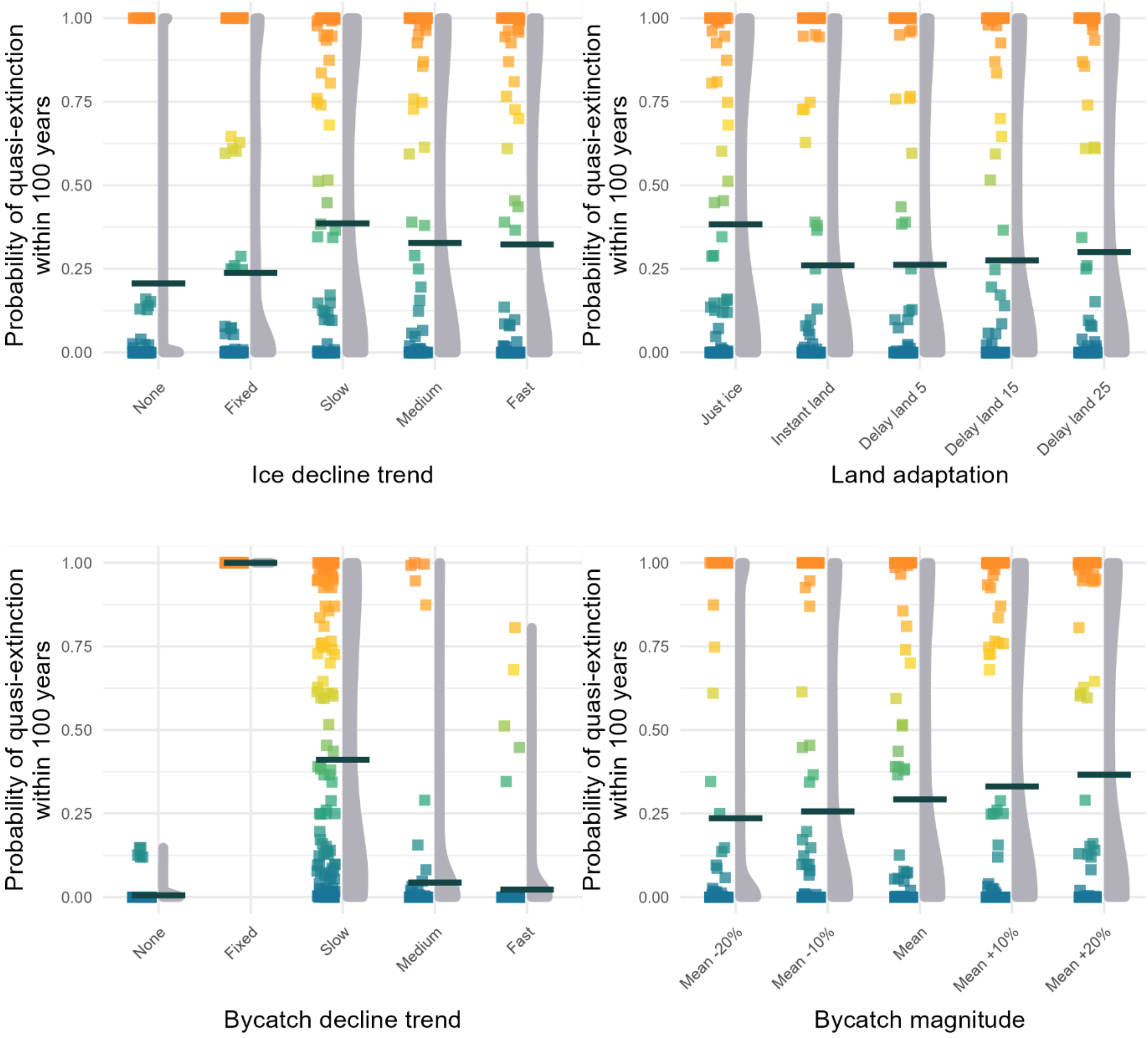

Figure 23. Four graphs which describe the quasi-extinction probability within 100 years for each the 625 different parameter combinations we evaluated. Within each graph, the x-axis indicates a specific parameter value within one of the 4 parameter classes, (i) ice decline trend (top left), (ii) land adaptation (top right), (iii) bycatch decline trend (bottom left), and (iv) bycatch magnitude (bottom right). The data is illustrated using a square point dot plot with the square dot plot points coloured according to their value on the y-axis. The distribution of the data points across model runs with a specific value within a parameter class is shown alongside each square point dot plot and illustrated using a half-violin plot with equal scaling. The average probability of quasi-extinction across model runs with a specific value within a parameter class is shown as a horizontal black line.

4.5. Discussion

During this analysis we developed a population projection model that was designed to evaluate the sensitivity of future Caspian seals to bycatch, and climate impacts that may lead to a loss of ice cover. The results of our simulations implied 4 key findings. First, current levels of bycatch are predicted to lead to quasi-extinction regardless of other factors. Second, predictions are sensitive to the initial estimates of contemporary bycatch rates. Third, dependent on other parameters, rates of land adaptation and ice cover loss can have inconsistent effects on quasi-extinction risk. Fourth, behavioural adaptation to land breeding may only play a minor role in mitigating the loss of sea ice and does not affect quasi-extinction to any great extent when considered across all parameter combinations.

During our analyses, we considered how threats that impact Caspian seal can change over time. This was is important for two reasons: firstly, this species is at risk of impacts from climate change (Kovacs et al., 2012; Albouy et al., 2020), which will become increasing impactful over the next 100 years (Shahgedanova et al., 2009; Koenigk et al., 2013; Tamura-Wicks et al., 2015) and secondly, the ability for Caspian seals to adapt to breeding on land is unknown and the behaviour of other ice-breeding phocids suggests that the adaptation rates are varied (Jüssi et al., 2008; Stenson and Hammill, 2014). If Caspian seals breed on ice when annual conditions are unstable (Stenson and Hammill, 2014) and the proportion of suitable ice decreases (Tamura-Wicks et al., 2015; Nandini-Weiss et al., 2020), then interference may arise between mortality associated with breeding on unstable ice and breeding on land. For example, when the rate of mortality from breeding on unstable ice is sufficiently high, increasing proportions of unstable ice could result in higher mortality rates than those seen when ice-breeding seals breed on land. This type of interference could emerge based upon current knowledge about how land and ice breeding impacts seals, whereby the pre wean mortality rate of grey seals pups born on land can be over 14% (Baker, 1984; Twiss et al., 2003), although approximately 75% of pups are thought die during exceptionally poor ice years when pups cannot finish nursing (Goodman 2022, personal communications). In addition, it is important to consider how bycatch threats evolve because bycatch in the Caspian mostly occurs within illegal fisheries and case studies on managing poaching have shown that reducing poaching rates is generally a slow process (Hauenstein et al., 2019; Acharya et al., 2020).

When bycatch rates remain at contemporary levels (Svolkinas, 2021) or higher, our projections suggest that its demographic impacts are high enough to result in quasi-extinction before 3 generations. These results are not surprising, given the well reported threat that human impacts can have upon pinniped populations. For example, these results align with analyses which have investigated the drivers of the extinction of the Japanese sea lion (*Zalophus kaponicus)* and the Caribbean monk seal (*Monachus tropicals*), where over-hunting by humans (Lee et al., 2022), and indirect impacts associated with intensive overfishing of their prey and overhunting by humans (McClenachan and Cooper, 2008; Baisre, 2013) are noted as a primary driver of their extinction. Furthermore, our results indicate that a reduction in bycatch should occur within 40 years. Although these actions must happen quickly, optimism for their prospects of future recover can be found in the literature. For example, following the cessation of extensive human caused mortality, formerly exploited pinnipeds have shown a surprisingly high capacity to recover from very low population numbers. Those populations that had previously approached near extinction due to bycatch and poaching, presumably to levels far below their carrying capacity, have since recovered at annual rates of between 5 and 9% (Harding et al. 2007; Kauhala et al. 2019).

One of our most concerning results is that we found the simulated populations are highly sensitive to our initial estimates of bycatch mortality. In our simulations we addressed sensitivity within the estimates presented in by simulating scenarios where the mean estimate was 10% and 20% greater or lower than the values reported (Svolkinas, 2021). These results showed that our projections are sensitive to the effect of bycatch, providing that bycatch declines within 80 years. However, what is concerning is that the bycatch rates used are reported as an estimate for the minimum bycatch of Caspian seals (Svolkinas, 2021). These results therefore highlight that the impact of bycatch mortality is likely to have upon contemporary Caspian seals and the urgency with which its impact must be addressed.

In this study, we specifically constructed our population projections to address change and interaction between demographic parameters over time. This design allowed us to potentially identify patterns that may emerge because of changes in different rates. One of these emergent patterns appears when comparing the quasi-extinction risk within 3 generations and within 100 years if bycatch rates decline slowly over 80 years. In these scenarios, our simulations suggest that Caspian seals may recover after facing near extinction, with declines well below the quasi-extinction before recovering towards the end of our projections. Interpreting these results as an expectation that the population is likely to recover is, however, highly tenuous. In reality, the exceptionally small population would be extremely vulnerable to extinction vortices and Allee effects, which can negatively impact pinnipeds with low population sizes (Nagel et al., 2021), but this could not be adequately represented in our simulations.

Another emergent pattern is the inconsistent effect of ice loss dependent upon our assumptions about land adaptability. For example, if Caspian seals do not possess an ability to adapt to land breeding and continue breeding upon ice until there is no ice within breeding areas, we can estimate a higher probability of quasi-extinction when ice cover declines slowly compared to when ice declines quickly. This is a counter-intuitive result because studies upon ice breeding seals typically associate ice loss to negative demographic impacts (Baker, 1984; Twiss et al., 2003; Jüssi et al., 2008; Stenson and Hammill, 2014), and a higher rate of ice loss suggests less ice overall. However, in our study, this pattern emerges because of the simulated Caspian seals spending a longer amount of time breeding within conditions where the extra mortality because of breeding upon land is lower than the extra mortality because of breeding upon poor ice. Although counter-intuitive, this result is consistent with other studies that have shown negative impacts of ice loss, because it emerges due to an increase in the time that Caspian seals experience negative impacts of ice loss relative to our estimates for negative impacts of breeding upon land from the literature (Jüssi et al., 2008). Although overall we did not find a highly prominent impact of behavioural adaptation to land breeding, and this did not impact quasi-extinction risk to any great extent, when considered across all parameter combinations.

Furthermore, the likelihood of Caspian seals to readily adapt to land breeding when it would result in higher pup survival is mostly unknown, however, a few arguments could be made in either case. Some white coated Caspian seal pups have been observed on land, although 99.9% of Caspian seal pups are born on the northern ice sheet (Wilson et al., 2017). However, the historical variation in Caspian climactic conditions may imply that the species has evolved within highly extreme conditions which may indicate a tolerance to variation in the environment. The Caspian Sea level changed dramatically during the Late Pleistocene with water levels ranging widely between the global sea level and ~-50 meters below sea level over the last 100 thousand years (Mamedov, 1997). In addition, the Caspian Sea level was ~-36 meters 10,000 years ago and since then has fluctuated anywhere between levels lower than contemporary levels of ~-28 meters and -20 meters (Dolukhanov et al., 2010). Assuming the sea level fluctuations within the last 100,000 years are indicative of the conditions Caspian seals have evolved within, it may be the case that the population has some adaptability to breeding upon land, if at some point in its history breeding upon ice was irregular. Although, in summary, based upon the known ecology of this species and the expected timelines for sea ice to decline or become inaccessible due to sea level rises, it seems unlikely that Caspian seals would be capable of adapting to land breeding faster than the rate of ice sheet decline, and to alleviate a series of generations which are likely to be born upon extremely poor ice conditions before the ice sheet disappears completely. These concerns may be presented with some optimism however, given the recent success in creating artificial breeding substrates within the ice-breeding Saimaa seal (*Pusa hispida saimensis*) (Kunnasranta et al., 2022), and a similar approach may be suitable in the Caspian if land adaptation rates are of some concern.

Overall, the results of our study suggest that reducing bycatch rates may be the most essential component of any Caspian seal conservation programme, and to avoid the quasi-extinction of this species, these reductions should occur within 40 years. However, when interpreting these results, it is important to clarify the simplified construction of our projections. Future developments of our projections could improve the sophistication of our trend estimations, particular for the decline in ice sheet conditions. For example, here we functionally describe the predicted increase in poor ice cover alongside the predicted decrease in the Caspian Sea level as a joint parameter which encompasses predictions for sea temperature to rise and the sea level to decline. This is a notable simplification of reality, and future projections of Caspian seal populations may wish to integrate climate forecast models to help ground truth the risk of this species to future climate change. Furthermore, whilst our parametrization of sporadic disease events may describe the impact of disease within larger population sizes, as the simulated population becomes smaller, the population is likely to be more at risk of allele effects and sporadic extinction vortex events that could push the Caspian seal into extinction due to the absence of a population buffer (Nagel et al., 2021). This risk is not comprehensively addressed within our simulation and may be improved through a direct modelling of disease transmission. Finally, regarding disease transmission, the increased immunity of individuals who survive previous infection may provide some buffered resistance within consecutive disease events (Kennedy et al., 2000; Wilson et al., 2014; Namroodi et al., 2018), however we could not capture this effect effectively within our model.

In this study, we constructed a mechanistic stage structed population model to generate population projections that simulate Caspian seal population numbers over the next 100 years. We demonstrate that reducing the rate at which Caspian seals die within illegal fisheries must be a high priority for conserving this Endangered species and show that if bycatch rates bycatch rates do not decline quickly or within 40 years, the species may reach the threshold to be classified as a Critically Endangered species according to Criterion A of the IUCN Red List (IUCN, 2012). We provide evidence to suggest that, in most scenarios, bycatch threats far outweigh future risks associated with climate change. However, the increase in poor ice cover can have a significant impact upon the population viability in the future, especially if bycatch rates take more than 40 years to decline to negligible levels.

4.6. References

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4.7. Supplementary materials

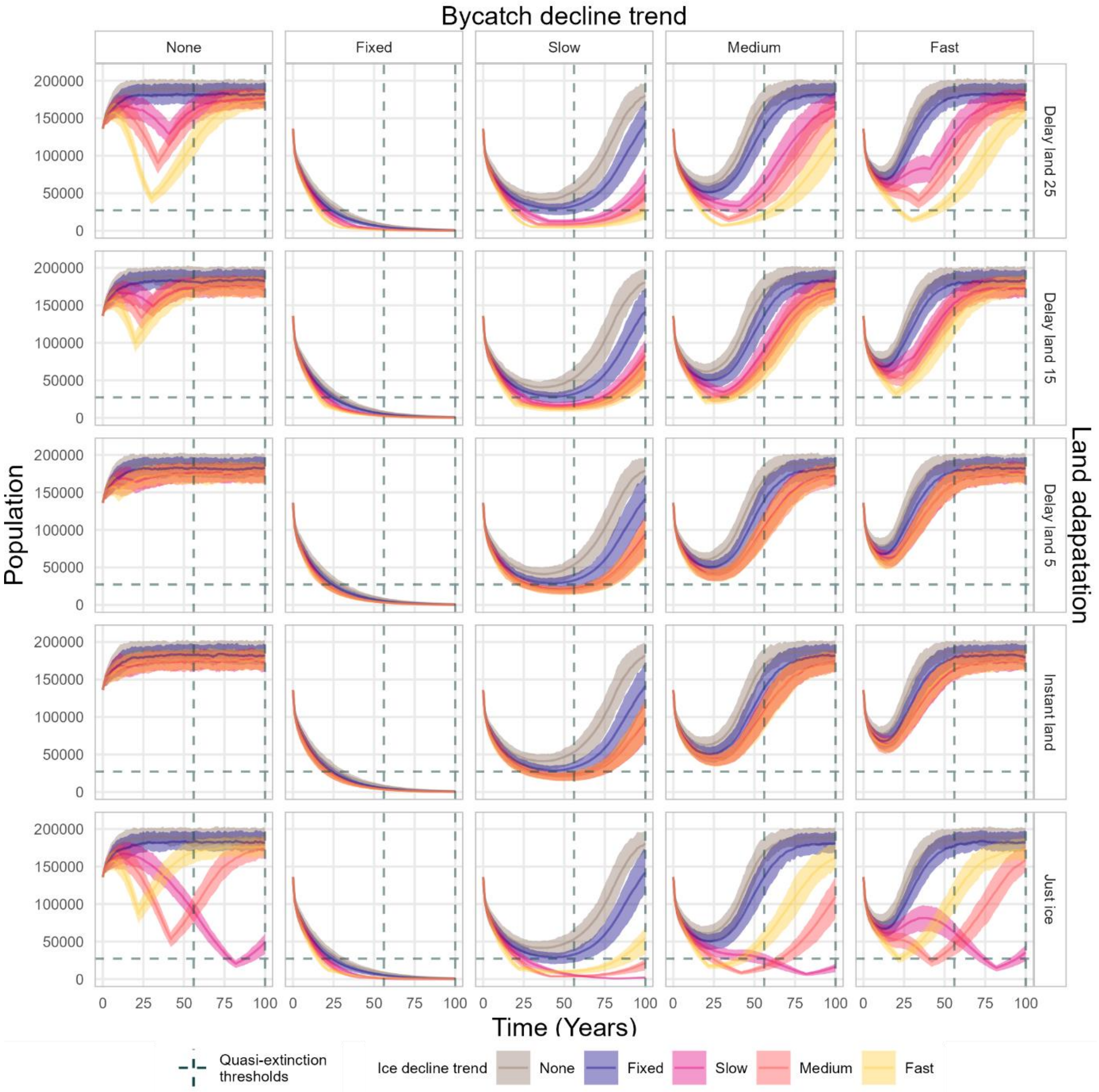

Figure S 1. Temporal summaries for the total population of all scenarios where the bycatch magnitude parameters were 20% lower than the values estimates from (Svolkinas, 2021), and therefore, represents 1/5 of the 625 scenarios. The parameters shown to vary are (i) *Bycatch decline trend* on the secondary x-axis (top), (ii) *Land adaptation* on the secondary y-axis (right), and (iii) *Ice decline trend* within each graph and coloured according to their value, none (grey), fixed (blue), slow (purple), medium (pink), and fast (yellow). The mean population for each unique combination of the 4 modelled parameters is shown by mean lines along with error ribbons that indicate the sample interquartile. Thresholds relating to quasi-extinction are shown by a horizontal dashed line and two vertical dashed lines highlighting 3 generations and 100 years. The horizontal line represents an 80% decrease from the current population size of 136000. The first column “None” indicates that these summaries have no extra-mortality contribution due to bycatch. The second column “Fixed” indicates that these summaries have an extra-mortality contribution due to bycatch that is equal to contemporary levels. The third, fourth, and fifth columns “Slow” (80 years), “Medium” (40 years), and “Fast” (20 years) indicate the varying speeds that bycatch mortality may decrease from contemporary levels.

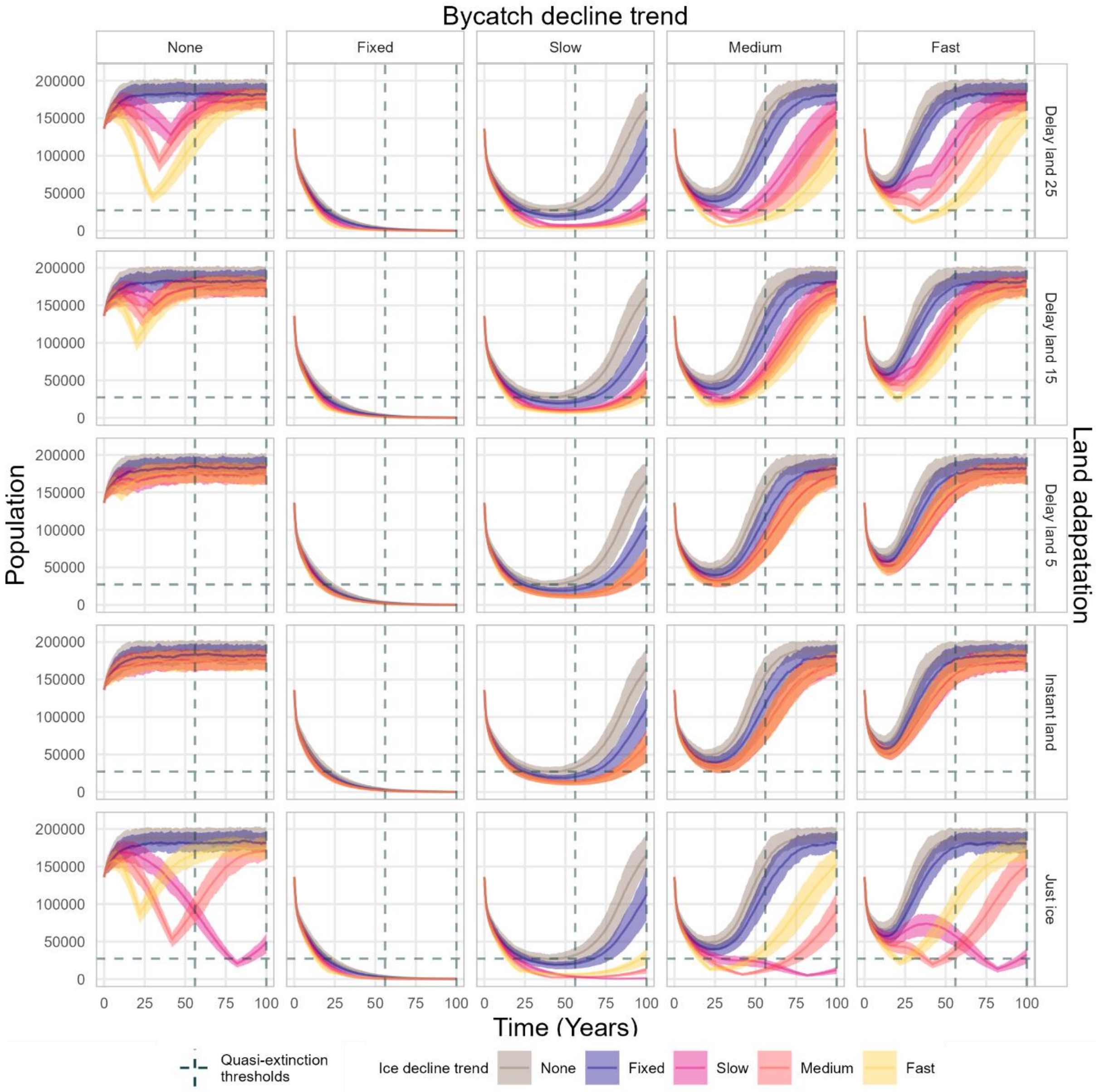

Figure S 2. Temporal summaries for the total population of all scenarios where the bycatch magnitude parameters were 10% lower than the values estimates from (Svolkinas, 2021), and therefore, represents 1/5 of the 625 scenarios. The parameters shown to vary are (i) *Bycatch decline trend* on the secondary x-axis (top), (ii) *Land adaptation* on the secondary y-axis (right), and (iii) *Ice decline trend* within each graph and coloured according to their value, none (grey), fixed (blue), slow (purple), medium (pink), and fast (yellow). The mean population for each unique combination of the 4 modelled parameters is shown by mean lines along with error ribbons that indicate the sample interquartile. Thresholds relating to quasi-extinction are shown by a horizontal dashed line and two vertical dashed lines highlighting 3 generations and 100 years. The horizontal line represents an 80% decrease from the current population size of 136000. The first column "None" indicates that these summaries have no extra-mortality contribution due to bycatch. The second column "Fixed" indicates that these summaries have an extra-mortality contribution due to bycatch that is equal to contemporary levels. The third, fourth, and fifth columns "Slow" (80 years), "Medium" (40 years), and "Fast" (20 years) indicate the varying speeds that bycatch mortality may decrease from contemporary levels.

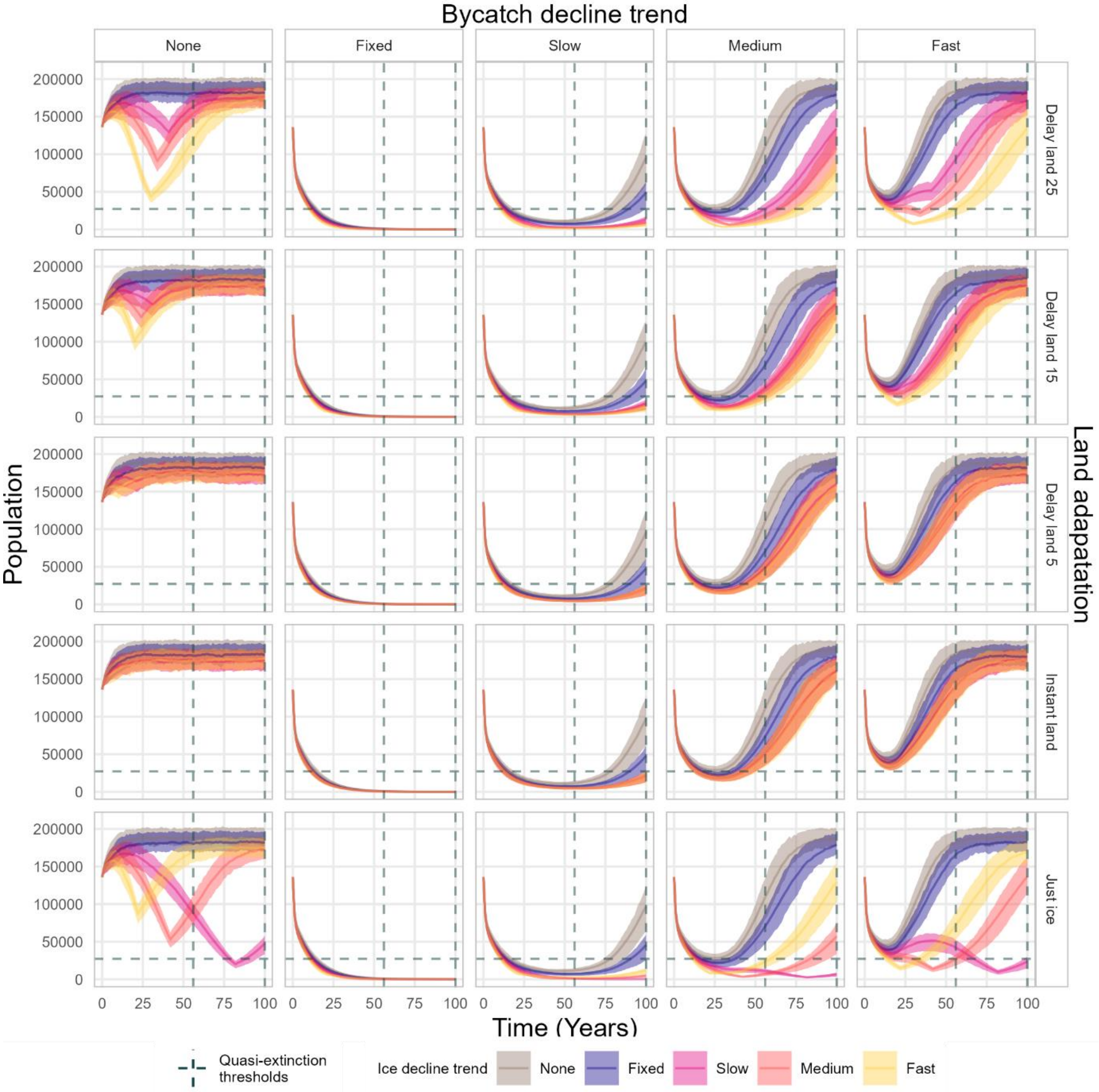

Figure S 3. Temporal summaries for the total population of all scenarios where the bycatch magnitude parameters were 10% higher than the values estimates from (Svolkinas, 2021), and therefore, represents 1/5 of the 625 scenarios. The parameters shown to vary are (i) *Bycatch decline trend* on the secondary x-axis (top), (ii) *Land adaptation* on the secondary y-axis (right), and (iii) *Ice decline trend* within each graph and coloured according to their value, none (grey), fixed (blue), slow (purple), medium (pink), and fast (yellow). The mean population for each unique combination of the 4 modelled parameters is shown by mean lines along with error ribbons that indicate the sample interquartile. Thresholds relating to quasi-extinction are shown by a horizontal dashed line and two vertical dashed lines highlighting 3 generations and 100 years. The horizontal line represents an 80% decrease from the current population size of 136000. The first column "None" indicates that these summaries have no extra-mortality contribution due to bycatch. The second column "Fixed" indicates that these summaries have an extra-mortality contribution due to bycatch that is equal to contemporary levels. The third, fourth, and fifth columns "Slow" (80 years), "Medium" (40 years), and "Fast" (20 years) indicate the varying speeds that bycatch mortality may decrease from contemporary levels.

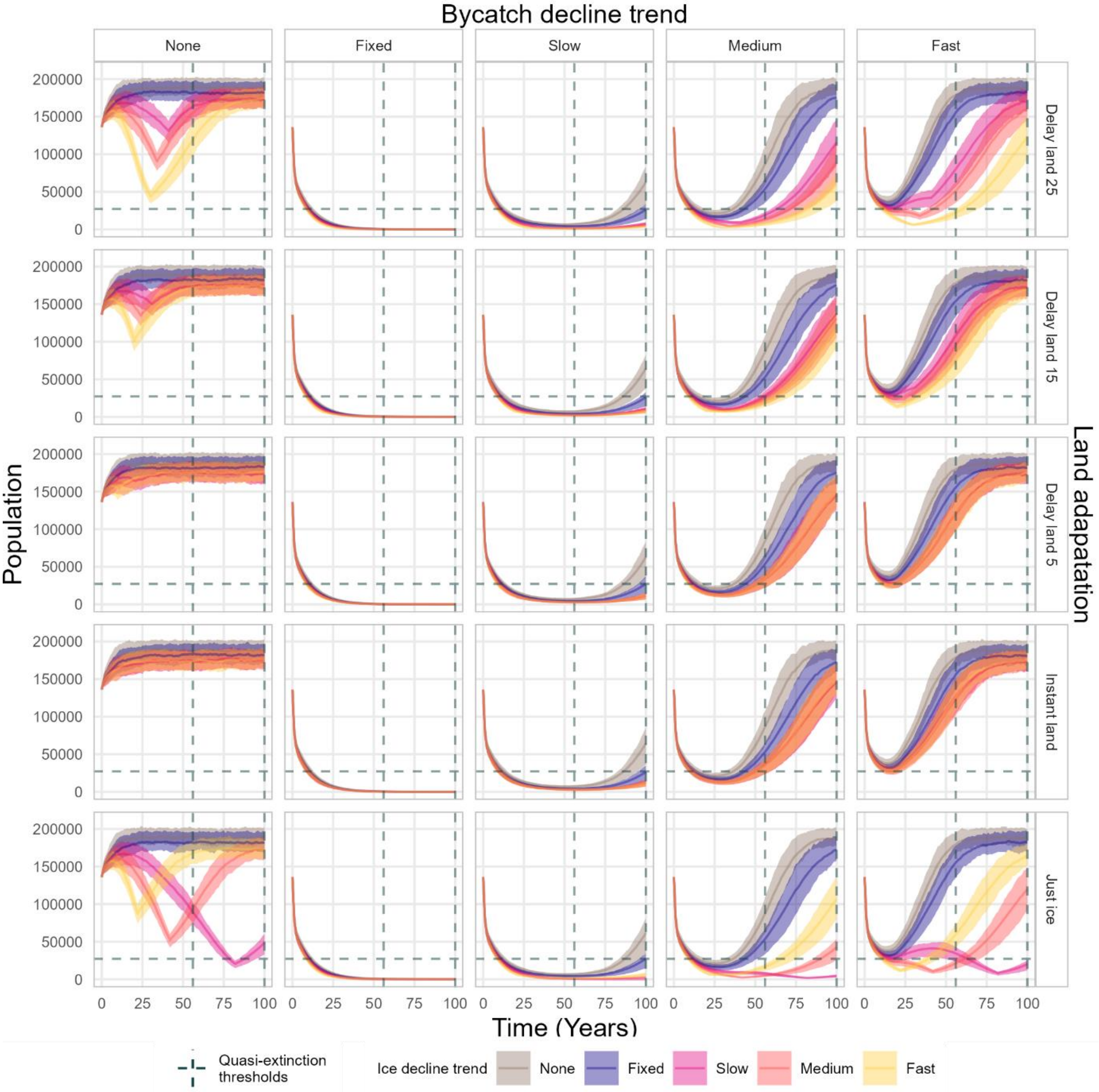

Figure S 4. Temporal summaries for the total population of all scenarios where the bycatch magnitude parameters were 20% higher than the values estimates from (Svolkinas, 2021), and therefore, represents 1/5 of the 625 scenarios. The parameters shown to vary are (i) *Bycatch decline trend* on the secondary x-axis (top), (ii) *Land adaptation* on the secondary y-axis (right), and (iii) *Ice decline trend* within each graph and coloured according to their value, none (grey), fixed (blue), slow (purple), medium (pink), and fast (yellow). The mean population for each unique combination of the 4 modelled parameters is shown by mean lines along with error ribbons that indicate the sample interquartile. Thresholds relating to quasi-extinction are shown by a horizontal dashed line and two vertical dashed lines highlighting 3 generations and 100 years. The horizontal line represents an 80% decrease from the current population size of 136000. The first column "None" indicates that these summaries have no extra-mortality contribution due to bycatch. The second column "Fixed" indicates that these summaries have an extra-mortality contribution due to bycatch that is equal to contemporary levels. The third, fourth, and fifth columns "Slow" (80 years), "Medium" (40 years), and "Fast" (20 years) indicate the varying speeds that bycatch mortality may decrease from contemporary levels.

5. Chapter five - General discussion

5.1. Research summary

Across this thesis I deployed several novel methods to increase our understanding of Caspian seal ecology as well as addressing several unresolved threats that may impact Caspian seals. In this final chapter, I provide a brief recap of the key findings and discussion points of each research chapter and contextualize these findings regarding the wider literature. I follow on from this recap by discussing the combined contributions of each chapter together and relate these points to existing research. Finally, I discuss progress in data-driven ecological research and make a series of suggestions for future research that may contribute to a continual evaluation of Caspian seal ecology and threat status.

5.1.1. Chapter Overview

Following the general introduction, chapter two evaluated the relationship between breeding density and the stability of contemporary ice conditions and assessed how this relationship related to the nursing time of Caspian seals. In this chapter, I used a visual image-tracking algorithm to develop a series of alternative metrics that describe ice stability over space and time. These metrics were then used as environmental covariates to explain the breeding densities of seal pups, and to generate continuous spatial maps that identify breeding hotspots. I found that pup densities were ~1.9 times higher on ice that had been continually frozen and stable since near the start of the breeding season, when compared to freshly frozen ice or ice that had remained frozen since before the breeding season. In addition, the use of visual image tracking allowed us to measure the length of the entire ice covered season. In the context of the wider literature, these results were concerning because we discovered that the total length of the ice season is only a few days longer than the 3-4 weeks that are required to complete weaning (Wilson et al., 2017). Furthermore, other studies have provided evidence that a lack of stable ice may increase the pre-wean mortality of ice-breeding seal pups (Kovacs et al., 1985; Jüssi et al., 2008; Stenson and Hammill, 2014) and climate projections predict a shortening of the ice available season and an overall decline in ice cover (Shahgedanova et al., 2009; Koenigk et al., 2013; Tamura-Wicks et al., 2015). To summarise, our findings indicate that most pups are located on ice that has been frozen for about 10-15 days prior to our survey, totalling approximately 15-20 days over the entire ice forming season. Given that Caspian seal pups nurse for about 3-4 weeks, 15-20 days is likely just meeting the minimal duration to prevent Caspian seals from premature water contact, especially very young pups without sufficient blubber (Frisch and Øritsland, 1968). Therefore, as climate change projections expect a future reduction in the length of the Caspian ice season (Tamura-Wicks et al., 2015), Caspian seals are likely to become increasingly vulnerable in the future.

In Chapter three, I studied Caspian seal movements using a state space model metric as a proxy for foraging activity (Jonsen et al., 2020). This metric was then integrated within a hierarchical framework which I used to account for individual variability, spatiotemporal correlations, and the relationship between foraging and habitat features. In this study, I showed that Caspian seals significantly vary their habitat use across different seasons and highlighted that foraging hotspots occur nearby river inlets and shelf-like gradients in the middle and south Caspian. In the context of the wider literature, these results support several other studies on the foraging behaviour of other pinnipeds, such as those that forage nearby river mouths during the out migrations of salmon (*Oncorhynchus tshawytscha*) (Allegue, 2017), and those that forage near shelf like bathymetric features (Tucker et al., 2009; Jonsen et al., 2019; Nowak et al., 2020). Furthermore, these results are brought further into context through an understanding of the distribution of Caspian seal prey items. For example, river inlets and bathymetric features are associated with a higher occurrence of migratory fish that Caspian seals eat, and the transient migrations of these fish would support a seasonally flexible foraging strategy (Pochtoeva-Zakharova, 1999; Mamedov, 2006; Goodman et al., 2007; Golpour et al., 2013; British Petroleum, 2015).

Within the fourth and final research chapter of my thesis, I evaluated the sensitivity of future Caspian seals to future threats. This chapter took a different modelling approach, where I developed a stage-structured mechanistic population projection model to evaluate the effects of bycatch and sea ice decline on population demographics. Different scenarios evaluated the potential demographic impact of a range of sea ice loss predictions in the Caspian (Shahgedanova et al., 2009; Koenigk et al., 2013; Tamura-Wicks et al., 2015) as well as varying rates that bycatch may reduce from contemporary levels (Dmitrieva et al., 2013; Svolkinas, 2021). Although there are no explicit plans for a widespread reduction in bycatch rates, I chose to evaluate a future decline in bycatch because evidence from the literatures suggests that contemporary rates are highly likely to result in the extinction of Caspian seals and an important target for conservation action (Dmitrieva et al., 2013; Ermolin and Svolkinas, 2018; Svolkinas, 2021). During these simulations, I showed that climate change threats are less likely to cause quasi-extinction on their own and that bycatch rates have the largest impact on the quasi-extinction risk of Caspian seals. When bycatch rates remain at contemporary levels or higher (Svolkinas, 2021), our projections suggest that its demographic impacts are high enough to result in quasi-extinction before 3 generations. These results align with analyses that have investigated the drivers of the extinction of the Japanese sea lion (*Zalophus kaponicus*) and the Caribbean monk seal (*Monachus tropicals*), where over-hunting by humans and indirect impacts associated with an intensive overfishing of their prey are believed to be the primary drivers of their extinction (McClenachan and Cooper, 2008; Baisre, 2013; Lee et al., 2022).

5.1.2. Combined contributions

Each of the research chapters within this thesis are presented as distinct pieces of research that address specific gaps in our knowledge about Caspian seals ecology. Together, these chapters contribute unique insights that each address several potential but unresolved threats that may impact Caspian seals. The threats that they address are notable because they address knowledge gaps that form a notable component of the latest IUCN threat evaluation for Caspian seals (Goodman and Dmitrieva, 2016). In chapter two, I address an important gap in our understanding of Caspian seal breeding habitats. During this chapter I found that the future shortening of the ice-forming season due to climate change may impact Caspian seal pups whilst nursing within a few decades. In chapter three, I addressed a research gap in our understanding of where and when adult seals forage within specific habitats across the Caspian Sea. During this chapter I found that seals forage in proximity to different habitats during different seasons and that these differences may be related to the seasonal availability of migratory fish species. During my final research chapter, I evaluated how future change in climate and anthropogenic threats may influence the quasi-extinction risk of Caspian seals. During this chapter I found that current levels of bycatch are likely to lead to quasi-extinction and outweigh the risks associated with climate threats. When viewed together, the key contributions of each chapter combine to address outstanding knowledge gaps that were notable in the latest threat evaluation of Caspian seals (Goodman and Dmitrieva, 2016). Most notably, the potential impact of contemporary variability in climate conditions, if foraging and non-breeding behaviours interact or are associated with environmental factors across the Caspian Sea, and how bycatch related mortality rates interact and compare with other sources of mortality in Caspian seals (Dmitrieva et al., 2015; Goodman and Dmitrieva, 2016; Dmitrieva et al., 2016; Wilson et al., 2017; Svolkinas, 2021).

The findings of this thesis are important because Caspian seals are a highly vulnerable species, and we must better understand their sensitivity to future threats to improve conservation efforts. Although, there are a few conflicting ideas presented across each research chapter. For example, during chapter two we presented results that Caspian seals are very close to being threatened by ice loss and that the predicted decline in ice cover could be expected to impact young pups in the near future (Tamura-Wicks et al., 2015; Wilson et al., 2017). However, during chapter four we provided evidence to suggest that, in most scenarios, bycatch threats far outweigh future risks associated with climate change, such as a decline in ice cover and a shortening of the ice forming period (Shahgedanova et al., 2009; Koenigk et al., 2013; Tamura-Wicks et al., 2015). One potential explanation for these differences is that due to the extreme nature of bycatch in the Caspian, where 14-20% of the population may die from bycatch annually (Dmitrieva et al., 2013; Svolkinas, 2021). These rates have an exceptionally high impact on our projections of Caspian seal demography, which is evident by our results that when bycatch is absent, the population recovers over the next 100 years. Furthermore, in scenarios with lower bycatch, the impact of climate change and the distinction between the impact of different rates of change in breeding ice became much clearer.

5.1.3. Accounting for space and time

In addition to the combined ecological contributions that this thesis makes, during this thesis I used specific attributes from a selection of novel methods to address specific research gaps in our understanding of Caspian seal ecology. Together, these chapters contribute to highlighting the benefits of ecologists continuing to adopt the novel attributes of the latest statistical and quantitative methods. During chapters two and three I analysed Caspian seal pup distributions and adult foraging conditions. These chapters investigated how pup distributions and foraging activity relate to environmental covariates over space and time. This research involved using novel methods to account for random spatial and temporal phenomena, such as clustering and autocorrelation. This is especially important when analysing data from Caspian seals because spatial and temporal datasets from this species are highly clustered and autocorrelated. In the context of the wider literature, there may be several reasons for clustering and autocorrelation in both datasets. Some of these patterns may be explained by observable environmental covariates, however, others are more difficult to measure. The minimum distance between nursing Caspian seals is about 2 meters, which is less than the 5-10 meters seen in grey (*Halichoerus grypus*) and harp (*Pagophilus groenlandicus*) seals (Lydersen and Kovacs, 1999) and the 0.25-0.5 km seen in spotted seals (*Phoca largha*) (Rugh et al., 1997). Caspian seals also appear to have a higher tolerance to neighbouring mothers compared to grey seals (Boness et al. 1982), with Caspian seal mothers often sharing access holes in the ice sheet. Furthermore, previous research has implied the aggregation of mothers in breeding groups may be due to an increased from predators, or a preference for breeding near suitable ice structures. However, in general, this behaviour does not have a conclusive explanation. In this example, it is difficult to parameterize this behaviour using environmental covariates alone because the density of pups may be conditional on quantities that are difficult to measure, such as the timing and proximity of haul out in nearby mothers if mothers prefer nursing in proximity. In addition, if the approximately 2 meter proximity of nursing mothers is indicative of a preference for small scale ice features (Wilson et al., 2017), the distribution of specific ice features in the Caspian may be far lower than the current resolution of sea ice datasets in the Caspian (Heygster et al., 2009). To summarise, some of the variation in the dependent variables analysed during chapters one and two may be explained by environmental covariates. However, a wide range of other phenomena can also impact the distribution an animal. If these phenomena are not accounted for, our analyses are potentially sensitive to dependence-breaking phenomena such as spatial or temporal autocorrelation (Dormann et al., 2007). In addition, a highly relevant impact can occur in the context of identifying distribution hotspots, because unexplained spatial variability can reduce the fit of a model and result in poor predictive performance (Dormann et al., 2007).

5.1.4. Species distribution modelling

To map the distribution of a species over space, several different methods can be deployed that account for spatial processes. Some common methods that are applied in ecological research include the Besag York Mollié (BYM) model (Besag et al., 1991; Gange et al., 2018), and the stochastic partial differential equation (SPDE) model (Lindgren et al., 2022). SPDEs have been used during the analysis grey seal distribution (Sadykova et al., 2017) and are well integrated within the INLA modelling framework which provides a fast and flexible Bayesian modelling framework (Lindgren et al., 2015). SPDE methods provide researchers with a flexible approach to implement a range of continuous ‘random’ effects, including temporal, spatial, and spatio-temporal effects (Lindgren et al., 2022). SPDEs can be applied within a hierarchical model to parametrize spatial dependence structures by generalising Matérn covariance models (Lindgren et al., 2022). This is useful in the context of SDM research because it allows researchers to directly parametrize spatial processes. By parametrizing spatial processes, we can account for dependence breaking phenomena such as spatial autocorrelation, in addition to using parameters estimated during the model fit such as the range of the spatial correlation, alongside other covariates, to generate continuous spatial maps.

During chapters one and two, I used INLA-SPDE techniques to generate continuous maps for the distribution of seal pups and adult foraging intensity (Lindgren et al., 2015; Bachl et al., 2019; Krainski et al., 2020). During chapter one, I used a novel SDM method that can address a key issue when analysing aerial survey data. One recent innovation in community ecology is the use of joint models, including joint species distribution models (JSDM). JSDMs are multivariate models that analyse multiple species occurrences and estimate separate species level effects as well as effects that are estimated from more than one species (Martino and Rue, 2010; Lindgren et al., 2015; Sadykova et al., 2017; Tikhonov et al., 2020; Pichler and Hartig, 2021). Similar methods can be adopted for datasets that contain more than one type of data, such as aerial survey datasets. Aerial survey data is described by a spatial reference alongside a count variable which describes the number of individuals at each reference. In this example, two data likelihoods could be specified, a point process likelihood for the location of an observation and a Poisson likelihood for the number of individuals at a location. This structure forms a more robust statistical framework because the number of individuals at a location is modelled as a function of the point process likelihood, therefore, avoiding the need to include pseudo absences when fitting the model (Warton and Shepherd, 2010). These methods can be described as a marked point process model, which has been used to estimate the distribution of killer whales (Watson et al., 2019), however, they are not commonly used within pinniped research. In chapter one I implemented these methods to create a joint-likelihood model (Jaffa and Jaffa, 2019) that accounts for differences between the density of breeding sites and the number of seal pups observed at each location. I then used this model to predict the distribution of breeding sites and Caspian seal pups.

During chapter two, I used SPDE methods within a generalized hierarchical model that analysed seasonal variation in where the foraging activity occurred. Predictions from this analysis when then used to identity hotspots of foraging activity. These predictions where then fed into a prioritization algorithm to see if there was space to implement a protection scheme that covered an area that could represent the Aichi target of protecting 10% of marine habitats (CBD 2010) and more recent targets of 30% protection of marine habitats (Baillie and Zhang 2018; Dinerstein et al. 2019). From this research, I found that there existed sufficient space for high foraging use that could meet these targets with a low impact on vessel-based anthropogenic industries. This chapter demonstrated how understanding how and when animals use different areas could feed into policy decisions that may protect species. For example, the design of marine protected areas (MPAs) can be informed by the activity and distribution of a species. MPAs can reduce threats to marine life by limiting human activities within important habitats (Hoyt 2018) and are increasingly used within conservation actions globally (Boonzaier and Pauly 2016). However, although there is currently a low capacity to enforce protection in the Caspian, developing protocols that can inform the viability of protected areas is useful so we can begin to evaluate the feasibility of protecting this endangered species.

5.1.5. Nonlinear responses

Another technical attribute that I harnessed across chapters one and two involved parameterizing non-linear relationships between ecological responses and environmental covariates. My first chapter involved evaluating the relationship between breeding density and the stability of contemporary ice conditions and assessing how this relationship related to the nursing time of Caspian seals. Overall, higher ice stability is linked to higher pup survival in ice-breeding pinnipeds (Stenson and Hammill, 2014). However, in the Caspian, ice begins to form before the peak breeding period and the densest ice is often found away from the sea-ice interface (Heygster et al., 2009). In addition, the dispersal of pregnant Caspian seals is limited by the availability of leads in the ice sheet (Wilson et al., 2017). Therefore, because pregnant Caspian seals are unlikely to access the most stable ice, there is theoretical support for a non-linear relationship between pup densities and ice stability, because the most stable ice is less accessible to mothers at the start of the breeding period and the youngest ice is unsuitable or has formed after the peak breeding period. To test this hypothesis, I compared the fit of models that used linear and non-linear parameterizations for the effect of ice stability and found that the non-linear effect resulted in the most parsimonious explanation between ice stability and pupping densities. Furthermore, pup densities were significantly higher in a relatively narrow range of ice conditions found towards the middle of the overall availability of ice conditions.

When analysing foraging activity, the application of non-linear covariates was conceptually different to the implementation I used when analysing breeding distributions. Firstly, non-linear smoothing effects were used to account for temporal correlations in foraging activity for each individual separately. Secondly, previous research had identified three spatial clusters where the foraging activity occurred at its highest intensity (Dmitrieva et al., 2016) and these clusters were spatially aggregated around river inlets and prominent bathymetric features in the Caspian (Kosarev, 2005; Allen and Simmon, 2013). In these examples, a linear relationship may approximate the correlation between foraging intensity and distance to river inlets. However, when analysing this dataset as a time series, I used attributes associated with hierarchical modelling frameworks that allowed me to jointly estimate the average relationship between foraging and the environmental covariates, as well as non-linear seasonal deviations that describe an increase or decrease in the strength of the average relationship over time. Using this structure, I was able to identify significant temporal variability in the use of these areas over time, where the relationship between distance to these features and foraging activity peaked during different seasons. Furthermore, these patterns appear to be broadly associated with the seasonal availability of migratory fish species (Mamedov, 2006;

Kottelat and Freyhof, 2007; Bandpei et al., 2012; British Petroleum, 2015). Together, chapters one and two provide two examples where non-linearity in the response of an animal to the environment can be explained and modelled statistically, to produce unique insights, and to show how carefully considering a species' ecology can inform the design of hierarchically structured models.

5.2. Future directions

Ecological data science is fast becoming a field of big data analytics with several recent advancements leading to a wide variety of new insights (Farley et al., 2018; Nathan et al., 2022). This data revolution is likely to continue, and, in the future, several technological advancements may specifically aid pinniped research. One highlight is the increasing capacity of researchers to retrieve data remotely. These advancements are particularly powerful in the context of pinniped research because data is often retrieved using remote animal-borne trackers (Jonsen et al., 2005; Costa et al., 2010; 2014; Briscoe et al., 2018; Jonsen et al., 2020; Wege et al., 2021; Nathan et al., 2022), or during aerial surveys (Lonergan et al., 2011; Dmitrieva et al., 2015; Seymour et al., 2017; Morris et al., 2021; Lindsay et al., 2021). One of these advances includes the upcoming Copernicus Polar Ice and Snow Topography Altimeter (CRISTAL) satellite mission, which is expected to launch in 2027 and will provide ice extent, concentration, thickness, type, and drift, at a resolution of less than 80 m (Kern et al., 2020). These advances will vastly improve the reliability, and resolution of remote sensing sea ice datasets and will greatly increase the kinds of insights we can gain about the breeding conditions of ice-breeding pinnipeds.

Another major advancement in remote sensing technology includes the use of very high resolution (VHR) satellite imagery, that is accurate to approximately 30 to 50 cm, and been used to count adult Weddell seals (*Leptonychotes weddellii*) using satellite images (LaRue et al., 2020; LaRue et al., 2021). Although the resolution of visual spectrum satellite imagery is still too coarse to count white coated seal pups on ice. In the future, these advancements will directly impact biological questions that may extend the work presented in this thesis. For example, when evaluating climate change impacts such as the increasing instability of breeding ice. Eventually, these advancements in the remote monitoring of environmental conditions and breeding seals will align, which in combination with advancements in automated visual image classification and tracking (Li et al., 2018) may make it possible to directly monitor associations between early ice melt and individual seal pup detections throughout the breeding season.

Additional advancements to the protocols outlined within this thesis include increasing the automation of collecting and processing the data collected during aerial surveys. This may be achieved by using belly-mounted cameras in aircraft or drones (Morris et al., 2021; Heyer et al., 2021), or multi-spectral imagery, which may provide a more easily automated and quantified survey image (Seymour et al., 2017; Lindsay et al., 2021), and ship-based unoccupied aircraft systems (UAS) which are used within seal counts by NOAA in the Chukchi and Bering Sea (Moreland et al., 2013; Lindsay et al., 2021). Automated breeding season surveys would be particularly useful in the context of improving the ongoing monitoring of Caspian seals. At present, the data sets available during chapter one were collected and processed using a fully manual process. More recent advancements to data aerial survey strategies would significantly improve the speed at which breeding hotspots could be identified.

Alongside advancements with remote sense datasets, the field of animal movement is under especially rapid development and one major advancement is likely to be the application of high throughput tracking technologies (Nathan et al., 2022). At present, evaluating the impact of anthropogenic disturbance upon foraging marine mammals in remote areas is difficult due to the unreliable identification of potential disturbance-causing events. This is because the resolution of tracking data in remote areas typically has a precision of a few hundred meters or a few kilometres. This makes the accurate identification of individual disturbance events unreliable, particularly when a coarse spatial association may be expected. For example, pinnipeds and fishing industries may target the same groups of species resulting in a spatial association that may or may not be indicative of disturbance-causing events. However, in the future, high throughput tracking technologies will increase the resolution of pinniped tracking data to a few meters (Nathan et al., 2022), which may provide a method for directly measuring non-lethal impacts such as displacement. These advancements would have significant impact on frameworks that assess disturbance impacts, such as the population consequences of disturbance framework (New et al., 2014, 2015), because a direct measure for displacement could directly parametrise non-lethal energetic impacts associated with disturbance. Furthermore, another similar advancement could include combining animal tracking with other high-dimensional data collection methods. For example, by combining animal tracking with animal-borne video cameras researchers detected specific foraging events in Baikal seals (*Pusa sibirica*) (Watanabe et al., 2020). Applying next generation tracking methods in the Caspian will greatly increase our knowledge of Caspian seals. However, their application is likely to be some way off yet, in part, due to regional development, the remoteness of at-sea regions, and an inability to retrieve tags that are lost at sea.

5.3. Concluding remarks

The main contributions of my thesis use a range of methods to provide precise insights into the breeding and foraging ecology of Caspian seals. Each chapter is presented as a distinct piece of research that each harnesses attributes associated with specific analytical frameworks to test specific ecological theories that may explain Caspian seal biology but are not easily approached using alternative methods. During the first chapter, I found that climate threats have the potential to impact Caspian seal pup production soon. During the second chapter, I found that Caspian seals use different habitats during different seasons and protected areas could be implemented that would have a minimal impact on shipping industries and meet conservation targets. Finally, I found that reducing bycatch rates is essential if Caspian seals are to have a realistic chance of surviving past the next century, with this chapter forming the basis for an overall conservation recommendation that reducing bycatch is the most essential step towards conserving Caspian seals.

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