Killer whale predation of seals in the inshore waters of Shetland: investigating the ecological drivers and consequences of an apex predator-prey interaction

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THESIS ABSTRACT

The impact of predation has important consequences for individual fitness and the potential to culminate in population level effects. Understanding the causes and consequences of predator-prey interactions is therefore a mainstay in ecological research. This thesis explores the predator-prey interactions of killer whales (*Orcinus orca*) and seals in inshore Shetland. Data was derived from dedicated land-based field research and community-led monitoring efforts. A multivariate approach was used to explore potential environmental, ecological, spatial, and temporal drivers of predator and prey co-occurrence and species-specific capture probability. Killer whale diet composition with associated uncertainties in prey identification were quantified through an expert elicitation process and used to inform species- and age-class consumption estimates. Using a bioenergetic approach, the energetic requirements of inshore-foraging killer whales were estimated for the year 2021. Uncertainty in parameter estimates were explored through a Monte Carlo uncertainty analysis, with plausible ranges of killer whale consumption estimates incorporated as a harvest-type parameter in an age and sex-segregated Leslie Matrix population model. Population trajectories for both harbour (*Phoca vitulina*) and grey (*Halichoerus grypus*) seals were simulated under different assumptions of input parameters (e.g., changes to vital rates and composition in killer whale) over a 35-year prediction period. Findings from this thesis highlight the potential importance of near-shore areas for killer whale foraging effort and prey species refuge. In comparison to grey seals, harbour seals were found to have a higher probability of capture and consumption given an observed encounter with a killer whale. For harbour seals, populations trajectories typically resulted in a decline despite assumptions as to input parameters, whereas grey seal trajectories exhibited an increase. Overall, findings suggest killer whale predation may have implications for the depleted harbour seal population in Shetland, and demonstrate the capabilities of community-led monitoring to complement dedicated sampling efforts and inform research objective.

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1.1 Predator-prey interactions & ecological consequences

Predator-prey interactions are a cornerstone of ecology, playing an integral role in shaping species demographics, community structure, and ecosystem function (Sih et al. 1985; Krebs et al. 1995; Suraci et al. 2022). From a classical perspective, predator-prey interactions are viewed as a simple consumptive relationship between two species, whereby predators have a negative effect on prey through consumption, and prey provide a positive benefit to predators through nutritional content (consumptive effects) (Figure 1.1). In this simplistic view, predator consumption rates vary as a function of prey density (termed functional response, Holling, 1959), with predators mediating population parameters through capturing and consuming passive prey, reducing prey density whilst increasing the success of their own species through nutritional gain (termed numerical response, Holling, 1959; Paine, 1980). Classical understanding of predator-prey interactions fundamentally changed with the recognition of predator-induced nonlethal effects on prey (Lima 1998; Schmitz et al. 2004; Peckarsky et al. 2008). That is, predator presence can have negative effects on prey population without direct consumption, whereby prey incur fitness costs by altering phenotypically plastic traits such as behaviour, physiology, and morphology in order to reduce their risk of mortality by predation (Lima and Dill 1990). Together, consumptive and non-consumptive effects have the potential to drive predator-prey spatial use, population vital rates, species viability, and indirect interactions (Lima 2002; Dill et al. 2003; Werner and Peacor 2003; Preisser et al. 2005; Sih 2005).

Modern perspectives view predator-prey interactions as adaptive foraging games, whereby predator success is contingent on their ability to successfully locate, capture and consume prey (foraging traits), and prey success is contingent on their ability to successfully evade and escape predation (vulnerability traits) (Schmitz 2017) (Figure 1.1). To explore the complexities of predator-prey interactions across ecological contexts, predator and prey should be viewed beyond simple taxonomic identity and considered with regards to their respective functional traits. That is, morphological, physiological, or behavioural traits that are expressed in phenotypes of individual organisms in response ecosystem properties, such as abiotic (e.g., refuge availability) and biotic (e.g., predator density) factors (Naeem and Wright 2003; Schmitz et al. 2015; Schmitz 2017). Predator-prey interactions, and the outcome of adaptive foraging games, are therefore contingent upon and mediated by the state-dependent functional traits of one player relative to the other (Kotler 2016). For this reason, predator-prey interactions are considered a strong evolutionary driving force (Dawkins and Krebs 1979) shaping the fitness of both predator and prey species through a combination of direct consumptive and indirect non-consumptive effects (Lima and Dill 1990; Peckarsky et al. 2008). Predator-prey interactions are therefore adaptive, dynamic, complex, and have important consequences for the population structure, function, and resilience of both predator and prey species within their wider ecosystem (Peckarsky et al. 2008; Laundre et al. 2010; Peacor et al. 2020; Sheriff et al. 2020).

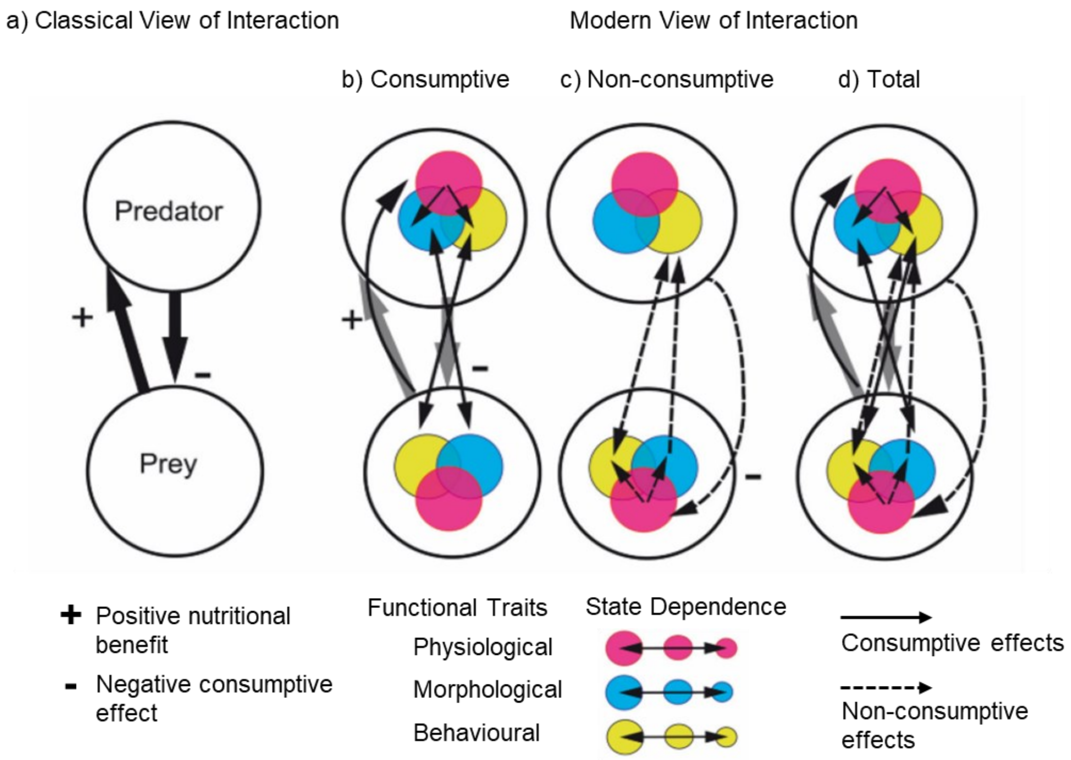

Figure 1.1. Classical vs modern views of predator-prey interactions from Schmitz 2017. a) Classical perspective whereby predators have a negative consumptive impact on prey, and prey provide a nutritional benefit to predators; b-d) Modern perspective whereby interactions are viewed as a multifaceted relationship between physiological, morphological, and behavioural predator and prey functional traits. Interactions are made up of both consumptive (b) and non-consumptive (c) interactions, for a total (d) combined interaction reflecting a complex adaptive game involving responsive feedback between predator and prey traits. Interactions are dependent on and mediated by the state-dependence magnitude (size of state dependence circles) of predator traits versus prey traits, for example good or poor body condition (physiological), large or small body size (morphological), or vigilant or inattentive (behavioural).

1.2 The predation sequence

Predation itself is the culmination of a sequence of events occurring between predator and prey, from spatial overlap through encounter and attack to outcome (termed predation sequence: Lima and Dill 1990) (Figure 1.2). At each stage, the predation sequence is mediated by the functional traits of both predator and prey, with the overall outcome determined by the relative magnitude of predator foraging traits versus prey vulnerability traits (Schmitz 2017; Suraci et al. 2022). For example, despite spatiotemporal overlap, prey may reduce predator encounters through crypsis and the use of localised refugia; if an encounter does occur, the predator may already be satiated and not motivated to attack the prey; if the predator does choose to attack, escape and physical defences of the prey may prevent their capture and consumption (Suraci et al. 2022). Viewing the predation sequence through the lens of both predator and prey functional traits is therefore integral to understanding the mechanisms underpinning context-dependent predator-prey interactions, quantifying top-down predator mediated effects, as well as assessing the capacity of both predator and prey species to adapt to changing environmental conditions.

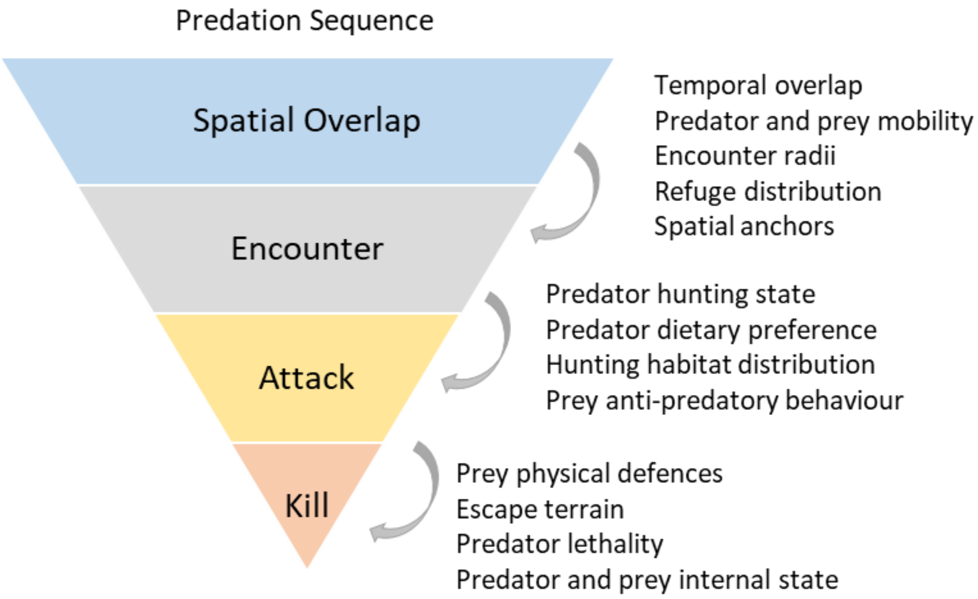

Figure 1.2. Depiction of the hierarchal predation sequence with factors that influence the progression between stages of the sequence, from Suraci et al., 2022. Later (lower) stages of the sequence are rarer and dependent on the outcome of the previous stage. Predator and prey functional traits and environmental variation can influence the likelihood that one stage will progress to the subsequent stage, with the sequence capable of ending at any stage.

To fully understand the complexity and context dependency inherent in predator-prey relationships, interactions should be examined across the progressive stages of the predation sequence rather than in isolation (Suraci et al. 2022). Traditional economic models propose predators should seek out areas of high prey density to maximise their foraging efficiency patches (i.e., by increasing spatial overlap), foraging more in areas of dense, high-quality prey and less in sparse, lower-quality patches (Marginal Value Theorem, Charnov 1976). However, for highly mobile animals foraging in a multi-prey system, spatial overlap and high prey density alone is not necessarily synonymous with foraging efficiency, and instead predators may optimise foraging by selecting prey based on relative abundance (encounter probability), vulnerability (capture probability), and nutritional value (Pyke 1984). For example, predators known to preferentially predate young age-class of a prey species have switched to predating more abundant adult age-class during years of low productivity (Reimer et al. 2019), or switch to hunting low-energetic-state individuals when high-energetic-state individuals become more vigilant (Embar et al. 2014). Just as predators are capable of making adaptive foraging decisions at each stage of the predation sequence to increase their foraging efficiency, prey are capable of employing predator avoidance strategies to reduce their chances of capture and consumption.

Prey can evade predators by modifying their activity patterns across contexts and spatiotemporal scales, such as a fine-scale or a large-scale shifts in micro- and macro-habitat usage respectively (Wirsing et al. 2008). Morphologically, cryptic colouration, or physical defences can reduce prey chance of detection and capture, and behaviourally, increased vigilance and mobbing can facilitate predator detection and deterrence, respectively (Helfman 1989; Hunter and Skinner 1998; Graw and Manser 2007; Caro et al. 2012). Antipredator behaviour employed by prey to reduce their predation risk, i.e., the probability of being captured given an encounter with a predator, typically incurs physiological costs (e.g., energetic cost of escape or increased stress response) and opportunity costs (e.g., interrupted feeding or moving to a less profitable habitat) (Heithaus and Dill 2006; Frid et al. 2007; Wirsing et al. 2008; Sheriff et al. 2020). For highly mobile prey, the stochastic variation in predation risk results in risk-balancing behavioural decision making, whereby antipredator behaviour must be balanced with other fitness-critical behaviours. The risk allocation hypothesis proposes that the magnitude of the response to the perceived predation risk should be a function of the frequency of the exposure to the risk. For instance, anti-predator behaviour should prevail in high-risk situations that are brief and infrequent; animals may choose to prioritise being safe over feeding, and instead feed during interim periods of low-risk. Alternatively, if high risk situations and lengthy and frequent, then animals may have no choice but to feed during high-risk periods or else risk starvation (Lima and Bednekoff 1999).The greater the perceived risk is relative to the cost of the response, the more likely an animal is to engage in anti-predator behaviour (Frid and Dill 2002). However, differences in prey states and traits may further influence prey decision making and risk-balancing. For instance, individuals in a poor body condition may prioritise foraging over predator avoidance if the risk of starvation outweighs the risk of predation (i.e., based on nutritional condition) (Heithaus et al., 2007). Furthermore, cognitively complex individuals may strategically alter their response based on knowledge of perceived threat (Deecke et al. 2002) or known proximity to refuge (safety) (Dill and Houtman 1989; Bonenfant and Kramer 1996).The outcome of the predation sequence is a result of context-dependent, reciprocal interactions between predator and prey, contingent on the relative magnitude of their respective traits.

Predator-prey interactions are therefore multifaceted, varying spatiotemporal and in relation to prey density, ontogeny, and phenotypically plastic individual traits. The consequences of consumptive and non-consumptive effects may be of particular importance in shaping the fitness of long-lived, highly mobile predator and prey species capable of responding to each other in behaviourally sophisticated ways (Brown et al. 1999; Wooster et al. 2023). Investigating the ecological drivers and consequences of predator-prey interactions in marine mammals would further understanding of the top-down effects of predators on prey populations, and the capacity of both predator and prey to adapt to environmental changes, thus informing the conservation and management of both the predator and prey populations.

1.3 Apex predator: Killer whale

Many apex predators are recognised as playing a keystone role in ecosystems (Estes et al. 2011; Ripple et al. 2014). Due to their top position on the trophic ladder, apex predators are capable of influencing ecosystems by mediating the density of their prey which are often meso-predators themselves. As a result, changes in the density and distribution of apex predators can elicit strong direct and indirect effects on species and ecological communities (Estes et al. 1998; Ripple et al. 2001; Sandin et al. 2008; Estes et al. 2011; Ripple et al. 2014). Apex predators are typically characterised by slow life history traits, such as large body size, slow growth rates, late sexual maturity, low fecundity, and long lifespans (Pauly et al. 1998). In the marine environment, apex predators are considered sentinel species given they exhibit observable responses to environmental variability or change (Fleming et al., 2016), including anthropogenic impacts on ecosystems (Sergio et al., 2008), and play important roles in marine food webs (Estes et al., 2016).

The killer whale (*Orcinus orca*) is a widely distributed apex predator species, most abundant in temperate waters of high marine productivity at higher latitudes (Forney and Wade 2007). The highest densities are observed in coastal North Pacific, North Atlantic, and higher latitudes of the Southern Ocean (Forney and Wade 2007) although it should be noted records are biased towards coastal areas and seasons with greatest sighting effort. The killer whale is currently considered a single species (although see Morin et al. 2024) due to taxonomic uncertainties (Reeves et al. 2004), however numerous ecologically divergent lineages displaying differences in diet, morphology, and behaviour are recognised throughout their global distribution (de Bruyn et al. 2013). From the perspective of predator-prey interactions, killer whales have been found to exert top-down effects in various ecosystems by both reducing meso-predator density through direct consumption and by prompting changes in prey behaviour and distribution due to predation risk (Jefferson et al. 1991; Estes et al. 1998; Breed et al. 2017). Studying the foraging behaviour of apex predators such as killer whales can provide valuable insights into the mechanisms influencing the abundance, distribution, movements, and resilience of both predator and prey populations (Womble et al. 2007; Lennox et al. 2023).

1.3.1 Predator movements & prey distribution

Predators are capable of locating and tracking prey across dynamic and variable landscapes using predictable patterns in seasonal and geographical variation in prey distribution and previous foraging success (Bradshaw et al. 2004; Biuw et al. 2009; Iorio-Merlo et al. 2022). The spatiotemporal occurrence of killer whales has been linked with the presence of predictable and abundant prey resources. In the Northeast Atlantic, sub-populations of offshore killer whales follow the seasonal movements of Norwegian spring-spawning (NSS) herring (*Clupea harengus*) and Icelandic summer-spawning (ISS) herring stocks (Similä et al. 1996; Foote et al. 2011; Samarra et al. 2017). In the British Isles (including Northern Ireland), killer whales have been opportunistically observed by fishery and marine mammal trained observers aboard pelagic Scottish fishing vessels in offshore waters of the northern North Sea predating on mackerel (*Scomber scombrus*) during the mackerel fishery season months of January and February. No sightings, however, were made by fishery observers aboard vessels during herring fishery seasons of June to September (Luque et al. 2006), suggesting (at time of study) the killer whales did not interact with the herring fishery, although seasonal bias in offshore observer effort should also be noted here, with no marine mammal trained observers aboard herring vessels. Inshore, killer whales are sighted year-round in the Northern Isles (Orkney and Shetland), with sightings increasing during the summer months of May to August and the autumn/winter months of October to November (Evans 1988; Bolt et al. 2009), coincident with harbour (*Phoca vitulina*) and grey (*Halichoerus grypus*) seal pupping seasons respectively (Thompson et al. 1989; SCOS 2022). Seasonal movements between Iceland in Winter and Shetland in Spring/Summer have been observed for a proportion of killer whales identified from photo-ID research (Foote et al. 2010; Samarra and Foote 2015). Early research using social network analysis identified a small number of individuals (less than 10) repeatedly sighted in both East Iceland and the Northern Isles (Foote et al. 2010; Beck et al. 2014) with more recent citizen science efforts cataloguing identified individuals finding evidence of double this number moving between Iceland and Scotland (Mrusczok and Scullion 2019). Broad scale killer whale movements may therefore be influenced by spatiotemporal variation in prey abundance, however, to understand finer scale movements and to quantify potential impacts on prey populations, understanding of predator foraging specialisation and diet composition is required.

1.3.2 Ecotypic foraging behaviour & population consequences

Foraging specialisation is a key marker of ecotypic variation in well-studied killer whale populations worldwide (Baird 2000; Riesch et al. 2012; de Bruyn et al. 2013). In the Northeast Pacific, three genetically distinct specialist ecotypes are identified: coastal ‘Resident’ fish-eating killer whales, sympatric ‘Transient’ mammal eating killer whales, and allopatric ‘Offshore’ killer whales found in outer continental waters (Ford et al. 1998; Dahlheim et al. 2008). Less is known about the latter ecotype, but they potentially specialise in eating fish including sharks (Bigg 1982; Baird and Stacey 1988; Ford et al. 1998; Dahlheim et al. 2008). In Antarctica, four ecotypes are described: ‘type A’ specialising on minke whales (*Balaenoptera acutorostrata*), ‘type B’ on pinnipeds, ‘type C’ on fish (Pitman and Ensor 2003; Morin et al.

2010), and 'type D' about which less is known but are potentially fish-specialists (Morin et al. 2010; Pitman et al. 2011). By contrast, the picture is less clear in the Northeast Atlantic where the ecological divergence and potential prey specialisation of killer whales appears more complex.

Early research proposed two ecotypes in the North Atlantic based on stable isotope analysis and tooth wear (linked to different prey types): Type 1 were proposed to be generalists associated with Atlantic herring, potentially feeding primarily on fish but with individual whales also consuming seals to varying extents (Foote et al. 2009; Vongraven and Bisther 2014; Jourdain et al. 2019); Type 2 appeared to be prey-specialists feeding on cetaceans (e.g., minke whales) (Foote et al. 2009). More recently, however, the dichotomous labels of Type 1 and Type 2 have been re-evaluated given a lack of data supporting the discrete classifications (Foote 2023). For instance, recent research in Norway found no evidence of strict mammal- versus fish-eating ecotypes in observations or stable isotope analysis (Jourdain et al. 2020). Instead, seal-eating killing whales were found to predate on a range of species whereby seals made up a significant portion of the killer whales' diet (i.e., were not opportunistic or sporadic foraging events) as evident in isotopic niche clustering, but individual killer whales also foraged on fish to varying extents, adapting to seasonal abundance of herring, lumpfish, and seals accordingly (Jourdain et al. 2020). In Iceland, the foraging ecology of killer whales appears more complex than a simple herring, or mixed herring and seal diet (Samarra et al. 2018); killer whales have been observed seasonally predating other prey such as birds (eider ducks, *Somateria Mollissima*), cephalopods, fish, and marine mammals (Samarra et al. 2018).

Prey availability, foraging specialisation, and diet flexibility, or lack therefore, can have important consequences and impact population distributions and demographics in killer whales (Ward et al. 2009; Ford et al. 2010). Historical movements of killer whales between Iceland and Norway were observed in association with Atlantic herring aggregations (Similä and Urgate 1993; Foote et al. 2010); however, the collapse of the Atlanto-Scandian herring stock in the 1960's (Jakobsson and Stefánsson 1999; Kvamme et al. 2003) was hypothesised to cause a shift in killer whale distribution and has potentially driven populations to seek alternative prey resources such as seals, which would indicate a capacity to adapt to shifts in prey resources and changing ecosystems (Jourdain et al. 2019; Jourdain et al. 2020). In the North Pacific, a reduction in fish prey availability influenced the survival and reproduction of highly specialised fish-eating killing whale ecotypes to the extent the population is considered endangered, contrasting to the mammal eating killer whale population which is not (Ward et al. 2009; Ford et al. 2010; Reeves et al. 2017). Foraging specialism may therefore reflect spatiotemporal availability of prey, or a preference for a particular prey type (Krahn et al. 2008; de Bruyn et al. 2013). Furthermore, foraging flexibility may not be an innate quality shared across discrete killer whale populations or ecotypes, but instead contingent on ecotypic characteristics and where populations lie on the specialist-generalist foraging gradient.

Prey specialisation is predicted to enhance fitness of killer whales in the short term (Whitehead and Ford 2018); however, longer-term consequences of a specialist diet may make certain ecotypes less resilient to fluctuating prey resources and more vulnerable to certain pollutants. For instance, mammal-eating killer whales are vulnerable to both bioaccumulation and biomagnification of lipophilic contaminants through prey consumption, including anthropogenically produced pollutants such polychlorinated biphenyls (PCBs) (Desforges et al. 2018). Indeed, mammal-eating killer whales around the world were found to have pollution burden substantially higher than fish-eating killer whales (Ross et al. 2000; Andvik et al. 2020) with concentrations shown to exceed thresholds for health effects on immune and hormone systems, which may ultimately influence reproductive fitness and population survival(Jepson et al. 2016; Desforges et al. 2018; Andvik et al. 2020). Understanding prey specialization in killer whale populations is therefore integral to identifying specialist ecotypes, assessing the capacity of populations to adapt to seasonally abundant prey, predicting consequences of specialist diets, and quantifying the top-down predator effects on prey populations, informing the conservation and management of both the apex predator and their prey species.

Longitudinal studies are required to investigate the consequences of predator prey interactions, from spatiotemporal overlap, through prey specialization and foraging success, to population-level consequences for both predator and prey (Jourdain et al. 2017). Whilst such studies are underway for sub-populations of Northeast Atlantic killer whales such as in

Norway (Jourdain et al. 2017; Vogel et al. 2024) and Iceland (Samarra et al. 2017), from which considerable advances in understanding of foraging ecology have been obtained, there is a paucity of published information for killer whales around the British Isles. In Scotland, groups of killer whales have been observed predating on fish offshore and marine mammals inshore (Luque et al. 2006; Bolt et al. 2009; Deecke et al. 2011); however, at present, there are a lack of studies quantifying the foraging ecology and prey specialization of these populations. In the Northern Isles and north coast mainland Scotland, killer whales are becoming increasingly monitored year-round due to expanding citizen science efforts (Hall et al. 2019). Dedicated research efforts into this study population therefore creates an opportunity to quantify killer whale diet, foraging behaviour and predator-prey interactions, furthering understanding of potential prey-specialization in the sub-population, and their capacity to adapt to changes in the marine environment, including anthropogenic change.

1.4 Predator-prey interactions: Killer whales and seals in coastal Scotland

Two species of phocid seal occur in the British Isles, the harbour seal and grey seal. Belonging to wider populations distributed throughout the Northeast Atlantic, the UK hosts 30% of Europe’s harbour seal population, with 79% of the UK population found in Scotland (SCOS 2022). Approximately 38% of the world’s grey seal population breed in the UK, of which 88% are found in Scotland (SCOS 2022). The UK is therefore considered an important area for both seal species, and from an apex predator-prey perspective, reflects a considerable prey resource to mammal-hunting killer whale frequenting Scottish waters. Although overlapping in their distributions, harbour and grey seals vary in their abundance, ecology, morphology, physiology, and life-history strategies; traits which may mediate their availability and vulnerability to predators (Russell and Mcconnell 2014; Russell et al. 2019; Thompson et al. 2019; Carter et al. 2020). Furthermore, killer whale predation is proposed as a potential driver of regionally declining harbour seal populations (Bolt et al. 2009; Arso Civil et al. 2018; SCOS 2022). Determining the extent to which killer whale preferentially predate different age classes of harbour versus grey seals would therefore provide valuable insights into the potential role killer whale predation may play in regional population trajectories.

As previously described, foraging specialisation may reflect spatiotemporal availability of prey or a preference for a particular prey type (Krahn et al. 2008; de Bryun et al. 2013). The distribution, density, and behaviour of harbour and grey seals, viewed here as killer whale prey, varies across spatiotemporal scales according to ecological and species-specific characteristics (Russell and Mcconnell 2014; Russell et al. 2019; Thompson et al. 2019; Carter et al. 2020); factors which may influence their presence in killer whale diet. On the broadest scale, divergent population trends have been observed both within and between the two seal species since monitoring began in the early 1990's (SCOS 2022). Grey seal populations are largely stable or increasing around the UK (Russell et al. 2019; Thomas et al. 2019), and whilst the UK population of harbour seals is stable overall, regional populations have undergone dramatic declines around the north and east coasts of Scotland (Morris et al. 2021). Whilst regional differences in overall seal abundance may be driven by population trajectories, seasonal differences in seal species relative abundance may be driven by life-history cycles. For instance, harbour seals pup in the summer months of June-July, and moult in August; grey seals pup in the months of August-December, and moult in December-April, depending on their location around the UK (Pomeroy et al. 1999; Thompson et al. 2010; Hanson et al. 2013; SCOS 2022). From a predator perspective, prey selection may not be dictated by abundance alone, but also context dependent and contingent on the functional traits of the predator and prey (Schmitz 2017; Suraci et al. 2022). For example, grey seals are physically larger than harbour seals but typically forage further offshore; whilst they may offer a higher energetic reward if caught, chances of a killer whale encountering a grey seal may be lower, in comparison to a coastal foraging harbour seal, if killer whale foraging effort is primarily focused inshore (i.e., high spatiotemporal overlap but low encounter probability)(Jones et al. 2015; Carter et al. 2020). Similarly, naïve pups and juveniles of both species may be easier to capture and handle in comparison to adults (Baird 1994), however given the lower calorific reward due to their smaller size, they may not be selected if alternative adult prey is also available (Reimer et al. 2019). A complex interaction of prey (e.g., seals) species availability (abundance and distribution) and vulnerability (e.g., age classes) therefore likely influences killer whale prey selection and thus the total context and age-stage dependent predation effects experience by the two species.

Exploring the factors influencing predator-prey interactions from spatiotemporal overlap to capture and consumption would therefore provide valuable insights into killer whale foraging ecology and their potential impacts on seal populations in coastal Scotland. This is of particular importance given the strong spatial overlap in killer whale presence and regionally declining harbour seal populations (i.e., around the north coast and Northern Isles of Scotland) (Scullion et al. 2021). Furthermore, given that both recruitment failure and an increase in adult mortality must be occurring to produce the observed declines (Hanson et al. 2017), understanding of age- and stage-specific predation pressure is crucial when identifying potential drivers of demographic changes. Investigating the predator-prey interactions of killer whales and seals across the predation sequence has therefore substantial potential to shed light into the factors mediating top-down predation pressure beyond simple spatial overlap.

1.5 Study area & predator and prey populations

Within the British Isles, killer whales are seen year-round in inshore waters of the Northern Isles of Shetland and Orkney, and more seasonally around the north and west coast of mainland Scotland (Scullion et al. 2021) (Figure 1.3). Around 200 different individuals have been identified in the Scottish Killer Whale Photo Identification Catalogue 2021 (Scullion et al. 2021). At present there is insufficient evidence to label certain individuals as resident or migratory, and a lack of genetic analysis preludes concrete conclusions as to the relatedness of known individuals. However, through continued photo identification efforts, stable social relationships are observed at a scale of years to identify groups, here termed pods. Several pods are observed to be site-faithful to the Northern Isles and are consistently re-sighted throughout the year in inshore-foraging areas (e.g., 27s, 64s, and 65s). Other pods exhibit more nomadic movement patterns, with irregular sightings made between Scotland and Iceland (e.g., 12s, 15s, 19s). Additionally, roving lone males (e.g., ID 018) and roving male alliances of stable associations (e.g., Hulk, ID 62 and Nott, ID 155; John Coe, ID W001 and Aquarius, ID W008) are sighted intermittently.

Data used in this thesis were collected around coastline of the Shetland Isles (henceforth termed Shetland); an archipelago and the northern most part of the United Kingdom, located around 170km northeast of mainland Scotland, 80km northeast of Orkney, and 200km west of Norway. Shetland was selected as an appropriate study area based on previous sightings data of killer whales from Shetland Cetacean Group, Shetland Biological Record Centre (SBRC), Sea Watch, and aerial surveys of seal populations conducted by the Sea Mammal Research Group (SMRU) (Figures 1.4 – 1.5). Building on existing data sets and previous research (e.g., Bolt et al. 2009; Deecke et al. 2011; Samarra and Foote, 2015), a pilot field season was conducted by ECOPredS project PI Dr. Isojunno in summer 2019 to gain further insights into the logistics and feasibility of land-based data collection for seal monitoring and killer whale focal follows. Following this, data collection and fieldwork protocols were refined throughout the duration of my PhD field seasons (2021-2023), with two sampling periods of summer (June-July) and autumn (October-November) established to overlap with harbour and grey seal breeding seasons, respectively, coinciding with observed peaks in killer whale presence. With data collected primarily conducted from land, data used as part of this thesis was within 2.5km of the Shetland coastline, henceforth termed ‘inshore’ for the purpose of this thesis (Figure 1.6).

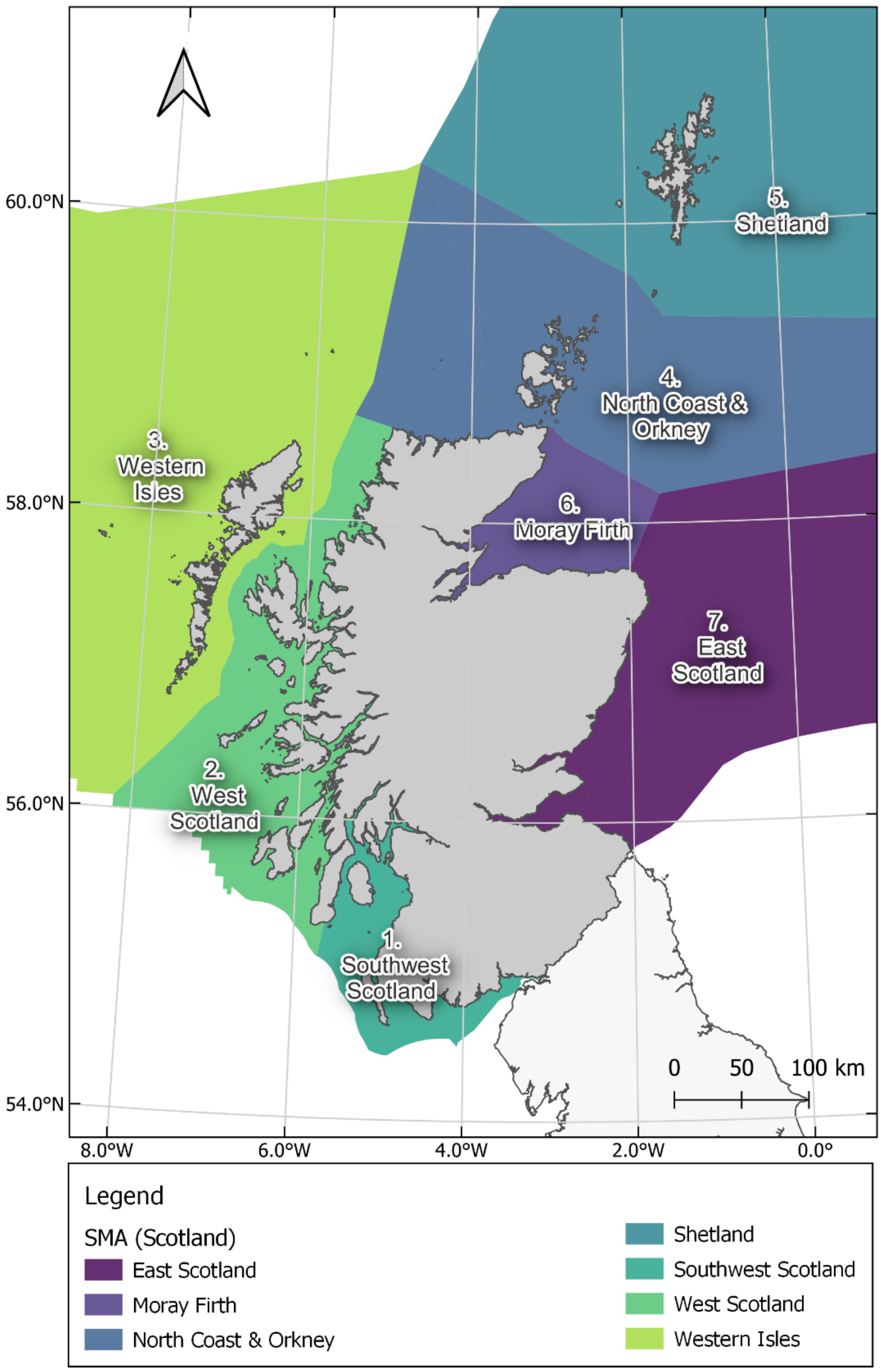

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Figure 1.3. Seal Management Areas (SMAs) of Scotland clipped to UK EEZ. SMAs in Scotland used by the Sea Mammal Research Unit (SMRU) to monitor and report on population size and trend estimates for harbour and grey seals in UK waters.

Seal Management Areas (SMAs) are used by the Sea Mammal Research Unit (SMRU) to report population sizes and trend estimates for harbour and grey seals in UK waters (SCOS 2022) (Figure 1.3). SMA boundaries were devised based on latest biological knowledge of seal populations, taking into account considered constraints on data collection and management requirements (SCOS 2022). Whilst SMA boundaries do not translate to discrete populations (i.e., movement of individuals between SMAs is likely, particularly for grey seals) they were designed to allow for local and regional management of seal populations in response to environmental effects and anthropogenic impacts (e.g., to set potential biological removals, PBRs, for seal species) (SCOS 2022). The Shetland SMA is one of seven SMAs in Scotland and is divided into three sub-regions: the North & East (N&E), the Southeast (SE) and the West (W) SMA subregions. On a finer spatial scale, Special Areas of Conservation (SACs) (EU Habitats Directive, Council Directive 92/43/EEC) are established for both seal species, identified as areas important for resting and breeding (Figure 1.6).

In the Shetland SMA, counts of harbour seals declined in a stepwise drop by approximately 40% between 2001 and 2005, when counts were 4,994 and 3,038 respectively (Figure 1.4 & 1.5) (Morris et al 2021). Since 2005, counts of harbour seals have remained stable at a depleted level across the SMA as a whole, however there have been significant regional differences in trends between the SMA sub-regions. In the North and East SMA subregion, counts declined markedly by approximately 60% from approximately 3,000 in the late 1990's to approximately 1,200 in 2005, after which they have remained stable or slightly increasing. A continual although less extreme decline was observed in the Southeast SMA subregion, with counts declining from approximately 1,600 in the early 1990's to fewer than 500 in 2017. In contrast, counts in the West SMA sub-region have remained stable since monitoring began in early 1990's (Morris et al. 2021). Of the two harbour seal SACs in Shetland, the Yell Sound SAC has remained stable at a depleted level after a marked stepwise decline between 2001 and 2005, however abundance in the Mousa SAC has exhibited a continual decline (SCOS, 2022) (Figure 1.4). Counts of grey seals within the Shetland SMA have remained stable since 1995 (Figure 1.4), although a non-significant reduction in numbers was observed in the most recent counts between 2015 and 2019 when the detection-corrected (i.e., accounting for the proportion of seals hauled out during survey) population estimate was 3,760 individuals (SCOS 2022).

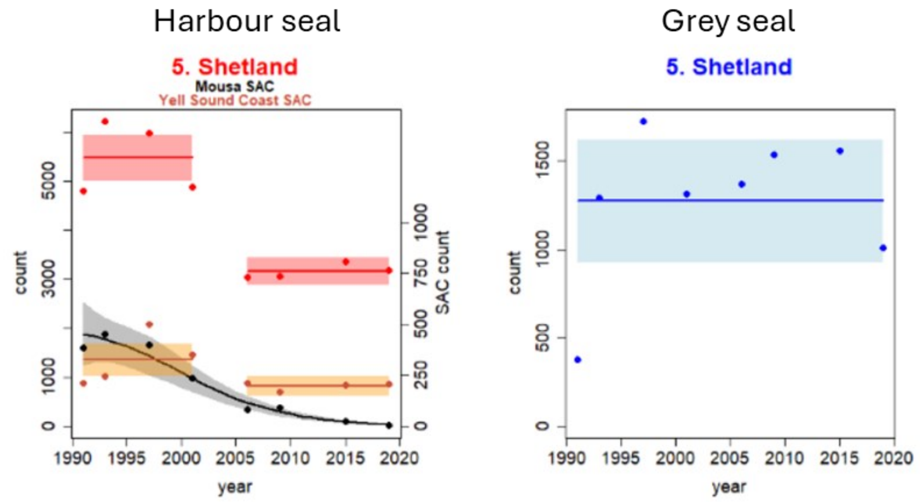

Figure 1.4. Predicted trends and associated 95% confidence interval for harbour seals (left, red) and grey seals (right, blue) from August seal counts in Shetland, from SCOS 2022.Harbour seal predictions depict the stepwise decline for the whole SMA (red) and the Yell Sound SAC (orange), and the continued decline in the Mousa Sound SAC (black). Note the difference in axis for the SACs. Grey seals predictions for the whole SMA are roughly stable, although a drop in numbers is observed between the final two surveys.

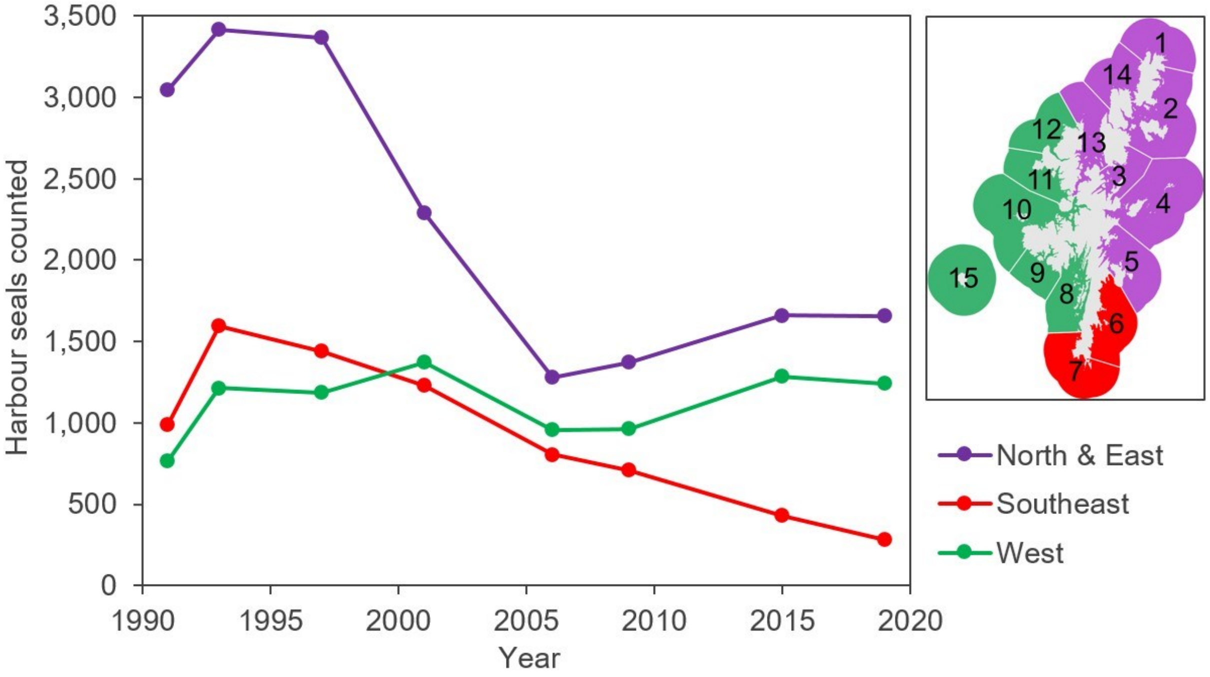

Figure 1.5. Harbour trends in the North & East, Southeast, and West Shetland SMA subunits from Sea Mammal Research Unit (SMRU) aerial counts 1991 – 2019 (Morris et al. 2021)

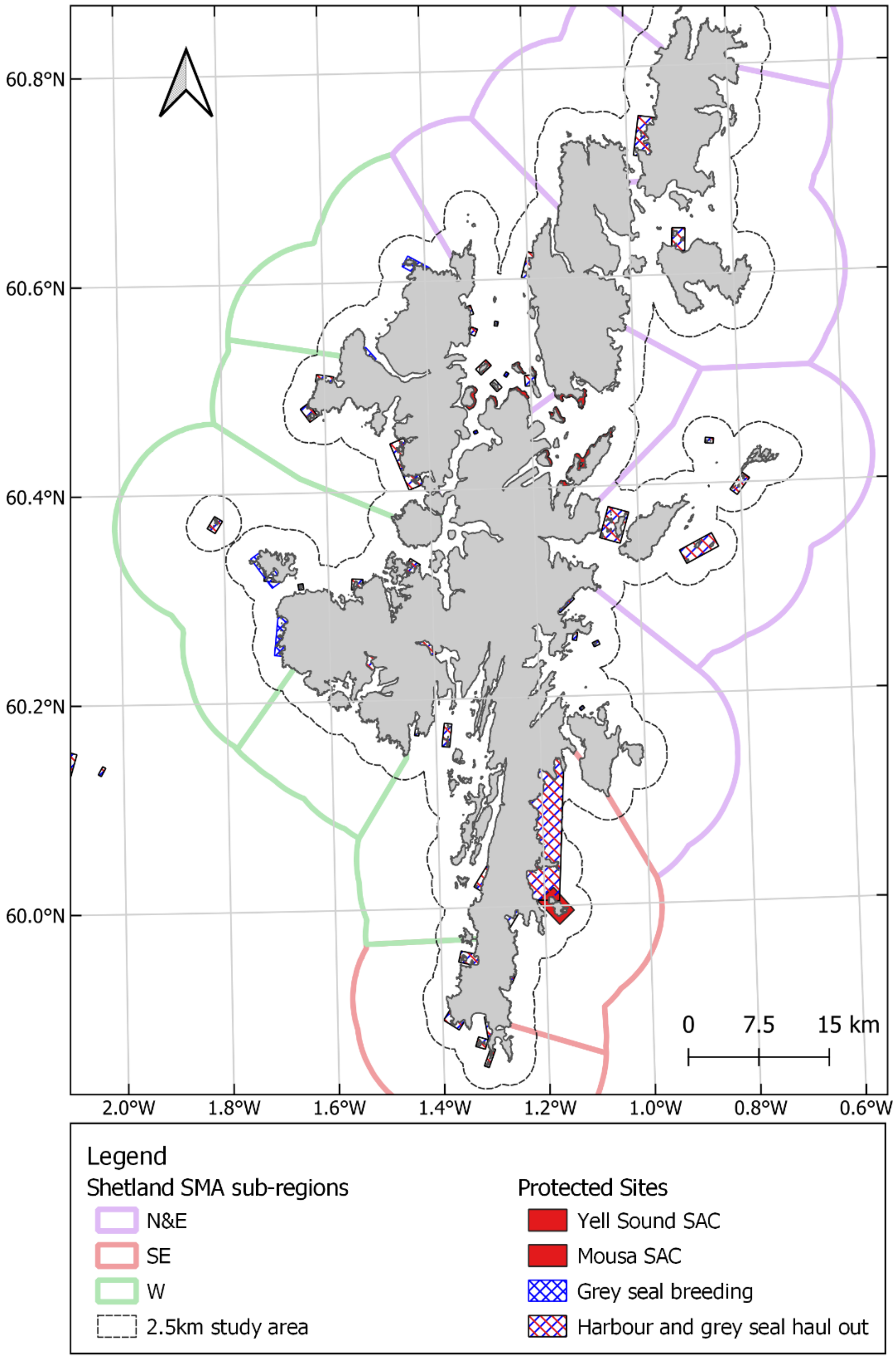

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Figure 1.6. Shetland study area. Map of the study area, with data collected for this thesis within 2.5km of the coastline (dashed black boundary). Coloured boundaries depict SMA sub-regions (N&E, SE, and W) within the Shetland SMA used for seal population monitoring and reporting. Solid red boundaries depict designed Special Areas of Conservation (SACs) for harbour grey, with blue and red crossed boundaries depicting Marine Scotland designated haul-out sites for grey seal breeding (blue) and harbour and grey seal haul-out (red and blue).

1.6 Thesis overview

Statement of collaborations:

Data used in this thesis reflects a collaborative effort of ECOPredS project members, citizen scientists, and project collaborators, including volunteer drone pilots. From the ECOPredS project team, preliminary fieldwork was conducted by Dr. Isojunno in Summer 2019, and I conducted 5 field seasons throughout the duration of this PhD: Summer and Autumn in 2021 and 2022, and Summer in 2023. Dr. Isojunno was also present during Summer 2022 and Autumn 2021 fieldwork. Citizen science efforts and contributions primarily came from members of the Shetland Orca Sightings network, a social media sightings group managed by Karen Hall (Nature Scot and PhD co-supervisor) and Hugh Harrop (Shetland Wildlife). Scotland-wide sightings were contributed by the Sea Watch Foundation. Drone footage of killer whales was primarily contributed by Nick McCaffrey (Southspear Media & Surveys), Richard Shucksmith (Shetland Ecology), and Hugh Harrop, with additional footage provided by Vivian Clark and Gary Buchan. Master's student Chloé Deleu conducted quality and content scoring, and behavioural annotation of a subset of drone footage used to inform analysis as part of this PhD and wider ECOPredS research. Leslie Matrix population modelling was adapted from a pre-existing model developed by Dr. Eiren Jacobson and Dr. Monica Arso Civil.

Overview of Chapters:

In Chapter 2, the first data chapter, I investigate the co-occurrence of killer whale foraging effort and seal prey availability, as observed during PhD land-based fieldwork (2021-2023). The aim of this Chapter is to investigate potential spatiotemporal, environmental, and life-history traits that may drive seal aggregations, and whether killer whales exhibited increased foraging effort in association with such drivers. That is, whether killer whales focused foraging efforts in times and locations of high seal prey abundance. Land-based surveys were conducted to quantify seal species counts with repeated visits to land-based and boat-based surveys sites across five and two field seasons, respectively. Land-based focal follows of killer whales were conducted across five field seasons to quantify proportion of time spent foraging in comparison to other behaviours (e.g., travelling). Spatiotemporal and environmental variables were explored as part of a multivariate approach to predict seal counts and killer whale foraging effort.

In Chapter 3, I investigate prey consumption by killer whales as observed from PhD fieldwork, drone-based observations, and citizen science contributions (2016-2023). The aim of this Chapter is to explore spatiotemporal patterns in predation success and capture probability between prey species. An expert-elicitation process was conducted to identify prey species in media (e.g., photo, drone still) with associated confidence in identification. Spatiotemporal, environmental, and ecological variables were then explored as part of the multivariate approach to predict probability of predation success given an observed predatory-prey encounter.

In Chapter 4, I develop a comprehensive ethogram for inshore-foraging killer whales for the application to behavioural data collection across observer platform. The aim of this Chapter is to produce an extensive list of killer whale behaviours, both behavioural states and surface-events, with objective definitions to facilitate consistent reporting and data collection on the study population. Additionally, the ethogram was applied to drone-based observations to quantitatively summarise the time spent by killer whales in different behavioural states (activity budget) as observed in inshore Shetland.

In Chapter 5, I investigate the consumptive impact of killer whales on harbour and grey seal populations in Shetland. The aim of this chapter is to estimate the calorific requirements of the killer whale study population as present in in-shore waters of Shetland in the year 2021, and how many seals would hypothetically need to be consumed to meet these requirements. A bioenergetic model was developed with input parameters and their associate uncertainties to estimate sex and age-class specific calorific requirements for killer whales as predators, and species sex and age-class specific calorific values for harbour and grey seals as prey. The range of values estimated to be consumed for each seal species, based on the diet composition derived from Chapter 3, was then incorporated in a Leslie Matrix model to explore potential predicted trajectories for harbour and grey seal populations over a 35-year period under different scenarios (e.g., seal vital rates, killer whale diet composition).

2 CHAPTER 2. PREDATOR AND PREY CO-OCCURRENCE: QUANTIFYING VARIABILITY IN SEAL PRESENCE AND INSHORE- FORAGING KILLER WHALES

Abstract

Within an area of predator-prey overlap, predators may utilise space to increase foraging opportunities across spatiotemporal scales. In this Chapter, I investigate the co-occurrence of killer whales foraging behaviour and seal prey availability as observed using land-based surveys (2021-2023). Potential spatial, temporal, environmental, and life-history drivers of seal aggregation are explored to investigate whether killer whales foraging behaviour is related to times and locations associated with high seal prey abundance. Seal surveys were conducted during autumn and winter months to measure the abundance and composition (species and age classes) of seals on and around haul outs. Killer whale focal follows were carried out to quantify proportion of time spent foraging in comparison to other behaviours (e.g., travelling). Spatiotemporal, environmental, and ecology variables were explored as part of a multivariate approach to predict seal counts and killer whale foraging effort. Seal counts and haulout composition were found to vary significantly both spatial and temporally (e.g., between SMA subregion, year and season), and in relation to environmental variables (e.g., shoreline type and sea state). Killer whale foraging was found to vary significantly in relation to sea-state. The only common predictor of seal counts and killer whale foraging effort was sea state, with more seals and a higher probability of foraging observed at lower sea states. Biological explanations for these results may be relevant, however detectability biases should not be ruled out. Biologically, seals may select sheltered haulouts for fitness-critical behaviours such as resting and breeding, and killer whales may forage at lower sea states to reduce risk of injury or stranding. However, it is plausible that more seals were observed at lower sea state due to higher detectability, and indicators of killer whale foraging (e.g., blood or slick on water surface) may be more readily observable during lower sea states. Results

from this Chapter highlight the complexities of studying predator-prey space use concurrently, and challenges associated with land-based observations.

2.1 Introduction

Spatiotemporal overlap is a fundamental prerequisite for predator-prey interactions (Lima and Dill 1990). Within this overlap, predators are expected to utilize space in a way that maximises foraging success, which is a function of prey density and predator foraging decisions (Sih 2005). Prey are expected to utilize space in a way that balances the risk of predation and other behaviours critical to survival (e.g., foraging, breeding) (Stephens and Krebs 1986; Grand and Dill 1999). As a result, conflict arises between predator and prey habitat selection; predators are expected to aggregate in areas of high prey density, and prey in areas of low predation risk (Sih 1984; Suraci et al. 2022). Studying predator and prey space use concurrently is therefore integral to understanding predator-prey interaction rates and quantifying the strength of predation pressure on prey communities (Luttbeg and Sih 2004)

The marine environment represents a highly heterogeneous, three-dimensional landscape where the distribution of prey may vary spatiotemporally in relation to intrinsic requirement (e.g., breeding, foraging, predator avoidance) and environmental factors (e.g., habitat, proximity to refuge) (Nathan et al. 2008; Benoit-Bird et al. 2009). If prey are restricted in their space use due to environmental (e.g., resource concentration) or intrinsic (e.g., physiological) constraints, then predators may be able to increase spatial overlap by showing preference for areas of high resource value for prey, regardless of whether the prey are present themselves (Hammond et al. 2007). Over broader spatial scales, predators may be able to gather this historical knowledge through successful foraging experiences, improving their ability to track and anticipate patterns of prey aggregations (Biuw et al. 2009; Wooster et al. 2024). For example, if mobile prey exhibits seasonal migrations (e.g., to breeding grounds) or are constrained by spatially fixed resources (e.g., watering holes), predators may be able to increase spatial and temporal overlap by seeking out areas of high resource value for prey (Sih 2005; Hammond et al. 2007; Suraci et al. 2022). Across smaller spatial scales, predators can make informed foraging decisions through the use of sensory cues (e.g., olfactory and visual) to locate prey aggregations (Lawson et al. 2019). Investigating the environmental factors and species characteristics that affect predator and prey space use is crucial for understanding the potential scale and concentration of predator-prey overlap within and area of shared space (Luttbeg and Sih, 2004; Suraci et al. 2022).

Unlike other cetaceans, killer whales are not known to migrate to specific breeding or calving grounds (Corkeron and Connor 1999). Instead, killer whales exhibit seasonal shifts in movement and distribution patterns for the purpose of locating prey (Nichol 1990; Estes et al. 2007). Killer whales may utilize a combination of historical knowledge and environmental cues to improve their ability to track and anticipate prey aggregations, increasing their foraging opportunities across spatiotemporal scales (Wooster et al. 2024). For example, in the Northeast Pacific, post-reproductive females were observed leading group movement in years of low prey abundance, proposedly due to their historical ecological knowledge of foraging grounds (Brent et al. 2015). In Antarctica, Weddell seal (*Leptonychotes weddellii*) hunting specialists (Type B eco-type) focus hunting efforts in areas of pack ice – the preferred haul-out habitat of resting Weddell seals (Pitman and Durban 2012). In the present study population, the inshore waters of Scotland could be considered the overall prey patch to which killer whale pods routinely return for foraging opportunities (Bolt et al. 2006; Scullion et al. 2021). Understanding how aggregations of seals vary spatiotemporally and in relation to ecological and environmental factors within this patch may therefore provide insight into their predictability as a prey resource to inshore mammal-hunting killer whales. That is, whether killer whales can effectively track and predict seal movements in order to increase spatiotemporal overlap for foraging opportunities within an area of shared space.

Whilst harbour and grey seals overlap within their wider distribution in Scottish waters, they showed marked regional difference in their at-sea distribution and coastal haul-out usage dependent on ecological variation and life-history strategies (Thompson 1989; Russell and McConnell 2014; Carter et al. 2020; SCOS 2022). Coastal haul-out sites are used for fitness critical behaviours such as resting, moulting, and breeding (Thompson 1989). Harbour seals pup during the summer months (July – August) and are typically considered income breeders, whereby mothers continue to forage during the lactation period until pups are fulling weaned after four to six weeks (SCOS 2022). Grey seals pup during the autumn/winter months (August-December) and employ a more capital-breeding strategy, whereby females accumulate large fat reserves during the year and fast whilst continually feeding their pups on land for approximately three weeks, although occasional foraging trips may occur during nursing (Pomeroy et al., 1999; Radford et al., 1978). The spatial, temporal, and physiological constraints of breeding may therefore limit the habitat and space use of seal species in a way predictable to foraging killer whales. That is, if seals are constrained and remain in close proximity to haul-outs for the purpose of fitness-critical behaviours such as breeding, then free-ranging killer whales may be able to increase spatiotemporal overlap with their prey by utilizing these inshore areas at concurrent times for foraging opportunities.

In the present study area of inshore Shetland, killer whales have been observed predating on both harbour and grey seals (Bolt et al. 2009; Deecke et al. 2011) with land-based sightings of killer whales proposed to peak in months coinciding with seal species breeding seasons, summer and autumn/winter respectively (Hall et al. 2019). In comparison to other regions of Scotland, harbour and grey seals in Shetland exhibit a highly coastal distribution in their at-sea movements as observed from GPS-GSM telemetry tagged individuals (Carter et al., in prep), with a majority of tagged harbour seals observed to spend at least half of their time at sea within 100m of land (Carter et al., in prep). Data is available on the longer-term trends in harbour and grey seal abundance for the Shetland Seal Management Area (SMA) and sub-regions therein, with abundance estimates and trends reported across five-year survey cycles (Morris et al. 2021; SCOS 2022). Opportunistic sightings of killer whale presence are available from community-led monitoring efforts (e.g., Shetland Biological Record Centre and Sea Watch Foundation), which has seen an increase in reporting with the advent of social media groups (e.g., Shetland Orca Sightings in 2016) facilitating the dissemination of sightings information. However, the spatial and temporal scale at which this data is available and the variability in observer effort makes it challenging to explore the degree of overlap in and concentration of predator foraging effort in relation to variability in prey presence. Instead, fine-scale data on predator and prey co-occurrence is required for a detailed understanding of predator-prey spatiotemporal overlap, particularly in relation to ecological and environmental variables that may influence the capacity of predators to adapt foraging decisions in response to fluctuations in prey distribution and density (Benoit-Bird et al. 2013).

The aim of this Chapter is to investigate potential drivers of seal aggregations, as killer whale prey, around inshore Shetland through land-based field observation conducted during summer and autumn PhD field seasons. By collecting data on the variability in seal haul-out usage at the same scale killer whale focal follows were conducted, the co-occurrence of killer whale foraging effort could be explored in relation to their prey availability. If seal counts are found to be predictable in relation to spatial, temporal, environmental and life-history factors, then killer whales may be able to maximise their foraging efficiency by focusing hunting efforts in times and locations of high seal density (i.e., high prey abundance) or predictable (i.e., consistent prey abundance). To test this, I conduct a two-fold investigation. First, I will quantify the overall number and consistency in both seal species (combined) as observed around coastal haul-out sites to investigate the broader predictability of seals as killer whale prey. Given variation in the overall density of seals seen around haul-out sites may vary seasonally in relation to species-specific breeding constraints, I also investigate harbour seal predictability relative to total observed seal abundance. Second, I will quantify killer whale foraging effort in relation to environmental and ecological predictors of seal species to investigate whether killer whales exhibit evidence of exploiting seals as predictable in-shore prey aggregations. This comparative approach allows for the direct comparison of predator and prey space use and will further understanding of how predators may successfully locate prey within a dynamic and variable landscape.

2.2 Methods

2.2.1 Field data collection

Fieldwork was conducted during summer (June – July) and autumn (October – November) months to coincide with observed peaks in killer whale presence, and to capture seal variability across harbour and grey seal breeding seasons respectively. Field effort was primarily land-based, with the exception of boat-based seal surveys conducted across two field seasons (Section 2.2.1.1).

2.2.1.1 SEAL SURVEYS

Candidate survey sites were identified prior to fieldwork by examining existing datasets on seal haul-outs in Shetland, namely: SMRU aerial surveys (2015 and 2019 surveys) (Morris et al., 2021); preliminary data collection conducted by the Harbour Seal Decline project in 2015; preliminary ECOPredS fieldwork conducted in 2019; Special Areas of Conversation (SACs), designated haul-outs, and protected breeding haul-out sites (all of which are established based on evidence of high area usage by one or both seal species) (Habitats Directive – Council Directive 92/43/EEC; Marine (Scotland) Act, 2010). Additional candidate sites were also provided through advice from local wildlife experts and citizen scientists on the ground in Shetland.

During preliminary data collection of fieldwork, candidate sites were visited to assess their suitability as 'regular' monitoring sites – those to be repeatedly and routinely visited throughout PhD field seasons. Suitable sites were defined as those utilised by one or both seal species (including pupping and non-pupping sites) and at coastal locations known to be visited by killer whales. Additional considerations were taken to ensure sites were safely and readily accessible by foot (to increase coverage and data collection efficiency), consisted of a variety of habitat types (e.g., rocky skerries and sandy bays), and were distributed throughout the three Seal Management Unit sub-regions of Shetland (North and East, NE; Southeast, SE; and West, W). Additional regular sites were introduced during subsequent field seasons through project field observations and local recommendations.

Suitable land-based sites were challenging to establish for Yell Sound – an area where killer whales are frequently sighted – due to the topography of the region, the presence of the Sullom Voe Oil Terminal (resulting in a large proportion of the coastline being inaccessible), and the fact that seals typically haul out on islands and skerries in this area (SCOS 2022; Morris et al. 2021). Additional boat-based surveys were therefore conducted in this region for two field seasons, one in summer 2023 and one in autumn 2022. Boat-based monitoring sites were identified following the same procedure as the land-based sites, with additional information regarding haul-out locations available from tracks of harbour and grey seal GPS-GSM tags deployed in Yell Sound by SMRU in 2022 (Carter et al., in prep).

A total of 27 regular land-based monitoring sites were established around the coastline of mainland Shetland (Table 2.1, Figure 2.1). Ten sites were located in the North & East SMA subregion, 9 in the Southeast SMA subregion, and 8 in the West SMA subregion. 13 boat-based monitoring sites were established in Yell Sound within the North and East SMA subregion (Table 2.2, Figure 2.2)

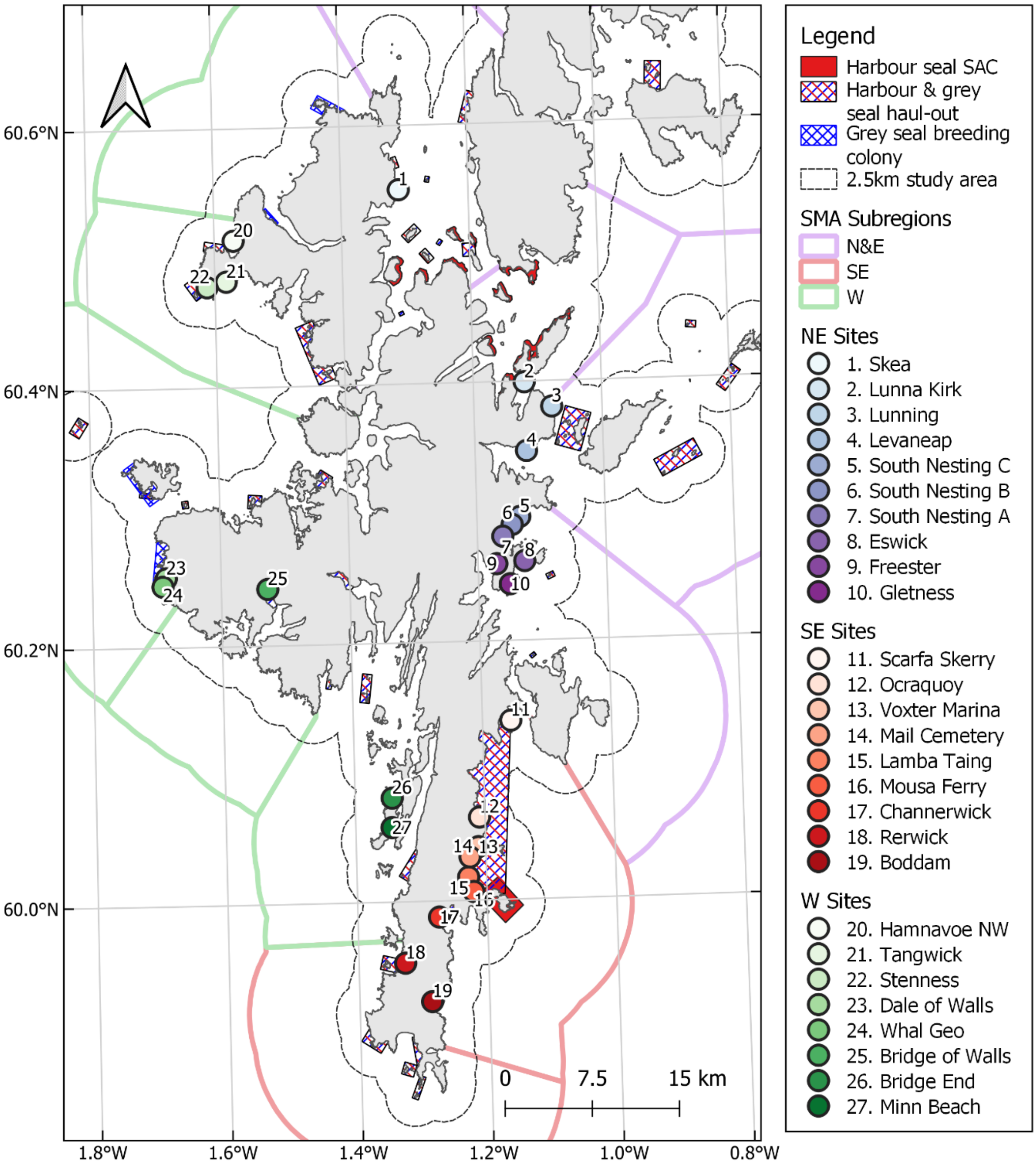

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Figure 2.1. Study area with land-based survey sites in each SMA subregion. Special Areas of Conservation (SACs) were designated under EU Habitats Directive as areas identified as important for haul-out and pupping. Designated haul-outs were designated under the Marine (Scotland) Act 2010 as areas important for resting, moulting or breeding.

Table 2.1 Summary information for land-based seal survey sites Where ‘sum’ = summer and ‘aut’ = autumn in season established column. Designated sites of type ‘haulout’ are designated for both harbour and grey seals, and ‘breeding, greys’ for grey seals only.

SMA subregion	Site name	Latitude	Longitude	Designated site name (type)	Season established
North & East SMA subregion (n = 10)	1. Skea	60.5501	-1.3094		Sum ‘22
	2. Lunna Kirk	60.3992	-1.1205	Yell Sound (SAC)	Sum ‘22
	3. Lunning	60.3799	-1.0786		Sum ‘22
	4. Levaneap	60.3461	-1.1199		Sum ‘22
	5. South Nesting C	60.2953	-1.1330	Scudliss Wick (haulout)	Sum ‘21
	6. South Nesting B	60.2893	-1.1455	Scudliss Wick (haulout)	Sum ‘21
	7. South Nesting A	60.2804	-1.1606	Scudliss Wick(haulout)	Sum ‘21
	8.Eswick	60.2611	-1.1275	Eswick Holm (haulout)	Sum ‘21
	9.Freester	60.2593	-1.1710		Aut ‘21
	10. Gletness	60.2435	-1.1509		Sum ‘21
South-east SMA subregion (n = 9)	11. Scarfa Skerry	60.1381	-1.1561		Sum ‘21
	12. Ocraquoy	60.0639	-1.2086	E South Shetland (haulout)	Sum ‘21
	13. Voxter Marina	60.0411	-1.2115	E South Shetland (haulout)	Sum ‘21
	14. Mail Cemetery	60.0334	-1.2250	E South Shetland (haulout)	Sum ‘22
	15. Lamba Taing	60.0179	-1.2279	E South Shetland (haulout)	Sum ‘21
	16. Mousa Ferry	60.0066	-1.2204	E South Shetland (haulout)	Sum ‘21
	17. Channerwick	59.9875	-1.2745	Channerwick and Hoswick (haulout)	Sum ‘21
	18. Rerwick	59.952	-1.3285	Colsay and Bay of Scousburgh (haulout)	Sum ‘21
	19. Boddam	59.9223	-1.2885		Sum ‘21
West SMA subregion (n=8)	20. Hamnavoe NW	60.5134	-1.5702		Sum ‘21
	21. Tangwick	60.4818	-1.5825		Sum ‘21
	22. Stenness	60.4779	-1.6126	Isle of Stenness (haulout)	Sum ‘21
	23. Dale of Walls	60.2535	-1.6856	Dale (breeding, greys)	Sum ‘21
	24. Whal Geo	60.2472	-1.6908	Dale (breeding, greys)	Aut ‘21
	25. Bridge of Walls	60.2438	-1.5280	Gruting Voe NW Head (haulout)	Sum ‘21
	16. Bridge End	60.0803	-1.3429		Sum ‘21
	17. Minn Beach	60.0576	-1.3443		Sum ‘21

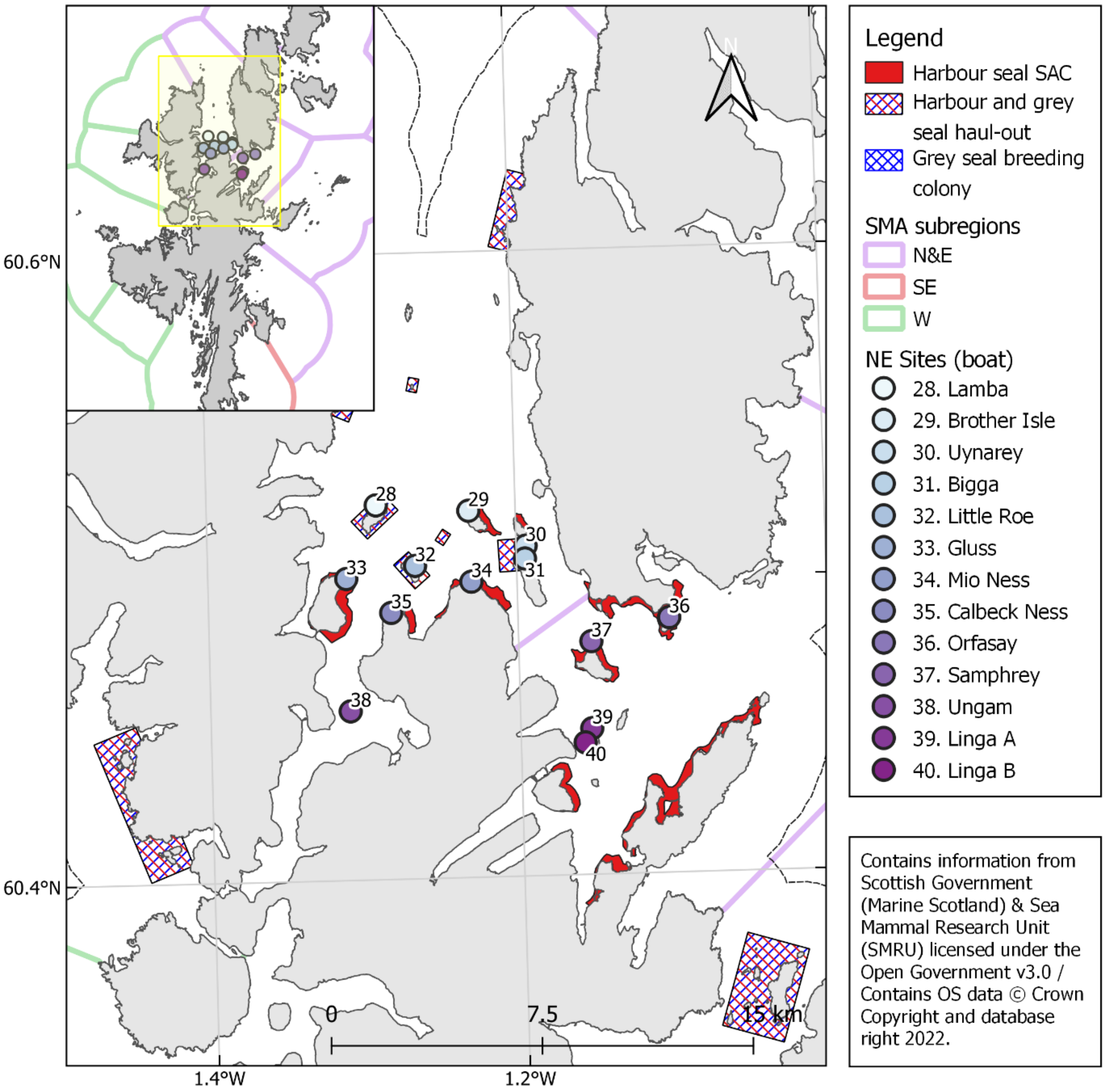

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Figure 2.2. Study area with boat-based survey sites within the N&E SMA subregion. SACs were designated under EU Habitats Directive as areas identified as important for haul-out and pupping. Designated haul-outs were designated under the Marine (Scotland) Act 2010 as areas important for resting, moulting or breeding.

Table 2.2. Information for boat-based seal survey sites. All survey sites were established in autumn 2022. Designated site type 'haulout' is designated for both harbour and grey seals, and 'SAC' for harbour seals.

N&E SMA subregion (n = 13)	Site name	Latitude	Longitude	Designated site name (type)
	28. Lamba	60.5196	-1.2900	Lamba (haulout)
	29. Brother Isle	60.5171	-1.2302	Yell Sound (SAC)
	30. Uynarey	60.5055	-1.1937	Yell Sound (SAC)
	31. Bigga	60.5014	-1.1944	Sligga Skerry & North End of Bigga (haulout)
	32. Little Roe	60.4999	-1.2656	Little Roe (haulout)
	33. Gluss	60.4963	-1.3103	Yell Sound (SAC)
	34. Mio Ness	60.4944	-1.229	Yell Sound (SAC)
	35. Calbeck Ness	60.4851	-1.2818	Yell Sound (SAC)
	36. Orfasay	60.4813	-1.102	Yell Sound (SAC)
	37. Samphrey	60.4744	-1.1529	Yell Sound (SAC)
	38. Ungam	60.4540	-1.3096	Ungam (haulout)
	39. Linga A	60.4466	-1.1539	
	40. Linga B	60.4421	-1.1584	

Data collected at seal monitoring sites followed a scan survey protocol (Martin & Bateson, 2007), with a minimum of 10 minutes spent at each land-based site per visit to standardise effort. Scans were conducted primarily using naked eye and binoculars, with a scope used for observing more distant haul-outs (~500m from the observer). Following preliminary observations, 10 minutes was considered sufficient to capture the composition of seals present without missing animals submerged underwater or miscounting (e.g., duplicate) individuals as they moved around the survey site. For boat-based sites, the boat was idled around 100m-300m from haul-outs for only as along as required for data collection, typically less than 10 minutes. This time constraint was in part due to time and fuel cost considerations, but also ensured chances of disturbance from vessel presence and noise was minimised for the seals (SMWWC 2017). Where possible, sites were visited at least once a week at various tidal states and times of the day to ensure unbiased sampling and even spatiotemporal data coverage across environmental conditions.

Data were collected at each site visit to capture seal species numbers in relation to environmental variability (e.g., sea state) and anthropogenic processes (e.g., boat presence) (Table 2.3). Species identification was based on distinct morphological differences between harbour and grey seals (e.g., pelage, head shape), with pups identified as individuals in clear association with a mother (mum-pup pair) or alone but of weaning age (pup). Where species ID could not be established (e.g., due to angle, obstruction, or distance) the animal was recorded as an ‘unknown’ individual. ‘Hauled out’ was defined as animal resting on land or rocks, and ‘in the water’ defined as those either swimming or resting (bottling) in the water. Environmental data was collected to explore how seal presence varied dependent on abiotic conditions (e.g., weather, sea state) that may influence both detectability and actual haul-out usage. Sea state, swell height, visibility, and cloud cover were estimated visually, with wind speed and direction obtained from the IOS weather app.

Table 2.3. Data variables collected during seal survey scans (table continues overpage)

Type	Variable	Description
Effort	Obs	Observer ID
	Date	Format dd:mm:yy
	Loc_name	Location name of seal site
	Start	Beginning of scan hh:mm
	Finish	End of scan hh:mm
Environmental	Sea_state	Beaufort scaled: 0=mirror calm; 1= slight ripples, no foam crests; 2 = small wavelets, glassy crests, but no whitecaps; 3= large wavelets, crests begin to break, few whitecaps; 4=longer waves, many whitecaps, 5= moderate waves of longer form, some spray, 6 and over = large waves, whitecaps everywhere, frequent spray.
	Swell	Swell height estimated in meters
	Visibility	Visibility: < 1km; 1-5 km; 6-10km; >10km.
	Cloud_cover	Cloud coverage as a percentage
	Weather	Calm; breeze; wind; partial sun; sun; overcast; haar; showers; rain; heavy rain; hail; snow; haar rain, wind rain.
	Wind_d	Wind direction on eight points compass: N; NE; E; SE; S; SW; W; NW
	Wind_mph	Wind speed in mph
Anthropogenic	Vessel_nm	Number of vessels <500m with motor off
	Vessel_m	Number of vessels <500m with motor on
Seal totals	Seal_total_H	Total number of seals hauled out
	Seal_total_S	Total number of seals in the water
Harbour seal presence	Pv_adult_H	Number of adult harbour seals hauled out
	Pv_adult_S	Number of adult harbour seals in the water
	Pv_pup_H	Number of harbour seal pups hauled out
	Pv_pup_S	Number of harbour seal pups in the water
	Pv_mum_pup_H	Number of harbour seal mum-pup pairs hauled out. Not included in total count, only to indicate pairs vs lone adults and pups.

	Pv_mum_pup_H	Number of harbour seal mum-pup pairs in the water. Not included in total count, only to indicate pairs vs lone adults and pups.
Grey seal presence	Hg_adult_H	Number of adult grey seals hauled out
	Hg_adult_S	Number of adult grey seals in the water
	Hg_pup_H	Number of grey seal pups hauled out
	Hg_pup_S	Number of grey sela pups swimming
	Hg_mum_pup_H	Number of grey seal mum-pup pairs hauled out. Not included in total count, only to indicate pairs vs lone adults and pups.
	Hg_mum_pup_H	Number of grey seal mum-pup pairs in the water. Not included in total count, only to indicate pairs vs lone adults and pups.
Unknown seal presence	Unk_adult_H	Number of unknown adults hauled out. When species ID cannot be confident due to distance, angle, or weather conditions.
	Unk_adult_S	Number of unknown adults in the water. When species ID cannot be confident due to distance, angle, or weather conditions.
	Unk_pup_H	Number of unknown pups hauled out. When species ID cannot be confident due to distance, angle, or weather conditions.
	Unk_pup_S	Number of unknown pups in the water. When species ID cannot be confident due to distance, angle, or weather conditions.
	Comments	Additional relevant comments e.g., on other prey presence (porpoise, otters), anthropogenic disturbance.

2.2.1.2 KILLER WHALE FOCAL FOLLOWS

Existing protocols and published literature were used to establish effort and follow protocols for killer whale data collection. Definitions of behavioural states were informed by published behavioural descriptions (e.g., Baird 1994; Deecke et al. 2005; Ashe et al. 2010; Jourdain et al. 2020) and adapted to the study population considering observations from preliminary fieldwork. Project data-collection protocols for land-based data collection of coastally foraging killer whale behaviour were available from the ECOPredS project (developed during preliminary fieldwork conducted by project PI Dr. Isojunno in summer 2019) and the Elephant Seal Research Group (ESRG) (F. Galimberti & S. Sanvito, personal communications, 2021). Following ethical approval, data contributed by experienced citizen scientists via sightings networks were used to supplement in-field data collection.

Killer whales were located following reports shared by citizen scientist via local sighting networks. Visual observations of pods were conducted from land using binoculars, sighting scopes and telephoto lens (Canon 70D with Ef 100-400mm lens). Observations were categorised either as point sightings or focal follows, which were made up of continuous re-sightings of the same group.

Focal follow data collection followed a continuous recording protocol (Martin and Bateson 2007). The beginning and end of follows were ad libitum (Altmann 1974), commencing when the whales were within line of sight and terminating when either the whales moved out of view, the observer had to move location (to re-sight the animals) or data collection was no longer possible due to environmental conditions (e.g., the onset of darkness or poor visibility). Observer and pod locations were obtained and recorded using mobile OS Unlimited map in OutDoors GPS IOS app. Observer location was exact based on GPS reference taken in-situ, and killer whale pod location were approximated based on cross-referencing bearings and distances with environmental landmarks in relation to the observer location. Visual data were collected on group size, composition (e.g., number of adult males, calves), ID, behavioural states (e.g., shorehugging, transit, milling), direction of travel, estimated distance to shore, and any evidence of predator-prey interactions visible at the surface (e.g., killers whale chasing visible prey, blood, slick or bird surface activity indicative of a kill). Environmental (e.g., sea state) and anthropogenic processes (e.g., boat presence, aquaculture) were also recorded. Visual data was collected as often as there were changes to any of the recorded variables described (Tables 2.4 – 2.5). When animals were sighted but a focal follow was not possible (e.g., due to animal’s distant position), data points were recorded as sightings with a point time, location, and as many recorded variables as possible.

Table 2.4 Data variables collected during killer whale follows (table continues overpage)

Type	Variable	Type	Description
Effort	Source	Categorical	Observer or citizen science source ID
	Date	Continuous	Format dd:mm:yy
	Time	Continuous	Point time for sighting hh:mm
	Start	Continuous	Start time for on-follow hh:mm
	End	Continuous	End time for on-follow hh:mm
	Location	Categorical	General location of data collection
	Lat & long (observer)	Continuous	Latitude and longitude of observer position
	Lat & long (start)	Continuous	Latitude and longitude of killer whale at follow start or position of point sighting
	Lat & long (end)	Continuous	Latitude and longitude of killer whales at the follow end
Environmental	Sea state	Integer	Beaufort scaled: 0=mirror calm; 1= slight ripples, no foam crests; 2 = small wavelets, glassy crests, but no whitecaps; 3= large wavelets, crests begin to break, few whitecaps; 4=longer waves, many whitecaps, 5= moderate waves of longer form, some spray, 6 and over = large waves, whitecaps everywhere, frequent spray.
	Vessel_nm	Integer	Number of vessels <500m with motor off
	Vessel_m	Integer	Number of vessels <500m with motor on
	Anthropogenic	Integer	Number of anthropogenic devices <500m (note device in 'comments')
Killer whale ID	No. in group	Integer	Number of killer whales in group
	Male	Categorical	ID of pod (if known)
	Female	Integer	Number of females (if known)
	Juvenile	Integer	Number of juveniles (if known)
	Calf	Integer	Number of calves (if known)
Behavioural	Direction	Categorical	Direction of travel on eight points compass: N; NE; E; SE; S; SW; W; NW or 'non-directional'
	Distance to shore	Continuous	Approximate distance to shore (meters)
	Group behaviour	Categorical	Transit; transit shorehugging; shorehugging milling (see behavioural definitions)
	Group distribution	Categorical	Tight, 0-1; close, 2-3; loose, 4+ body lengths apart.
Predator-prey	Predator-prey interaction	Categorical	None; chasing prey; circling; feed (blood, slick).
	Outcome	Categorical	Consume; escape (land); escape (dive); escape (anthropogenic); consume (blood or prey sharing).
	Prey ID	Categorical	Seal (Pv/Hg); seal (unknown species); porpoise; otter; mammal; sea bird; fish; unknown.

Notes	Comments	Text	Relevant comments, e.g., identification of anthropogenic devices, interaction with anthropogenic devices, evidence of disturbance.

Table. 2.5. Killer whale behavioural states as and definitions.

Behavioural State	Description
Transit	Group moves in a consistent direction; any turn of direction is completed by the whole group in another consistent direction. Surfacing typically synchronous.
Transit shorehugging	Group transit parallel to shoreline, in and out of bays, around headlands / skerries; turns only occur in the direction of shoreline/skerries and are completed by the whole group. Surfacing typically synchronous as with “transit”.
Shorehugging	Following contours of shoreline, in and out of bays, around headlands / skerries; turns only occur in the direction of shoreline/skerries and are completed by the whole group. Different to “transit shorehugging” by evidence of prey ‘searching’ or ‘inspection’ behaviour – side swimming underwater, asynchronous surfacing.
Milling	Group moves in multiple or inconsistent directions; individuals whales may swim in consistent direction while others do not.

2.2.2 Environmental covariates

Wind speed was missing during 2021 data collection (land-based only). To give a complete, consistent dataset across all years, average windspeed was appended to the entire dataset and used instead of windspeed taken in-situ during 2022 and 2023 for land-based data collection. In-situ windspeed was available for all boat-based data, and so was included in these models instead of average windspeed.

Shoreline habitat for survey sites was classified using Environmental Sensitivity Index (ESI) shoreline classifications provided by Marine Scotland (Marine Scotland National Marine Plan 2017). The dataset was established for oil spill contingency planning and provides habitat classification for the intertidal zone where seals aggregate to haul out. Of the habitat dataset explored for inclusion in analysis, the shoreline classification dataset was considered appropriate given spatial overlap with visual data collection. Alternative datasets considered for use had poor data coverage at the inshore scale of the present study area. Shoreline classifications are grouped into five categories, of which four were present around the Shetland coastline: rocky cliffs and bedrock; sand/gravel beach; sheltered rock, manmade, gravel or rock armour (riprap); sheltered tidal flats or salt marshes (Figure 2.3). Shoreline type was appended to the land-based and boat-based survey locations (summarised in Table 2.6.).

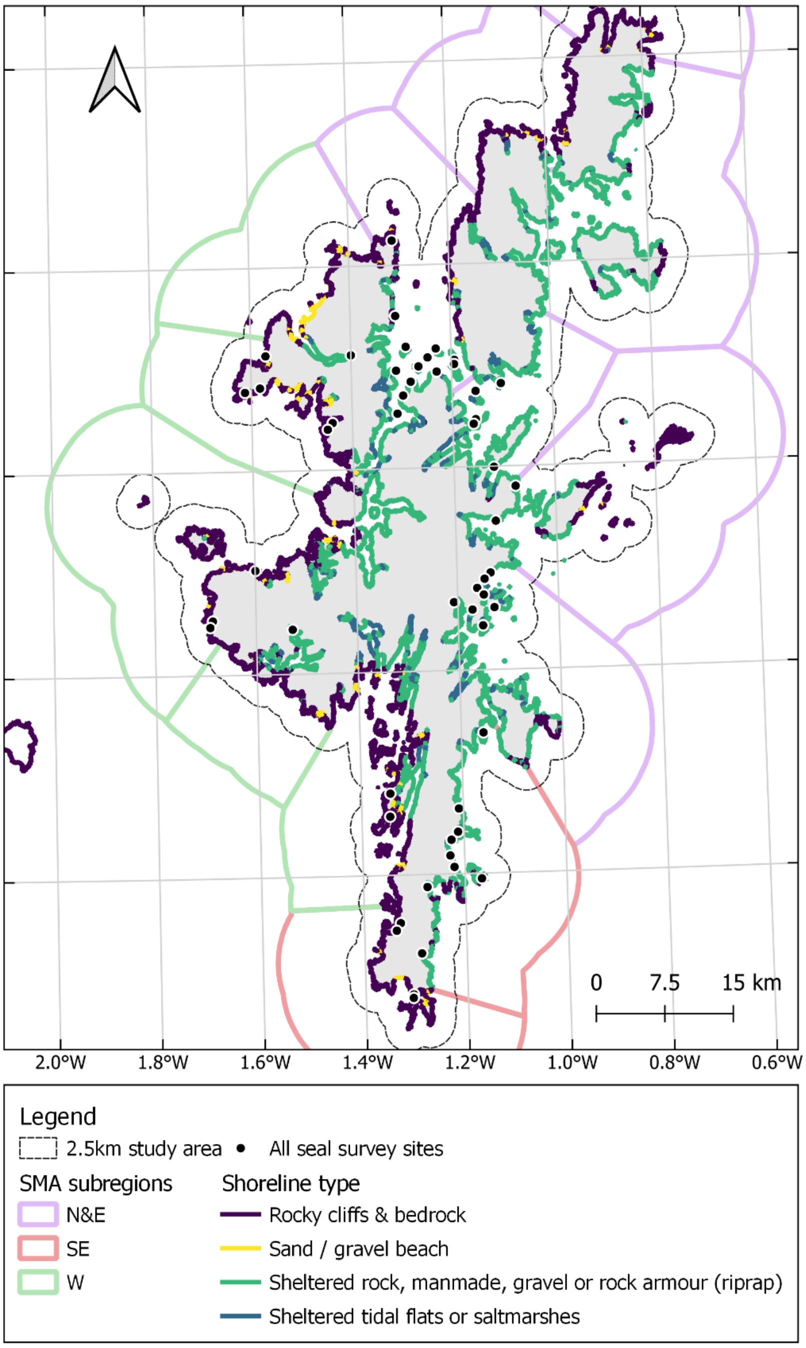

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Figure 2.3 Shoreline type around Shetland coastline as classified using Environmental Sensitivity Index (ESI) shoreline classifications. The dataset was established for oil spill contingency planning and provides habitat classification for the intertidal zone.

Table 2.6. Sample size for shoreline types at seal survey sites as summarised for each SMA subregion. Numbers in parentheses denote sample size of boat-based sites in the N&E SMA subregion and total.

Shoreline type	N&E	SE	W	Total
Rocky cliffs and bedrock	1 (2)	2	5	8 (2)
Sand/gravel beach	0	0	2	2 (0)
Sheltered rock, manmade, gravel or rock armour (riprap)	8 (10)	6	1	15 (10)
Sheltered tidal flats or salt marshes	1 (1)	1	0	2 (1)

2.2.3 Data processing

Land-based and boat-based sites were analysed independently during statistical analysis due to the different spatial and temporal scale of data collection. Land-based sites were grouped together by SMA subregion for statistical analysis to explore regional variation in seal numbers. Models for boat-based seal counts included site location as a factor covariate, due to the smaller number of sites and the fact that all sites were within the N&E SMA subregion.

To explore variation in killer whale foraging effort, behaviour states were grouped into two categories for analysis: (1) “foraging”, made up of behaviour states ‘shorehugging’ (indicative of prey searching) and ‘milling’ when observed in association with predator-prey interactions (e.g., after a kill), and (2) “other” , ‘transit’, ‘transit shorehugging’, and ‘milling’ not associated with predator-prey interactions). ESI shoreline classifications were used to assign a shoreline habitat to each focal follow, with the closest shoreline category append to each data row. To explore whether proximity to known seal haul-out sites influenced presence of foraging behaviour, the distance to closest regular monitoring site was calculated and appended to the data set. Closest shoreline and haul-out site were calculated in *R* using the *st_nearest_feature* and *st_distance* functions from the *sf* package.

2.2.4 Statistical analysis

2.2.4.1 VARIATION IN SEAL COUNTS

To investigate the variability in the number of seal counts between SMA sub-regions, years, and seasons, the coefficient of variation (CV) for total seal numbers was calculated. CV is a relative measure of the dispersion of data point around the mean (i.e., relative standard deviation); low CVs therefore indicate consistency in the number of seals observed, and high CVs indicate high variation in the number of seals observed.

A regression modelling approach was taken to model regional and environmental variation in the total number of seals. A Poisson generalised linear model (GLM) approach was applied using the *glm* function in the R package *lme4.* Total seal count (the response variable, discrete count data bound at 0) was specified a quasi-distribution to account for overdispersion in the count data.

Covariates were chosen to capture environmental, spatial, and temporal predictors of seal density, regardless of species composition. Interaction terms were included to test for differences in temporal (inter-annual or seasonal) trends across different regions. Variance inflation factors (VIFs) were calculated to identify and remove collinear predictor variables from the candidate set. Given the correlation of certain environmental variables (e.g., average wind speed and sea state), the variable that was considered of more biological importance was selected in final model; for example, the influence of windspeed is expected to be dependent on wind direction in relation to the site, whereas sea state captured in-situ site specific variability in the environmental condition, thus sea state was selected as a covariate.

Global model selection, testing for all combinations of the candidate predictor variables and interactions, was carried out using the *dredge* function in the R package *MuMIn*. The *dredge* function was used to rank the candidate models and identify those that best explained variation in the response variable after accounting for the number of estimated parameters in each model, calculated using Akaike Information Criterion adapted for the quasi-distribution (QAIC). The final model was selected as the model with fewest estimated parameters within 2 QAIC units of the lowest QAIC model (ΔQAIC <2). The final model was used for statistical inference and prediction with 95% normal confidence intervals. Statistical hypothesis tests (t-tests) were performed for each regression coefficient in the final model to assess effect sizes and uncertainty for each contrast, e.g., whether difference in counts between summer and autumn was statistically different from zero, with 5% significance level as a reference.

2.2.4.2 VARIATION IN HAUL-OUT COMPOSITION

A binomial GLM was used to investigate variables predicting the composition (i.e., proportion) of seal species at monitored haul-out sites. Species proportion, as a binomial response, was calculated by coding the number of harbour seals as ‘successes’, and the total seal counts minus the number of harbour seals (I.e., the presence of grey seals and unknowns) as the ‘failures’ per survey. The response variable was modelled using a quasibinomial distribution to account for over-dispersion in the data. Candidate covariates included in the model were selected to capture potential environmental, spatial, and temporal predictors, but also included the presence of harbour seal pupping sites (as a binary presence / absence variable for each year) to investigate whether the relative abundance of harbour seals increased at suitable breeding locations. Separate models were constructed for land-based sites and boat-based sites. Model selection was conducted using the same methodology for predicting the total seal numbers (Section 2.2.4.1).

2.2.4.3 VARIATION IN KILLER WHALE FORAGING EFFORT

A binomial GLM was used to investigate variables predicting foraging presence of killer whales. As a binomial response, foraging was coded as a binary presence / absence variable (foraging vs all other behavioural states). As with the model to predict seal species composition, the response variable was modelled using a quasibinomial distribution to account for over-dispersion in the data. Candidate covariates included in the model were selected to capture potential environmental, spatial, and temporal predictors, but also distance to nearest seal survey site to investigate whether foraging effort increased in proximity to known seal prey haul-out locations. Model selection was conducted using the same methodology for predicting the total seal numbers (Section 2.2.4.1).

2.3 Results

2.3.1 Summary of field effort and coverage

In total, 5 field seasons were conducted: Summer 2021 (14th June – 18th July), Autumn 2021 (26th October – 28th November), Summer 2022 (10th June – 17th July), Autumn 2022 (25th October – 24th November), and Summer 2023 (6th June – 18th July).

2.3.1.1 SEAL SURVEYS

Variability in the number of site visits across the seasons were due to methodological development and logistical constraints (Figure 2.4 – 2.5). For example, certain sites were only identified in later field seasons, as described in method development and were therefore absent from prior field seasons. Site visits were also constrained by logistical factors such as balancing seal survey effort with killer whale data collection and weather windows for boat-based surveys. Visits were also curtailed due to adverse weather conditions when survey effort was not possible, most notably for autumn 2022. Boat surveys were conducted in autumn 2022 and summer 2023 field seasons, with four surveys were conducted during each season, covering all 13 sites a total of eight times.

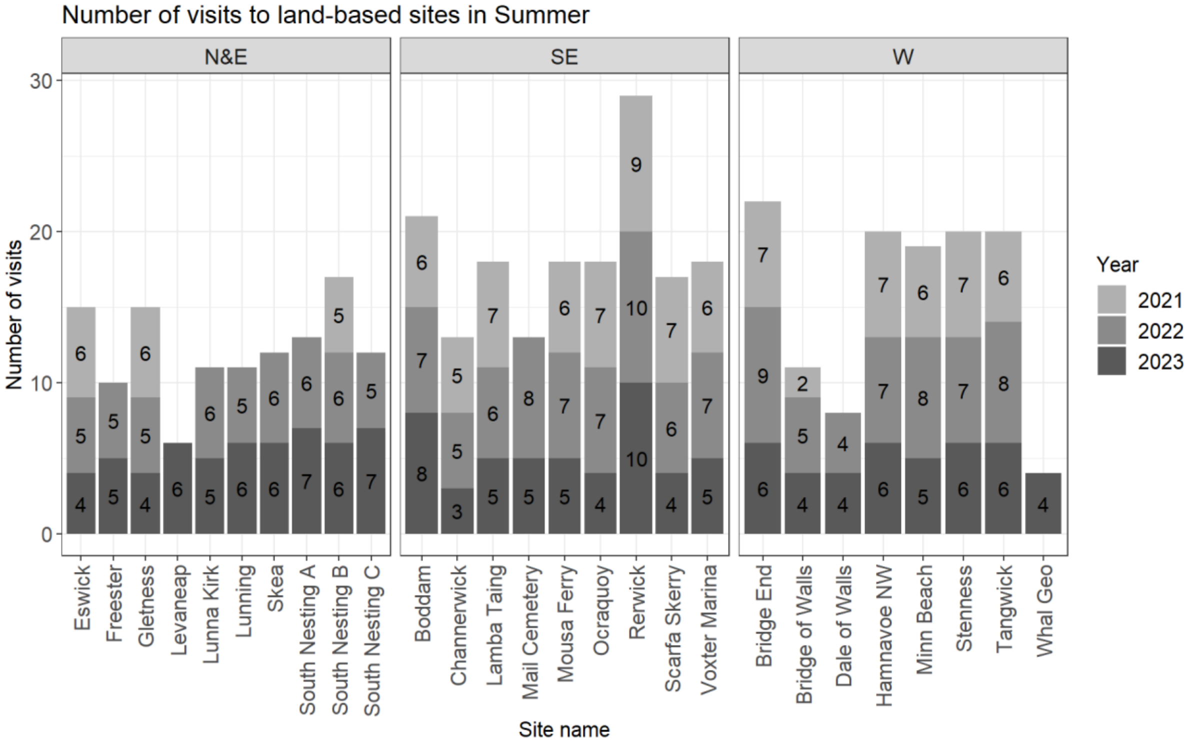
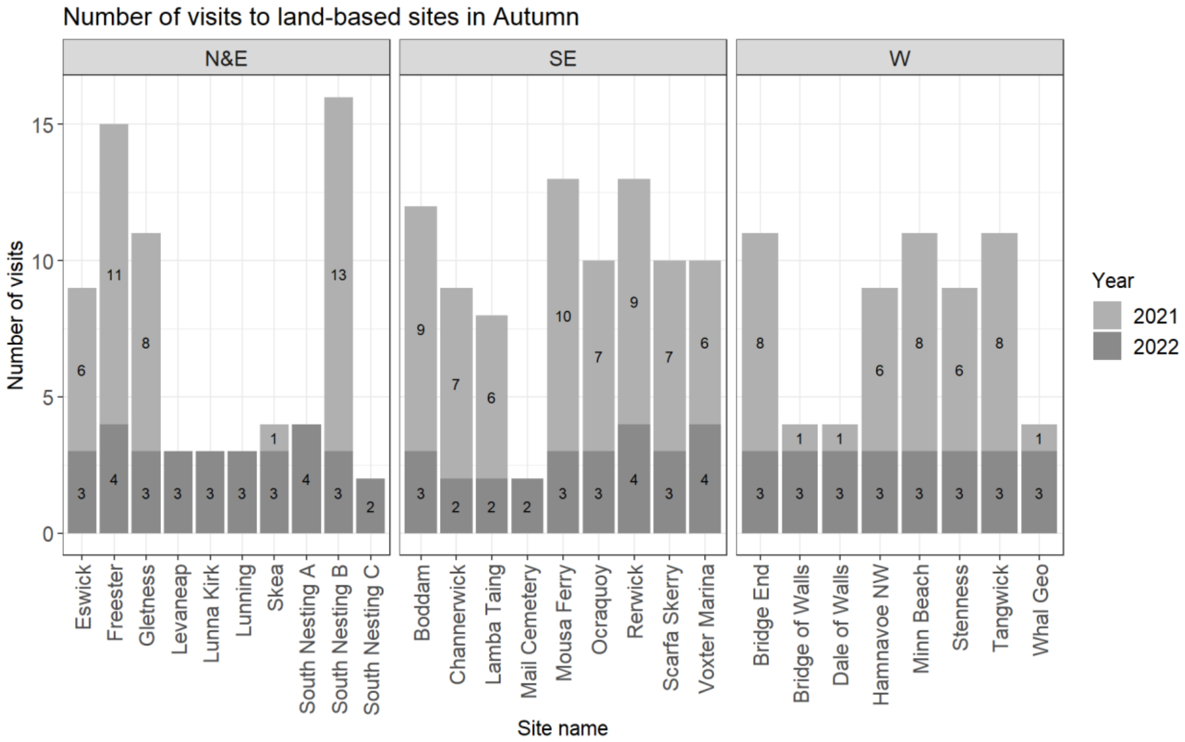


Figure 2.4. Seasonal coverage of land-based survey sites in summer (2021-2023). Number of visits to land-based monitoring site during summer fieldwork.



Region	Site name	2021	2022
N&E	Eswick	6	3
N&E	Freester	11	4
N&E	Gletness	8	3
N&E	Levaneap		3
N&E	Lunna Kirk		3
N&E	Lunning		3
N&E	Skea	1	3
N&E	South Nesting A		4
N&E	South Nesting B	13	3
N&E	South Nesting C		2
SE	Boddam	9	3
SE	Channerwick	7	2
SE	Lamba Taing	6	2
SE	Mail Cemetery		2
SE	Mousa Ferry	10	3
SE	Ocraquoy	7	3
SE	Rerwick	9	4
SE	Scarfa Skerry	7	3
SE	Voxter Marina	6	4
W	Bridge End	8	3
W	Bridge of Walls	1	3
W	Dale of Walls	1	3
W	Hamnavoe NW	6	3
W	Minn Beach	8	3
W	Stenness	6	3
W	Tangwick	8	3
W	Whal Geo	1	3

Figure 2.5. Seasonal coverage of land-based survey sites in autumn (2021-2022). Number of visits to land-based monitoring site during autumn fieldwork.

2.3.1.2 KILLER WHALE SIGHTINGS & FOCAL FOLLOWS

Killer whales were observed during each of the five field seasons, with the number of sightings and follows varying between each year and season (Figures 2.6-2.8). For 2021 and 2022, the number of sightings were higher in autumn compared to summer (autumn 2021, n = 36; summer 2021, n = 27; autumn 2022, n = 51, summer 2022, n = 46) (Figure 2.6). Summer 2023 had the highest number of sightings out of all field seasons (n=116) (Figure 2.6). The number of focal follows across field seasons varied between a minimum of two and a maximum of five (autumn 2021 n = 2; summer 2021, n = 3; autumn 2022, n = 3; summer 2022, n = 4; summer 2023, n = 5) (Figures 2.7 – 2.8), with the number of sightings within each follow ranging from a minimum of three to a maximum of 29. Focal follows typically occurred on different days, however two follows were conducted on the same day once in summer 2022 (one a lone bull ID 018, and one of the 27s pod) and once in summer 2023 (both the same pod, 64s) (Figures 2.7 – 2.8).

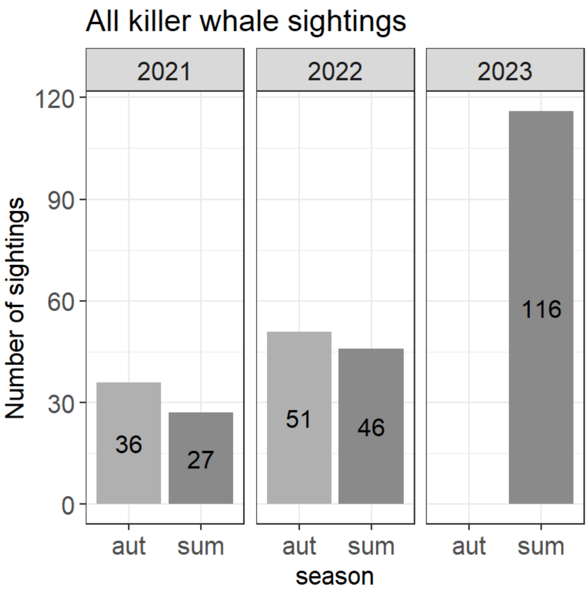


Figure 2.6. Summary of killer whale sightings in field seasons (2021-2023). Where aut = autumn, and sum = summer. Note only a summer field seasons was conducted in 2023.

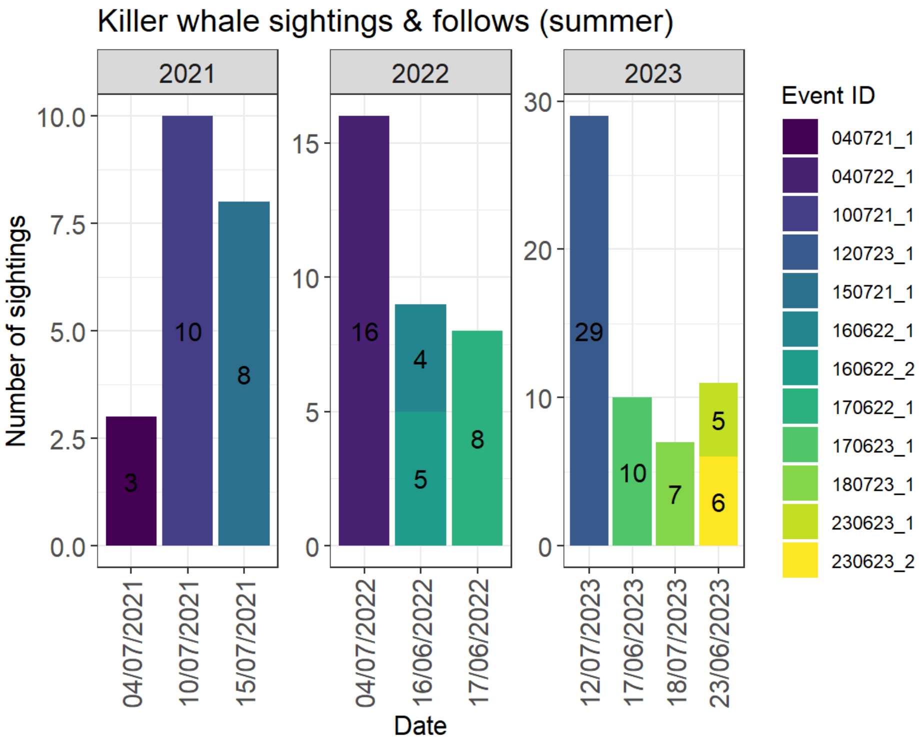


Figure 2.7. Summary of killer whale follows conducted in summer field seasons (2021-2023). Number in bars denote the number of sightings in each follow event. Event ID formatted as day, month, year, follow number (ddmmyy_#). Note different Y axis scale on each facet of plot.

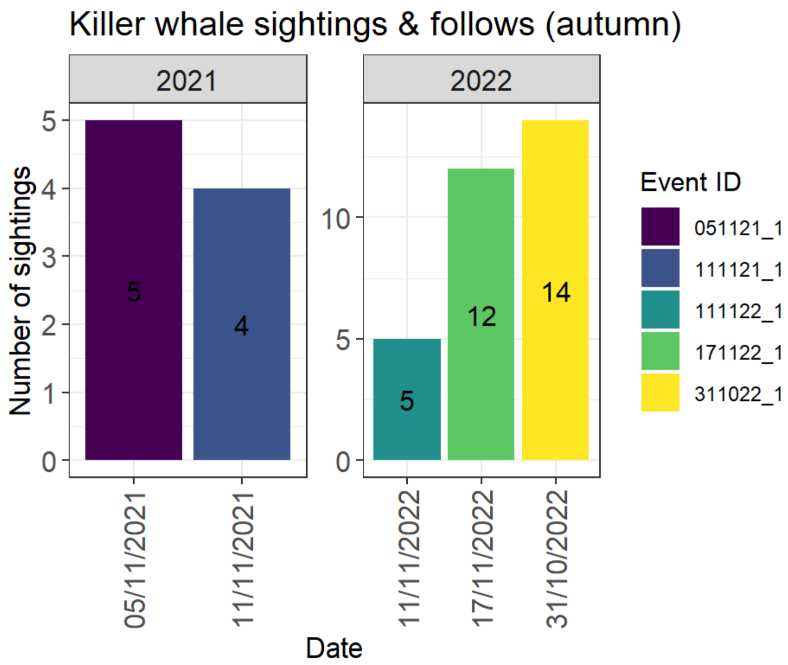


Figure 2.8. Summary of killer whale follows conducted in autumn field seasons (2021-2022). Number in bars denote the number of sightings in each follow event. Event ID formatted as day, month, year, follow number (ddmmyy_#). Note different Y axis scale on each facet of plot.

2.3.2 Variation in seal counts

2.3.2.1 SUMMARY STATISTICS

Land-based sites.

For land-based surveys, total seal counts across all SMA subregions tended to be higher in summer in comparison to autumn, though there was considerable variability between regions and years (Figure 2.9). Monitoring sites in the West SMA subregion contained the highest median number of seals, followed by the North and East and the Aoutheast regions, respectively (Figure 2.9, Tables 2.7 – 2.8). Overall, the CV was lower in summer (0.97) compared to autumn (1.04), indicating less variation in seal numbers in summer months across all field years when compared to autumn. This pattern was consistent for each SMA subregion; however, the level of variation was different across regions (SE summer = 1.01, autumn = 1.09; W summer = 0.63, autumn 0.7; NE summer = 0.93, autumn = 1.21) and indicated that variability was lowest within the west SMA subregion (Tables 2.7 – 2.8).

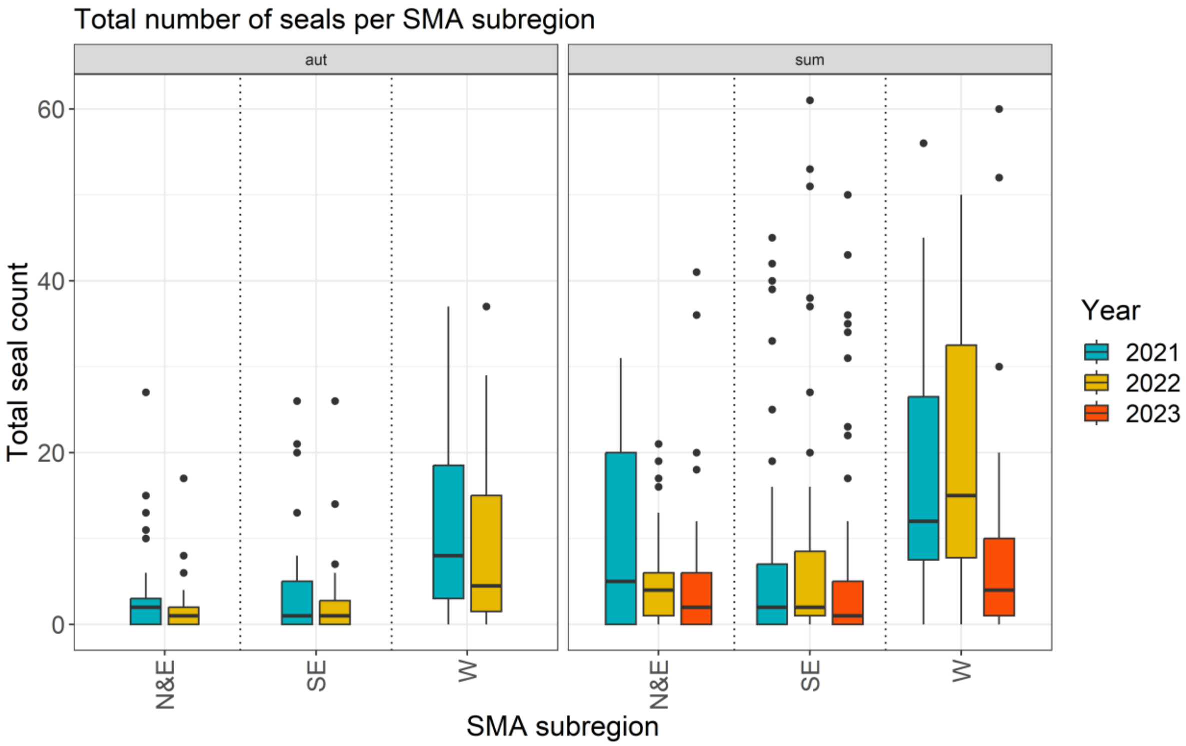


Figure 2.9. Box plot for total seal counts for land-based surveys (SMA subregions). Boxplots depicting the interquartile range (coloured box) with median (black bar), minimum and maximum (whiskers) and outliers (dots) of total seal counts for land-based sites, grouped by SMA subregion, and faceted by season and year. The total count includes both seal species counted on-water and on land. Boxplots depict the interquartile range (coloured box) with median (black bar), minimum and maximum (whiskers) and outliers (dots) of total seal counts.

Table 2.7. Summary statistics for total seal counts for land-based surveys (SMA subregions) by season. Min = minimum, max = maximum, SD = standard deviation, CV = coefficient of variation

SMA subregion	Season	Min	Mean	Median	Max	Sd	CV
N&E	Autumn	0	2.66	1	27	4.6	1.73
	Summer	0	5.68	3	41	7.78	1.37
SE	Autumn	0	3.49	1	26	5.85	1.67
	Summer	0	7.62	2	61	12.8	1.68
W	Autumn	0	10.8	6	37	11.0	1.02
	Summer	0	15.6	10	60	15.5	0.98

Table 2.8. Summary statistics for total seal counts for land-based surveys in each SMA subregion by year and season. Min = minimum, max = maximum, SD = standard deviation, CV = coefficient of variation.

SMA subregion	Year	Season	Min	Mean	Median	Max	SD	CV
N&E	2021	Autumn	0	3.23	2.00	27.00	5.36	1.66
		Summer	0	9.65	5.00	31.00	11.35	1.18
	2022	Autumn	0	1.94	1.00	17.00	3.37	1.74
		Summer	0	5.12	4.00	21.00	5.22	1.02
	2023	Summer	0	4.96	2.00	41.00	8.14	1.64
SE	2021	Autumn	0	3.75	1.00	26.00	5.96	1.59
		Summer	0	7.60	2.00	45.00	12.17	1.60
	2022	Autumn	0	2.88	1.00	26.00	5.65	1.96
		Summer	0	7.92	2.00	61.00	13.36	1.69
	2023	Summer	0	7.24	1.00	50.00	12.97	1.79
W	2021	Autumn	0	11.54	8.00	37.00	11.12	0.96
		Summer	0	17.34	12.00	56.00	14.57	0.84
	2022	Autumn	0	9.58	4.50	37.00	10.83	1.13
		Summer	0	20.65	15.00	50.00	16.10	0.78
	2023	Summer	0	8.27	4.00	60.00	12.68	1.53

Boat-based sites

For boat-based surveys, seasonal patterns varied across boat-based sites, with some sites (Lamba, Uynarey, Bigga, Little Roe, Orfasay, Samphrey, and Ungam) having higher median seal numbers in summer compared to autumn, and others (Brother Isle, Gluss, Mio Ness, Linga A, and Linga B) displaying the opposite (Figure 2.10, Table 2.9). The CV for total number of seals at boat-based sites was 0.72 compared to 0.71 in summer, indicating similar variability across both seasons (Figure 2.11).

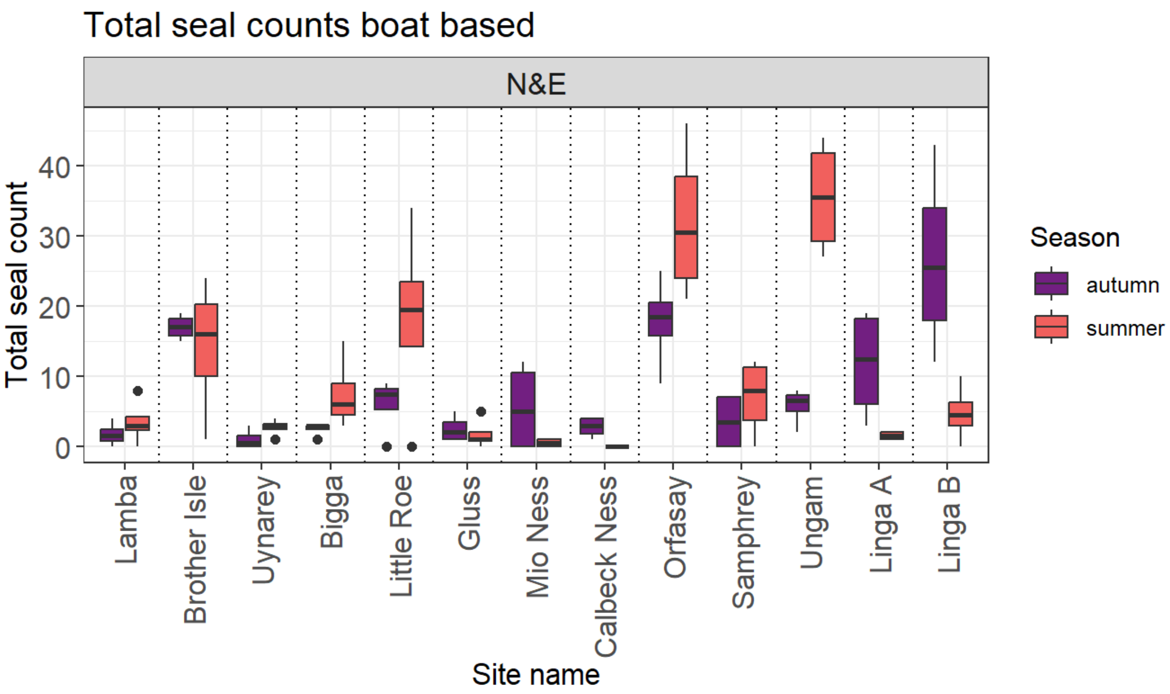


Figure 2.10. Boxplot for total seal counts for boat-based surveys. Boxplots depicting the interquartile range (coloured box) with median (black bar), minimum and maximum (whiskers) and outliers (dots) of total seal counts for land-based sites, grouped by survey site and coloured by year. The total count includes both seal species counted on-water and on land.

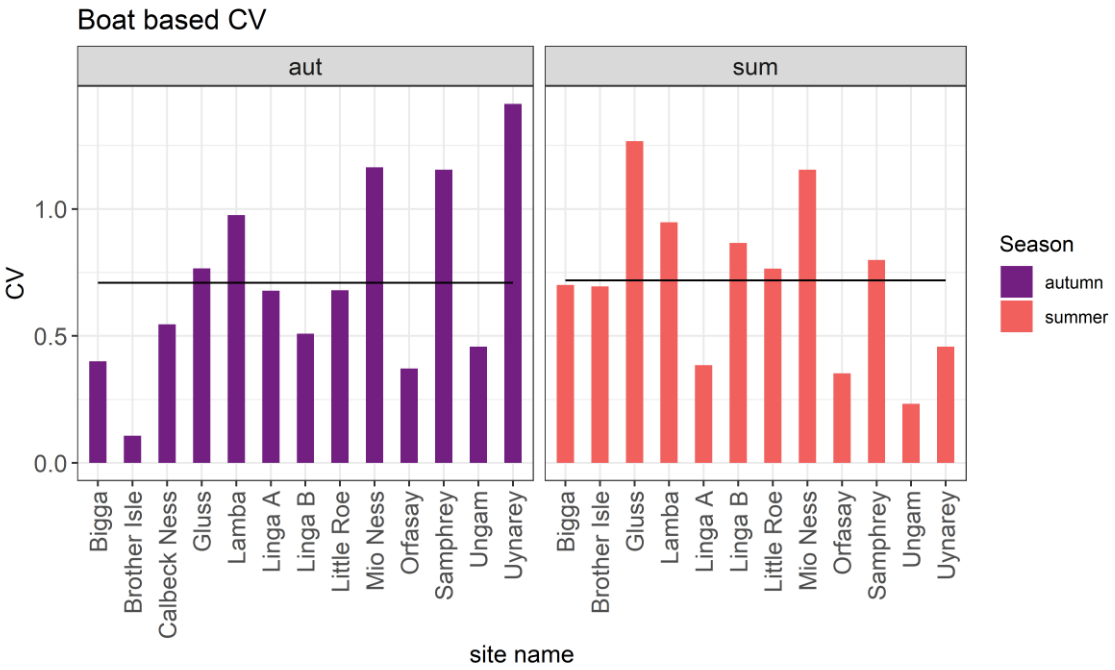


Figure 2.11. Bar chart for CV of each boat-based site, average across summer and autumn field seasons. Black line depicts mean CV for autumn and summer respective.

Table 2.9. Summary statistics for total seal counts at boat-based sites. Min = minimum, max = maximum, SD = standard deviation, CV = coefficient of variation.

Site name	Season	Min	Mean	Medan	Max	SD	CV
Bigga	Autumn	1	2.5	3	3	1.00	0.40
	Summer	3	7.5	6	15	5.26	0.70
Brother Isle	Autumn	15	17	17	19	1.83	0.11
	Summer	1	14.25	16	24	9.91	0.70
Calbeck Ness	Autumn	1	2.75	3	4	1.50	0.55
	Summer	0	0	0	0	0.00	NA
Gluss	Autumn	1	2.5	2	5	1.91	0.77
	Summer	0	1.75	1	5	2.22	1.27
Lamba	Autumn	0	1.75	1.5	4	1.71	0.98
	Summer	0	3.5	3	8	3.32	0.95
Linga A	Autumn	3	11.75	12.5	19	7.97	0.68
	Summer	1	1.5	1.5	2	0.58	0.38
Linga B	Autumn	12	26.5	25.5	43	13.48	0.51
	Summer	0	4.75	4.5	10	4.11	0.87
Little Roe	Autumn	0	6	7.5	9	4.08	0.68
	Summer	0	18.25	19.5	34	13.96	0.77
Mio Ness	Autumn	0	5.5	5	12	6.40	1.16
	Summer	0	0.5	0.5	1	0.58	1.15
Orfasay	Autumn	9	17.75	18.5	25	6.60	0.37
	Summer	21	32	30.5	46	11.28	0.35
Samphrey	Autumn	0	3.5	3.5	7	4.04	1.15
	Summer	0	7	8	12	5.60	0.80
Ungam	Autumn	2	5.75	6.5	8	2.63	0.46
	Summer	27	35.5	35.5	44	8.27	0.23
Uynarey	Autumn	0	1	0.5	3	1.41	1.41
	Summer	1	2.75	3	4	1.26	0.46

2.3.2.2 REGRESSION MODELLING

Land-based sites

To investigate regional and environmental drivers of variation in land-based counts, the following covariates were included as candidate covariates in the model selection for total number of seals: SMA subregion, year, season, sea state, precipitation (as a binary presence/absence), average windspeed, and shoreline type, with an interaction term between year and SMA subregion to investigate whether temporal trends varied across SMA subregions. Panel smooth plots and VIFs indicated correlations in model covariates which were to be expected (e.g., average windspeed and sea state, and season and sea state);

however, VIF values were less than the threshold of 3, so all covariates were retained for *dredge* model selection.

The QAIC model selection retained sea state, season, shoreline type, SMA subregion, year, and an interaction between year and SMA subregion. The selected model was the simplest model within ΔQAIC <2 that explained the data with fewest estimated parameters (Table 2.10). Overall, the final selected model explained 41% of the deviance in the data. Statistical support for each effect was assessed at the 95% significance level (Table 2.11). Sea state was a negative predictor of average number of seals, with 0.2-15% fewer seals expected for every unit increase of Beaufort sea state at 95% confidence (t=-2.0, p=0.046, Table 2.11, Figure 2.12). Higher numbers of seals were observed in summer in comparison to autumn, and fewer seals were observed in 2023 and 2022 in comparison to 2021 (Table 2.11, Figure. 2.13). Fewer seals were observed in the SE and W SMA subregion when compared to the N&E. However, the interaction term showed this trend was not consistent across years; more seals were estimated in the SE and W regions in 2022 compared to the intercept N&E region in 2021 (Table 2.11, Figure 2.15). Shoreline type of sand/gravel beach was estimated a greater number of seals on average, while sheltered rocky rubble shores and sheltered tidal flats were estimated to have fewer seals in comparison to rocky cliffs and bedrock (Figure 2.14).

Table 2.10. Model 1: GLM model selection for land-based surveys. Table shows the most parsimonious models based on QAIC (delta QAIC <2) from *dredge* model selection. The final model is highlighted in grey.

Response	Model	Covariates retained	Df	QAIC	Delta QAIC	Weight
Seal total	A	Precipitation + sea state + season + shoreline type + SMU region + average windspeed + year + SMU region: year	17.000	860.867	0.000	0.252
Seal total	B	sea state + season + shoreline type + SMU region + average windspeed + year + SMU region: year	16.000	861.100	0.233	0.225
Seal total	C	Precipitation + sea state + season + shoreline type + SMU region + year + SMU region: year	16.000	861.123	0.256	0.222
Seal total	D	Sea state + season + shoreline type + SMU region + year + SMU region: year	15.000	861.289	0.422	0.204
Seal total	E	Precipitation + season + shoreline type + SMU region + year + SMU region: year	15.000	862.785	1.918	0.97

Table 2.11. Model 1: GLM model output for land-based surveys. Where the intercept is autumn; NE; 2021; and rocky cliffs and bedrock.

	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	3.009786	0.244498	12.31005	2.70E-31	***
sea_state	-0.08661	0.043285	-2.00099	0.045831	*
seasonsum	0.630142	0.115393	5.460851	6.88E-08	***
Shoreline.type_descSand / gravel beach	0.264333	0.122235	2.162489	0.030964	*
Shoreline.type_descSheltered rocky rubble shores	-1.48691	0.132455	-11.2258	9.73E-27	***
Shoreline.type_descSheltered tidal flats	-2.70062	0.466475	-5.78943	1.12E-08	***
SMU_regionSE	-0.6891	0.232924	-2.95848	0.00321	**
SMU_regionW	-0.60692	0.243693	-2.49053	0.013017	*
year2022	-0.71734	0.255654	-2.80591	0.005176	**
year2023	-0.66152	0.265923	-2.48762	0.013123	*
SMU_regionSE:year2022	0.806344	0.309557	2.604832	0.009413	**
SMU_regionW:year2022	0.855241	0.284479	3.006344	0.002752	**
SMU_regionSE:year2023	0.48766	0.327603	1.488572	0.137111	
SMU_regionW:year2023	-0.13776	0.322438	-0.42724	0.669353	
Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1					
40.55% deviance explained					

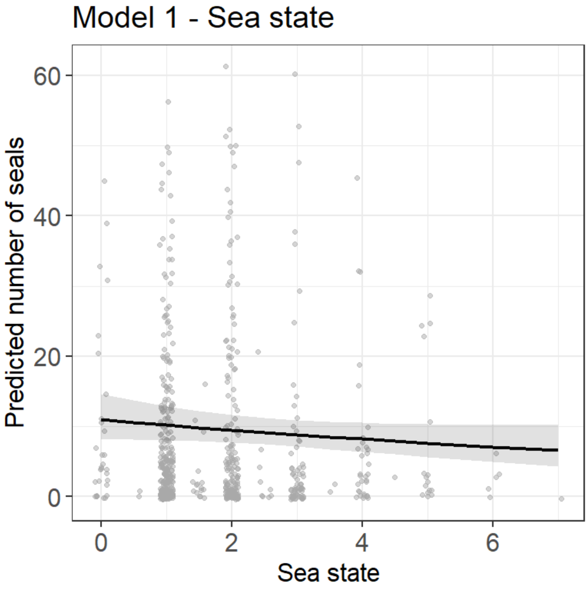


Figure 2.12. Model predictions for the effect of sea state on total number of seals. Model predictions are conditional on model reference levels, here adjusted for season = autumn, shoreline = rocky cliffs & bedrock, SMA subregion = N&E, and year = 2021. Ribbons depicted upper and lower 95% confidence intervals, and grey dots depict the raw data.

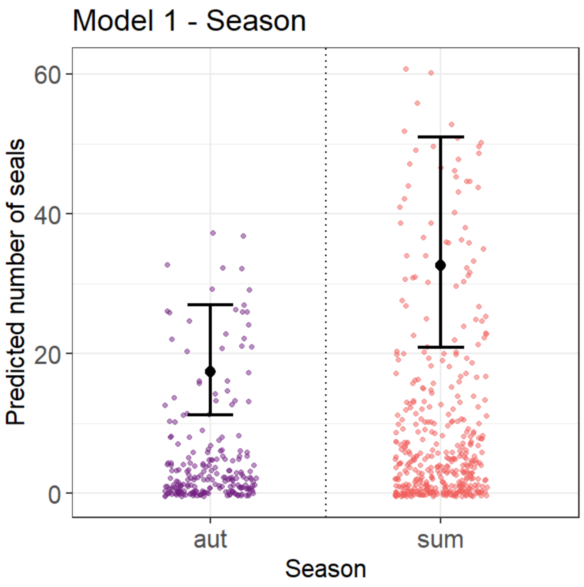


Figure 2.13. Model predictions for the effect of season on total number of seals. Predictions are conditional on model reference levels, here adjusted for sea state = 1.79 shoreline = rocky cliffs & bedrock, SMA subregion = N&E, and year = 2021. Error bars depict the upper and lower 96% confidence intervals with mean as a black dot. Colour dots depict raw data points.

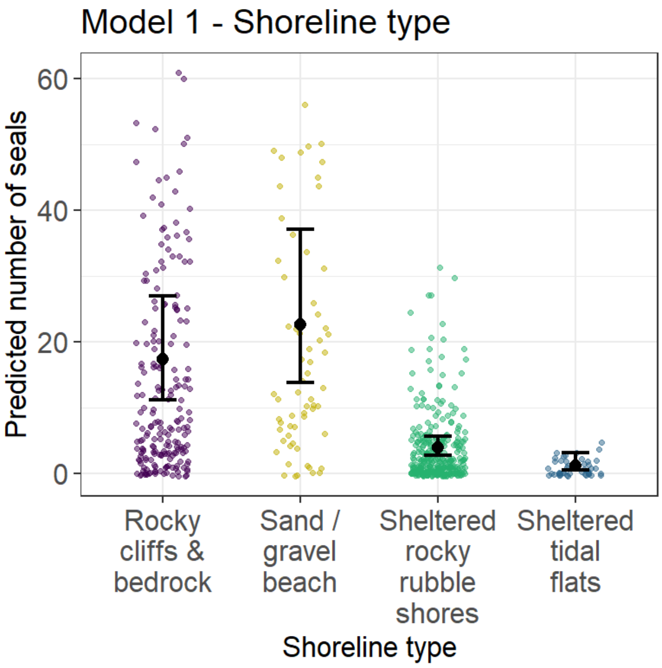


Figure 2.14. Model predictions for the effect shoreline type on total number of seals. Predictions are conditional on model reference levels, here adjusted for sea state = 1.79, season = autumn, SMA subregion = N&E, and year = 2021. Error bars depict the upper and lower 96% confidence intervals with mean as a black dot. Colour dots depict raw data points.

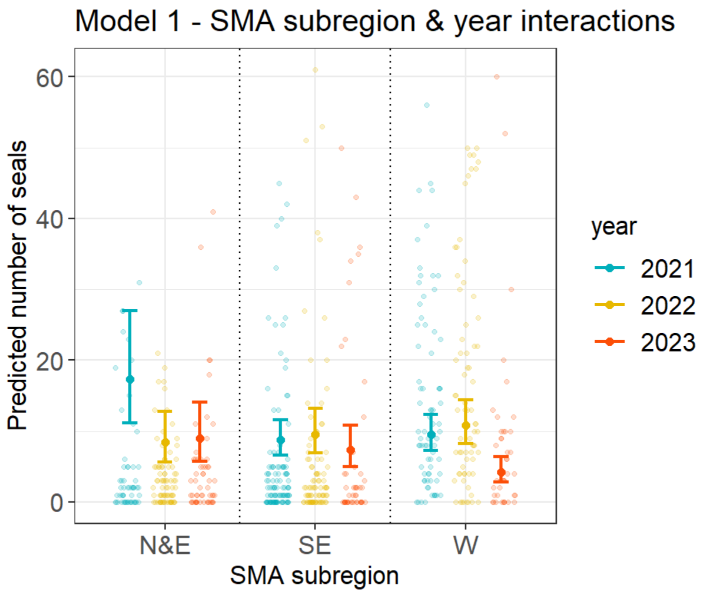


Figure 2.15. Model predictions for the effect of the interaction between SMA subregion and year on total number of seals. Model predictions are conditional on model reference levels, here adjusted for sea state = 1.79 shoreline = rocky cliffs & bedrock, season = autumn. Error bars depict the upper and lower 96% confidence intervals with mean as a dot. Colour dots depict raw data points.

Boat-based sites

To investigate spatial and environmental variation in boat-based counts, the following candidate covariates were included in model selection: sea state, precipitation, wind force, season, shoreline type and site. An interaction term between season and site was included to investigate varying seasonal trends within sites. All boat-based survey sites were within the N&E SMA subregion, so region was not included in the model. Surveys were only conducted in autumn 2022 and summer 2023, so year was not included (as season was captured instead). Wind speed was collected in-situ for all boat-based surveys, and so was retained for this data set. VIF calculations indicated strong correlation between variables, and upon examination of the data shoreline type and site were strongly correlated (because each site only contained one shoreline type). ESI shoreline types were not well represented in the data, with only one site for sheltered tidal flats (ESI 9&10), two for rock and manmade (ESI 1&2), and 10 for sheltered rocky rubble shores (ESI 8). Site location was therefore retained as a predictor variable and shoreline type removed. An interaction term was included for season and location to investigate varying temporal trends across sites.

Following QAIC model selection, the final model retained location, season, and the interaction term between location and season (Table 2.12). Overall, the model explained 75% of the deviance in the dataset. Although retained in the model, the seasonal contrast did not gain statistical support at the 95% level, but did meet at 90% (p=0.078) with more seals observed in summer compared to autumn. Brother Isle, Linga A, Linga B and Orfasay were positive predictors of seal total (Table 2.13, Figure 2.13). For the interaction term, fewer seals were observed at Linga A, Linga B and Mio Ness in summer when compared to autumn (Table 2.13, Figure 2.13).

Table 2.12 Model 2: GLM model selection for boat-based sites. Table shows the most parsimonious models based on QAIC (delta QAIC <2) from *dredge* model selection. The final model is highlighted in grey.

Response	Model	Covariates retained	Df	QAIC	Delta QAIC	Weight
Seal total	A	Site + season + site: season	27	216.111	0.000	0.332
Seal total	B	Site + sea state + season + site:season	29	216.514	0.403	0.271
Seal total	C	Ste + sea state + season + wind speed + site:season	30	217.750	1.639	0.146
Seal total	D	Site + season + wind speed + site:season	28	218.051	1.940	0.126
Seal total	E	Site + precipitation + season + site:season	28	218.078	1.968	0.124

Table 2.13. Model 2: Model output for boat-based surveys

Where in intercept is autumn and Bigga.

	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	0.916291	0.55468	1.651926	0.10257	
loc_nameBrother Isle	1.916923	0.594067	3.226778	0.001831	**
loc_nameCalbeck Ness	0.09531	0.766401	0.124361	0.90135	
loc_nameGluss	3.67E-15	0.784436	4.68E-15	1	
loc_nameLamba	-0.35667	0.864407	-0.41262	0.681014	
loc_nameLinga A	1.547563	0.610845	2.533477	0.013299	*
loc_nameLinga B	2.360854	0.580255	4.068651	0.000112	***
loc_nameLittle Roe	0.875469	0.660202	1.326063	0.188689	
loc_nameMio Ness	0.788457	0.66897	1.178615	0.242135	
loc_nameOrfasay	1.960095	0.592456	3.308423	0.001421	**
loc_nameSamphrey	0.336472	0.726247	0.463303	0.644437	
loc_nameUngam	0.832909	0.664409	1.253608	0.213729	
loc_nameUynarey	-0.91629	1.037712	-0.88299	0.379954	
Seasonsum	1.098612	0.64049	1.71527	0.090266	.
loc_nameBrother Isle:seasonsum	-1.27507	0.713757	-1.78642	0.077918	.
loc_nameCalbeck Ness:seasonsum	-18.4128	1844.705	-0.00998	0.992062	
loc_nameGluss:seasonsum	-1.45529	1.075837	-1.3527	0.180059	
loc_nameLamba:seasonsum	-0.40547	1.034176	-0.39207	0.696079	
loc_nameLinga A:seasonsum	-3.157	0.994219	-3.17536	0.002143	**
loc_nameLinga B:seasonsum	-2.81761	0.775361	-3.63394	0.000498	***
loc_nameLittle Roe:seasonsum	0.013793	0.761951	0.018103	0.985603	
loc_nameMio Ness:seasonsum	-3.49651	1.445139	-2.4195	0.01787	*
loc_nameOrfasay:seasonsum	-0.50926	0.691084	-0.7369	0.463392	
loc_nameSamphrey:seasonsum	-0.40547	0.860159	-0.47138	0.638682	
loc_nameUngam:seasonsum	0.721721	0.752106	0.9596	0.340222	
loc_nameUynarey:seasonsum	-0.08701	1.207933	-0.07203	0.94276	

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75% deviance explained

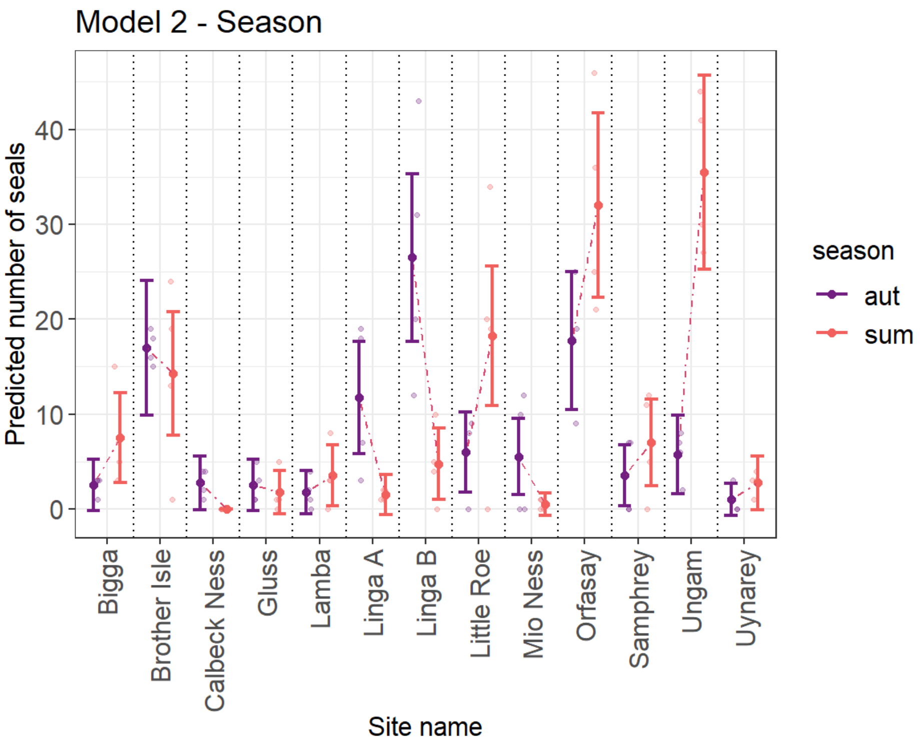

Figure 2.13. Model prediction for the effect of an interaction between location and season on total seal numbers. Location was a significant at the 95% level for Brother Isle, Linga A, Linga B, and Orfasay in comparison to the intercept of Bigga. For the interaction term, Linga A, Linga B and Mio Ness were estimated to have fewer seals in summer in comparison to autumn. Error bars depict the upper and low 95% confidence interval, with colour dot depiction the mean. Coloured dots depict the raw data, and dashed joining line depict direction of difference in mean between seasons at each location.

2.3.3 Variation in haul-out composition

2.3.3.1 SUMMARY STATISTICS

Land-based sites.

For land-based surveys, harbour seals were more numerous (higher median) than grey seals across all SMA subregions, both in summer and autumn (Figure. 2.14, Table 2.14 – 2.15). Both species had a higher mean in summer compared to autumn (harbour seal summer mean = 7.6, grey seal = 1.3; harbour seal autumn mean = 3.5, grey seal = 0.8), and a lower CV in summer compared to autumn (harbour seal summer CV = 1.4, grey seal = 2.7; harbour seal autumn CV = 1.9, grey seal = 3.1). CVs would suggest more consistent numbers of both species were observed during the summer seasons across all years, with harbours being more consistently observed than grey across both seasons. The number of 'unknown' seals observed was the highest in 2021 (summer mean = 1.6, autumn = 1.7) as the counts were carried out without a scope to aid ID of species at distant haul-outs during this first year.

Table 2.14. Summary for harbour seal at land-based sites. Min = minimum, max = maximum, SD = standard deviation, CV = coefficient of variation.

SMA subregion	season	year	Min	Mean	Medan	Max	SD	CV
N&E	autumn	2021	0	1.92	1	13	3.34	1.74
		2022	0	1.61	0	15	3.12	1.93
	summer	2021	0	8.53	4	30	10.42	1.22
		2022	0	4.59	3	21	5.17	1.13
	summer	2023	0	4.84	1.5	41	8.19	1.69
SE	autumn	2021	0	2.66	1	26	5.05	1.90
		2022	0	1.96	0	24	4.88	2.49
	summer	2021	0	6.66	2	45	11.49	1.73
		2022	0	6.03	1	51	11.29	1.87
	summer	2023	0	5.98	0	47	11.52	1.93
W	autumn	2021	0	7.10	3	37	9.91	1.40
		2022	0	6.88	1.5	37	10.55	1.53
	summer	2021	0	12.37	7	49	14.64	1.18
		2022	0	15.27	13.5	41	10.66	0.70
	summer	2023	0	7.49	4	47	10.69	1.43

Table 2.15. Summary for grey seals at land-based sites. Min = minimum, max = maximum, SD = standard deviation, CV = coefficient of variation.

SMA subregion	season	year	Min	Mean	Medan	Max	SD	CV
N&E	autumn	2021	0	0.18	0	5	0.82	4.59
		2022	0	0.32	0	2	0.60	1.86
	summer	2021	0	0.00	0	0	0.00	NA
		2022	0	0.41	0	5	1.04	2.55
	summer	2023	0	0.13	0	2	0.38	3.07
SE	autumn	2021	0	0.64	0	9	1.46	2.29
		2022	0	0.92	0	6	1.67	1.81
	summer	2021	0	0.81	0	15	2.42	2.98
		2022	0	1.89	1	18	3.55	1.88
	summer	2023	0	1.27	0	12	2.62	2.07
W	autumn	2021	0	0.79	0	5	1.15	1.45
		2022	0	2.71	0	29	6.17	2.28
	summer	2021	0	0.66	0	7	1.55	2.36
		2022	0	4.81	0.5	33	7.60	1.58
	summer	2023	0	0.78	0	15	2.50	3.20

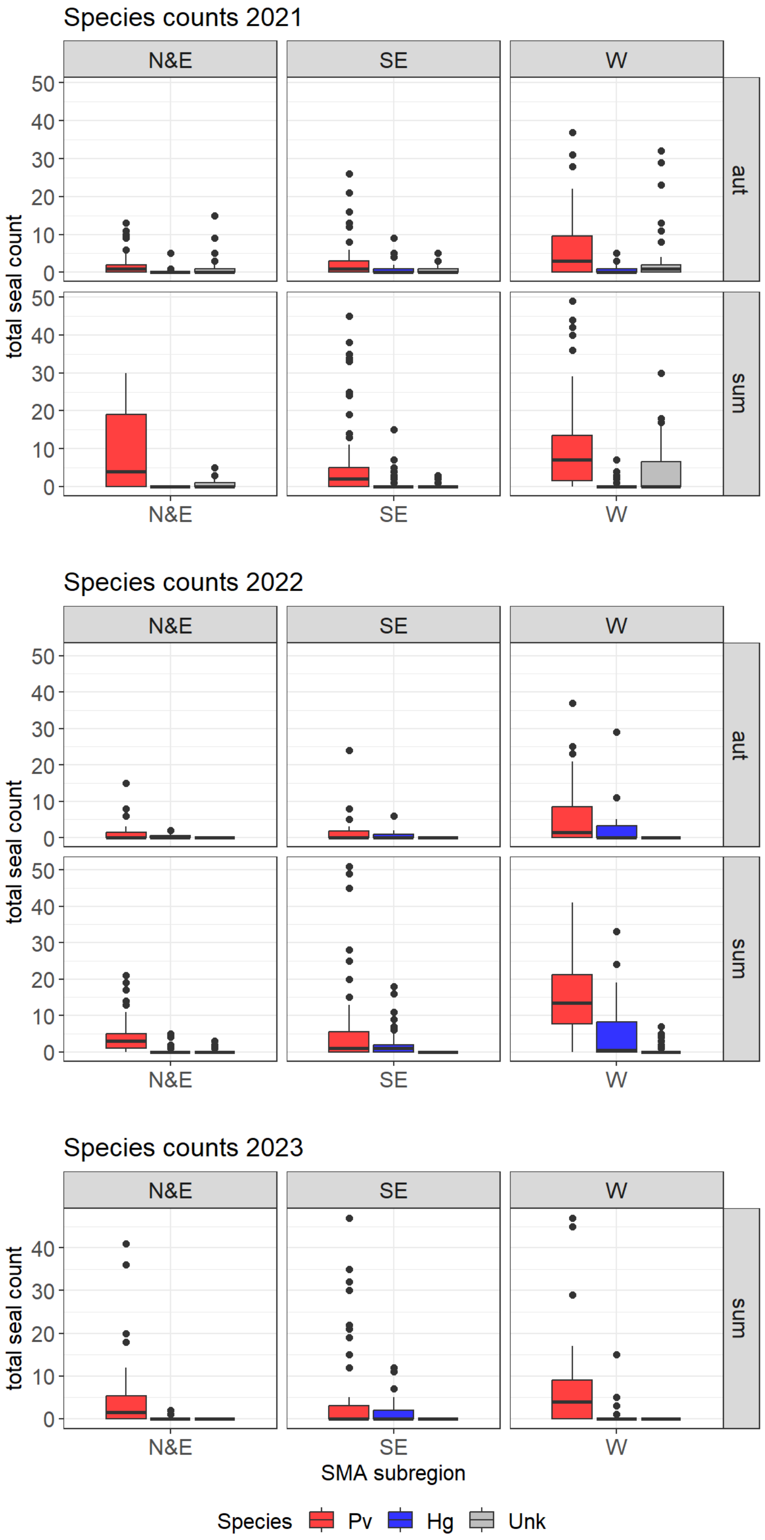

Figure 2.14. Box plot for total species counts for land-based surveys (SMA subregions) 2021-2023.Boxplots depicting the interquartile range (coloured box) with median (black bar), minimum and maximum (whiskers) and outliers (dots) of total harbour and grey seal counts for land-based sites, grouped by SMA subregion and coloured by species.

Boat-based sites.

For boat-based surveys, overall, harbour seals had a higher mean in both summer and autumn compared to grey seals (harbour summer mean = 7.5, grey seal = 2.4; harbour seal autumn mean = 4.7, grey seal = 3.3) (Figure 2.15, Table 2.16 – 2.17). The CV of grey seals was the same across summer and autumn months (1.69), with the CV of harbour seals lower in summer (1.37) compared to autumn (1.54). However, patterns of species composition varied at individual boat-based sites between seasons. In autumn, harbour seals were more numerous (higher median) at all sites with the exception of one (Brother Isle) which was a grey seal pupping site (Figure 2.15, Table 2.16 – 2.17). In summer, harbour seals were more numerous at 6 (Lamba, Brother Isle, Little Roem Gluss, Orfasay, and Ungam) out of the 12 sites, with grey seals more numerous at the others (Uynarey, Bigga, Mio Ness, Samphrey, Linga A and Linga B) (Figure 2.15, Table 2.16 – 2.17).

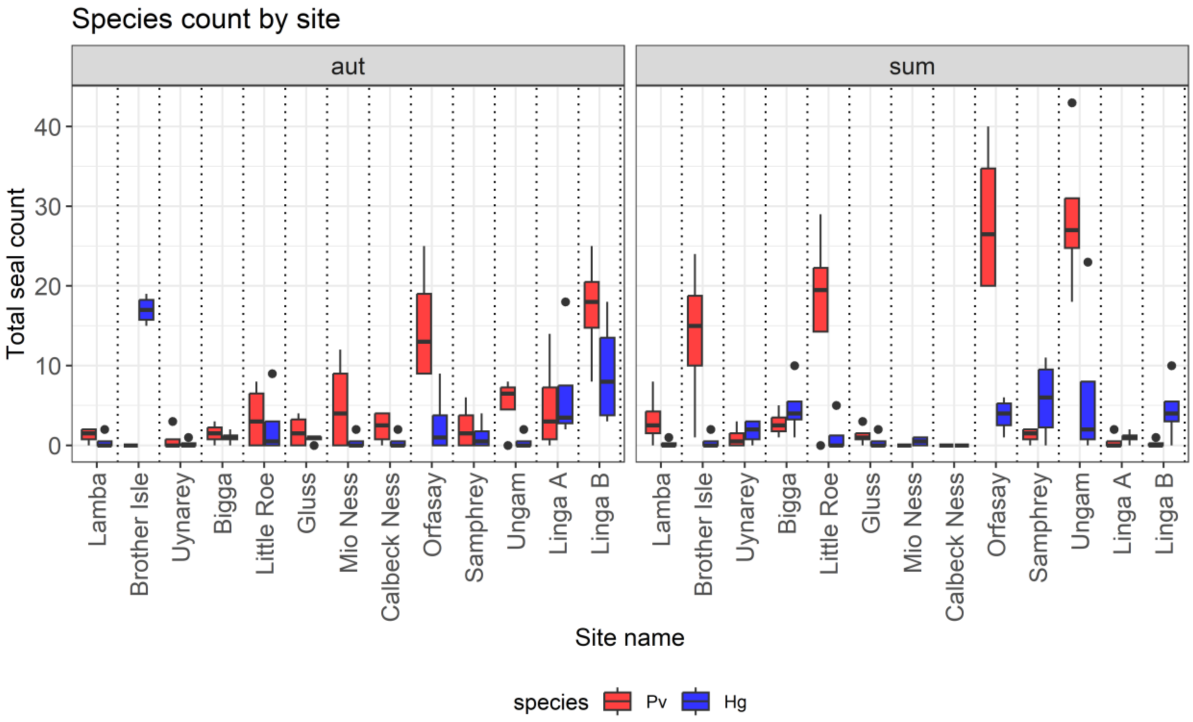

Figure 2.15. Total species counts for boat-based surveys (SMA subregions) 2021-2023. Boxplots depicting the interquartile range (coloured box) with median (black bar), minimum and maximum (whiskers) and outliers (dots) of total harbour and grey seal counts for land-based sites, grouped season and coloured by species.

Table 2.16. Summary statistics grey seals at boat-based sites. Min = minimum, max = maximum, SD = standard deviation, CV = coefficient of variation

Site	season	Min	Mean	Medan	Max	SD	CV
Bigga	Autumn	0	1	1	2	0.82	0.82
	Summer	1	4.75	4	10	3.77	0.79
Brother Isle	Autumn	15	17	17	19	1.83	0.11
	Summer	0	0.5	0	2	1.00	2.00
Calbeck Ness	Autumn	0	0.5	0	2	1.00	2.00
	Summer	0	0	0	0	0.00	NA
Gluss	Autumn	0	0.75	1	1	0.50	0.67
	Summer	0	0.5	0	2	1.00	2.00
Lamba	Autumn	0	0.5	0	2	1.00	2.00
	Summer	0	0.25	0	1	0.50	2.00
Linga A	Autumn	2	6.75	3.5	18	7.54	1.12
	Summer	0	1	1	2	0.82	0.82
Linga B	Autumn	3	9.25	8	18	7.09	0.77
	Summer	0	4.5	4	10	4.12	0.92
Little Roe	Autumn	0	2.5	0.5	9	4.36	1.74
	Summer	0	1.25	0	5	2.50	2.00
Mio Ness	Autumn	0	0.5	0	2	1.00	2.00
	Summer	0	0.5	0.5	1	0.58	1.15
Orfasay	Autumn	0	2.75	1	9	4.27	1.55
	Summer	1	3.75	4	6	2.22	0.59
Samphrey	Autumn	0	1.25	0.5	4	1.89	1.51
	Summer	0	5.75	6	11	5.12	0.89
Ungam	Autumn	0	0.5	0	2	1.00	2.00
	Summer	0	6.75	2	23	10.90	1.62
Uynarey	Autumn	0	0.25	0	1	0.50	2.00
	Summer	0	1.75	2	3	1.50	0.86

Table 2.17. Summary statistics harbour seals at boat-based sites. Min = minimum, max = maximum, SD = standard deviation, CV = coefficient of variation

Site	season	Min	Mean	Medan	Max	SD	CV
Bigga	Autumn	0	1.5	1.5	3	1.29	0.86
	Summer	1	2.75	2.5	5	1.71	0.62
Brother Isle	Autumn	0	0	0	0	0.00	NA
	Summer	1	13.75	15	24	9.64	0.70
Calbeck Ness	Autumn	0	2.25	2.5	4	2.06	0.92
	Summer	0	0	0	0	0.00	NA
Gluss	Autumn	0	1.75	1.5	4	2.06	1.18
	Summer	0	1.25	1	3	1.26	1.01
Lamba	Autumn	0	1.25	1.5	2	0.96	0.77
	Summer	0	3.25	2.5	8	3.40	1.05
Linga A	Autumn	0	5	3	14	6.38	1.28
	Summer	0	0.5	0	2	1.00	2.00
Linga B	Autumn	8	17.25	18	25	7.04	0.41
	Summer	0	0.25	0	1	0.50	2.00
Little Roe	Autumn	0	3.5	3	8	4.12	1.18
	Summer	0	17	19.5	29	12.19	0.72
Mio Ness	Autumn	0	5	4	12	6.00	1.20
	Summer	0	0	0	0	0.00	NA
Orfasay	Autumn	9	15	13	25	7.66	0.51
	Summer	20	28.25	26.5	40	9.95	0.35
Samphrey	Autumn	0	2.25	1.5	6	2.87	1.28
	Summer	0	1.25	1.5	2	0.96	0.77
Ungam	Autumn	0	5.25	6.5	8	3.59	0.68
	Summer	18	28.75	27	43	10.40	0.36
Uynarey	Autumn	0	0.75	0	3	1.50	2.00
	Summer	0	1	0.5	3	1.41	1.41

2.3.3.3 REGRESSION MODELLING

Land-based sites.

To investigate potential drivers of haul-out species composition at land-based sites, the following candidate covariates were included in model selection to predict the proportion of harbour seals: SMA sub-region, sea state, precipitation, average windspeed, year, season, shoreline type, and harbour seal pupping sites (presence/absence of pups at each site each year). An interaction term between year and SMA subregion was included to allow for different temporal trends between regions.

Following QAIC model selection, the final model contained precipitation, harbour seals using the site for pupping (presence/absence), shoreline type, SMA subregion, year, and the interaction term between SMA sub-region and year (Table 2.18). The final model explained 21% of the deviance in the dataset. The proportion of hauled-out harbour seals was estimated to be lower in the presence of precipitation (Table 2.19, Figure 2.16). A statistically significant difference was also found between harbour seal pupping versus other sites, with a higher proportion of harbour seals estimated in sites with pups that year (t=3.3, p<0.001, Table 2.19, Figure 2.17). A significantly lower proportion was predicted for sheltered rocky rubble shores (t=-2.84, p=<0.01) (Table 2.19, Figure 2.18). The west SMA subregion was estimated to have a lower proportion of harbour seals than NE, while no statistical support was found for a difference between NE and SE (Table 2.19) A significantly higher proportion was predicted for 2023 and 2022 than 2021; however the interaction term also showed differences across the SMA subregion significantly lower proportion of harbour seals was predicted in 2023 in the SE region in comparison to 2021 and 2022 (Table 2.19, Figure 2.19).

Table 2.18. Model 3: Model selection (with interaction) for land-based sites. Table shows the most parsimonious models based on QAIC (delta QAIC <2) from *dredge* model selection. The final model is highlighted in grey.

Response	Model	Covariates retained	Df	QAIC	Delta QAIC	Weight
Pv proportion	A	Precipitation + Pv_pupping + sea state + season + Shore line type + SMU region + year + SMU_region:year	17	645.11	0.00	0.44
Pv proportion	B	Precipitation + Pv_pupping + sea state + Shore line type + SMU region + year + SMU_region:year	16	645.36	0.25	0.39
Pv proportion	C	Precipitation + Pv_pupping + sea state + season + Shore line type + SMU region + average wind speed + year + SMU_region:year	18	647.01	1.90	0.17

Table 2.19. Model 3: Model output for QAIC-selected model (with interaction) for land-based sites

Where the intercept is rocky cliffs & bedrock; 2021; and NE.

	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	1.7011	0.439	3.866	0.00012	***
precipitation1	-0.51708	0.196	-2.626	0.00890	**
Pv_pupping1	0.610	0.184	3.314	0.0009	***
sea_state	-0.278	0.069	-3.984	7.86E-05	***
Shoreline.type_descSand / gravel beach	0.751	0.211	3.550	0.0004	***
Shoreline.type_descSheltered rocky rubble shores	-0.66	0.2348	-2.826	0.0049	**
Shoreline.type_descSheltered tidal flats	-0.787	0.789	-0.997	0.3191	
SMU_regionSE	-0.197	0.395	-0.500	0.6171	
SMU_regionW	-1.153	0.394	-2.921	0.0036	**
year2022	1.225	0.495	2.473	0.0137	*
year2023	2.462	0.839	2.933	0.0035	**
SMU_regionSE:year2022	-1.204	0.574	-2.098	0.0364	*
SMU_regionW:year2022	-0.669	0.534	-1.251	0.2112	
SMU_regionSE:year2023	-2.449	0.909	-2.691	0.0073	**
SMU_regionW:year2023	-0.718	0.935	-0.768	0.4424	
Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1					
20.7% deviance explained					

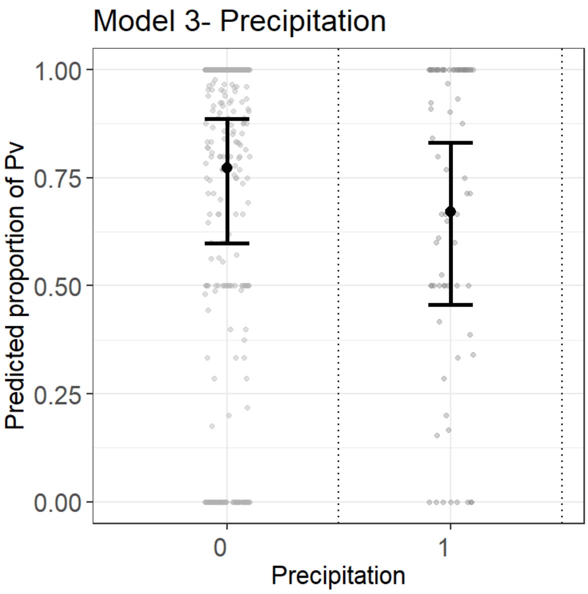

Figure 2.16. Model predictions for the effect of precipitation on the proportion of harbour seals (Pv). Model predictions are conditional on model reference levels, adjusted here for harbour seal pupping location = absent, sea state = 1.7, shoreline type = rocky cliffs and bedrock, SMA subregion = N&E and year = 2021. Error bars depict the upper and lower 96% confidence intervals with mean as a black dot. Grey dots depict raw data points.

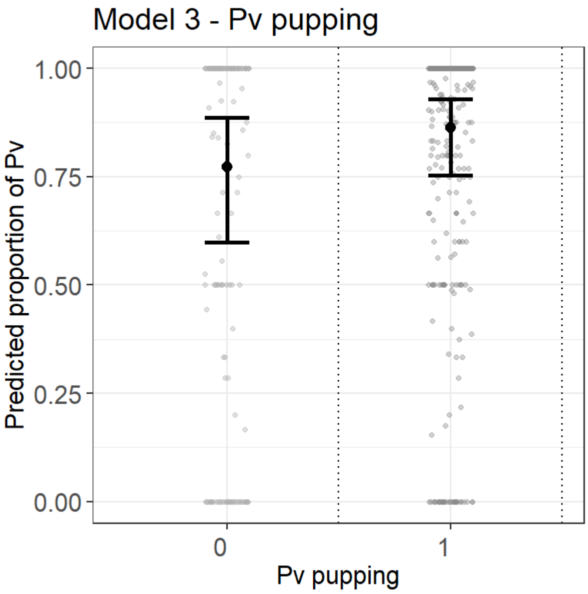

Figure 2.17. Model predictions for the effect of harbour seal pupping location on proportion of harbour seals (Pv). Model predictions are conditional on model reference levels, adjusted here for precipitation = absent, sea state = 1.7, shoreline type = rocky cliffs and bedrock, SMA subregion = N&E and year = 2021. Error bars depict the upper and lower 96% confidence intervals with mean as a black dot. Grey dots depict raw data points.

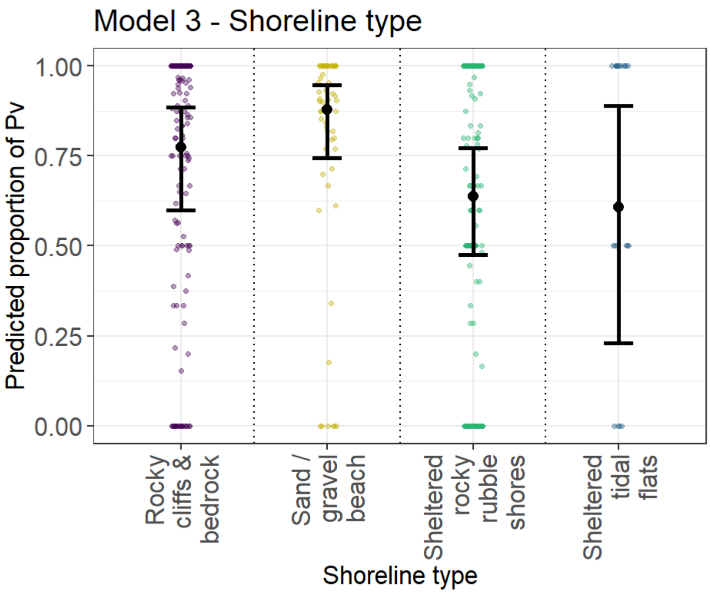

Figure 2.18. Model predictions for the effect shoreline type on proportion of harbour seals (Pv). Model predictions are conditional on model reference levels, adjusted here for precipitation = absent, sea state = 1.7, pupping site = absent, SMA subregion = N&E and year = 2021. Error bars depict the upper and lower 96% confidence intervals with mean as a black dot. Coloured dots depict raw data points.

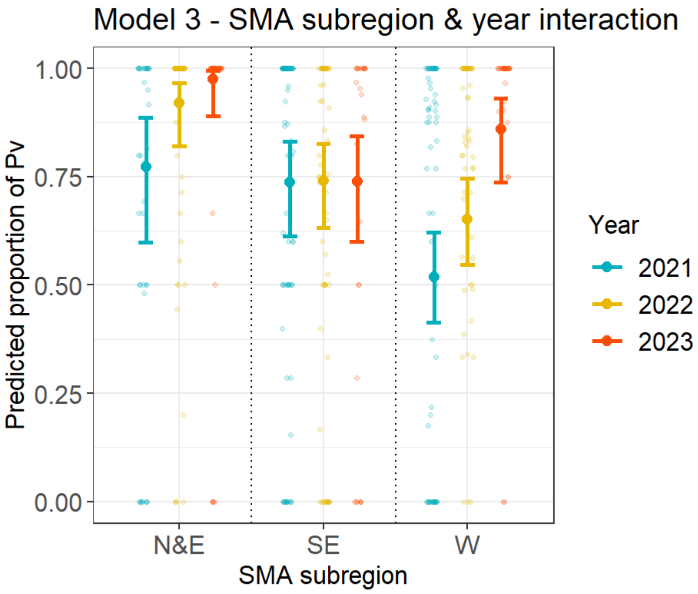

Figure 2.19. Model predictions for the interactive effect of SMA subregion and year on proportion of harbour seals (Pv). Model predictions are conditional on model reference levels, adjusted here for precipitation = absent, sea state = 1.7, pupping site = absent, shoreline type = rocky cliffs & bedrock. Error bars depict the upper and lower 96% confidence intervals with mean as a black dot. Coloured dots depict raw data points.

Boat-based sites.

To investigate potential drivers of haul-out species composition at boat-based sites, the following candidate covariates were included in model selection for boat-based surveys: shoreline type, sea state, precipitation, wind speed, season, harbour seal pup presence/absence and an interaction term between shoreline type and season to allow for difference temporal trends.

Following QAIC model selection, the final best fitting model retained harbour seal pupping, season, shoreline type, and an interaction between season and shoreline type (Table 2.20). The proportion of harbour seals was predicted to be higher in the presence of harbour seal pups (Table 2.21, Figure 2.20). A statistically significant difference was found between summer and autumn, with a high proportion of harbour seals estimated in summer (t=3.50, $p < 0.001$) (Table 2.21). The interaction term showed differences across shoreline types between seasons, with a higher proportion of harbour seal predicted in summer for rocky cliffs and bedrock, and lower proportion in summer compared to autumn for sheltered rocky rubble shores (Table 2.21, Figure 2.21).

Table 2.20. GLM model selection (with interaction) for boat-based sites. Table shows the most parsimonious models based on QAIC (delta QAIC <2) from dredge model selection. The final model is highlighted in grey.

Response	Model	Covariates retained	Df	QAIC	Delta QAIC	Weight
Pv proportion	A	Pv pupping + seasons + shoreline type + season:shoreline type	8	103.35	0	0.445
Pv proportion	B	Pv_puping + season + shoreline type + wind force mph + season:shoreline type	9	105.29	1.94	0.168
Pv proportion	C	Precipitation + Pv_pupping + season + shoreline type + season:shoreline type	9	105.29	1.94	0.168

Table 2.21. Model output for QAIC-selected model (with interaction) for boat based sites. Where the intercept is autumn; rocky cliffs & bedrock.

	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	-4.453	1.1425	-3.897	0.00020	***
Pv_pupping 1	1.8139	0.4645	3.9045	0.00019	***
Season summer	5.9816	1.7082	3.5015	0.00076	***
Shoreline: Sheltered rocky rubble shores	4.7213	1.1420	4.134	8.898549e-05	***
Shoreline: Sheltered tidal flats	3.0445	1.7911	1.699	0.0931	.
seasonsum:Shoreline.type_desc Sheltered rocky rubble shores	-6.584	1.7862	-3.686	0.0004	***
seasonsum:Shoreline.type_descSheltered tidal flats	-6.714	2.4097	-2.786	0.0066	**

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

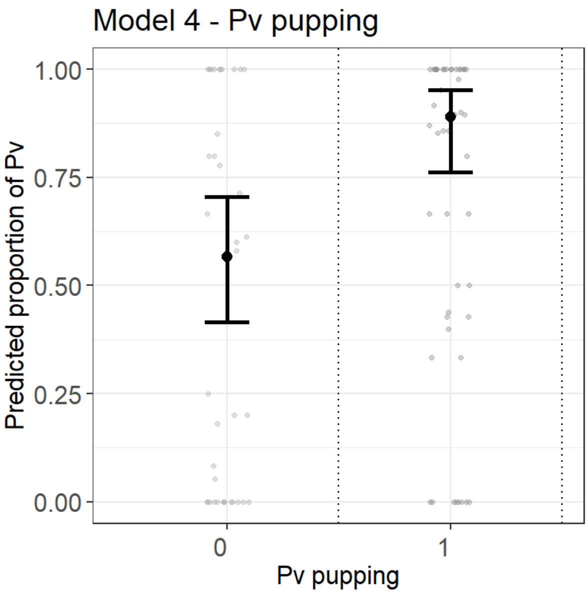

Figure 2.20. Model prediction for effect of Pv pupping site on harbour seal proportion. Model predictions are conditional on model reference levels, adjusted here for season = summer, shoreline tye = sheltered rocky rubble shores. Errors bars depict upper and low 95% confidence interval with mean. Grey dots depict raw data points.

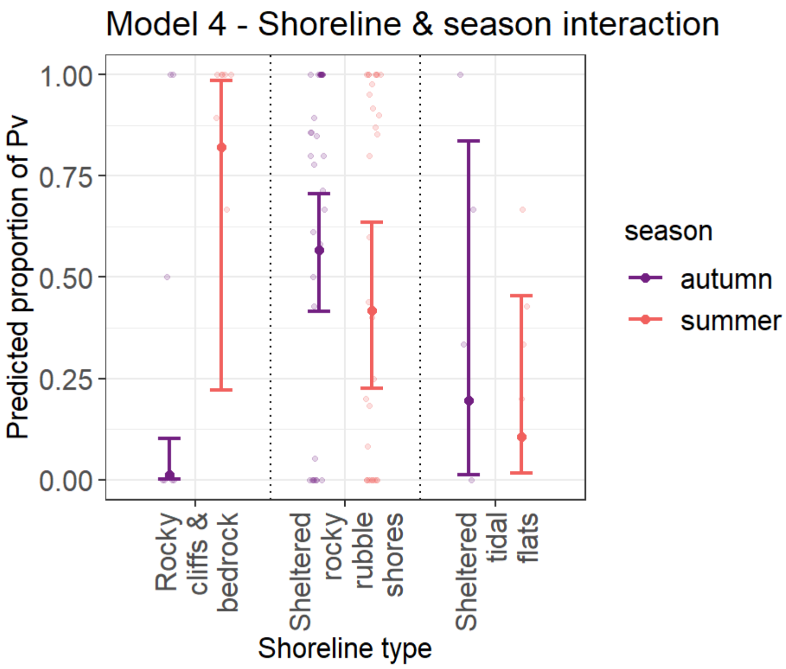

Figure 2.21. Model prediction for interactive effect of season and shoreline type site on harbour seal proportion. Model predictions are conditional on model reference levels, adjusted here Pv pupping site = absent. Errors bars depict upper and low 95% confidence interval with mean. Grey dots depict raw data points.

2.3.4 Regression model for killer whale foraging effort

To investigate potential drivers of killer whale foraging effort, year, SMA subregion, sea state, season, distance to nearest seal survey site, and shoreline type were included as candidate covariates. Following QAIC model selection the final model contained only sea state as a predictor and explained 4% of the deviance in the dataset (Table 2.22 – 2.23). A negative relationship was observed between sea state and killer whale foraging effort, with a lower proportion of foraging predicted at higher sea states (Table 2.23, Figure 2.22).

Table 2.22. GLM model selection for killer whale foraging effort. Table shows the most parsimonious models based on QAIC (delta QAIC <2) from *dredge* model selection. The final model is highlighted in grey.

Response	Model	Covariates retained	Df	QAIC	Delta QAIC	Weight
Foraging	A	Sea state	3	180.81	0	0.17
Foraging	B	Sea state + SMU region	5	180.86	0.05	0.16
Foraging	C	Sea state + season	4	180.95	0.14	0.16
Foraging	D	Sea state + season + SMA	6	181.51	0.7	0.12

Table 2.23. Model output for QAIC-selected model.

	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	1.15587	0.574463	2.012087	0.046116	*
sea.state	-0.54552	0.206791	-2.63804	0.009275	**
Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1					

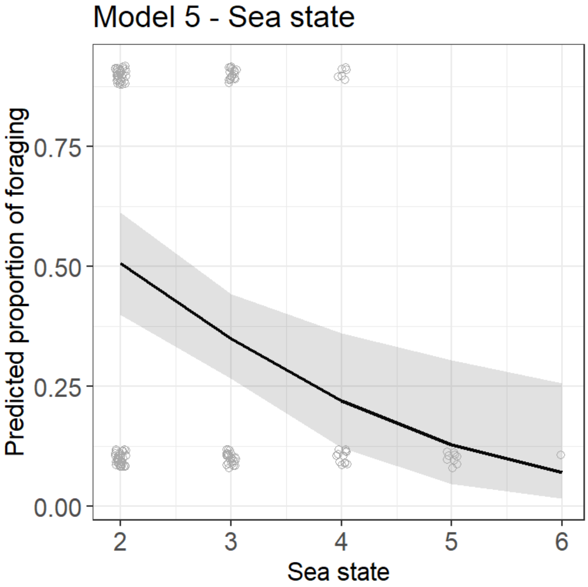

Figure 2.22. Model prediction effect of sea state on killer whale foraging. Ribbon depicts upper and low 95% confidence interval with mean. Grey dots depict raw data points.

2.4 Discussion

2.4.1 Predator-Prey Overlap

This Chapter aimed to investigate potential environmental, ecological, and spatiotemporal drivers of seal aggregations around inshore Shetland to explore their predictability as a prey resource for killer whales. The only common predictor observed between the total number of seals and killer whale foraging effort was sea state; more seals and a higher probability of foraging were both observed at lower sea state (Fig. 2.12, Fig. 2.22). This may be in part due to detectability biases associated with visual data collection methods, whereby false negatives may occur when the target species goes undetected (Wilson and Delahay 2001; Mackenzie and Royle 2005; Reid et al. 2013). In the present study, seals may have been missed during counts at surveys in higher sea states, and indications of killer whale foraging behaviour (e.g., blood or slick on water surface) may have been more readily observable during lower sea state. Alternatively, biological reasons for the observed relationships should also be considered. For seals, the pattern of a higher numbers observed at lower sea states held true for the counts of both seals hauled out and in the water during surveys, suggesting the effect was not wholly due to detectability but also due to seal behaviour. Seals primarily use haul-outs for fitness critical behaviours such as resting and breeding, and environmental variables are likely to influence site selection (Thompson 1989). In the present study, sea-state was taken as observed at the haul-out site and is likely a reflection of how sheltered a given site is. That is, even during poor weather conditions, sheltered sites would have had a lower localised sea-state; seals may preferentially select haul-outs based on this, particularly for pupping and resting purposes. To explore this, incorporating information on haul-out exposure would be prove worthwhile for future analysis.

For killer whales, foraging effort was investigated as the probability of foraging, in comparison to other behaviours, given the sighting of a pod where behavioural data could be collected. The finding that probability of foraging decreases as sea state increases would therefore suggest that to at least some extent, killer whales focus foraging effort (for seals) in times and areas of lower sea states. Foraging in lower sea states may increase the overlap with prey, as suggested by the finding of more seals at lower sea state, but may also present characteristics conducive to successful foraging, such as easier detectability and catchability of prey in coastal areas. Acoustic cues are often used in predator-prey detection, with killer whales passively listening for prey vocalisation as they search (Barrett-Lennard et al. 1996; Torres 2017). Such vocalisations may be harder to detect in coastal areas during higher sea states due to increased background noise (e.g., waves crashing on rocks) masking seal vocalisations (Erbe et al. 2016). Furthermore, foraging close to shore in higher sea states may prove risky to killer whales due a potential increase in stranding. It should be noted the present study focused on the inshore foraging of killer whales with follows typically occurring within 2km of the coastline, and thus conclusions can only be drawn in relation to this. It is possible that during times of higher sea states killer whales focus foraging efforts further offshore, outwith the observable behaviour collected here, and utilise inshore areas more for behaviours such as transiting. The fact that no support was found for the inclusion of other variables included in this study to predict killer whale foraging effort may suggest they deploy a more homogenous search pattern for prey throughout their wider range, regardless of the patchiness and predictability of prey. However, it is also plausible factors predicting killer whale foraging effort were not captured in the current analysis. For example, analysing habitat in terms of shoreline type was considered appropriate for seals given they utilise the intertidal zone when hauling out. For killer whales that always remain at sea, however, habitat characteristics as experienced at sea such a seabed substrate and shoreline gradient may be a more appropriate when exploring predictors of inshore-foraging effort.

The consequences of spatial overlap and prey predictability for predators will likely be scale dependent (Sih et al. 2005). For example, at a finer scale, foraging in patches of low prey density may not necessarily be costly for a predator, as it is simply a case of a meal sooner rather than later. At a larger spatial and temporal scales, however, poor tracking of prey would become costly as too many missed foraging opportunities will result in undernourishment (Stephen and Krebs 1997). The killer whales observed in this study range far beyond Shetland in search of prey, with pods venturing throughout the Northern Isles (Shetland and Orkney), the north coast of Scotland, and for some pods, Iceland, and the Faroe Islands. At this larger scale, killer whales may efficiently utilise space by moving between wider areas, possibly dependent on their prey density. Indeed, the nomadic pattern of Scottish-Icelandic pods is hypothesised to be due to prey switching between seasonally abundant herring in Iceland, and seals in Scotland (Samarra & Foote, 2015). At a finer scale, the use of space within a region of high prey density, regardless of the patchiness of prey therein, may be of less fitness consequence as a meal will be obtained, it’s just a matter of time and effort. In this context, Shetland itself may be an area of high, predictable prey density the killer whales utilise, but within this area they are less constrained in their use of space due to the wide and dynamic distribution of their prey.

Prey space use appeared to vary in relation to spatial-temporal and environmental characteristics. The total number of seals observed at haul-out sites varied regionally year on year, with the highest consistency observed in the SE SMA subregion (Figure 2.15). Typically, the pattern of total seals observed showed an inverse relationship with the composition of species at haul-out sites, measured as the proportion of harbour seals present. This would suggest that the observed differences in total number of seals may be driven more by the presence, or absence, of grey seals rather than harbour seals. Overall prey density may therefore be subject to species-specific constraints, resulting in a dynamically variable multi-prey prey field for coastally foraging killer whales.

2.4.2 Species-Specific Variability

Harbour seals were more numerous than grey seals across all regions and seasons. Given ecological differences between the two species, with harbour seals in Shetland typically spending a higher proportion of time closer to the shore in comparison to grey seals (Carter et al., in prep), it is possible the highly coastal nature of data collection may result in a lower proportion of grey seals present in this sample. However, despite regional declines, harbour seals are almost as numerous as grey seal within the wider Shetland SMA (Morris et al., 2021). Furthermore, a high density of grey seals are found away from the mainland sites surveyed in the present study, in remote islands and skerries (e.g., Out Skerries). The observed higher proportion of harbour seals in this study may therefore reflect both the overall species composition of the Shetland SMA, and the propensity for grey seals to utilise habitats further offshore. The extent to which grey seals may influence the inshore number of harbour seals, due to their movement between autumn/winter breeding grounds and other locations used for resting, moulting and foraging, is therefore an interesting aspect to consider.

Seasonal variation would suggest that a higher number of seals aggregate around coastal Shetland in summer months in comparison to autumn (Figure 2.14). The presence of harbour seals will increase at haul-outs in summer months due to breeding, with mum pup pairs and males of breeding age aggregating at pupping sites (Thompson and Miller 2010). Interestingly, however, the number of grey seals also appeared to generally increase at monitoring sites in the summer months; a time when space use would not be constrained by their breeding cycle, which occurs in autumn and winter months. In Shetland, grey seals typically pup in more remote, inaccessible areas, away from the mainland, such as the islands of East Linga, Griff Skerry, and Papa Stour (SCOS, 2022). Indeed, grey seal pups were only present at three of the land-based and one of the boat-based monitoring sites surveyed within this study. Grey seals may therefore increase prey density during the summer months due to a lack of constraints on space use; that is, they are free to move within their wider range and utilise areas that are possibly more important for foraging and resting, without having to prioritise space use to breeding habitats. The divergent constraints on harbour and grey seals during the summer months may cloud their overall predictability as killer whale prey. That is, whilst harbour seal numbers may be more consistent in summer months, overall seal prey density may be highly variable due to the movements of grey seals. This demonstrated how species-specific variability may influence the predictability of prey densities.

From a predator perspective, density alone may not reflect increased foraging opportunities, as successful predation is not only contingent upon detecting prey, but also capturing and consuming them (Lima & Dill, 1990). Larger aggregation may afford potential safety-in-numbers for prey species, through increased vigilance by prey and confusion by predators (the dilution effect) (McNamara and Houston 1992; Lima 1995). Predators may therefore increase their chances of foraging success by focusing efforts in areas of reliable prey aggregation even if such areas do not present the densest patch of prey (Suraci et al., 2022). In this scenario, predators still have a good chance of encountering prey, thus minimising their time-energy cost of finding prey, and potentially a higher chance of success if predation is strongly contingent on other aspects of the predation sequence (e.g., prey vulnerability). In the present study, the SE SMA subregion contained the most consistent total number of seals, and the most consistent proportion of harbour seals as observed around surveyed haul-outs. Whilst no evidence of increased foraging effort in their areas was found in the current analysis, further investigation of spatial-temporal and species-specific predictors of predation success would facility understanding of whether predators are better focusing efforts in areas where prey density may be lower, but more consistent and higher chance of capture (lower encounter, higher success), versus areas where prey density higher, but more variable and with a higher chance of escape (higher encounter, lower success) (Suraci et al., 2022).

2.4.3 Conclusions

Overall, this Chapter highlights the complexities of studying predator-prey space use in combination. The fact that killer whale foraging effort was not found to increase in relation to the spatial-temporal increases in prey density supports the notion that spatial overlap alone does not necessarily imply foraging success, however limitations of data collection and covariate data should be considered when drawing conclusions. Whilst harbour and grey seals are known to be two of the primary prey species of coastally foraging killer whales, other species such as harbour porpoise (*Phocoena phocoena*) may also be important contributors to their diet. Further exploration of the ecological complexities driving the spatiotemporal co-occurrence of predator and prey in this system should be explored.

3 CHAPTER 3. PREY CONSUMPTION BY KILLER WHALES: INVESTIGATING SPATIOTEMPORAL PATTERNS AND CAPTURE PROBABILITY BETWEEN PREY SPECIES

Abstract

The probability that prey is captured and consumed by a predator is contingent upon a variety of intrinsic (e.g., predator and prey traits) and extrinsic (e.g., environmental characteristics) conditions. In this Chapter, I explore that spatiotemporal patterns and capture probability of prey species by killer whales in Shetland. First, killer whale diet composition is estimated from an expert-elicitation process, which quantifies associated uncertainty in prey species identification from citizen science, drone, and field imagery collated between 2016-2023. Second, spatial, temporal, environmental and ecological variables are investigated as potential predictors of observed predation success. Targeted prey species identified as part of the expert elicitation process include harbour seals, grey seals, harbour porpoises, sea birds, and otters. Where prey species were identified, species-specific variability in capture probability was observed, with harbour seals having a higher probability of capture and consumption in comparison to grey seals. Predation events occurring further from the shoreline had a higher probability of success in comparison to those closer to shore, and the proportion of successful events was higher in the Southeast (SE) Seal Management Area subregion (SMA). Results from this Chapter provide new insights into the prey composition of inshore-foraging killer whales in Shetland, and how capture probability varies between prey species and across spatial scales.

3.1 Introduction

Spatial overlap, whilst a pre-requisite for predator-prey interactions, does not necessarily translate directly to increased predation risk, i.e., the probability that a prey will be killed by a predator. Predation risk varies dynamically dependent on prey-field structure and characteristics (Spitz et al. 2010), predator-prey behaviour (Sih 1984; Krebs et al. 2001) and is likely a function of predator-prey encounter rates and the probability of capture given an encounter, i.e., conditional capture probability (CCP) (Hebblewhite et al. 2005). Here, an encounter is defined as a situation where predator and prey are within detection range of one another, and one or both parties detect the other (Suraci et al., 2022). CCP can be mediated by intrinsic (e.g., predator and prey traits) and extrinsic (e.g., environmental) conditions (see Suraci et al., 2022 for review). Even when spatial-temporal overlap, and thus probability of encounter, is high, CCP and overall predation risk may be low. For example, predators may not be actively hunting because they are already satiated or chose not to attack prey and instead search for more profitable prey. Additionally, predator success rate may be low due to environmental circumstances (e.g., prey refuge availability) (Dill and Houtman 1989; Wirsing et al. 2010; Smith et al. 2019) and prey characteristics (e.g., camouflage or defence)(Wilson et al. 2018). Understanding the environmental and ecological drivers of CCP is therefore integral to quantifying species and context-dependent predation pressure, and level of consumption within a predator-prey community.

From a predator perspective, CCP is likely to be contingent on their motivational state (Stephen and Krebs, 1986). Predators that experience high resource availability may encounter prey without attempting to capture and consume prey, either due to satiation or prey preference, leading to a high encounter/low predation risk scenario for prey (Suraci et al. 2022). From the perspective of prey encountering a predator, CCP may be reduced by using environmental conditions conducive to evading (e.g., avoiding detection by the predator) escaping (e.g., fleeing if detected by the predator) predation. The potential for prey to escape predation typically translates to proximity to refuge – the closer prey is to refuge, the more likely it is to escape (Kramer and Bonenfant 1996). However, refuge alone does not preclude chances of predation. Prey intrinsic factors, both behavioural and morphological, may make certain prey species and age classes more vulnerable to predation at different times.

Increased vigilance, camouflage, defence, and locomotive escape tactics can all increase chances of evading predators (Wilson et al. 2013; Smith and Ruxton 2021). CCP, and the extent to which certain species or age classes are present in a predator's diet (predator diet composition), is therefore likely to reflect an interaction between environmental conditions, prey vulnerability, and predator preference.

To understand intrinsic and extrinsic drivers of CCP, and thus predation risk, from both the predator and prey perspectives, ecological and environmental complexities must be examined in combination. In the context of killer whales foraging in inshore waters of Scotland, the extent to which predators encounter, pursue, and successfully consume various prey types is largely unknown. Killer whales are known to predate harbour and grey seals (Bolt et al. 2009; Deecke et al. 2011), and are observed predating harbour porpoise, seabirds, and on-occasion, otters (*Lutra lutra*) in Scottish inshore waters (SBRC, unpublished data). However, there is a paucity of data on the extent to which they successfully target and consume different prey types. Understanding variation in predator success and prey evasion is integral for quantifying predation impact on prey populations, and assessing the capacity of predators to respond effectively to changes in prey density.

Within Scottish coastal waters, harbour and grey seals overlap in their broad-scale ranges but their distributions differ within those ranges (SCOS 2022). The spatiotemporal variation in the species abundance may influence their composition in the prey field, their encounter probability with killer whales, and risk of predation if killer whales switch between prey species based on their relative abundance. The UK population of grey seals has steadily increased over the last 60 years (Thomas et al. 2019), and plateauing of pup production in Orkney and the Hebrides suggests these areas may have reached carrying capacity (Russell et al. 2019). In contrast, whilst the UK population of harbour seals has remained stable in the last 20 years, there is marked regional variation in population trends with dramatic declines observed around the North and East coast of Scotland (Thompson et al., 2019). Furthermore, trends within regions vary between Seal Management Areas (SMA) sub-regions and Special Areas of Conservation (SACs). For example, whilst the Shetland Seal Management Area has remained stable overall at a depleted level after a stepwise decline, contrasting trends have been observed between the N&E, SE, and W sub-region, and the counts within the Mousa

SAC show exponential declines (Thompson et al. 2019; Morris et al. 2021). Encounter rates between killer whales and the two seal species may therefore depend on their relative abundance.

On a finer spatiotemporal scale, intrinsic prey characteristics may influence chances of encounter and CCP. Physiological, behavioural, and life-history constraints, such as those pertaining to breeding and foraging between the two seal species may be of importance. Harbour seals are considered income breeders, with pups weaning after four to six weeks during the summer and capable of entering the water soon after birth. Adult harbour seals typically forage close to coastal haul-outs (within 60 km, Thompson et al. 1996) and exhibit strong coastal habitat use (Carter et al. 2020; Cordes et al., 2011; Jones et al., 2015; Thompson et al., 1996). Grey seals are capital breeders, with pups weaned after a suckling period of 15-21 days during the winter and remaining on land between 9 and 40 days for a post-weaning fast (Pomeroy et al. 1999). Compared to harbour seals, adult grey seals generally travel further offshore when foraging (up to 145km, Thompson et al., 1996) and show wider foraging distribution (Thompson et al. 1996; Jones et al. 2015; Carter et al. 2020). In Shetland, recent GPS-GSM tagging of harbour and grey seals revealed high coastal usage by both species. On average, harbour seals spent at least half their time at sea within 240m of land and greys 1.2km (Carter et al. in prep). These intrinsic differences between the two species may therefore influence consumption rates, both through increased relative abundance and thus potentially encounter rates, and vulnerability due to physiological differences and life-history cycles.

The aim of this chapter is to investigate potential drivers of CCP for harbour and grey seals as prey species of coastally foraging killer whales in Scotland. If spatial, temporal, and/or environmental factors are found to influence predator success given a prey encounter, then killer whales may be able to maximise their CCP by focusing predation attempts in environments, areas and/or times conducive to high capture rates. If certain prey species and/or age classes are found to be more susceptible to predation, then killer whales may exhibit dietary preference consistent with higher probability of capture for given prey types. First, predation events observed around coastal Shetland will be used to characterise the diet composition of coastally foraging killer whales. Second, spatial, temporal, environmental and ecological variables will be investigated as predictors of observed predation success. From a prey perspective, estimates of predation rates will inform understanding of species and stage-dependent predation pressure. From a predator perspective, estimates of diet composition will inform calculations of consumption rates and quantity needed to meet killer whale energetic requirements, in addition to furthering knowledge on foraging plasticity of killer whales. Quantifying predictors of observed predation success will provide insights into predation risk beyond spatial overlap and facilitate understanding of species and context-dependent predation pressure.

3.2 Methods

3.2.1 Predation events

3.2.1.1 FIELD OBSERVATIONS

A primary aim of land-based fieldwork was to conduct focal-follows of coastally foraging killer whales and obtain data on predation events, particularly in relation to prey species identification and predator hunting success within and between prey species and age classes. PhD fieldwork was conducted across five seasons: summer 2021 (14th June – 18th July), autumn 2021 (26th October – 28th November), summer 2022 (10th June – 17th July), autumn 2022 (25th October – 24th November), and summer 2023 (6th June – 18th July). Field seasons were chosen to overlap with harbour and grey seal breeding seasons, summer and autumn respectively, and expected peaks in killer whale observations to investigate temporal patterns in prey species and age-class specific predation. During fieldwork, killer whales were located following reports shared by citizen scientists via local sighting networks, with focal-follows conducted as outlined in Chapter 2 (Section 2.2.2.2). During follows, I documented predation events using a telephoto lens (100-400mm mounted on a Canon 70D body), binoculars, and sighting scope. Metadata including time, date and estimated location of predation events were taken in field (see Chapter 2 section 2.2.2.2), with prey species ID assigned from images where possible.

During initial field seasons (summer and autumn 2021), the sample size of predation events obtained during focal-follows was low (n=5), and prey species identification was only confidently obtained for 40% (n=2/5) of events. Often, the only indication a predation had occurred was the presence of blood, oil slick (from marine mammal blubber), and seabirds scavenging on the water surface, with no prey species directly observed. To supplement in-field effort of predation events and increase observation periods outwith project fieldwork months (June and July, October and November), drone observations and citizen science photo and video contributions were incorporated into data collection methods on killer whale predation events. Importantly it should be noted that predation events here include both predation attempts, where killer whales pursued a prey that escaped, and successful predation events, where killer whales captured and consumed the prey.

3.2.1.2 DRONE OBSERVATIONS

Recreational and commercial drone operators regularly use semi-professional unmanned aerial vehicles (UAV's), here termed drones (e.g., DJI Phantom, DJI Mavic Pro 2), to observe killer whales in coastal Shetland. Raw drone footage, unedited and uncropped, from experienced pilots was contributed to the ECOPredS research project on 4TB hard drives and via file transferring platforms (e.g., WeTransfer). Footage was submitted under participant agreement and ethical approval from the University of St. Andrews Teaching and Research Ethics Committee (UTREC) and University of St. Andrews Animal Welfare and Ethics Review Board (AWERB) (approval number EC19008). Ethical approval for the inclusion of drone footage for research objective was obtained 1st April 2021. Footage collected prior to this data was considered retrospective and collected independently by pilots. Footage obtained after this date was considered prospective and was collected under ECOPredS recommended flying parameters.

Operational requirements & procedures

To ensure footage included in analysis was collected responsibly, retrospective footage was required to meet minimum safety standards for legal and responsible recreational flights in concordance with Civil Aviation Authority (CAA) law and with due regard for animal welfare (Appendix A2.1). For footage collected after 1st April 2021, a Standard Operating Procedure (SOP) was developed in collaboration with experienced drone pilots in order to ensure prospective footage was collected at an optimal angle and altitude for analysis, maximising efficiency in future footage collection whilst minimizing research effects (Appendix A2.2). As part of the SOP, a recommended minimum flight height was established based on field experience and altitudes detailed for optimizing data collection whilst mitigating disturbance to marine mammals, as detailed in drone-based research literature. The minimum flight height for prospective footage was initially (April 2021) recommended at 15m for killer whales and 30m for seals, based on acceptable altitudes described for phocid seals (grey seal) and delphinids (bottlenose dolphin) (Pomeroy et al. 2015; Giles et al. 2020; Ramos 2022). In accordance with the growing body of literature (e.g., Cheney et al., 2022; Aubin et al., 2023), the minimum height for dedicated research flights was later increased (May 2023) to 30m for killer whales. This increase aligns with licencing requirements for research flight elsewhere in the world (e.g., Pacific North-West ,Weiss et al. 2021) and NatureScot aspirations for inclusions of drone flight parameter recommendations for all marine mammals in the Scottish Marine Wildlife Watching Code (SMWWC 2017) (K. Hall, personal communications, May 2023). The iterative nature of the SOP ensured dedicated research flights were conducted not only in compliance with current CAA safety standards and adhered to CAA recommended flying parameters, but also with appropriate consideration for the welfare of primary study species (killer whales and seals) and secondary species (e.g., birds) present in the operating environment, as detailed in the most recent published literature.

Drone altitude assessments

Drone altitude as available in flight-log data is calculated as vertical distance from take-off location, which for flights launched from land is typically a vantage point above sea level and thus does not reflect the true vertical distance of the drone above target species. Laser rangefinders can be used to determine flight height above sea level (e.g., Glarou et al., 2022), however given the opportunistic nature of data collection by volunteer pilots such methodology was not employed here. To estimate drone height in raw footage submitted by project participants, I conducted calibration flights of a known height and object length using a DJI Mavic Pro 2, a drone operating system frequently used by project participant drone pilots (2018-2023) (Appendix A2.3). Repeated measurements of the object, here representing a killer whale of 7m length in nadir position in centre frame, were taken in pixels per cm over multiple videos and stills using the software Image J. Measurements were used to calculate the mean vertical and horizontal proportion an adult killer whale of average North-East

Atlantic body length (7m, Foote et al., 2009) would occupy in a 1920x1088 frame (full HD). Measured proportions were compared to theoretical predicted proportions calculated using manufacturer specifications of drone field of view and aspect ratios to check the validity of frame ratios across different drone systems (e.g., DJI Mavic Pro 2, DJI Mavic Pro 3). Proportions measured in calibration flights were typically higher when compared to theoretical calculations; for example, a 7m killer whale took up ~70% of the vertical frame at 15m in calibration flights, and ~60% of the vertical in theoretical calculations. At 30m, a 7m whale took up ~35% of the vertical frame in calibration flights and ~30% in theoretical calculations. Calculated proportions were used to visually assess the average minimum flight height of prospective footage to ensure minimum requirements for inclusions in analysis were met as in relation to the SOP. Behavioural metrics by target species to the presence of the drone, eg., side on swimming by killer whales which could indicate looking up at the drone, and head-up alert or fleeing behaviour by seals, were monitored to determine if clear behavioural response occurred in the presence of the drone.

Quality and content scoring

Raw drone footage was subject to quality and content scoring to ensure minimum requirement for inclusion in analysis were met, and to evaluate data available in footage for research objectives as part of the wider ECOPredS project, e.g., for C. Deleu's MSc research or Dr. Isojunno's body condition project. Quality and content scoring was conducted by members of the project team, including myself, project PI Dr. Isojunno and MSc student C. Deleu. Parameters included in quality scoring included those pertaining to drone camera capabilities and flyer operations, such as media quality (1-3; grainy, fair, clear), minimum flying distance (1-3; close, medium, far), and viewing angle (1-3; horizontal, medium, steep) (Table 3.1, Figures 3.1 – 3.3, Appendix 2.4). With regards to available data, scoring noted the start and end time (mm:ss) of drone on follow, when the killer whales were in continual view, and the presence or absence (coded 0 or 1) of the following parameters: opportunity for photogrammetry, prey presence, predator prey interaction, shoreline visibility, killer whales within 100m of the shoreline, presence of boats, and presence of fish or shellfish farms. Relevant comments were taken such as other drones present in the footage or killer whale interacting with fishing gear (Table 3.1, Appendix 2.4). Drone footage assigned the closest flying distance (1) was further analysed to ensure minimum inclusion requirements for the footage type (retrospective or prospective) were met. Drone footage that met minimum requirements and were scored as containing prey and/or predator were subsequently analysed for predator prey interactions, (e.g., predator chasing prey, prey fleeing to refuge, predator consuming prey). Where interactions occurred, I extracted stills for collation into the predation event database for the purposes of identifying prey species therein.

Table 3.1. Variables collected during drone quality and content scoring.

Variable	Description
Quality	Perceived quality of footage: 1 (grainy); 2 (fair); 3 (clear)
Minimum distance	Drone minimum distance: 1 (close); 2 (medium); 3 (far)
Viewing angle	Drone viewing angle: 1 (horizontal); 2 (medium); 3 (steep)
On follow	Start and end time (mm:ss) when drone is following killer whale, i.e., whale is in clear continuous view.
Photogrammetry	Opportunity for photogrammetry, whale is in center of frame and in nadir position: 1 (present); 0 (absent)
Prey presence	Prey species present in footage: 1 (present); 0 (not present)
Predator & prey presence	Predator and prey present in same frame: 1 (yes); 0 (no)
Shoreline present	Shoreline is visible in the footage: 1 (present); 0 (absent)
Shoreline proximity	Animals <100m from shoreline: 1 (yes); 0 (no)
Boat	Boat(s) visible in footage: 1 (yes); 0 (no)
Fish farm	Fish or shellfish farms visible in footage: 1 (yes); 0 (no)
Comments	Additional notes e.g., other drones present, interactions with fishing gear, sea birds or blood present.

Figure 3.1. Media quality as categorised in quality and content scoring. On full zoom in VLC player, media quality was assigned as 1) grainy: image is pixelated, individuals can be seen but quality it not high enough to see ID markings; 2) fair: image is clear but slightly pixelated, distinct marking such as dorsal nicks can be seen; 3) Good, image is very clear with minimal pixilation, distinct ID markers such as scars can be seen. Image credit: R. Shucksmith & N. McCaffrey.

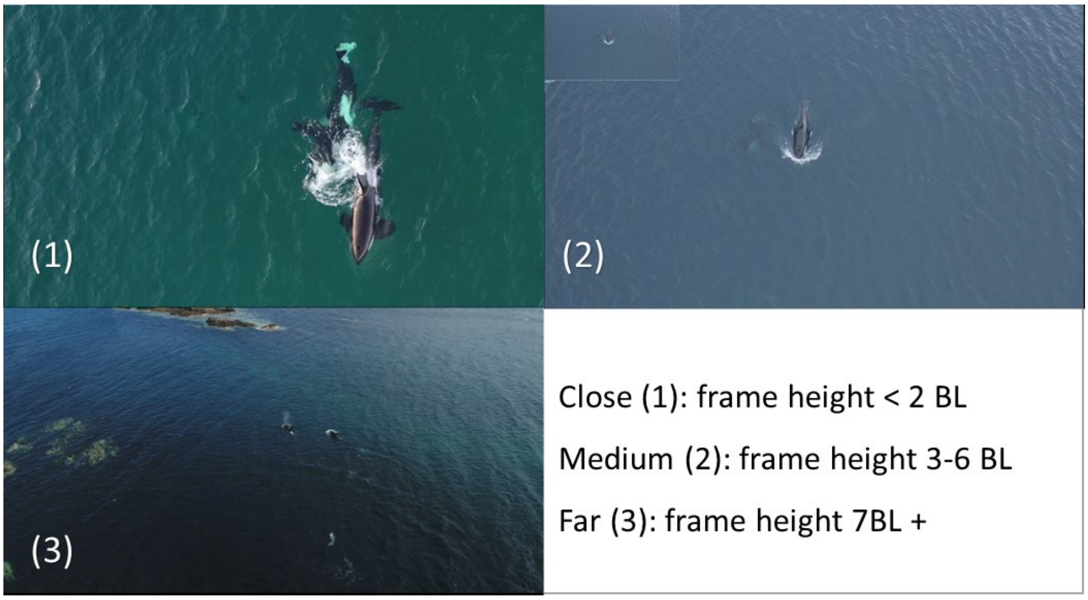

Figure 3.2. Minimum flying distance as categorised during quality and content scoring. Frame height was measured as the number of adult body lengths (BL) in the vertical frame. Drone footage in category 1 was further assessed against minimum flight height requirements. Image credits: R. Shucksmith & N. McCaffrey.

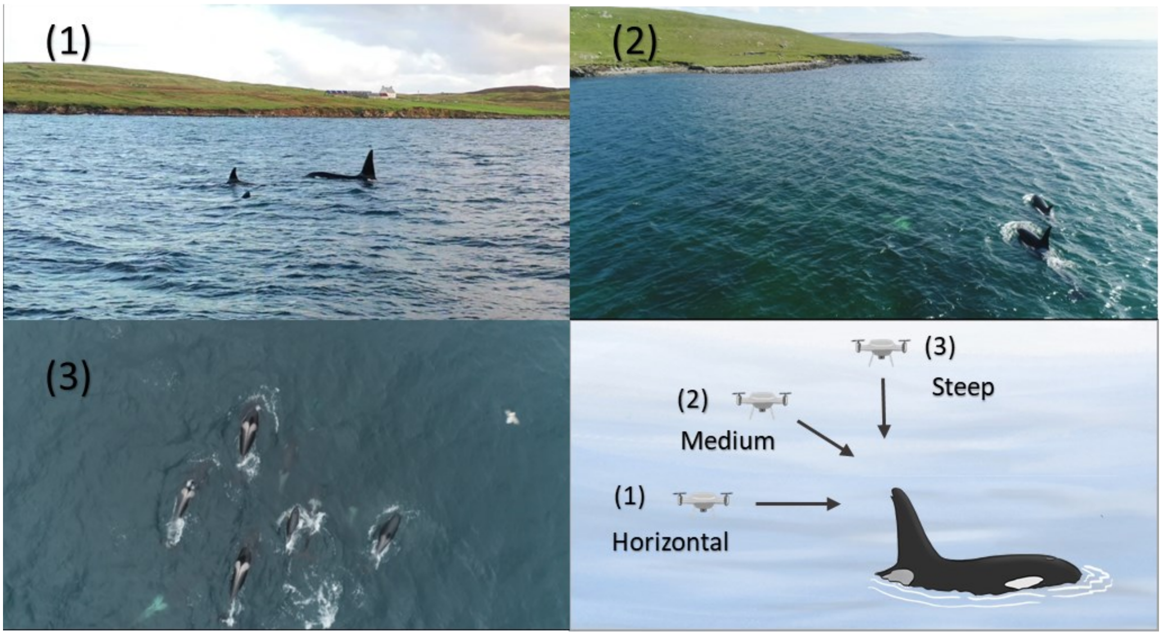

Figure 3.3. Viewing angle as categorised during quality and content scoring. Viewing angle was assigned either 1) Horizontal: where the drone is side-on, dorsal fin silhouette and eye patch shape can be seen during surfacing, 2) Medium: As if viewing from a height, dorsal fin silhouette can be seen but eye patch is unclear due to angle; 3) Steep: Nadir position, saddle patch shape clear during surfacing, dorsal fin and eyepatch unclear due to angle. Image credits: R. Shucksmith & N. McCaffrey. Drawing: J. Sutherland.

3.2.1.3 CITIZEN SCIENCE OBSERVATIONS

Citizen scientists, members of the public, regularly post photos and videos of killer whale encounters to the social media site Shetland Orca Sightings, managed by H. Harrop and K. Hall. Following ethical approval from the University of St. Andrews University Teaching and Research Ethics Committee (UTREC) (approval number EC19008) and permission from group owners, I conducted a systematic desk-based search to identify and extract predation events. The social media page was searched using key words including “hunt”, “prey”, “attack”, “forage”, “seal”, “porpoise”, “otter” and “fish”. Images were saved following permission from the original owner, and high-quality images were requested via email where available. Predation events were obtained between 2016, when the Shetland Orca Sightings Facebook group was established, and summer 2023 when PhD fieldwork ended. The conception of the social media group denoted the onset of citizen scientists documenting killer whale presence in a public forum, facilitating the recording of opportunistic observations for data collection purposes, with reporting effort increasing year on year as the group’s following increased in numbers. Additional predation events were also contributed directly by citizen scientists via email, following increased awareness of the project's objective through field and social media presence. Images from citizen scientists were collated into the predation events database for subsequent analysis on prey species ID.

3.2.1.4 METADATA AND PREDATIONS EVENTS DATABASE

Metadata regarding date, time (where available), location and pod ID were obtained for each predation event to compile a predation events database for analysis. For data collected in fieldwork, metadata was obtained in-situ and through analysis of photos as part of focal-follow protocols (see Chapter 2 section 2.2.2.) For drone footage, time and date metadata was extracted in R, with GPS location of the events obtained either through submitted flight logs or by cross refencing date and time of observations with killer whale sightings data provided by the Shetland Biological Records Centre (SBRC) (coordinated by K. Hall). Metadata for citizen science predation events were extracted from social media posts or through request from the original media owner. Pod ID was often reported in relation to predation events, e.g., through social media posts or naming of drone footage files. To ensure pod ID was accurately assigned, I visually inspected images and checked individual ID markers in reference to the Scottish Photo Identification Catalogue (Scullion et al. 2021) (Figure 3.4). Killer whales exhibit unique markings, including eyepatch and saddle-patch shape that are consistent from birth, and scars and nicks that can be used to re-identify individuals through time. Pod IDs as assigned by reports and visual inspection were cross referenced with IDs noted in sightings data from the SBRC. Where pod ID could not be confidently established for a predation event, it was labelled unknown.

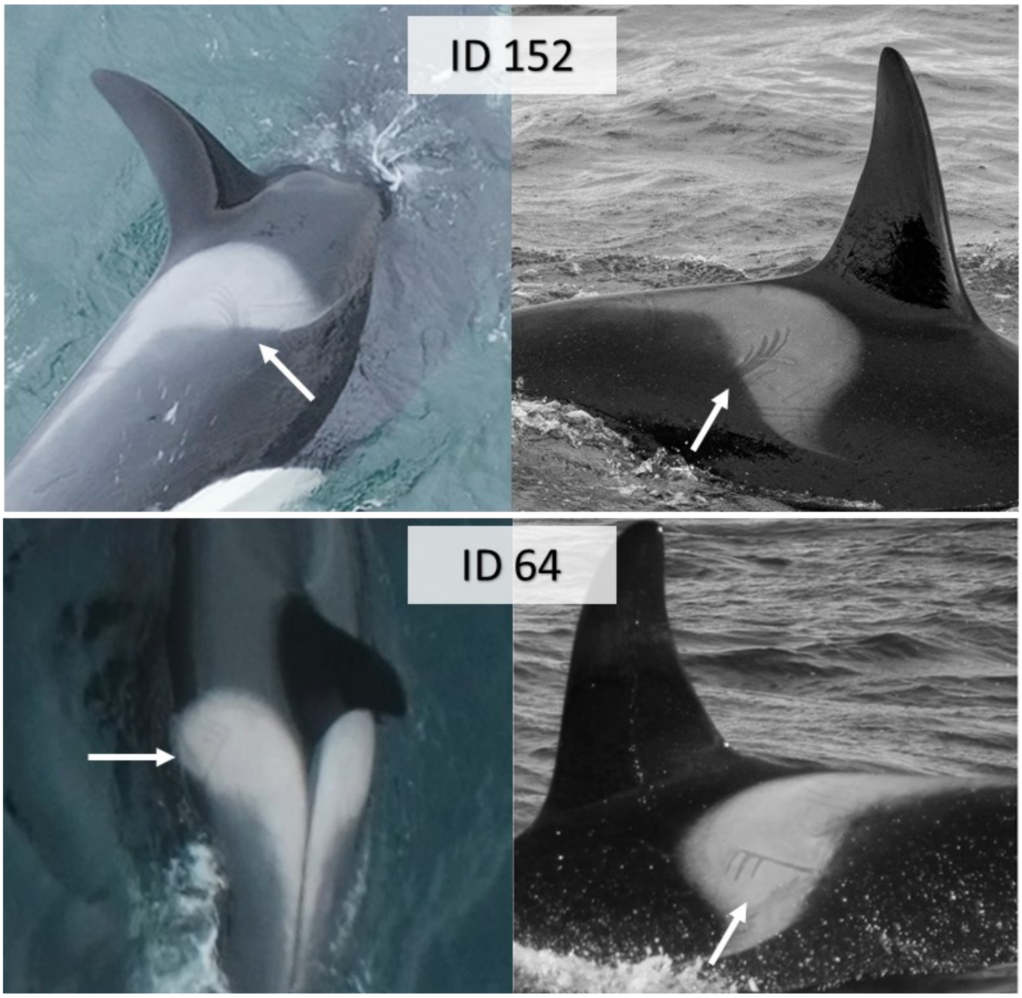

Figure 4.4. Photo ID of individuals from drone footage. Individual markings such as saddle patch scars, nicks, dorsal fin an eyepatch shape were used to identify individuals in drone footage. Example here shows individual markings for individual ID 152 from the 27s pod (top) and matriarch ID 64 from the 64s pod (bottom) as seen in drone footage (left) and as published in the Scottish Photo Identification Catalogue 2021 (Scullion et al., 2021). Images are cropped to show detail. Photo credit: N. McCaffrey & Scullion et al., 2021.

Predation event outcome was assigned based on examination of images in the database with additional information obtained from the original owner when required. Outcome was grouped into eight discrete categories: consume (e.g., killer whales seen capturing and consuming prey), escape to land (e.g., seal hauled out), escape to shallows (e.g., animal takes refuge close to shoreline), escape to anthropogenic refuge (e.g., animal uses anthropogenic device such as navigation buoy for refuge), escape to depth (e.g., animal dives), escape to unknown (e.g., no predation is observed but it unclear where prey escapes to), and unknown outcome (e.g., drone footage ends before outcome is observed or observer was not certain of the outcome).

Images acquired from fieldwork, drone footage, and citizen science observations were collated into a predation events database (Table 3.1, Figure 3.5). Each predation was assigned a unique "Event ID" based on the date and location from metadata, to ensure no duplicates were present in the dataset. Where events where present both in drone footage, citizen science observations, and/or fieldwork, images were collated under the same event ID and all used for prey identification.

Table 3.4. Variables collated in predation events dataset.

Variable	Type	Description
Event ID	Factor	Individual ID assigned to predation event
Source	Categorical	Source of events (social media group, drone, fieldwork, submission)
Date	Continuous	Date of predation event
Pod	Categorical	Pod ID
Location	Text	Location reported or observed
Latitude & longitude	Continuous	Latitude and longitude of predation event
Media	Categorical	Type of media of event (photo, video still, drone still, report)
Outcome	Categorical	Outcome of predation event (consumed; escaped – land; escaped – shallows; escaped – dive; escaped – anthropogenic; unknown)
Notes	Text	Additional relevant comments e.g., specific anthropogenic refuge prey used

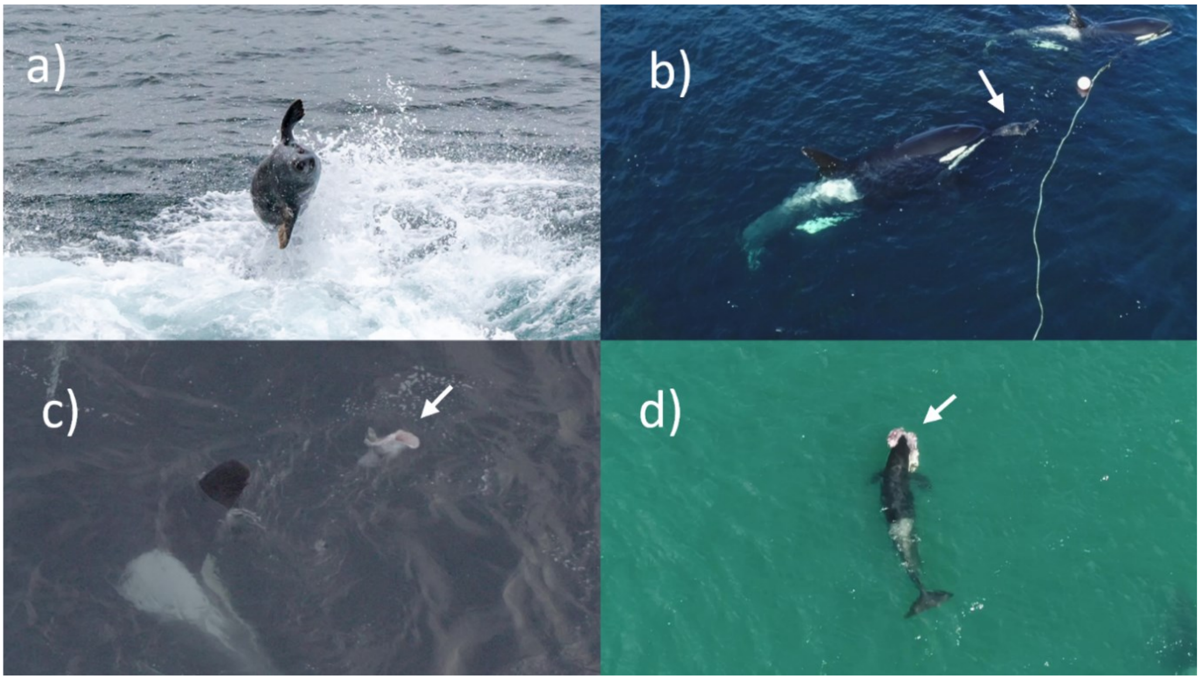

Figure 3.5. Examples of media and image quality classification included in predation events dataset. Good quality photo of prey (grey seal) during attack, b) Good quality drone still of prey (harbour seal) during attack, c) Good quality drone still of prey (seal) remains; d) Fair quality drone still of prey (unknown mammal) remains. Images are cropped. Photo credit: R. Shucksmith & H. Perry.

Habitat covariates

To investigate whether and how habitat influenced observed predator success, shoreline habitat associated with predation events was assigned using Environmental Sensitivity Index (ESI) shoreline classification provided by Marine Scotland (Marine Scotland National Marine Plan, 2017). This index, which was developed for oil sensitivity mapping, classifies the Scottish coastline into five categories: rock and man-made; sand, gravel and rock armour; exposed tidal flats; sheltered rock, man-made or rock armour; and sheltered tidal flats or salt marshes. This dataset was selected for habitat classification as it was developed for the intertidal zone and thus had good resolution at the coastal scale visual observations of predation events were conducted (<1km to the coastline). Alternative datasets (e.g., JNCC SeaMapper) had poor resolution at the coastal scale and often habitat or substrate information did not overlap with predation observations. The shoreline category for each predation event was calculated in R using the *st_nearest_feature* function from the sf package, which identified the habitat classification for the closest shoreline in a straight line from the point of predation event.

Spatial and temporal covariates

Distance to shoreline was calculated for each predation event to investigate whether proximity to shore, and thus prey refuge, influenced predator success. Closest shoreline and distance to shore were calculated in R using the *st_nearest_feature* and *st_distance* functions from the *sf* package and appended to the predation events dataset. To investigate how predation attempts and predator success varied spatially around Shetland, predation events were summarised in each SMA subregion using the *st_within* join the from the *st_join* function in the *sf* package in R. Temporal covariates including weekday (Monday through Sunday, numerical 1 through 7), day of the month (numerical 1 through 31), month (numerical, 1 through 12) and year were assigned using the *lubridate* package in R.

3.2.2 Expert elicitation for prey identification

Images of predation events varied in quality on information available dependent on the source of the image (e.g., camera capabilities), and the state of the prey species therein (e.g., intact or remains). Some images depicted prey species clearly (e.g., high-quality photographs of prey mid-capture), whilst others were less clear (e.g., grainy footage of prey fleeing, or animals disfigured from partial consumption) (Figure 3.5). Identifying prey species in all predation events was therefore objectively challenging, particularly in relation to discerning identification of seal species (harbour vs grey) and age classifications (pups vs 1+ years). To formally identify species in predation events and quantify associated uncertainty in species and seal age classification based on subjective probabilities, an expert elicitation for prey identification protocol was established (section 3.2.2.1). Using expert's assessments on a subset of predation events, a 'confidence threshold' was established against which confidence in my species identification for the full dataset could be assessed (section 3.2.2.2).

3.2.2.1 EXPERT PANEL AND PROTOCOL

Experts invited to join the panel were researchers that had expertise in the identification of UK seal species (harbour and grey seals), as seal species and age-class was expected to be the most challenging to accurately identifying in comparison to e.g., porpoise or seabirds. The panel consisted of experts in various data collection-methods and observer platforms (e.g., behavioural observations, telemetry tagging, aerial surveys, ground-counts) to ensure the panel represented a broad experience base with different approaches to seal identification (e.g., morphology, behaviour, pelage, size). In total, 10 experts were requested to independently review a sub-sample of images (drone stills, video still, photos) collated on killer whale predation events (n=37) with the purpose of identifying prey species (harbour seal, grey seal, porpoise, sea bird, otter), age class (pup vs 1+ years for seal species), and associated level of uncertainty for each event.

A protocol was developed based on published literature for robust, repeatable, and structured approaches for expert elicitation in ecology (Hemming et al., 2018). Experts were provided with metadata on image type and quality, but information on date and location were withheld to prevent potential bias based on expectations of certain seal species or age classes being more abundant in certain areas or times of year (e.g., breeding seasons) thus influencing identification. Assessments were conducted independently to avoid potential peer influence in species identification, e.g., less experienced individuals agreeing with those perceived as more experienced. An information and guidance document containing example assessments, killer whale size guide, and prey species size guides were provided to experts prior to the assessment to reduce subjective assumptions on predator-prey size ratios (Appendix A2.5).

The assessment followed a ‘roulette method’ (Haran et al., 2010; Goldstein and Rothschild, 2014), where experts were asked to create a realistic and plausible representation of the probability distribution for the prey ID. Experts were tasked to assign subjective probabilities (as a percentage) for each prey type, equivalent to ‘bins’ in the roulette method, including age class (pup vs 1+year) for seals to give a species total of 100. Experts were provided a comments field where they could make additional notes on each event, describing how a decision was reached, e.g., seal species based on head shape or pelage, age class based on size, whether certain media type were more informative (Table 3).

3.2.2.2 SPECIES IDENTIFICATION CONFIDENCE THRESHOLD

Given the time commitment expected to examine images and complete assessments for the full dataset (n = 127) experts were asked to assess a sub-sample (n=37) of predation events. Prior to experts returning their scores, I independently assessed images for all predation events and assigned species probabilities following the same ‘roulette method’ protocol detailed in Section 3.2.2.1. To ensure species identification in full dataset was not biased by my prior knowledge of predation events (e.g., the date it occurred), a ‘confidence threshold’ was established using expert scores. For example, if I was confident the depicted prey was a harbour seal pup, partially influenced by the fact that the event occurred in July (peak pupping time) close a harbour seal pupping site, but the experts’ confidence did not meet the established threshold, then there was not sufficient confidence in my assessment to assign the species and age class to the event. By doing this, my prior knowledge and expectations of most likely species as obtained by collating the predation images was accounted for. Expert scores for the 37 events contained in the elicitation process were compared to my assessments for the same sub-set. The confidence level at which my scores were in complete agreement with the expert scores was then assigned as the confidence threshold at which prey species ID could be assigned. As a result, prey species assigned in the final dataset reflected subjective probabilities as supported by expert obtained confidence levels.

3.2.3 Data processing & covariate selection

Following the expert elicitation protocol and my scoring of the full dataset, the most likely prey species from the following categories was calculated for each predation event: fish, porpoise, otter, seabird, harbour seal pup, harbour seal 1+ years, grey seal pup or grey seal 1+yrs. The confidence for species identification in each event was compared to the confidence threshold established, and only assigned to the event if the threshold was exceeded. Where confidence was not sufficient at age-class level for the two seal species, identification would be made at the species level (harbour vs grey seal). If confidence was not sufficient at species levels, but there was confidence at a higher taxonomic class level (i.e., a mammal based on blubber prey remained) then identification would be classified as unknown mammal. Where identification was uncertain across all species, identification was assigned as unknown. Based on this approach, prey identification was assigned to the full predation events database.

For statistical analysis of the influence of variables on predator success, predation outcome categories were grouped into three categories: consume, escape (regardless of method – land, shallows, dive, or anthropogenic), and unknown. Events where the outcome was unknown were excluded from statistical analyses. Events with prey ID assigned unknown or unknown mammal were not included in statistical analysis to investigate prey species vulnerability due to bias towards a consumptive outcome (primarily being observed as prey remains). Outcome, as a binary covariate (0 = escape and 1 = consume), was used as the response variable to investigate ecological and environmental predictors of predator success.

To investigate environmental, spatial, and temporal patterns of predation success, the following candidate covariates were included for analysis: SMA subregion, shoreline type, month, distance to shore, and prey species ID. Given the expected increase in data collection over the years (2016-2023) due to increase in effort and reporting, both from citizen science reports and the presence of PhD fieldwork (2021-2023), predation events were investigated on a temporal scale of months and not years.

3.2.4 Statistical analysis

3.2.4.1 EXPERT ELICITATION

A multinomial regression was used to model the most likely prey species from expert elicitation scores and for the full predation events dataset. Percentages were modelled as a multinomial variable, considering each percentage as a frequency of choice. No random effects were included, with individual expert scores treated as independent and weighted equally. The function *mblogit* from the *mclogit* package in R was used to model most likely prey ID with associated confidence as the response variable, and event_ID weighted by percentages as the predictor variables.

3.2.4.2 SPATIAL, TEMPORAL, AND ECOLOGICAL PREDICTORS OF PREDATOR SUCCESS

A binomial GLM was used to investigate environmental, spatial, temporal and prey species variables predicting predator success, coded as a binomial response variable (0 = escape, 1 = consume) in the full predation event dataset where the outcome was known. The response variable was modelled using a quasibinomial distribution to account for any over-dispersion in the dataset. Candidate covariates included in the full model included: SMA subregion, shoreline type, month, distance to shore (in meters) and prey ID. Given the inclusion of prey ID is expected to reduce the explanatory power of the spatiotemporal covariates of interest, the full model was fitted both without (model 1) and with (model 2) prey species ID as a covariate. The small sample size of the response variables and categorical nature of candidate covariates prevented the inclusion of interactive terms in the full model. Global model selection was carried out using the *dredge* function in the R package *MuMin.* Global model selection tests all combinations of candidate predictor variables and ranks the candidate models by identifying those that best explain variation in the response variable after accounting for the number of estimated parameters in each model, calculated using Akaike Information Criteria adapted for quasi-distribution (QAIC). The final model was selected as that with the fewest estimated parameters within 2 QAIC units of the lowest QAIC model (ΔQAIC <2).

3.3 Results

3.3.1 Expert Elicitation & Prey Identification

For the subset of predation events assessed by expert, harbour seal adult (1+ years) was the most frequently assigned prey type (n=17), followed by grey seal adult (n=13), harbour seal pup (n=4), porpoise (N=1), otter (N=1), and seabird (N=1), while grey seal pup, fish, and other were assigned zero times each by the multinomial model (Figure 3.6). On average, confidence on most likely prey was approximately 0.6 (60%) (min = 0.27, median = 0.63, mean = 0.64 and max = 1.0), but means varied considerably between species (porpoise = 0.71, otter = 0.88, seabird = 0.80, harbour seal pup = 0.40, harbour seal adult = 0.60, and grey seal adult = 0.74). There were only 4 events where confidence in prey species across experts was greater than 0.95 (95%).

Given the uncertainty in species identification, particularly surrounding seal age-class (min = 0.27 and max = 0.47% harbour seal pup), probability scores for seal species were grouped to species level (harbour vs grey), regardless of age class. When considering seals at a species level, harbour seal was the most frequently assigned prey type (n=23), followed by grey (n=11), with otter, porpoise and seabird assigned once each (Figure 3.7). The average confidence on most likely prey subsequently increased to ~80% (min = 0.45, median = 0.82, median = 0.78, max = 1.0). Mean confidence in species increased to ~70% for harbour seals (mean = 0.73) and 85% for grey seal (mean = 0.85).

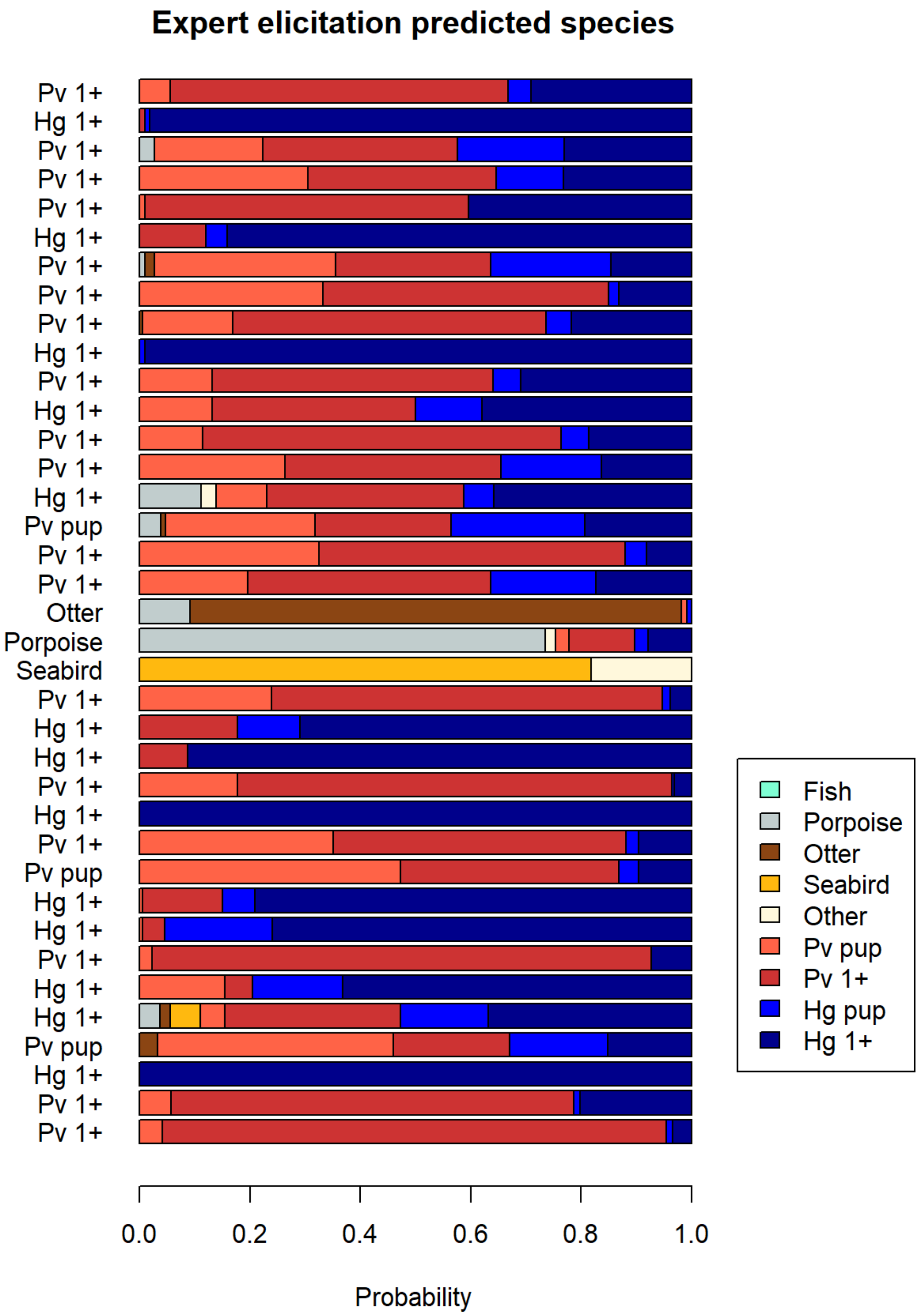

Figure 3.6. Expert elicitation most likely prey species & age class based on multinomial GLM results. Each row represents a predation event in the expert elicitation. Colours represent the proportion of species assigned to each event from the multinomial regression model, which modelled the most likely prey species across expert elicitation scores. Proportions were modelled as a multinomial variable, considering each proportion as a frequency of choice. The most likely prey species for each predation event (row) is detailed on the Y axis, where Pv_pup = harbour seal pup, Pv_ot = harbour seal adults (1+years), Hg_pup = grey seal pup, Hg_ot = grey seal adult (1+ years).

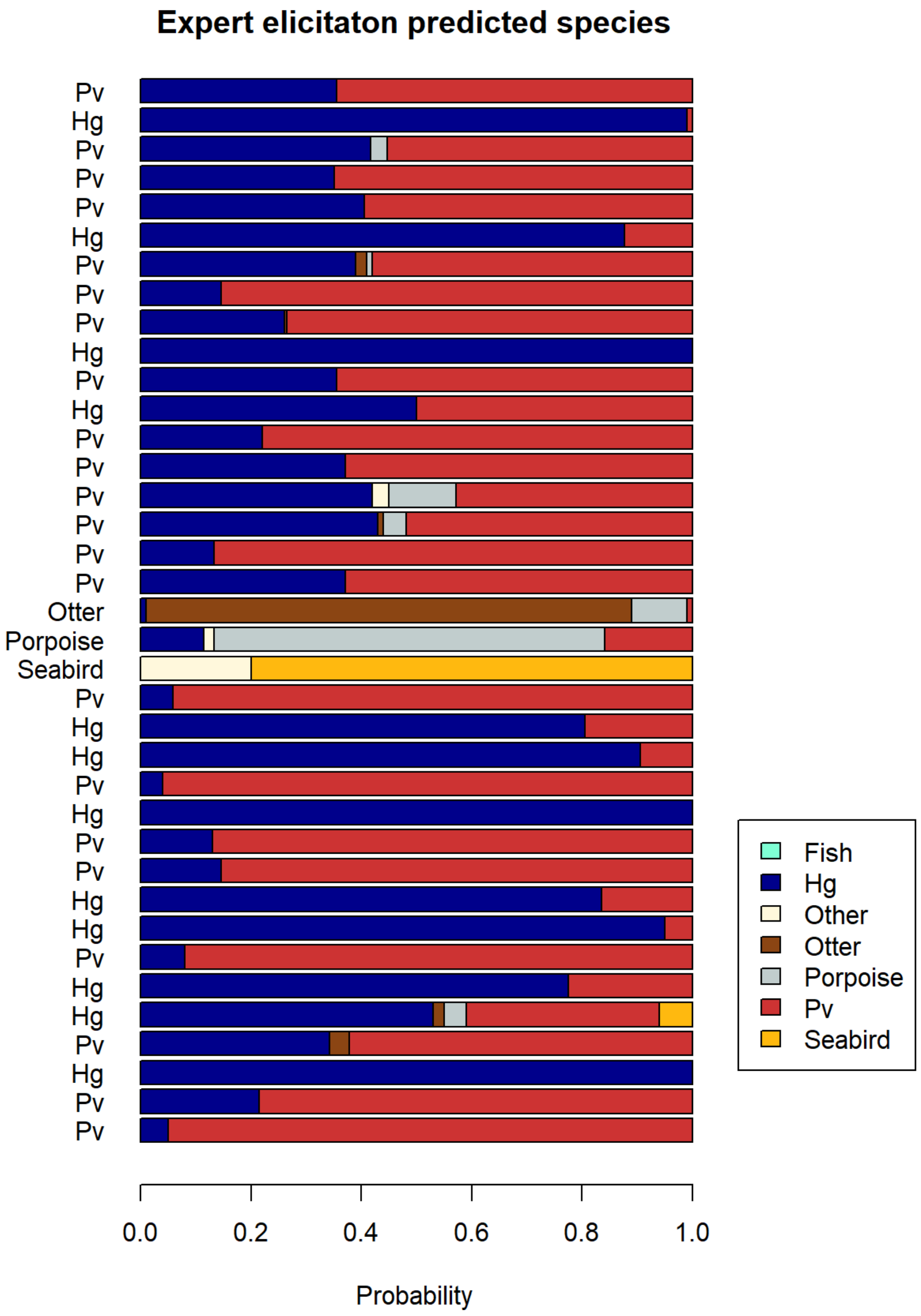

Figure 3.7. Expert elicitation most likely prey species based on multinomial GLM results. Each row represents a predation event in the expert elicitation, in the same order as Figure 3.7. Here, harbour seal pup and harbour seal 1+yrs scores were grouped together as harbour seal (Pv), and grey seal pup and grey seal 1+yrs scores were grouped together as grey seal (Hg). The most likely prey species for each predation event (row) is detailed on the Y axis, where Pv = harbour seal pup and 1+ yrs and Hg = grey seal pup and 1+yrs.

For the 37 events included in the expert elicitation, most likely prey type, including species age class, was assigned consistently between the experts and myself for 30 out of 37 events (Figure 3.8). However, there was considerable differences in assigned probabilities between myself and the experts for certain events, with up to 50% difference in probability of most likely prey species. When grouping seals at a species level (harbour vs grey seal), most likely prey species was assigned consistently between the experts (median 89%) and myself when my confidence was ≥65% (Figure 3.9). That is, when I was ≥65% confident prey type was either harbour seal, grey seal, harbour porpoise, otter, seabird or unknown mammal, the experts were in complete agreement with my assessment with a median confidence of 89% amongst them. Given this, the confidence threshold for prey type assignment for my assessment of the full predation events dataset was set at ≥65%. Using the confidence threshold of ≥65%, harbour seal (n=25), grey seal (n=20), otter (n=2), porpoise (n=7) and seabird (n=6) were assigned to 60 out of the total 127 events. Where confidence in individual seal species was <65%, but ≥65% for either a harbour or grey combined, prey ID was assigned as seal (n=52). Where my confidence that prey was either a harbour, grey, or harbour porpoise was ≥ 65%, ID was assigned unknown mammal (n=15) (Figure 3.10).

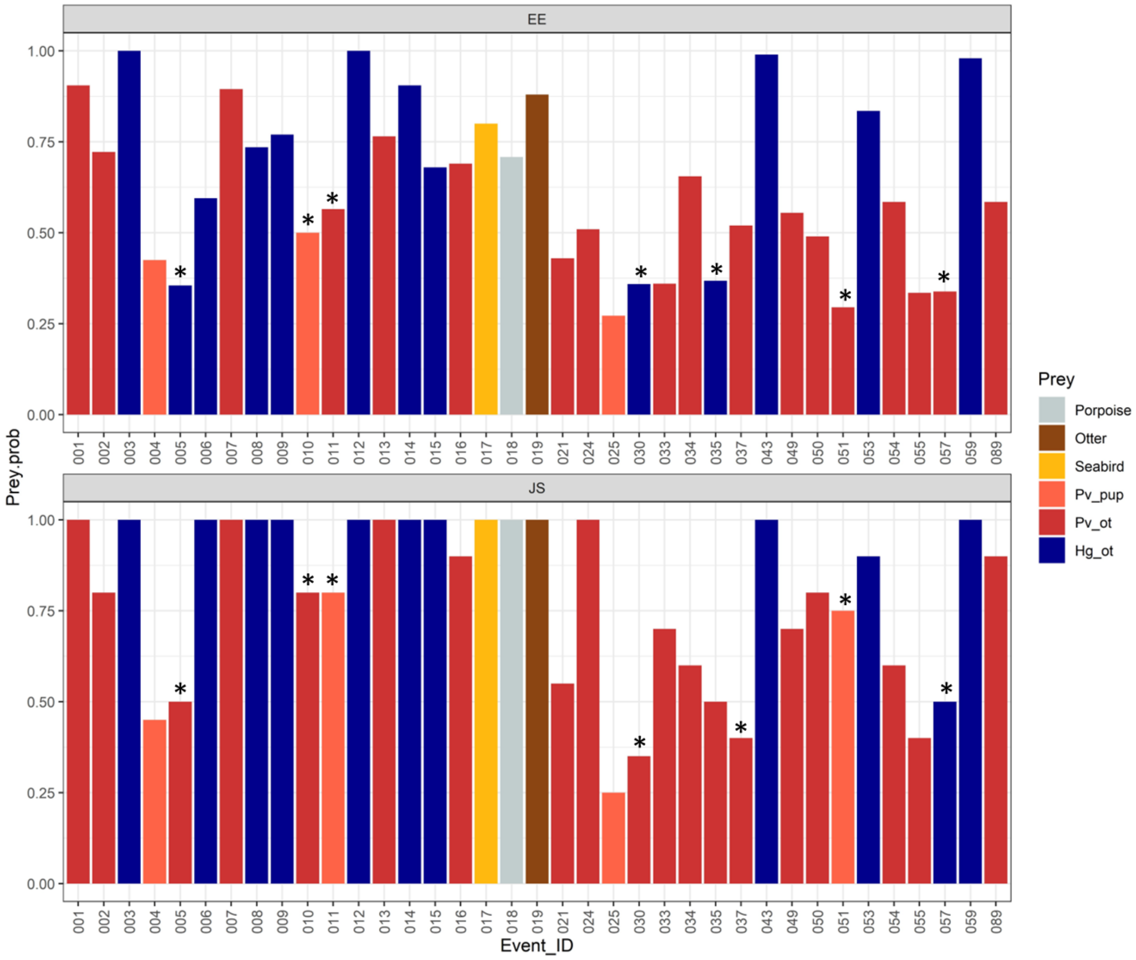

Figure 3.8. Expert elicitation and JS most likely prey species and age classes based on multinomial GLM results. Bar chart depicts the assigned probability for the most likely prey species and age class for each predation event, as assigned by the expert panel (EE, top) and myself (JS, bottom). Asterisks indicate events where most likely prey species was assigned differently between the two groups (n=7).

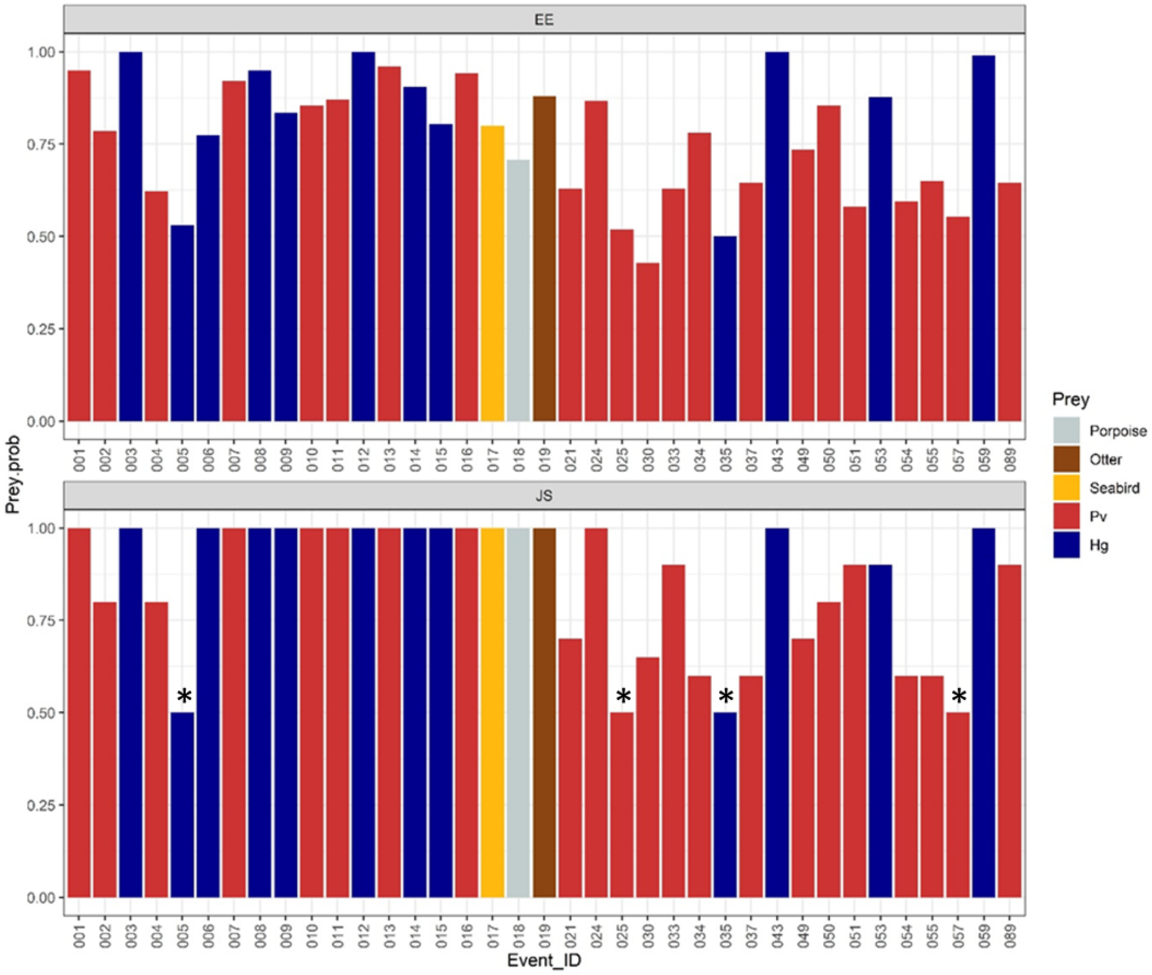

Figure 3.9. Expert elicitation and JS most likely prey species based on multinomial GLM results. Bar chart depicts the assigned probability for the most likely prey species, with harbour and grey seals grouped at the species level, for each predation event, as assigned by the expert panel (EE, top) and myself (JS, bottom). Asterisk on the JS panel indicate where my confidence in seal species was split equally between species (0.5 grey seal, 0.5 harbour seal) and thus does not reflect true agreement with the experts. Where I was ≥65% (0.65) confident in seal species, there was complete agreement in the experts assigned most likely prey and mine.

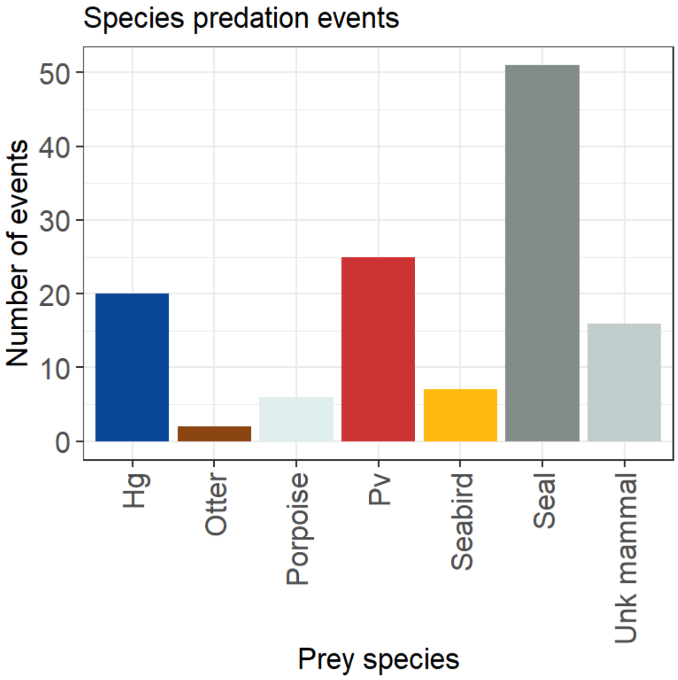

Figure 3.10. Total number of each species assigned in final predation events dataset (n=127). Where confidence in each species (Hg = grey seal, other, porpoise, Pv = harbour seal, seabirds) met established confidence threshold of 65%. Seal category reflects where there was confidence (≥ 65%) the prey item was a seal, but individual species (harbour vs grey) was uncertain (<65%). Unk mammal = unknown mammal, where it was confident the prey type was of mammalian class (≥ 65%) but of uncertain species.

3.3.2 Predation Events

In total, 127 predation events were collated between 11th January 2016 and 18th July 2023 from drone footage (n=70), citizen science (n=41), and fieldwork observations (n=16) (Figure 3.11, Figure 3.12). With data pooled across all years, events were observed in every calendar month with a noticeable peak in July (n=50) (Figure 3.12). Predation events were recorded in all SMA subregions (N&E, SE & W), but were most frequent in the N&E SMA region (N&E n=53, SE n=39, W n=35) (Figure 3.13). Harbour and grey seal predation events were recorded in all SMA regions, seabirds (N=6) and porpoise were present in the N&E (n=1) and SE (n=6) regions, and otters (N=2) were only present in the W region (Figure 3.13). At a species level for seals, grey seal observed predation events peaked in July (n=8) and harbour seal in August (n=8) (Figure 3.14).

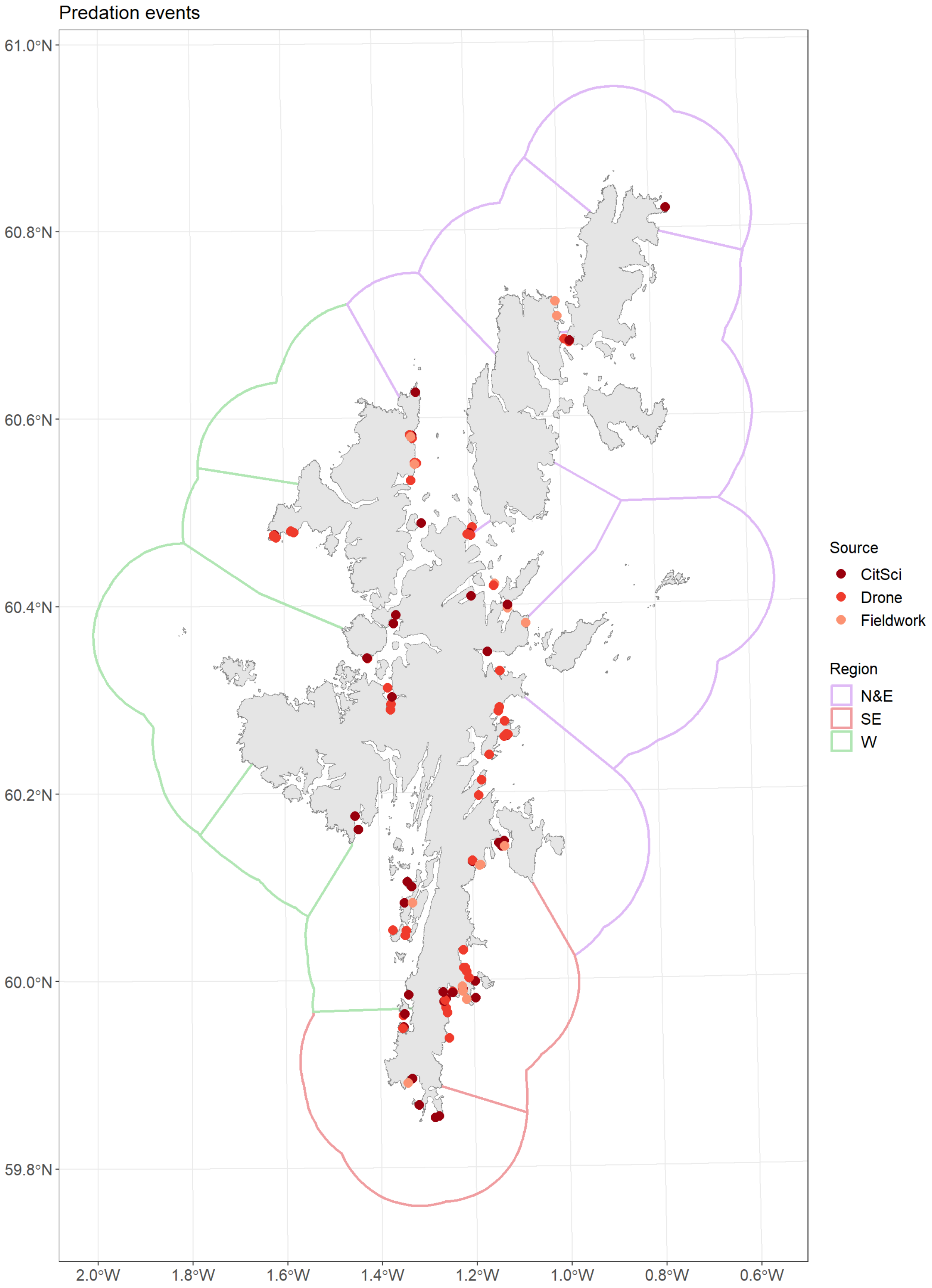

Figure 3.11. Predation events collated in final dataset (n=127). Dots indicate location of predation event within SMA subregion boundaries, colour coded by source (CitSci = citizen science, drone = drone footage submission, fieldwork = fieldwork observations).

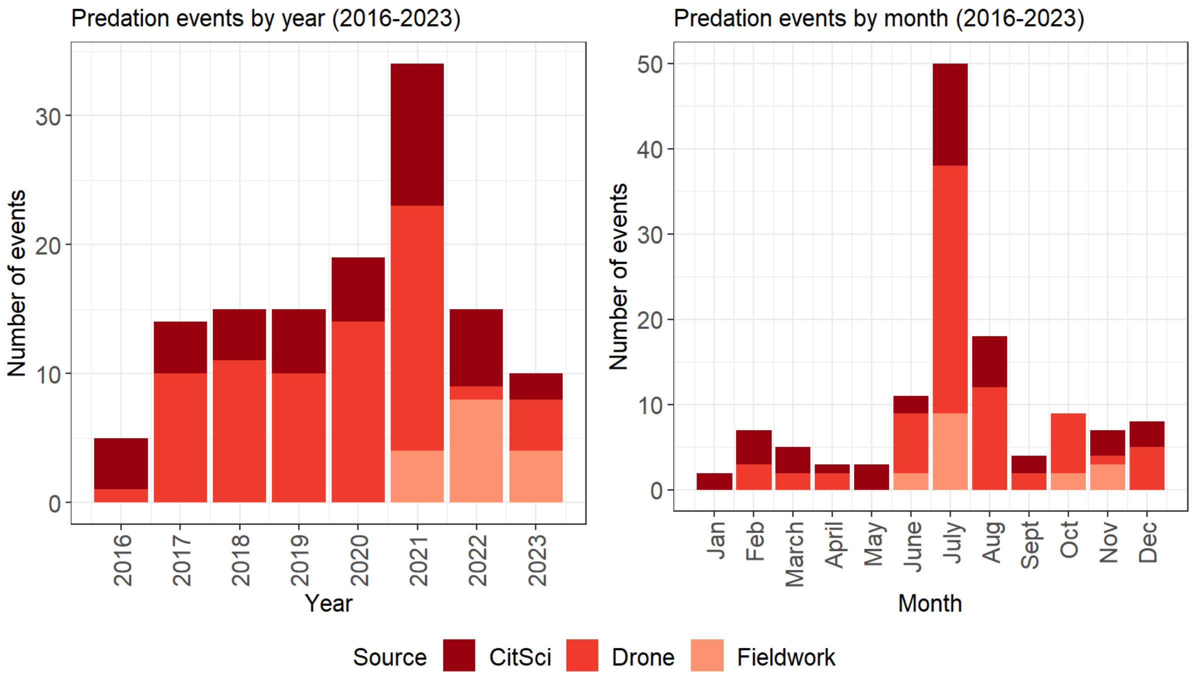

Figure 3.12. Predation events in each month with data pooled across all years (2021-2023) (left) and by year (right). Predation events as collated in the final dataset between January 2016 and July 2023.

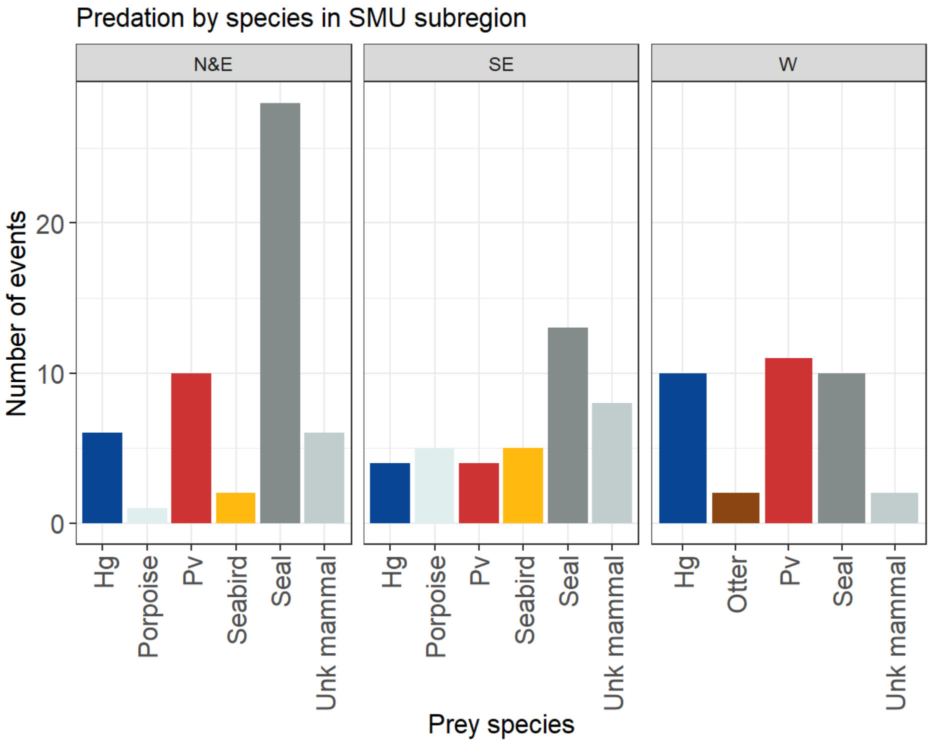

Figure 3. 13. Predation events by species classification in each SMA subregion.

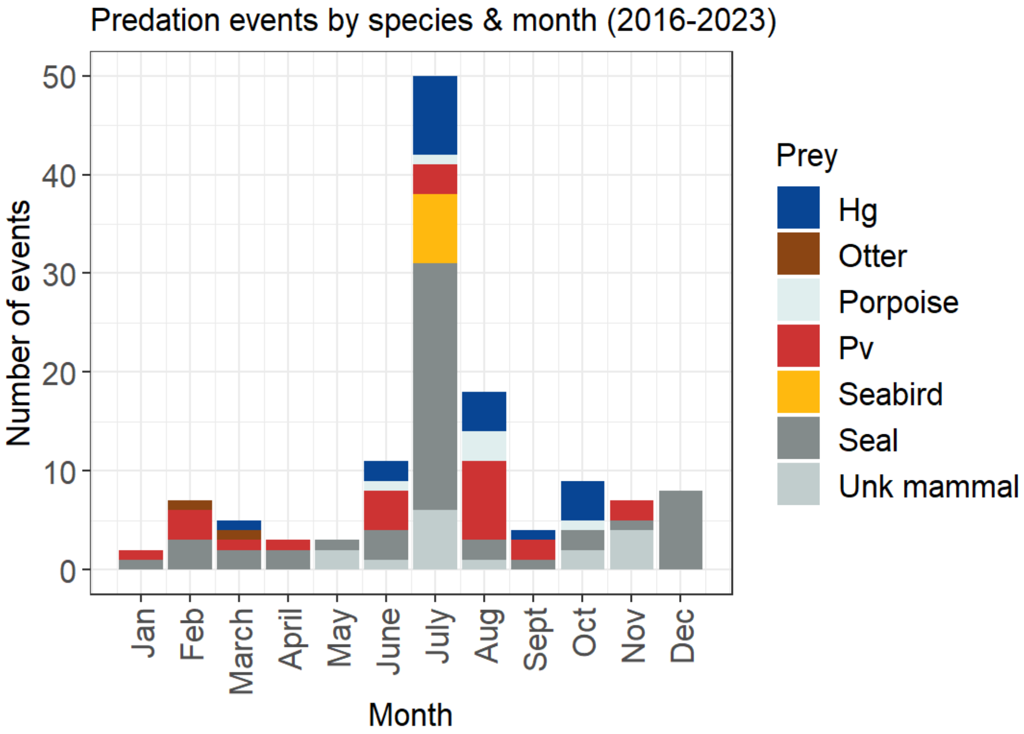

Figure 3.14. Predation events by species in each month with data pooled across years (2016-2023). Predation events by species as collated in the final dataset between January 2016 and July 2023.

A majority of predation events resulted in consumption (n=87, 69%). The most frequently observed method of natural escape was to move to shallow water (n=18) compared to moving to land (n=8) and diving (n=1) (Figure 3.15 – 3.16). Escape to anthropogenic refuges was observed twice, once where a seal took refuge under a boat and once when a seabird (black guillemot, *Cepphus grylle*) took refuge on a navigational buoy. Grey seals showed a higher propensity to escape (65%, n = 13/20 events) than harbour seals (28%, n = 7/25 events). Where prey could be identified to seal but not to species, seals escaped 27% of events (n = 11/51), likely reflecting a combination of harbour and grey seal predation events. Sample sizes for other species were smaller, with escapes observed for porpoise (n=1/6) and seabirds (n=1/16) for 17% of their respective events. Of the two otter events, the otter escaped on one occasion and the outcome of the other was unknown. Unknown mammals were always consumed (100%, 16/16) and were primarily identified based on prey remains. Whilst included in summary plots here, unknown mammals were not included in statistical analysis in investigate predictors of predation success due to their strong bias towards a consumptive outcome, as previously noted.

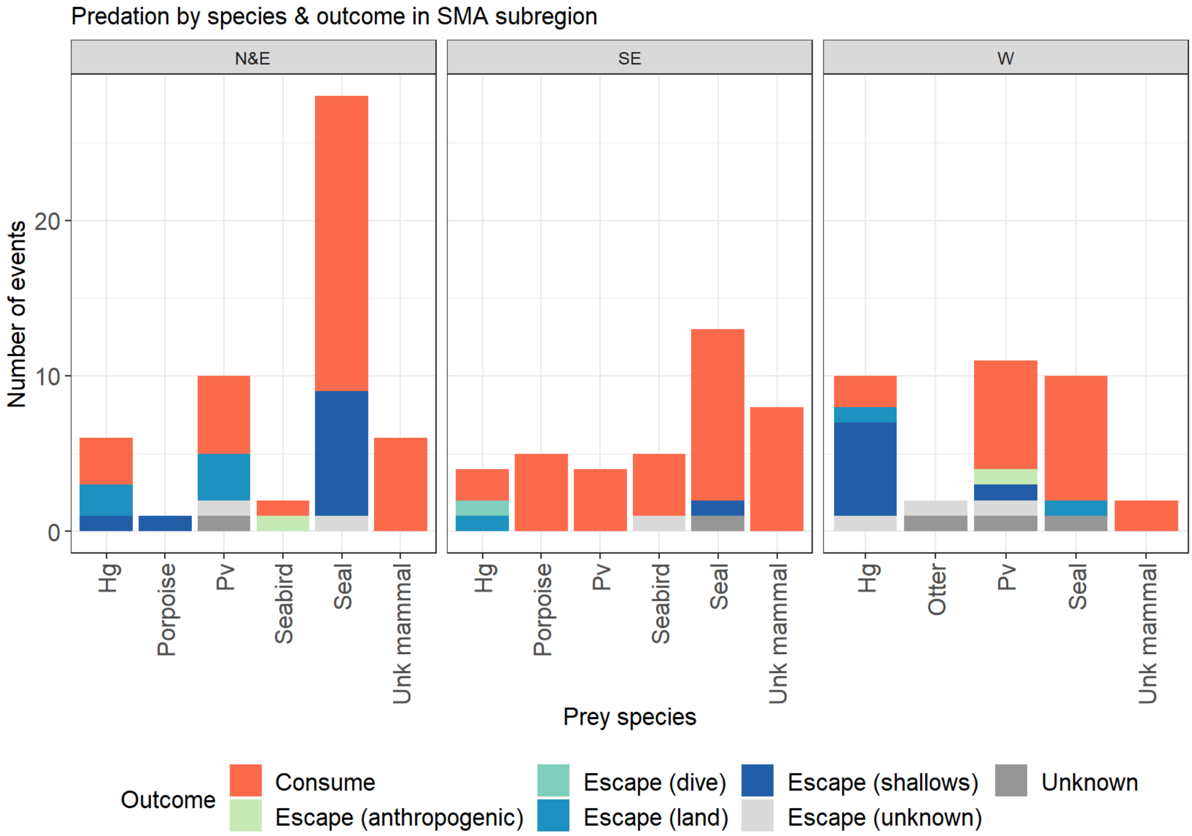

Figure 3.15. Predation events by species & outcome in SMA subregion. Anthropogenic escapes involved a seabird taking refuge on a navigation buoy, and a harbour seal taking refuge under a boat.

Given potential reporting bias by citizen scientists towards successful predation events (i.e., those most likely to be noticed and documented), the frequency of outcomes reported via citizen science was compared to those documented in the scoring of drone footage. Whilst the collection of drone footage may still be biased towards more noticeable events, the review of all raw footage for any predator-prey interactions likely reduces this type of reporting bias in the sample. Escapes were observed for 34% (n=24/70) of predation events in drone footage, and 24% (n=10/31) in citizen science observations suggesting some potential reporting bias in citizen science observations, but not a substantial amount (Figure 3.16).

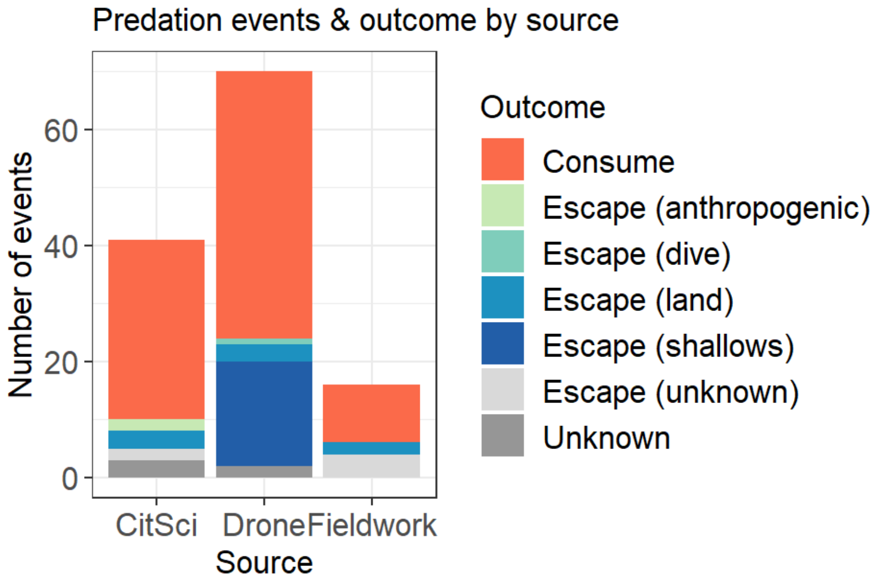

Figure 3.16. Predation event outcomes by data source. Drone footage represents more systematic data collection, as all raw footage was analysed, and citizen science (CitSci) represents more opportunistic data collection. The proportion of escapes observed in drone footage (34%) and citizen science (24%) was not substantially different, suggesting there may not be a strong reporting bias in citizen science towards successful predation events (i.e., those most likely to be noticed).

3.3.3 Spatial, temporal, and ecological predictors of predator success

Of the five candidate covariates included in the full model, distance to shore, SMA subregion, and prey species were retained in model selection. For the model without prey species included as a covariate (model 1), distance to shore was estimated to have a positive relationship with the probability of consumption. Predation events occurring further from the shoreline had a higher probability of consumption (t=2.47, p =0.01, Table 3.5), with marginal effects predicted probabilities increasing from 0.57 at ~10m to 0.92 at ~550m (Figure 3.17). Predation events within the SE SMA subregion had a higher probability of consumption compared to the intercept of the N&E region and the W region (t=2.24, p = 0.01, Table 3.5), with marginal effects predicted probabilities of 0.89 from the SE, 0.64 for the N&E and 0.62 for the W regions (Figure 3.18). This model explained 11.2% of the deviance in the dataset.

Table 3.5. Binomial GLM parameter estimates for factors influencing predation success. Interact for SMA region is N&E. Estimates are shown on logit-scale.

	Estimate	Std. Error	t value	P Value
(Intercept)	-0.21	0.45	-0.47	0.64
as.numeric(dist)	0.003	0.002	2.18	0.03*
SMASE	1.54	0.62	2.50	0.01*
SMAW	-0.09	0.48	-0.19	0.85
Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 Deviance explained: 11.2%				

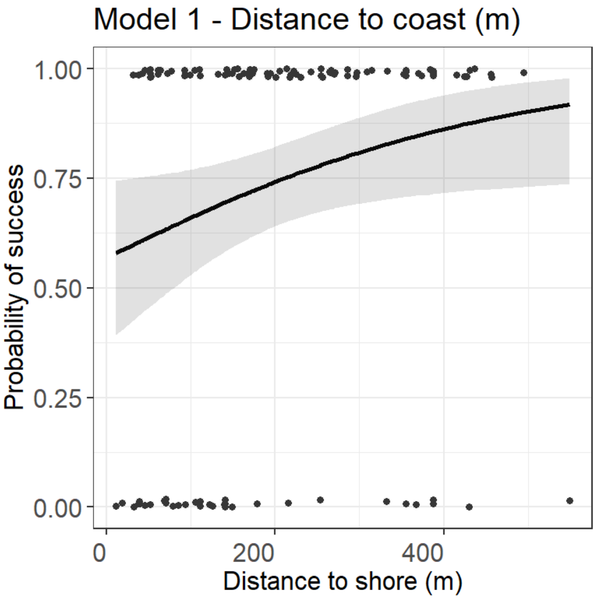

Figure 3.17. Model 1 predictions for the effect of distance to coast on probability of predation success. Plot made using *ggemmeans* function from the *ggeffect* package. *ggemmeans* plots the marginal effects, with non-focal predictors set to their mean numerical value or marginalized over levels for factors. Black dots depict raw data points, with small random noise added to show spread of the data.

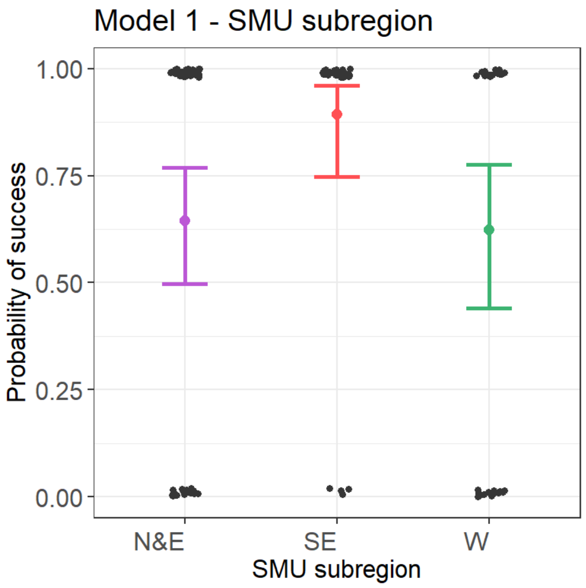

Figure 3.18. Model 1 predictions for the effect of SMA subregion on probability of predation success. Plot made using *ggemmeans* function from the *ggeffect* package. *ggemmeans* plots the marginal effects, with non-focal predictors set to their mean numerical value (here, 206m for distance to shore) or marginalized over levels for factors. Black dots depict raw data points, with small random noise added to show spread of the data.

For the model containing prey species as a covariate (model 2), the positive relationship with shoreline remained (t=2.6, p = 0.01, Table 3.6), with marginal effects predicted probabilities increasing from 0.41 at ~10m to 0.93 at ~550m (Figure 3.19). The SE SMA subregion had a higher probability of consumption compared to the intercept of the N&E region and the W region (t=2.1, p=0.01, Table 3.6), with marginal effects predicted probabilities of 0.67 from the SE, 0.2 for the N&E and 0.33 for the W regions (Figure 3.20). For prey species, seals (t=2.3 p = 0.001, Table 3.6) and harbour seals (t=2.35 p = 0.02, Table 3.6) were estimated to have a higher probability of consumption when compared to the intercept of grey seal, with marginal effects predicted probabilities of 0.2 for grey seal, 0.58 for harbour seal, 0.72 for seal, 0.4 for porpoise, and 0.35 for seabird (Figure 3.21). This model explained 21.3% of the deviance in the dataset.

Table 3.6. Binomial GLM parameter estimates for factors influencing predation success with species included as a covariate. Interact for SMA region is N&E and for species is grey seal (Hg). Estimates are shown on logit-scale.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-2.50	0.81	-3.07	0.00
as.numeric(dist)	0.01	0.002	2.63	0.01**
Prey_finPorpoise	0.98	1.31	0.75	0.45
Prey_finPv	1.69	0.72	2.35	0.02*
Prey_finSeabird	0.75	1.14	0.66	0.51
Prey_finSeal	2.30	0.69	3.34	0.001**
SMASE	2.10	0.77	2.74	0.007**
SMAW	0.67	0.61	1.10	0.27

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
Deviance explained: 21.3%

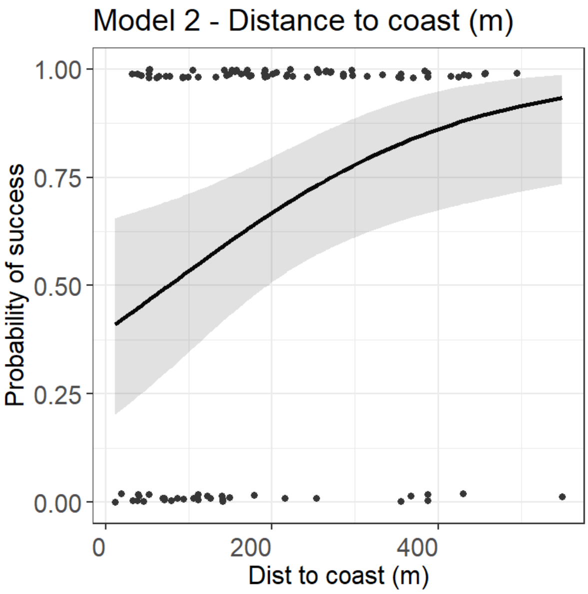

Figure 3.19. Model 2 predictions for the effect of distance to coast on probability of predation success. Plot made using *ggemmeans* function from the *ggeffect* package. *ggemmeans* plots the marginal effects, with non-focal predictors set to their mean numerical value or marginalized over levels for factors. Black dots depict raw data points, with small random noise added to show spread of the data.

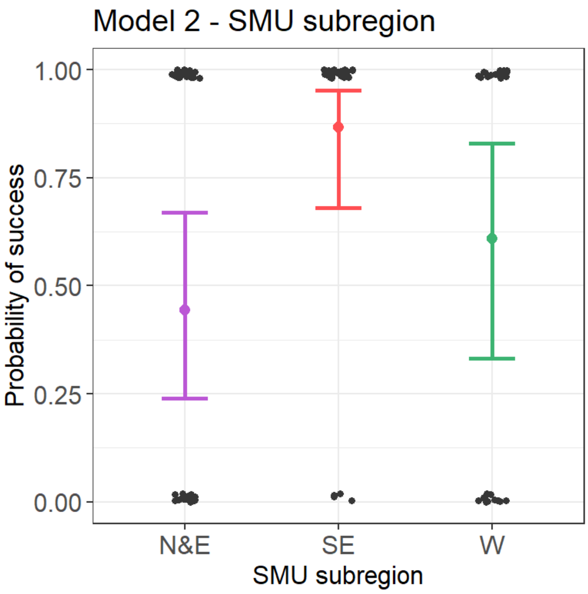

Figure 3.20. Model 2 predictions for the effect of SMA subregion on probability of predation success. Plot made using *ggemmeans* function from the *ggeffect* package. *ggemmeans* plots the marginal effects, with non-focal predictors set to their mean numerical value (here, 200m for distance to shore) or marginalized over levels for factors. Black dots depict raw data points, with small random noise added to show spread of the data.

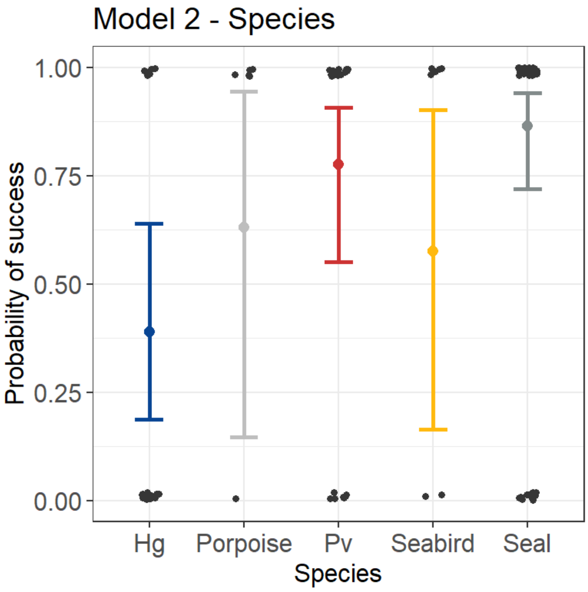

Figure 3.21. Model 2 predictions for the effect of species on probability of predation success. Plot made using *ggemmeans* function from the *ggeffect* package. *ggemmeans* plots the marginal effects, with non-focal predictors set to their mean numerical value (here, 200m for distance to shore) or marginalized over levels for factors. Black dots depict raw data points, with small random noise added to show spread of the data.

3.4 Discussion

The aim of this Chapter was to characterise the prey composition of coastally foraging killer whales as observed in Shetland, and to investigate potential spatial-temporal, environmental, and ecological drivers of conditional capture probability (CCP) for targeted prey species. In this study, I found that predation events further from the shoreline had a higher chance of success than those closer to shore (range ~10m – ~550m), and proportion of success was higher in the SE SMA subregion of Shetland. Where prey species were identified, harbour seal predation events had a higher probability of success in comparison to grey seals. Here, I discuss findings in light of methodological limitations, drawing conclusions on the potential causes and consequences of the observed variation in conditional capture probability (CCP) from both a predator and prey perspective.

3.4.1 Prey composition of inshore-foraging killer whales in Shetland

Published literature to date describing predation events of inshore-foraging killer whales in Scotland have detailed harbour seals as the primary or focal prey species (Bolt et al., 2009; Deecke et al., 2011; Hague et al., 2022) however there have been many unpublished observed but documented predation events on other species. Here, I systemically quantify the prey composition from observational data, whilst considering uncertainties in species and age class identification. Killer whales were observed targeting and successfully consuming a variety of prey species, including harbour seals, grey seals, harbour porpoise, and seabirds. Whilst otters were identified as targeted, no successful predation was confirmed.

It was historically proposed that killer whales are seen in greater numbers during harbour seal breeding seasons with the purposes of targeting harbour seal pups (Bolt et al. 2009), however year-round observations of killer whale foraging inshore propose a peak in summer and autumn months to coincide with harbour and grey seal breeding seasons respectively (Scullion et al. 2021). Here, harbour seal pups were assigned most likely prey species for only three of the 37 predation events assessed by the expert panel (Figure 3.6), although confidence in age classification was low amongst experts (median 40%, maximum 47%). For harbour seals aged 1+ years, however, confidence in age class identification was higher (median 60%, max 90%), and was assigned to 18 out of the 37 events in the elicitation process.

This would suggest harbour seals of all age classes are targeted by killer whales, and perhaps a higher proportion of adults than previously expected (Bolt et al. 2009). Whilst adults were more numerous in the elicitation dataset, it should be noted that pups may be underrepresented in predation events observations due to their small size and thus expected smaller handing time. That is, is it plausible more pups are taken but little evidence of the predation event (e.g., prey handling, prey remains, blood or slick) is observed at the surface.

With regards to understanding the potential consumptive impacts on vulnerable prey populations, understanding the age-class composition of individuals removed from the population is integral to quantifying population level consequences (Hanson et al. 2013). For the regionally declining harbour seal, it has been proposed that a significant number of adults must have been removed from the population for the observed declines to have occurred and/or prevent population recovery (Hanson et al. 2013; Hanson et al. 2017), however current consumption estimates have only assumed a killer whale diet composition of pups (Bolt et al. 2009). The confirmation that adults as well as harbour seal pups are prevalent in killer whale diet therefore represents a significant advancement in our capacity to estimate the top-down pressure elicited by the apex predator on vulnerable prey populations by taking into account age-class specific consumption estimates.

Grey seals of ages 1+ years were also assigned most likely prey species for 13 out of the 37 predation events in the elicitation dataset, confirming previous documentation that grey seals are regularly targeted by inshore-foraging killer whales in Shetland. No grey seal pups were identified as most likely prey species in the expert elicitation dataset, however a predation event included in the full predation events dataset showed killer whales consuming both a pregnant female grey seal and her unborn pup. The event was observed via drone in October 2020, with the pup removed from utero and amniotic sac during prey handing, and both mother and pup were consumed simultaneously by members of the 27s pod. Whilst not included in this dataset, stomach content analysis of a killer whale, juvenile male ID 151 from the 27s pod, that was found dead stranded in Orkney in October 2021 was identified as containing grey seal pup lanugo pelage, along with other unidentified seal species pelage (SMASS 2021). The pup pelage with fore flipper and claws still intact was viewed as too small to have been a pup at full term (S. Moss & C. Sparling, personal communications, February

2024), and indeed the time of the stranding (October) is prior to the start of grey seal pupping in the Northern Isles, suggesting the remains were likely a pup still in utero. This would suggest the drone observation of the pregnant female was not an isolated incident and raises important considerations with regards prey selection and consumptive impact. From a prey capture point of view, pregnant females may be easier to capture due to physiological constraints that limit their capacity to escape (e.g., reduced locomotion capacity due to increased buoyancy from fat stores). From a killer whale energetics point of view, targeting pregnant females may be an efficient method of prey acquisition if pregnant females are easier to capture and yield a higher calorific reward. If females of breeding age and stage are removed through predation, consumptive impacts on prey populations may have considerably consequences for population structure and fitness.

In combination, the variety of prey species identified through the expert elicitation process suggests a more varied diet for killer whales in inshore Shetland than previously described in the available literature and corroborates sightings observations over a number of years. Harbour seals of all age classes and grey seal adults were identified, with seals comprising the highest proportion of prey species observed in this dataset. The presence of other species, such as harbour porpoise, has important implications for species specific consumption estimates if energetic requirements of killer whales are met through the consumption of various mammalian prey (Ferguson et al. 2012). Whilst seabirds were identified as consumed, their energetic content is likely to be negligible given the requirements of killer whales; for instance, the seabird identified through the elicitation process was an eider duck chick. Attacking prey for purposes other than energetic gain is detailed in the literature(Jefferson et al. 1991; Gaydos et al. 2005), and here it is plausible that seabird consumption may be more to do with play or prey targeting practice than with nutritional acquisition.

Overall, the elicitation process gleaned valuable insight into the various prey consumed by killer whales, including the extent to which killer whales consume seals versus other prey species, highlighting the need to consider consumptive impacts in a multi-prey diet (Ferguson et al. 2021). Furthermore, the process demonstrated the challenges associated with obtaining confidence in prey identification through visual observations alone. To improve the elicitation process and increase confidence in the final prey species and age class identification, a two-stage delphi protocol could be adopted (Hemming et al. 2018). With this, experts would have the opportunity to review anonymised scores, discuss discrepancies in assessments, and together provide a best estimate for prey and age class identification for each predation event. This protocol was explored as part of the expert elicitation process conducted here, however due to time commitments and logistical constraints it was not feasible in the given timeframe.

To further understanding of killer whale prey composition, other methodologies such as stable isotope analysis of killer whale blubber biopsies (Herman et al. 2005; Jourdain et al. 2020) and an e-DNA analysis of prey remains from killer whale faeces could be explored (Visser et al. 2021; Reidy et al. 2022). Stomach content analysis from dead stranded individuals would also be worth considering where samples are available from necropsy (e.g., from SMASS). Whilst not within the scope of this study, alternative methodology may prove a valuable avenue to pursue for future quantification of killer whale diet given uncertainties surrounding visual observations alone. Nevertheless, the non-invasive methodology here undoubtably furthers understanding of the diversity of prey species and age-classes taken by coastally foraging killer whales as observed here in Shetland.

3.4.2 Spatial, temporal, and ecological predictors of prey capture

Predation risk depends not only the probability of an encounter, but perhaps more importantly the probability of capture given an encounter (Hebblewhite et al. 2005). If predators have low lethality given environmental conditions, e.g., refuge availability, or prey characteristics, e.g., vigilance and escape capabilities, then the chances of capture given an encounter (conditional capture probability) may be low (Suraci et al., 2022). Here, I observed that harbour seals had a greater probability of predation in comparison to grey seals (Figure 21), and predation events that occurred further from the shoreline had a greater probability of success (consumption) in comparison to those closer to the shoreline (Figures 3.17 and 3.19). These results would suggest that probability of capture given an encounter (conditional capture probability, CCP) is mediated both by intrinsic (prey characteristics), and extrinsic (environmental) characteristics, resulting in variable predation risk from coastally foraging killer whales.

For the purposes of investigating species-specific variability in predation rates, harbour and grey seals were analysed at the species level, regardless of age-class, to increase confidence in species identification for the full dataset (see section 3.2.2.2 and section 3.3.1). The sample size of for harbour and grey seals was considerably lower than for seals of an unknown species (n = 25 for harbour seal, n = 20 for grey seals, n = 52 for unknown seals) (Figure 10). Whilst harbour seals were observed to have a higher probability of predation in comparison to grey seals, the highest probability of all prey species was observed for unknown seals (Figure 3.21). Species-specific conclusions should therefore be made with caution, given the proportion of harbour and grey seals in the unknown seal species category is largely uncertain. To overcome this uncertainty, the proposed second stage of the expert elicitation process (see section 3.4.1) could be implemented to increase the number of harbour vs greys identified in the current dataset. Furthermore, an increase in the overall sample size through new data collection would improve modelling capabilities by allowing the inclusion of interactive relationships between species and other variables of interest, such as month and SMA sub-region, in the model selection process. Nevertheless, the finding that harbour seals have a higher probability of consumption in comparison to grey seals despite the fact that the number of predations attempts on the two species were not dissimilar (Figure 3.10) provides new insight into the predation risk experienced by harbour and grey seals and demonstrates the complexities of predator-prey interactions beyond simple spatial overlap.

With regards to prey species composition as observed in this study, data collection limitations should be taken into consideration. The current dataset depicts the prey composition of inshore-foraging killer whales as identified in field, citizen science, and drone observations; all of which are primarily focused on the Shetland mainland. Whilst harbour seals are found distributed around the Shetland mainland, the large concentrations of grey seals are found around islands and skerries further offshore (e.g., Out Skerries) (SCOS 2022). The number of grey seals predation events captured in this dataset may therefore underrepresent the actual number targeted by killer whales if attempts are made in areas of high grey seal density outwith the scope of land-based data collection in this study. Furthermore, observer-based bias associated with citizen science observation (Arazy and

Malkinson 2021) may result in a disproportionate number of events reported for summer months (Figure 3.12), when extended daylight hours, calmer weather and an increase in tourism may influence the capacity to detect, observe, and report predation events. This may therefore result in an overrepresentation of harbour seal pup and 1+years age classes in the observed data, given harbour seal breeding and moulting occur in June and July, and August respectively. To address the issues of effort and reporting bias, spatial and temporal effort correction of data should be incorporated into future analysis. With regard to increased reporting opportunity from increased daylight hours, a reporting index could be calculated by dividing the number of predation events observed per by day the total number of daylight hours. This would be interesting to explore, especially given the small increase in predation events also seen in the overall dataset October through December (Figure 3.12), which may prove more comparable to summer with daylight hours accounted for.

Landscape features and the distribution of refuges has important implications for both predator success and prey capacity to escape. Here, a majority of unsuccessful predation events occurred when seal species and harbour porpoise fled to the shallows, with predation events found to have a lower chance of success closer to the shoreline (Figures 3.17 and 3.19) (max 550m in the present dataset). The only unsuccessful predation event on a harbour porpoise was when the individual fled to the shallows and took refuge amongst rocks and kelp to escape the killer whales, highlighting the importance of shallow refuge across prey species. When spatial overlap with predators is high, prey are expected to under-utilise high risk areas, i.e., those with increased chances of consumption given a predator-prey encounter (Wirsing et al. 2008). For instance, in the Northeast Pacific harbour seals under-utilised profitable prey patches at depths overlapping with predator sleeper shark presence (Frid et al. 2007); in South Africa, Cape fur seals showed an aversion for deep-open water habitats in the presence of white sharks, instead utilizing more structurally complex habitats to move between foraging grounds (Wcisel et al. 2015). Here, prey species in Shetland may reduce their risk of predation by over-utilizing coastal areas which may be more conducive to escape, reducing their capture probability given an encounter with a killer whale.

Telemetry data as obtained from GPS-GSM biologging tags attached to harbour (n=25) and grey seals (n=9) in Shetland in 2023 showed strong coastal movements for both species

(Carter et al., in prep). Interpolated location fixes taken every 30 minutes suggests tagged harbour seals spend at least half their time within 200m of land; highly coastal in comparison to the average of ~3km for harbour seals tagged on the west coast of Scotland (Carter et al., in prep), where predation risk may be lower due to a decline in the West Coast Community killer whale pod and lack of semi-resident Northern Isle Community killer whale pods (Scullion et al. 2021). Grey seals tagged in Shetland appear to spend at least half of their time within 4km of land; whilst notably greater than harbour seals in Shetland, this is still relatively coastal in comparison to the average of ~18km for west coast grey seals (Carter et al., in prep).

From a predation risk and landscape of fear hypothesis, the highly coastal nature of seals in Shetland may indicate a behavioural pattern consistent with safer habitat selection. That is, when balancing the conflicting demands of resource acquisition (nourishment) and predator avoidance (Sih 1980; Lima and Dill 1990; Lima 1998), seal species in Shetland may choose to allocate more time to safer habitats, here those in greater proximity to shoreline refuge. The disparity in distance to land between the two species is characteristic of their more general behaviour, with harbour seals exhibiting more coastal ranges compared to grey seals (Carter et al., 2020) in UK waters. However, the fact that harbour seals had a higher probability of consumption in comparison to grey seals in this study may also shed light on the drivers of strong coastal distribution of harbour seals in Shetland. That is, if risk of predation upon encountering a killer whale is higher for harbour seal, as suggested here, the pressure to stay closer to shore and thus refuge may be greater than for grey seals, who have a lower probability of consumption given a predation attempt by killer whales.

To further investigate the propensity for seal species in Shetland to utilize shallows habitats, it would be interesting to compare harbour and grey seal behaviour in the presence and absence of killer whales on a more localised scale. That is, whether seals exhibit more coastal hugging when the threat of predation is high, i.e., when killer whales are present in coastal waters, in comparison to when threat is low, i.e., when killer whales are absent. For instance, during periods of high predation risk from white sharks, Cape fur seals preferred safer, shallow water compared to periods when white sharks were absent (Martin and Hammerschlag 2012; De Vos et al. 2015). Alternatively, the persistent threat of predation may be such that seals are in a continual state of perceived risk and thus prioritise proximity to refuge regardless of actual predator presence (Wirsing et al. 2008). Further analysis of telemetry data to quantify seal behavioural budgets, e.g., time spent foraging, transiting, and resting both in the presence and absence of killer whales on both a localised (e.g., within Shetland) and broader spatial scale (e.g., Northern Isles vs west coast of Scotland) may improve understanding of the non-consumptive impact of killer whale predation on seal species. That is, whether predation risk results in reduced foraging opportunities in favour of less profitable but safer habitats, which could result in population-level fitness consequences (Luttbeg and Sih 2004; Heithaus and Dill 2006; Sheriff et al. 2020).

Here so far, proximity to shore has been described somewhat synonymously with safer habitat. In practice, shoreline structure and associated habitat are far more complex, and perhaps proximity to suitable habitat refuges would be a more appropriate descriptor. However, in the current study no statistical support was found between habitat types and predation outcome. Given the small size and relative statistical complexities of the categorical shoreline data, it is possible the current dataset was not sufficient in size to have the statistical power to detect an effect of habitat type on predation outcome. Furthermore, the influence of observer bias should also be considered when interpreting the relationship, or lack therefore, with habitat in this current dataset. The capacity to observe killer whales in easily accessible shorelines may influence the scope of data collected from land-based observations. That is, more observations may be made in shallow gradient shorelines with open view of the sea simply because killer whale detectability is increased in such environments. Here, prey escaping to the shallows may be reported more frequently in the dataset in part because it is more readily observable from land-based observations and captured more in drone footage given the requirement to maintain a visual line of sight from the land-based launch position.

Increasing the sample size of predation events would undoubtedly increase the capacity to detect patterns of predator success across habitats, however it is also possible other habitat characteristics would better explain suitable refuge than those included in the current shoreline classification dataset. Given the apparent propensity for seals to use shallow habitats for refuge, quantifying habitat characteristics such as seabed geomorphology and shoreline gradient in combination with substrate type may be prove valuable to investigate.

This may also prove important for predator and prey detection, with killer whales better able to detect seals in habitats favourable to echolocation. Future analysis could include such candidate covariates to further explore how CCP is mediated by habitat complexities beyond simple shoreline type classifications.

The increase in presence of anthropogenic structures in the marine environment has been hypothesised to alter predator-prey interactions, with predators potentially attracted to prey aggregations created through anthropogenic niches (Fleming and Bateman 2018) and prey using anthropogenic structures as artificial refuge (Hague et al. 2022). Here, anthropogenic refuge was only utilised successfully on two occasions, once with a seal taking refuge under a boat and once when a black guillemot took refuge on a navigational buoy. Whilst a seal was seen taking temporary refuge in an anthropogenic devise (in a muscle line) in the dataset, the seal was ultimately flushed out and consumed by the killer whales (Hague et al. 2023). The current dataset would therefore suggest natural refuge is primarily utilised to escape predation by killer whales in Shetland, despite the prevalence of aquaculture sites. However, the limitations of coastal data collection may have limited the presence of anthropogenic refuge within the dataset, and thus conclusion drawn here are not without considerations.

On a broader spatial scale within Shetland, the SE SMA sub-region had a higher probability of predation success in comparison the N&E and W SMA sub-regions. Given the small sample size in the current dataset, it is challenging to interpret the potential drivers of this finding. That is, it is possible that habitat features and/or prey species variability contributed to a high CCP in this sub-region, however the small sample size and categorical shoreline data precluded the inclusions of interaction terms in model selection to investigate such relationships. An increase in sample size and incorporation of alternative habitat data would undoubtedly aid further exploration and interpretation of this finding and may prove particularly worthwhile given the declining population trajectory of harbour seals in the SE SMA sub-region of Shetland (Morris et al. 2021).

Temporal trends would be interesting to explore, especially with regards to how predation varies in the relation to prey-field structure, e.g., during seal breeding seasons when the relative abundance of pups and adults of breeding age are expected to increase. Temporal patterns were challenging to detect in the current dataset without effort correcting data collection. Predation events pooled across sample years (2016-2023) for statistical analysis given expected variability in reporting effort, and whilst month was included as a candidate covariate in the full model, it was not retained in the final model after global model selection. The number of predation events recorded in this study increased year on year from 2016 to a peak in 2021, before falling again in 2022 and 2023 (Figure 12). Again, this is likely an artefact of data collection methods and limitations and not necessarily a reflection of variability in predation presence. For example, an increase in citizen science reporting is expected following an increased following of social media sites, an increase in drone effort following growing popularity for recreational and commercial purposes, and the commencement of dedicated PhD fieldwork in 2021. Whilst such limitations hinder the capacity for temporal exploration in the current dataset, the wealth of information gained via citizen science and drone contributions should not be overlooked.

3.4.3 Conclusions

The findings of this Chapter represent considerable new insights into the prey composition of coastally foraging killer whales, and how prey capture probability varies spatially with regards to predator-prey behaviour and environmental characteristics. Killer whales were observed to have a mixed mammalian diet, targeting mammalian prey of both harbour and grey seals, and harbour porpoise. The presence of both pup and 1+year age class for seal species has important implications for estimating the consumptive impact on population structure, particularly with regards to regionally declining harbour seal populations. Furthermore, the fact that harbour seals had a higher probability of being consumed given an encounter may suggest that even if they are not preferentially targeted, they may be more present in killer whale diet due to increased capture probability. Given the present study reflects inshore-foraging behaviour of killer whales in Shetland only, it would be interesting to expand data collection to other areas of northern Scotland (e.g., Orkney and north-coast mainland Scotland) and further from the shoreline to explore consistency in predator success rates and prey escape tactics within their wider range. Further investigation into prey identification, species-specific capture probability, and species-specific anti-predator behaviour would undoubtably increase understanding of the spatiotemporal patterns and capture probability between prey species, furthering insight into species and context-dependent predation pressure.

4 CHAPTER 4. BEHAVIOURAL REPERTOIRES AND ACTIVITY STATES: DEVELOPING AN ETHOGRAM USING DRONE FOOTAGE TO CONSTRUCT ACTIVITY BUDGETS FOR INSHORE-FORAGING KILLER WHALES

Abstract

Understanding the behavioural repertoire of a species is a fundamental aspect of various facets of ecological research. Further, establishing consistent terminology and behavioural definitions in terms can facilitate reporting and transferability between observers, data-collection platforms, and studies. In this Chapter, I develop a comprehensive and repeatable ethogram for inshore-foraging killer whales and apply it to drone-based observational data to quantitatively summarise activity budgets. First, I conducted a literature review of published behavioural studies of functionally similar ecotypes to produce an extensive list of killer whale behaviours with objective definitions to establish consistent reporting and data collection for the present study population. Second, the derived ethogram is applied to ~14 hours of drone footage collected as part of community-led monitoring efforts, analysed here to summarise daily and overall activity budgets for inshore-foraging killer whales in Shetland. Mean daily activity and overall activity budgets revealed that the highest proportion of time was spent transiting, followed by milling, foraging, shorehugging, resting, and transit shorehugging, with seasonal variability in foraging observed across daily means. Results from this Chapter represent an important first step in quantifying the behavioural budgets of inshore-foraging killer whales and demonstrate the capacity for community-led monitoring efforts to facilitate seasonal and interannual fine-scale data-collection.

4.1 Introduction

How an animal spends its time and interacts with its environment has critical implication for its survival and fitness. Animals must adaptively allocate time to fitness-enhancing behaviours in relation to individual (e.g., age, sex, body condition), social (e.g., group size and composition), and environmental (e.g., habitat, prey availability) variability (Gabrielsen et al. 1987; Collins et al. 2016; Stirling et al. 2016). Behavioural time allocations can be further influenced by anthropogenic disturbance (e.g., noise pollution) and environmental change (e.g., habitat loss), with animals altering their behavioural activity to avoid or modulate their exposure to different types of cost-benefits and risks-opportunities in the environment (Lusseau et al. 2009; Pirotta et al. 2013; Noren et al. 2016). Understanding the behavioural repertoire, here termed ethogram, of a given population is a fundamental aspect of ecological research, from quantifying baseline activity levels to monitoring and predicting the capacity of a population to cope with anthropogenically induced environmental change.

Quantifying the behavioural and physiological responses of individuals is the first step in estimating population consequences of disturbance (PCoD) (Pirotta et al. 2018). Various methods can be used to measure and quantity responses, for example the use of animal-borne loggers to monitor changes in the movements, vocalisations, and activity in response to military sonar, seismic surveys, and pile driving (Dunlop et al. 2013; Russell et al. 2016; Wensveen et al. 2017; Isojunno et al. 2018). Visual observations have been used to quantify fitness-enhancing behaviours such as foraging and resting to estimate changes in activity budgets in the presence of anthropogenic activity, including whale watching (Williams et al. 2002; Christiansen and Lusseau 2015; New et al. 2015) and vessel activity (Williams et al. 2006; Lusseau et al. 2009). However, to measure such changes and quantify the response of individuals and populations to stressors, a baseline understanding of behavioural repertoires and associated activity budgets must first be ascertained.

Baseline data on the behavioural repertoire of a species must be collected before further analytical procedures can be introduced (Lehner 1992). To systematically measure behaviour, continuous events and movements must be divided into discrete units or categories following pre-specified rules (Martin and Bateson 2007). One fundamental and traditionally adopted method of achieving this is the development of an ethogram – a catalogue of mutually exclusive and objectively scorable behaviours exhibited by a species in the habitat under study (Altmann 1974; Drummond 1985; Muller et al. 1998; Martin and Bateson 2007; Howe et al. 2015; Baker et al. 2017). By describing and defining the behavioural inventory of a species, behaviours can be more accurately quantified within a population (i.e., collected consistently amongst observers), compared more thoroughly between populations (i.e., across studies) as well as understood in terms of their causative and function basis (Purton 1978).

Ethograms are typically study-specific, describing behaviours relevant to the specific needs of the study (partial ethogram), and often vary in their behavioural definitions and terminology (Martin and Bateson 2007). It can therefore be challenging to directly compare the results of individual studies despite them focusing on similar research questions (Stanton et al. 2015). While intraspecific variation in behaviour and behaviour types is expected, establishing consistent terminology applicable across different populations of a species would undoubtedly facilitate the collection of standardised, replicable, and objective observational data, particularly where research is collected by multiple observers.

Visual observations are a cornerstone of various facets of killer whale research, from identifying and characterising ecotypes to assessing their vulnerability to disturbance. Behavioural specialisations have resulting in local behavioural and genetic differentiation amongst sympatric ecotypes (Hoelzel et al. 1998). Identifying the behavioural repertoire of a population is a key aspect in understanding their fundamental ecology. Numerous studies have described the behavioural repertoire of killer whale populations worldwide, quantifying activity budgets and identifying important habitats for foraging, resting, and breeding (Baird and Dill 1995; Saulitis et al. 2000; Deecke et al. 2011; Noren and Hauser 2016; McInnes et al. 2024; McRae et al. 2024). Advancements in technology have resulted in more effective observational and recording methods. For instance, early studies employed boat-based follows with voice-note annotations to record at-surface observable behaviours. More recently, an increasing number of studies are using unmanned aerial vehicles (UAVs, henceforth termed drones) to collect visual observation data for analysis in computer applications). Drones offer a relatively non-invasive, cost-effective alternative to traditional methods of data collection at high spatial-temporal resolutions (Fiori et al. 2017). To name but a few applications, drone-based data collection has been used to measure cetacean body condition (Christiansen et al. 2016; Noren et al. 2019; Durban et al. 2021), monitor health (Pirotta et al. 2017; Horton et al. 2019), and quantify social structures (King et al. 2021; Weiss et al. 2021).

The aim of this chapter is to develop a detailed ethogram for inshore-foraging killer whales observed in inshore Shetland and to provide quantitative data on the frequency of different behavioural states observed. First, I conduct a literature review to collate behavioural definitions from functionally similar studies on killer whale populations to develop a comprehensive and repeatable ethogram for the current study population. Second, the ethogram is applied to drone-based observational data to quantitatively summarise activity budgets. Drone footage used in this analysis was collected as part of community-led monitoring efforts and contributed voluntarily to the ECOPredS project by professional drone pilots and wildlife experts. An overarching objective of this Chapter is to demonstrate the potential for community-led monitoring to collect observational data for quantitative analysis to inform research objectives. More generally, outputs from this Chapter aims is to provide a tool for future behavioural research and community-led monitoring that will give insight into the behavioural repertoire and activity budget of coastally foraging killer whales in Shetland by developing clear definitions and standardised terminology for behaviours. This will facilitate baseline data collection against which changes can be measured, contributing towards the management and conservation of inshore-foraging killer whales in response to anthropogenic disturbance and activity.

4.2 Methods

4.2.1 Literature review & definition collation

The first part of this study was to develop a comprehensive ethogram for inshore-foraging killer whales as observed around coastal Scotland. Previous studies detailing behavioural definitions in ethograms, often called behaviour categories or activity stats amongst of terminology, were collated as part of a desk-based literature review. For well-studied ecotypes and those subject to longitudinal studies (e.g., transient, and resident killer whales in the Pacific Northwest), some consistencies were observed in behavioural definitions between studies on the same populations. However, discrepancies exist between studies, depending on research questions and between populations, dependent on ecotypic specialisation. To summarise information considering variation between study populations and research topic, information was noted as part of the literature review included source (e.g., literature reference or online source), location (region), study population (more specific area of study and/or ecotype where applicable), paper topic (e.g., foraging behaviour, social interaction), terminology (e.g., behavioural category, activity state), behaviour name (e.g., foraging, travel, feeding), and definition (as defined in the study).

Definitions collated as part of the literature review were then used to develop a comprehensive and repeatable ethogram for use on inshore-foraging killer whales around coastal Scotland. So as not to falsely imply knowledge of an animal's internal state or the biological function of a behaviour pattern, the final ethogram developed as part of this studies aimed to describe the behaviour in terms of its structure (Martin & Bateson, 2006). That is, neutral terms are used to described behaviour as it is observed, from which function can be inferred. For example, 'body contact' is the structure and observable behaviour, with 'social bonding' an inferred function.

4.2.2 Comprehensive ethogram

An existing focal-follow protocol developed for the ECOPredS project and used during PhD fieldwork was used as the foundation for ethogram development (Appendix A4.1). Names and definitions collated as part of the literature review informed a detailed description of a comprehensive list of behaviours for the study population. Whilst behavioural terms were refined here based on analysis of drone footage, describing the behaviours in terms of their structure means they can be easily applied to other forms of data collection, such as land-based focal follows. In the ethogram, behaviours are defined as either a behavioural state (with a duration, denoted in Tables 4.1-4.3 with a dash) or a discrete point event (with no duration, denoted in Tables 4.1-4.3 with a dot), and were grouped into a movement (containing transit, shore-hugging, milling, or resting; Table 4.1) or predator-prey behavioural category (containing 'passing by prey', 'orienting response', 'chasing', 'circling', 'grab or touch', 'fly', 'feeding', 'blood', 'outcome unknown'; Table 4.2). Modifiers denote additional information that can be applied to a specific behavioural state. Some modifiers were shared across the two behavioural categories (e.g., group size, group distribution; Table 4.4) whilst others were unique to the predator-prey category (e.g., prey species, prey response; Table 4.5). Labelling, drone, anthropogenic, individual distance to shore, surface events, and other events each had their own category (summarised in the additional categories table, Table 4.6) with their own unique modifiers.

Table 4.1. Behaviours within the movement category.

Movement categories			
Type*	Behaviour	Description	Modifiers
-	Transit	Group moves in a consistent direction; any turn of direction is completed by the whole group in another consistent direction.	Group size, group distribution, swim speed, inspection.
-	Shore-hugging	Following contours of shoreline, in and out of bays, around headlands / skerries; turns only occur in the direction of shoreline/skerries and are completed by the whole group	Group size, group distribution, swim speed, inspection.
-	Milling	Group moves in multiple or inconsistent directions; individuals whales may swim in consistent direction while others do not	Group size, group distribution, swim speed, inspection.
-	Resting	Group is not actively moving; either drifting with current or stationary. Potentially resting	Group size, group distribution, swim speed, inspection.

* In type, – denotes a sate event

Table 4.2. Behaviours within the predator-prey category

Predator-prey categories			
Type*	Behaviour	Description	Modifier
-	Passing by prey	Passing/swimming by potential prey (seals either hauled out on land or in-water, swimming past eider ducks, otters, porpoise, etc)	Group size, group distribution, swim speed, prey species, prey location, prey behaviour, prey condition
-	Orienting response	An orientation response towards prey by at least one member of pod - indicates prey has been detected and potentially selected for foraging attempt	Group size, group distribution, swim speed, prey species, prey location, prey behaviour, prey condition
-	Chasing	Actively pursuing/attempting to capture prey; fast directed movement towards prey by at least one member of pod.	Group size, group distribution, swim speed, prey species, prey location, prey behaviour, prey condition
-	Circling	Circling/corralling prey species, e.g. prey in middle of group, killer whale circling to prevent escaping	Group size, group distribution, swim speed, prey species, prey location, prey behaviour, prey condition
-	Grab or touch	A group member has a hold of, or substantial contact, with whole prey	Group size, group distribution, swim speed, prey species, prey location, prey behaviour, prey condition
·	Fly	Prey is thrown into the air	
-	Feed	Whales are observed consuming prey. Prey sharing modifier.	Group size, group distribution, swim speed, prey species, prey location, prey behaviour, prey condition, prey sharing
-	Blood	Blood visible	
·	Outcome unknown	Predation attempt/event outcome, modifiers: consumed, escaped, unknown	

* In type, – denotes a sate event and • a point event

Table 4.3. Behaviour in the additional (labelling, drone, anthropogenic, shore distance, surface events, other events) categories.

Additional categories			
Type	Category name	Description	Modifier
-	Labelling	Start and end of the "on-follow" period(s)	
-	Drone	A second drone visible in footage	Numeric
-	Anthropogenic	Presence of human activities (presence of boats, fish farms, etc with a threshold distance, e.g., 200 m)	Anthropogenic
·	Individual distance to shore	Measure minimum distance to shore every time there is more than >1 BL change in the minimum distance	Numeric, age-class
·	Surface event	See modifiers list for possible different surface events	Surface event
·	Other event	See modifiers list for other possible surface events	Other event

*** In type, – denotes a sate event and • a point event**

Table 4.4. Movement & predator-prey behaviour modifiers

Movements & predator-prey behaviour modifiers			
Set name	Type	Categories or value	Description
Group size	Numeric	Number of individuals	Number of individuals to which the annotated behaviour applies
Group distribution	Multiple selection	Tight 0-1	Tight distribution, animals generally 0-1 body lengths from each other
		Close 2-3	Close distribution, animals generally 2-3 body lengths from each other
		Loose 4+	Loose distribution, animals over 4 body lengths from each other
Swim speed	Multiple selection	Slow or normal	Normal/slow movement speed
		Fast	High speed indicated by water displacement/splashes, fluke prints visible at surface, often porpoising out of the water
Inspection	Single selection	Inspection	Inspecting (body tilt, moving in/out) shoreline whilst shorehugging
		No inspection	Passing parallel with shoreline not showing evidence of inspection

Table 4.5. Predator-prey only behaviour modifiers

Predator-prey behaviour modifiers			
Set name	Type	Categories or value	Description
Prey species	Multiple selection	Seal	Harbour or grey seal
		Porpoise	Harbour porpoise
		Otter	Otter
		Mammal	Unknown mammal species
		Seabird	Include only seabird species that are known to have been attacked (eider ducks, guillemots)
		Fish	Fish
		Unknown	Prey species remains unidentified
Prey location	Multiple selection	Land	The prey animal is on "land" if its body is supported by land or an anthropogenic structure
		Water	The prey animal is in water if it is swimming or floating, not supported by land/structure
Prey behaviour	Multiple selection	No response	The prey animal is not exhibiting a measurable response (it might have responded prior to observation by hauling out, for example)
		Vigilant	Prey observed scanning environment and watching killer whales
		Avoidance	Attempting to avoid or escape killer whales by moving away from them
		Refuge	Taking refuge in natural features (shallow water, on land)
		Refuge anthropogenic	Taking refuge in anthropogenic structures (e.g., mussel lines, fish farms, boats)
Prey sharing	Multiple selection	Calf	Age class involved in prey sharing / feeding (Table 6)
		Juvenile	Age class involved in prey sharing / feeding (Table 6)
		Adult male	Age class involved in prey sharing / feeding (Table 6)
		Adult female or juvenile	Age class involved in prey sharing / feeding (Table 6)
Condition	Multiple selection	Injured	Visible injury or bloody form prey upon escape
		Uninjured	No injury visible on prey upon escape

Table 4.6. Additional categories (labelling, drone, anthropogenic, shore distance behaviour) modifiers

Additional categories (labelling, drone, anthropogenic, shore distance behaviour) modifiers			
Set name	Type	Categories or value	Description
Number	Numeric	Number of drones	Number of drones visible within the frame
Distance to shore	Numeric	Body lengths	Number of body lengths from shore of individual closest to shore. Input 50 if BL cannot be estimated accurately, or -1 when shoreline is not visible (i.e., distance is unknown)
Anthropogenic	Multiple selection	Boat motor	Boat with motor present within frame
		Boat no motor	Boat without motor present within frame
		Fish farm	Fish farm present within frame
		Shellfish farm	Shellfish farm present within frame
		Creel pot	Buoy present at surface indicating presence of creel pot within frame
		Object interaction	Interaction with objects such as rope, seaweed/kelp.
Age class	Multiple selection	Calf	Small calf swimming in echelon position with its mother
		Juvenile	Clearly smaller body than adult, but not calf; swims independently /outside echelon position of adults
		Adult male	Distinct tall dorsal fin
		Adult female or juvenile	Adult-sized whale without tall dorsal fin

Table 4.7. Surface event behaviour modifiers

Surface-event behaviour modifiers			
Set name	Type	Categories or value	Description (source, CWR[1])
Surface events	Multiple selection	Aerial scan	“Raises its head at an angle starting from a horizontal position”
		Back breach	“Leaps out of the water and exposes two-thirds or more of its body and then lands on its back”
		Belly flop	“Leaps out of the water and exposes two-thirds or more of its body and then lands on its stomach”
		Full breach	“Leaps out of the water and exposes two-thirds or more of its body and then lands on its side”
		Fluke lift	“Moves its flukes up and down above the water surface in a fluid motion with no force”
		Fluke wave	“Lifts its flukes and part of its caudal peduncle above the water, pauses for at least two seconds, and then brings its flukes down with no force”
		Half breach	“Leaps out of the water and exposes only half of its body, landing on its side”
		Inverted pectoral slap	“While on its back, raises its pectoral flippers straight up and slaps the dorsal surfaces down on the water's surface”
		Inverted tail lob	“While on its back, raises its flukes above the water's surface and brings them down with force”
		Lunge	“Breaks the surface of the water with its rostrum, melon and a large part of its body in a charging mode”
		Pectoral slap	“Lies on its side, lifts a pectoral flipper, and slaps it on the water's surface with force”
		Pectoral wave	“Lifts a pectoral flipper in the air for at least two seconds and brings it down with no force”
		Roll	“Rolls halfway, or all the way around in the water, along its longitudinal axis”
		Spyhop	“Raises its head vertically above the water, at least above its eye level, and then slips back below the water's surface”
		Tail lob	“Lifts its tail flukes above the water and brings them down with force”
		Tail thrashing	“Violently thrashes a tail fluke through the water surface”

[1] CWR: https://www.whaleresearch.com/orca-behaviors

Table 4.8. Other event behaviour modifiers

Other event behaviour modifiers			
Set name	Type	Categories or value	Description
Other	Multiple selection	Bubble blowing	releasing air through its blowhole whilst still under water
		Male genitals	Visible penis outside of body
		Mating	a male inserts its penis into a female's genital slit
		Body contact	Two members of the pod touch each other

4.2.3 BORIS data collection

Multiple software applications have been developed to collect behavioural observation, both in-situ (real-time) and from video recordings (post-hoc). Here, the Behavioural Observation Research Interactive Software (BORIS) desktop application was selected for behavioural data collection. BORIS is an open-source software, with a user-friendly and flexible interface. Although not used here, a mobile application is available for use on Android devices for real-time data collection. An advantage of the BORIS software is the ability to create a custom ethogram, where behaviours can be set as a state event (with a duration) or a point event (no duration), grouped into categories (for time budget analysis), and assigned to subjects (individual or groups). Each behaviour can be assigned two or more modifiers (numerical input, single selection, multiple selection) for additional specificity in data collection, and contextual variables that were video specific (i.e., do not change in the video file, e.g., weather, observer ID) can be recorded for each observation. To facilitate data collection, an exclusion matrix can be set for behaviours which cannot co-occur, for example resting and transiting. With the exclusion matrix, the onset of one behaviour will stop the current excluded state. Ethograms can be exported and shared, facilitating collaborative working between project members, and annotated files can be saved and edited without having to recode an entire observation. Once an observation is coded, the data can easily be exported as a CSV file for data processing and statistical analysis.

Behavioural data were collected from drone footage contribute to the ECOPredS project collected by a professional drone pilot on Shetland. Prior to behavioural scoring, footage was subject to quality and content scoring to ensure it was collected legally, responsibly, and with due consideration for primary and secondary animal welfare (See Chapter 3 Section 3.2.1.2, Appendix A2.1 and A2.2). A custom ethogram was created in BORIS using the comprehensive ethogram definitions as detailed in Tables 1-8, with an exclusion matrix applied to behavioural states in the movement and predator-prey behavioural categories (Table 4.9). To investigate inter-observer reliability, and thus the clarification of definitions included in the ethogram, a sub-set of videos were scored by myself and another, independent observer. Behavioural scoring was compared between the two observers for discrepancies; if any were found, behavioural definitions were refined and, if required, additional modifiers were created to further specify behaviour in the form of its observable structure.

Table 4.9. Exclusion matrix for movement and predator-prey behavioural states. Bold text indicated movement states.

Behavioural State	Shore-Hugging	Milling	Resting	Transit	Chasing	Feed	Grab or touch	Orienting response	Passing by prey	Circling
Shore-Hugging		x	x	x						
Milling	x		x	x						
Resting	x	x		x						
Transit	x	x	x		x					
Chasing				x		x	x	x	x	x
Feed					x		x	x	x	x
Grab or touch					x	x		x	x	x
Orienting response					x	x	x		x	x
Passing by prey					x	x	x	x		x

Only video footage files containing killer whales were subject to behavioural scoring, with the length of time the whales were visible in frame recorded as the labelling period, termed the “on-follow time”. During follows, the start and end time of each behaviour was labelled according to the ethogram definitions. All behavioural data was collected at the group level, except distance to shore which was coded as the number of body lengths from the individual closest to shore of individual closest to shore (where visible). Given behavioural data were collected at the group level, a change in behaviour of the majority of group was required for a change in behaviour recorded (e.g., if the majority of the group switched from milling to travelling, the video labelling would change). Minimum distance to shore, however, was recorded every time the distance of the closest individual to the shore changed by one adult body length. The full set of drone footage was scored by a single observer.

4.2.4 Activity budget

Behavioural data collected in BORIS was exported as CSV files for data processing and activity budget analysis in R Studio. During data processing, drone metadata was appended to BORIS observational data. Drone metadata included data extracted from video files including full filename and file path, date and time stamp, duration (in seconds), frame height and width (in pixels), number of frames per video, frame rate, and metadata manually scored as part of quality and content scoring such as drone minimum distance, viewing angle, predator and/or prey presence, presence and proximity to shoreline, sighting conditions (sea state, weather), boat and/or fish farm presence, pod ID (where available), and associated comments (See Chapter 3 Section 3.2.1.2, Appendix A2.4) . A time series of behavioural states was then created by assigning a start (onset of a behavioural state) and end (change of behavioural state or end of follow) time to data rows. Distance to shore (a point event) was interpolated across behavioural states to explore how time spent in different behaviours behaviour (e.g., transiting versus predator-prey behaviours) varied as a function of distance to shore. During data processing, distance to shore was grouped into three categories: Less than or equal to 10 body lengths (when distance to shore could be estimated), greater than 10 body lengths (when the shoreline was visible but an accurate distance beyond 10 body lengths could not be estimated), or unknown (when the shoreline was not visible in frame). The duration of time spent in each behavioural category was then summarised for each of the distance to shore categories.

For the purposes of summarising activity budgets, i.e., the duration (in hours) and proportion (duration as a proportion of total behaviour observed), only state events and associated individual distance to shore were included in quantitative analysis. Behavioural categories used for the activity budget largely reflected those defined as behavioural states in BORIS (transit, shorehugging, milling, and resting) except for predator-prey behavioural states (blood, chasing, feed, circling, grab or touch, orienting response) which were grouped together as “foraging” for comparison with other studies. Note that ‘passing prey’ was not included in foraging, given no interaction with the prey species was observed. An additional behavioural state of “transit shorehugging” was defined to differentiate between animals following the shoreline when travelling compared to searching for prey. That is, animals often followed the shoreline closely whilst exhibiting transit behaviour (moving in consistent direction as a group) and showed now evidence of investigating the shoreline; “transit shorehugging” was therefore defined as when animals were ‘shorehugging’ (behavioural state) and showed ‘no inspection’ (modifier). In comparison, animals were also observed following the shoreline closely whilst exhibiting prey search behaviour (e.g., side on swimming, circling skerries, animals moving in different directions); “shorehugging” was therefore defined as when animals were ‘shorehugging’ (behavioural state) and showed signs of ‘inspection’ (modifier). Daily activity budgets were calculated by summing the total time spent in each behavioural category per day, then dividing by the total daily observation duration. To determine an overall activity budget, the time spent in different behavioural categories was summed over all observations and divided by the total observation duration.

4.3 Results

BORIS analysis was conducted on 347 video files as obtained from drone flights conducted between 2016 and 2021. In total, 14.59 hours of killer whale follows were obtained across all years, of which 10.31 hours were obtained from summer months (June – August), 2.74 hours from autumn months (September – November), and 1.54 hours from winter-spring months (January – April). No footage was collected in the months of May or December. The number of hours varied between years, with a maximum of 3.35 hours obtained in 2021, and minimum of 0.89 hours obtained in 2016.

4.3.1 Activity durations

Duration of time spent in behavioural categories varied in relation to distance to shore categories (Figure 4.1, Table 4.10). The most frequent behaviour observed was transiting at an unknown distance to shore, with transiting also occurring at equal to or less than 10 body lengths to shore. Foraging behaviour was only observed when the shoreline was also visible (less than or equal to 10 body lengths, or greater than 10 body lengths to shore), with a majority of foraging observed at greater than 10 body lengths to shore. As expected, shorehugging and transit shorehugging only occurred when the shoreline was visible. The majority of the milling behaviour was observed when distance to shore was unknown (i.e., the shoreline was not visible in frame), but milling was also observed at less than or equal to 10 body lengths to shore. Resting was only observed at an unknown distance to shore.

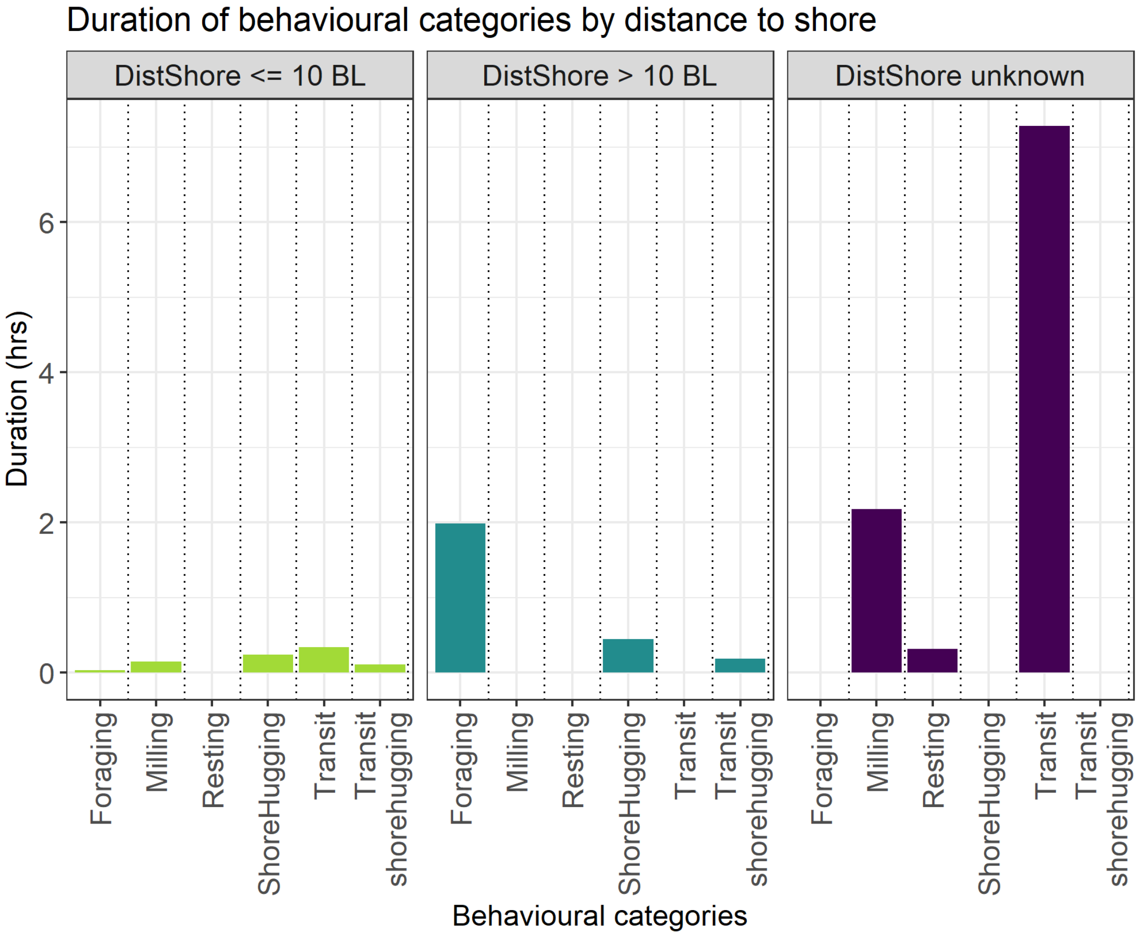

Figure 4.1. Duration (hrs) of each of the behavioural categories, grouped by distance to shore category. The total duration (hours) observed in each behavioural category, where predator-prey behavioural states are grouped together as “foraging”. Distance to shore grouped into three categories: less than or equal to 10 body lengths (BL), greater than 10 body lengths, and distance unknown (when the shoreline was not visible).

Table 4.10. Duration (hrs) observed in behavioural categories, grouped by distance to shore category.

	Distance to shore in BL & behaviour duration (hrs)		
Behavioural category	<=10 (hrs)	>10 (hrs)	Unknown (hrs)
Foraging	0.035	1.985	0
Milling	0.149	0	2.180
Resting	0	0	0.317
Shorehugging	0.238	0.449	0
Transit	0.338	0	7.278
Transit shorehugging	0.106	0.184	0

4.3.2 Daily activity budgets

Across all seasons, transit was the highest proportion of the daily activity budget (>0.5, Table 10) followed by milling (>0.1, Figure 4.2, Table 4.11). The proportion of time spent foraging varied between seasons, with the highest proportion observed in autumn (0.208), followed by summer (0.097) and then winter-spring (0.044) (Table 4.11). The proportion of time spent shorehugging was similar in winter-spring (0.056) and summer (0.058), and lower in Autumn (0.019). Transit shorehugging was the lowest proportion of daily activity budget, at >0.05 for all seasons.

Table 4.11. Mean proportion of time spent in each behavioural category per season. Where n = the number of observation days per season from which mean proportions were calculated

Season	n	Transit	Shorehugging	Foraging	Transit shorehugging	Milling
Winter-spring	10	0.640	0.056	0.044	0.013	0.099
Summer	19	0.501	0.058	0.097	0.040	0.218
Autumn	9	0.549	0.019	0.208	0.010	0.224

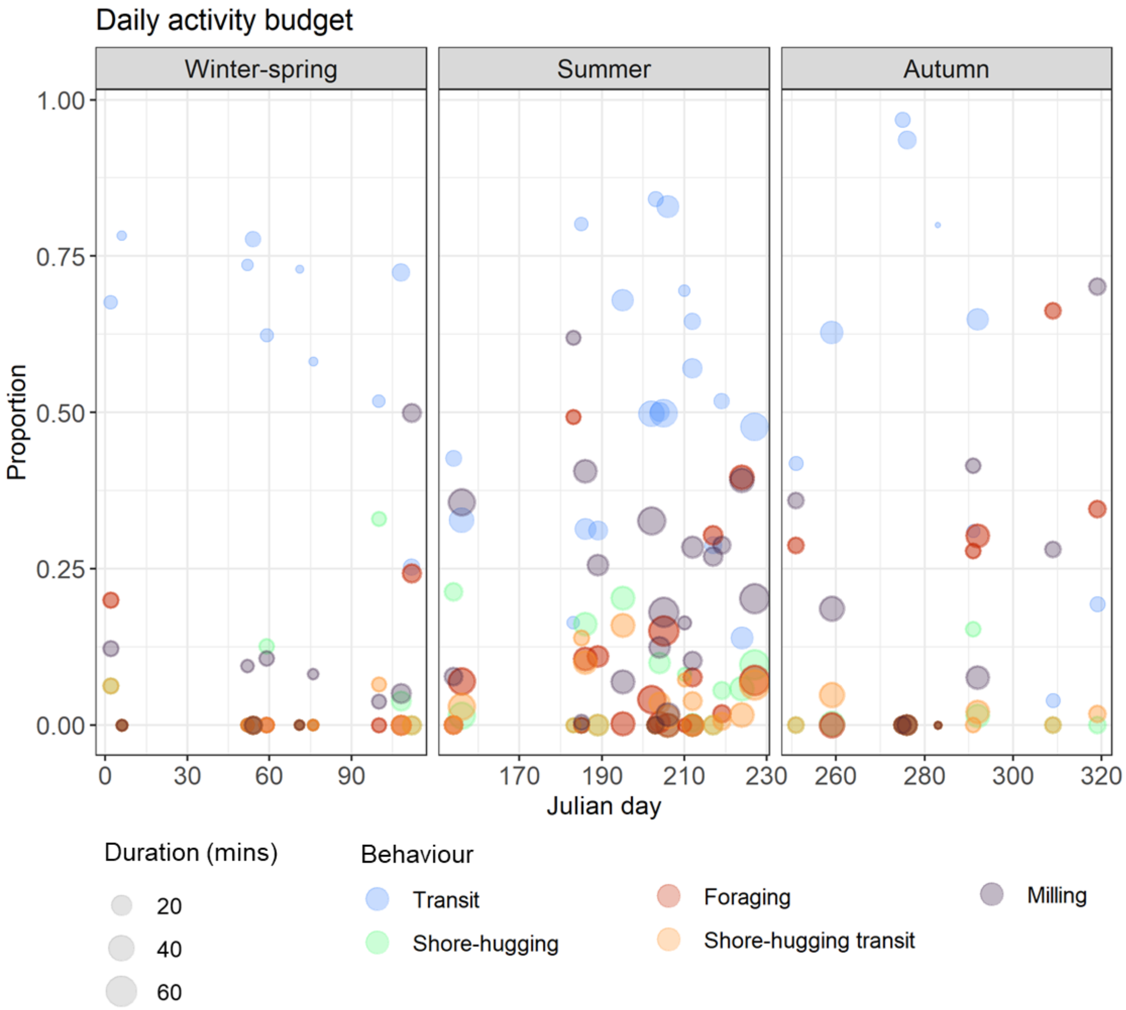

Figure 4.2. Daily activity budgets grouped by season. Proportion of time spent in each behavioural category per observation day (Julian day). The size of the circle represents the duration of footage per day, with larger circles indicating longer duration of footage.

4.3.3 Overall activity budgets

Transiting represented the high percentage 57.4% of the activity budget. Milling represented 17.6%, followed by foraging which accounted for 14.0%, with remaining budget account for by shorehugging (5.2%), resting (2.4%), and transit shorehugging (2.2%). Of behavioural states in the foraging category, feeding accounted for a majority (63%) of the foraging activity budget.

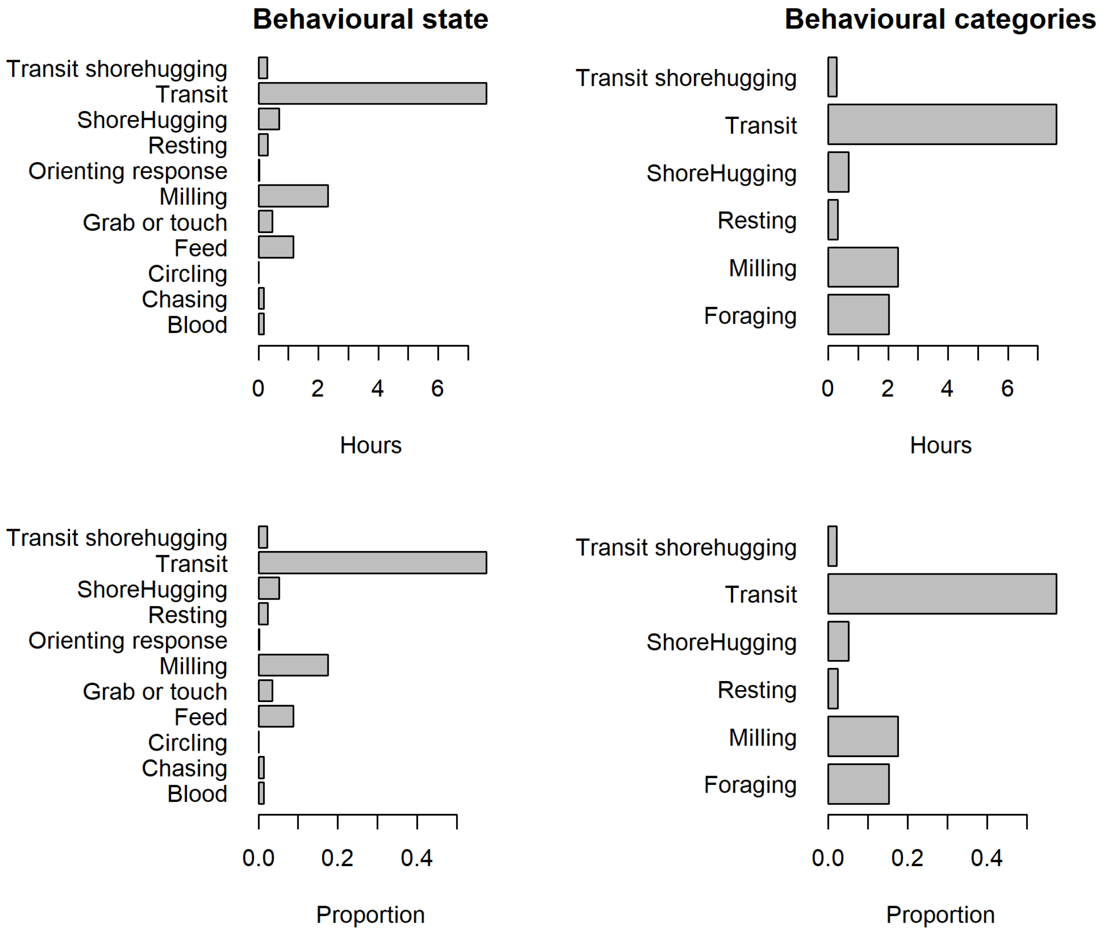

Figure 4. Overall activity budgets for behavioural states and behavioural categories. With total duration observed in hours in the upper panels, and proportion of time spent in lower panels.

Table 4.12. Total durations (hrs) and proportion of time observed for behavioural categories and predator-prey (foraging) states.

Behavioural category	Duration	Percentage (%)
Transit shorehugging	0.290	2.2
Transit	7.617	57.4
Shorehugging	0.687	5.2
Resting	0.317	2.4
Milling	2.329	17.6
Foraging (individual states)	2.020	14.0
Orienting response	0.027	0.2
Grab or touch	0.468	3.5
Feed	1.166	8.8
Chasing	0.183	1.4
Circling	0.001	0.0
Blood	0.175	1.3

4.4 Discussion

The aim of this chapter was to develop an objective and repeatable ethogram for inshore-foraging killer whales observed in coastal Shetland and apply it to drone-based video data to quantify activity budgets. As previously described, behaviours as defined in an ethogram should avoid subjectivity and functional inferences; that is, they should describe the basic observable patterns that from the behavioural repertoire of a given species (Martin and Bateson 2007). Here, eleven behavioural states were identified based on objective definitions (Table 4.1-4.2). Movement states were defined as transit, transit shorehugging, resting, and milling (Table 4.1), and predator-prey states defined as orienting response, chase, circling, grab or touch, feed, and blood (Table 4.2). The subsequent mean daily activity budgets across seasons (Table 4.11) and overall activity budgets (Table 4.12), showed that the highest proportion of time was spent transiting, followed by milling, foraging, shorehugging, resting, and transit shorehugging, although some seasonal variability in foraging was observed across daily means (Table 4.12).

Activity budgets are often used to quantify fitness-enhancing behavioural such as foraging, travel behaviour, and resting (Noren and Hauser 2016). In the present study, killer whales spent the highest proportion (~0.5-0.6 / ~50-60%) of time transiting (synonymous with travelling in previous studies) as observed both in their daily activity budgets (winter-spring mean: 64% / 0.64; summer mean: 50% / 0.5; and autumn mean: 55% / 0.549) (Table 10) and overall activity budgets (57% / 0.57) (Table 4.12). In the overall activity budget around 14% (0.14) of time was spent foraging, with seasonal differences in mean daily foraging budgets observed between winter-spring (4% / 0.04), summer (9% / 0.09) and autumn (20% / 0.2). In comparison with previous studies that quantified the activity budges of killer whale populations, the proportions and percentages reported here fall within the ranges of those previously published (Table 4.13).

Studies investigating the activity budgets of killer whale populations have typically focused on the well-studied ecotypes in the northeastern Pacific: mammal-eating Transients (e.g., Baird 1994; McInness et al. 2024) and fish-eating Residents (e.g., Ford 1989; Williams et al. 2006; Holt et al. 2013; Noren and Hauser 2016) (Table 4.13). Reported ranges of the proportion of time spent travelling for Residents range between 4.2% (Ford, 1989) to 70.4% (Noren et al., 2016) and foraging between 12.5% (Williams et al. 2006) and 66.5% (Ford, 1989). For Transients, time spent transiting ranges between 9.34% (McInnes et al. 2024) and 13.1% (Baird 1994), and foraging between 63.13% (Baird 1994) and 84.16% (McInnes et al. 2024). However, it is important to highlight that differences in activity budgets may in part be due to actual variation in populations' behavioural budgets, and/or sampling methodologies and discrepancies in behavioural definitions; comparisons between studies should there be made with caution.

Table 4.13. Activity budgets reported from studies across killer whale populations. Data collection protocol, sample size, and percentage occurrence of each activity is compared against those observed in the present study. NA = data was not reported. Additional information in brackets indicate whether prey search behaviour was included in 'transit' or 'forage' with additional descriptors as reported in source studies included for clarity.

Source	Population	Method	Transit	Forage	Resting	Socialising
Present study	Inshore Scotland	14.59 hrs of observation	57.4% (+2.2% transit shorehugging)	14% (+5.2% search phase, i.e., shorehugging)	2.4%	NA
Noren and Hauser 2016	Southern Resident	571 scans	70.4%	21.0% (including search phase of foraging)	6.8%	1.8%
Holt et al., 2013	Southern Resident	289 scans	53.6% (including search phase of foraging)	39.1%	NA	NA
Ashe et al., 2010	Southern Resident	764 scans	63.5% (forage/travel)	24.6%	8.2%	3.7%
Ford 1989	Southern Resident	416 hrs of observation	4.2%	66.5% (including search phase of foraging)	13.2%	11.6%
Williams et al., 2006	Northern Resident	2000 hrs of observations	53% (travel / forage)	12.5% (feed)	15.2%	2%
Baird 1994	Transient (offshore and near shore)	434 hrs of observations	13.10% (fast and normal)	63.13% (including search phase of foraging)	1.7%	3.78%
McInnes et al., 2024	Transient (offshore)	270hrs of observation	9.34%	84.16% (including search phase of foraging)	0.97%	5.54%

Differences in activity budgets reported between studies could reflect real differences in the behavioural budgets of the study-populations. This type of comparison is particularly pertinent for investigating change in activity budgets of a given study-population over time, particularly in relation to environmental and ecological covariates that may influence fitness (Gelatt et al. 2002; Christiansen et al. 2013). The differences in proportions of time spent foraging versus transiting in resident killer whales, for example, has been hypothesised to be a result of their changing population status and potentially linked to changes prey abundance and/or increased anthropogenic disturbance (Noren and Hauser 2016). Historical estimates (e.g., Ford 1989), where a higher proportion of time was observed spent foraging, are based on data collected during a period (1978-1983) where the resident killer whale population was stable or increasing. By comparison, more contemporary (2006-2009) estimates (e.g., Noren and Hauser 2016) where transiting behavioural was more prevalent, the population was decreasing. The differences could indicate an increase in transit time to move between and locate suitable feeding areas and have implications for time available to other behaviours such as rest and socialising (Noren and Hauser 2016). Data in these studies were collected from the core summer critical habitat of southern resident killer whales, which overlaps with the migration route of their primary prey species, chinook salmon (*Oncorhynchus tshawytscha*), comprising 90% of their summer diet (Ford and Ellis 2006). Salmon abundance varies considerably spatially and temporally (Lackey 2003) and is an important driver of both the reproductive success and mortality in resident killer whales (Ward et al. 2009; Ford et al. 2010); changes in activity budgets could therefore reflect variability in foraging efficiency as a result of changes in prey abundance. Indeed, activity budgets have been shown to change in response to prey availability in other marine mammals (Boyd 2004; Friedlaender et al. 2009) and it is proposed that historical knowledge of salmon foraging grounds is the reason post-reproductive females lead group collective movements during years of low salmon abundance (Brent et al. 2015). However, it should be noted that an alternative hypothesis proposed that the observed change in activity budgets may also be due to increase vessel activity from whale watching operators in the area which resulted in reduced time spent foraging by the killer whales (Lusseau et al. 2009). Quantifying the activity budgets of killer whales can therefore provide valuable insights into the bottom-up effects of fluctuations prey availability and facilitate understanding of the impacts of anthropogenic disturbance on study populations.

Alternatively, differences in activity budgets between studies, and even within study populations, may be due to differences in data-collection methods including study area and/or season, observer platform, sample size, and sampling method. Seasonality and geographic locations have been shown to influence activity budgets in delphinids(Stockin et al. 2009). In the case of activity budgets summarised for transients, it should be noted that Baird 1994 investigated the activity budget of both nearshore and offshore foraging Transients, whereas McInnes et al. 2024 investigated offshore individuals only. The higher proportion of time spent foraging observed by McInnes et al. 2024 for offshore transients (84% compared to previously estimated 33-63%) was suggested to be due to the increased handling time of larger prey species (e.g., grey whale calf, *Eschrichtius robustus*, and elephant seal, *Mirounga angustirostris*) found in the deep submarine canyon (the study area) compared to smaller prey species (e.g., harbour seals) typically encounter in coastal waters, as observed by Baird (1994). In the present study, the data collection was limited to at-surface and near-shore waters of Shetland, with land-launched drone footage typically obtained <1km from the shoreline. Given it is hypothesized that killer whales travel to inshore waters of Scotland for the purposes of exploiting abundant seal prey resources (Scullion et al. 2021), the activity budget presented an over-emphasis towards foraging-related effort. Despite this, the proportion of time spent foraging in the present study is typically less than those previously reported for killer whales (Table 4.13).

The lower proportion of time spent foraging compared to other studies, is likely in part due to differences in the definition of foraging. Critically, studies differ in the inclusion of the prey-searching aspect of foraging in either the transit category or the foraging category (Table 12). Here, prey-searching was not included in either the foraging or transiting category given the potential subjectivity of the behavioural definition. That is, prey-searching being a functional inference of an observable behaviour, which varies considerably dependent on the target prey. In the present study, shorehugging may be indicative of prey searching. Indeed, shorehugging (with inspection of shoreline) and transit shorehugging (with no inspection) were termed and defined as such to discern between the two behavioural states, with the former presumed to be locating prey and the latter to be a form of travel. The difference between these two states, and indeed the inferences made about transiting behaviour in general, is likely of particular importance for this study given the highly coastal nature of the data collection. That is, 'coastal-hugging' behaviour as observed from telemetry data for seal-hunting killer whales in Norway was defined as directional travel within 6.9km (+/-10km) from the shore (Vogel et al. 2024). Using the same definition, all movement behaviour observed in the present study could be considered foraging-related travel or prey-searching within the killer whale's wider range. By defining foraging in the present studying as containing only objective, observable behaviours related to prey acquisition and consumption (e.g., chase, circle, grab or touch, feed), the duration of time spent in different movements behaviours can be better compared in terms of those exhibited for the purpose of travelling versus the localised search for prey.

With regards to sampling methods, difference in activity budgets have been observed between focal follow and scan sampling methodology (see Mann 1999 for review). Focal follows, as used in the present study, are proposed to yield a more accurate picture of an individual's activity budget by capturing the sequence and transition of behaviours in comparison to scan sampling (Karniski et al. 2015). A further contributing factor to the differences in observed time spent foraging in the present study in comparison to others may also be due to the use of drone footage for data collection. Given the majority of cetacean activity occurs below the surface, behavioural data collected from boat-based observations are likely subject to biases towards conspicuous surface behaviour and assumption made about group activity state (Mann 1999; Fiori et al. 2019). For example, concurrent boat-based and drone-based surveys conducted on bottlenose dolphins yielded considerably different activity budgets, with drone-based observations revealing 55% more travelling than real-time boat-based observations (0.38 and 0.25 respectively) and 58% less foraging in drone-based observations than boat-based observations (0.03 and 0.07 respectively) (Fettermann et al. 2022). The authors propose differences are likely due to the benefits associated with drone-based data collection, such as sampling the behaviour of the whole group, retrospective analysis of drone imagery to accurately categorise behavioural states without real-time observational biases, and minimizing assumptions about what the whales are doing out of sight below the surface (Fetternmann et al., 2020).

Retrospective analysis of drone footage proved particularly important for the current study, given field-based observation were conducted from land, with the whales often at a distance or partially out of view. An example from the current study where land-based observations and drone-based observations were made concurrently yielded a different classification of behavioural activity in the field is an event where a harbour porpoise was killed. From land, it appeared the whales were milling post feed on a harbour porpoise, whereas drone footage revealed they were still prey-sharing. The use of drone footage to conduct focal follows in this study greatly facilitated the ability to observe and record individual predator-prey behavioural states, such as orientating response or circling prey, which may be more challenging to observe real time from at-surface behaviour observed in the field.

4.4.1 Conclusions

The activity budgets reported here represent an important step in understanding the behavioural budgets inshore-feeding killer whales in Shetland. Furthermore, this Chapter demonstrates the capacity of community-led monitoring via drones to provide seasonal and inter-annual coverage to monitor and quantify the fine-scale behaviour of killer whales, although sampling and detection biases (e.g., between seasons) should be noted. Whilst behavioural terms were refined here based on analysis of drone footage, describing the behaviours in terms of their structure means they can be easily applied to other forms of data collection, such as land-based focal follows. Refining of behaviour definitions may be appropriate, such as ‘shorehugging’ and ‘transit’, with ‘transit shore-hugging’ instead discernible by distance to shore. The ethogram and activity budgets reported here can be considered a starting point from which future studies can build. For instance, using the GPS locations as obtained from drone metadata or by cross-referencing footage with concurrent sightings data, habitat variables could be incorporated into analysis to explore how fine scale behaviour and activity budgets vary in relation to environmental covariates. Further activity states, such as socialising, could be explored by examining behaviours indicative of social bonding (e.g., body contact and the visibility of male genitals without the occurrence of mating), and spatial arrangements in terms of group distribution could be explored in relation to different activity states (Noren and Hauser, 2016).

5 CHAPTER 5. KILLER WHALE CONSUMPTION ESTIMATES IN A MULTI-PREY SYSTEM: REGIONAL POPULATION LEVEL CONSEQUENCES OF INSHORE-FORAGING KILLER WHALES ON HARBOUR & GREY SEALS

Abstract

Quantifying the consumptive impacts of predators is integral to understanding the potential top-down effects on prey populations. Predation by killer whales has been implicated in the decline of marine mammal populations worldwide. In the north and east of Scotland, killer whale predation has been hypothesised as a potential driver of regional declining harbour seal populations. In this Chapter, I quantify the energetic requirements and prey consumption rates of inshore-foraging killer whales, and explore the predicted consequences of these on harbour and grey seal populations trajectories. First, a bioenergetic approach was taken to estimate the daily energetic expenditure and prey consumption requirements for inshore-foraging killer whales in Shetland for the year 2021, with a Monte-Carlo uncertainty analysis conducted to derive 95% confidence ranges. Consumption estimates and associated uncertainties derived from bioenergetic modelling were incorporated into an age- and sex-segregated Leslie Matrix model to simulate harbour and grey seal population trajectories across as 35-year period in the Shetland Seal Management Area (SMA). Scenarios of plausible future population trajectories were simulated to explore potential population impacts of killer whale predation on each seal species under various assumptions (e.g., predator and prey population parameters, compositions of prey species in killer whale diet). Overall, harbour seal predicted trajectories typically exhibit declines, whereas grey seals generally increased or were stable. Simulations suggest that killer whale predation may be sufficient to result in a decline of or hinder the recovery of harbour seal populations in Shetland; however, uncertainties in input parameters should be considered

when drawing conclusions on potential consequences of killer whale predation on population trajectories.

5.1 Introduction

Predation is the mechanism that controls the flow of energy from one organism to another (Sih et al. 1985). Predators capture and consume prey, reducing prey population density whilst fuelling predator population (Holling 1959). As an ecological process, predation can act as a strong selective force and have important implications for population processes, dynamics, and life history strategies of prey (Abrams 2000; Croft et al. 2009; Calsbeek and Cox 2010). Quantifying the energetic requirements and prey consumption rates of a predator population is therefore critical to understanding the top-down effects they elicit on a given prey population (McNamara and Houston 1987; Sinclair et al. 1998).

Killer whales represent the highest trophic level of any marine mammal (Pauly et al., 1998) and are apex predators throughout their range. The nutritional requirements and prey consumption rates of killer whale populations may therefore be of significant importance; killer whale predation impact has been hypothesised as being the primary driver of the decline of several marine mammal populations worldwide (Springer et al. 2003; Williams et al. 2004; Herman et al. 2005; Springer et al. 2008; Estes et al. 2009, but see Springer et al. 2003 for debate) potentially resulting in top-down predator control (Estes et al. 1998; but see Kuker and Barrett-Lennard 2010). However, many of the underlying assumptions in these studies are associated with significant uncertainty, from estimates of the energetic requirements of killer whale populations (Maniscalco et al. 2007) to the nutritional value of prey beyond calorific content (MacHovsky-Capuska and Raubenheimer 2020). Furthermore, for predators that consume multiple prey species, it can be particularly challenging to quantify predation impact on individual prey species when consumption rates may vary both within and between prey species depending on which type of prey a predator selects (Ferguson et al. 2011). Quantifying the top-down effects of predator consumption on prey populations requires an understanding of the total energetic requirements of a given predator population and individuals therein, and how these requirements may be met by targeted prey species.

5.1.1 Energetic requirements: Basal and field metabolic rates

Basal metabolic rate (BMR) reflects the baseline energy expenditure required to maintain body processes when an animal is mature, non-reproductive, resting, fasting, and within a thermoneutral environment (Kleiber 1961). BMR is generally calculated in relation to an animal's mass (M in kilograms) and can be estimated as a function of $3.52M^{0.74}$, with this exponent found to be robust for terrestrial mammals of sizes from mice to elephants (Kleiber 1961; McNab 1986; Williams et al. 2001). Alternatively, BMR can be expressed in terms of energetic (calorific) requirements, calculated as $70M^{0.75}$ kilocalories a day (kcal d^{-1}) for terrestrial mammals (Kleiber 1961).

Field metabolic rate (FMR) is a measure of energy expenditure that takes into account the additional energetic requirements of free-living animals on a daily basis (Nagy, 1994). For this reason, FMR is a more ecologically relevant measure of daily energetic expenditure, and thus energetic requirements in wild animals. FMR is typically expressed as a multiple of Kleiber's (1961) predicted BMR (hereafter, BMR_K) for terrestrial mammals in kilocalories per day (kcal d^{-1}). It can be influenced by a combination of intrinsic and extrinsic factors, such as costs associated with growth, reproduction, digestion, thermoregulation, and locomotion (activity state) (Nagy 1994). Considerable variation has been found in FMR between species and taxa, much of which is accounted for by thermal physiology, with endothermic mammals and birds having FRMs 12 to 20 times higher than ectotherms of equivalent size (Nagy 2005). BMRs and FMRs of marine mammals are often higher than those of terrestrial mammals(Williams et al. 2001; Noren and Rosen 2023), likely due to physiological adaptions to life in the marine environment with considerable variation between taxa (see Noren and Rosen 2023 for review). Mean FMRs for marine mammals range from 1.1 to 6.1 times BMR_K dependent on species, as calculated based on a review of 'gold standard' estimates for a variety of taxa (Noren & Rosen, 2023). Published empirical measurements of field metabolic rates are only available for three species of odontocetes (Beluga whale *Delphinapterus leucas*, bottlenose dolphin *Tursiops truncatus*, harbour porpoise *Phocoena phocoena*), with the average across species as 3.52 (+/- 0.62) times BMR_K (Noren et al., 2023). Whilst there have undoubtably been advancements in understanding of the energetic requirements of free-ranging marine mammals, there is still considerable uncertainty surrounding estimates for cetaceans in particular (Noren & Rosen, 2023). Nevertheless, available estimates of FMRs provide the cornerstone of quantifying the energetic expenditure of wild animals and provide a useful tool in estimating the energetic requirements for species where direct quantification of energetic expenditure and prey intake rate is challenging to observe (Noren and Rosen 2023).

5.1.2 Energetic requirements of killer whales: Past research

Previous studies of daily energy expenditure and prey requirements for killer whales have typically focused on ecotypes in the North Pacific Northwest, e.g., fish-eating resident (Kriete 1995; Williams et al. 2006; Noren 2011) and mammal-eating Bigg's ("transient") killer whale populations (Baird and Dill 1996; Williams et al. 2004; Maniscalco et al. 2007; Shields et al. 2018). Given the lack of measured FMRs for killer whales, alternative approaches have been employed to estimate their energetic requirements. Approaches have involved using respiration rates as indicators of respiration rates and cost of transport (Roos et al. 2016), extrapolating FMRs from allometric relationships of at-sea metabolic rates of other marine mammals(Costa and Williams 1999), estimating FMRs from daily activity budgets of free-ranging animals using BMRs measured in captive killer whales (Kriete 1995; Williams et al. 2006; Maniscalo et al. 2007) or estimating the rate of energy intake through observations of prey intake by wild (Baird and Dill 1996) and captive (Barrett-Lennard, et al. 1995) individuals, with a correction factor applied to account for the sedentary activity level and smaller size of captive killer whales.

Historical studies using the doubly labelled water method on captive marine mammals result in FMR estimates that are on average five to six times the Kleiber (1961) predicted BMR, BMR_K (Costa and Williams 1999), which has previously been extrapolated to estimate field metabolic rates for killer whales (e.g., Williams et al., 2004; Noren 2011; Shields et al. 2018). However, a recent review of 'gold standard' estimates for a variety of marine mammal taxa calculated mean FMR ranges from 1.1 to 6.1 multiples of BMR_K, finding considerable variation in BMR, FMR, and the relationship between the two measures (BMR as a proportion of FMR) between species (Noren and Rosen 2023). Estimates of FMR and prey consumption rates using such approaches have varied greatly between studies (e.g., Williams et al., 2004 compared to Maniscalo et al., 2007), likely reflecting a combination of parameter estimate uncertainty (e.g., metabolic and prey intake estimates) and variation in predator population requirements (e.g., population size and demography).

Energetic requirements vary as a function of intrinsic characterises such as body size, age, and sex (Kleiber 1961; Kriete 1995). Bioenergetic models should therefore be parametrised with specific population requirements. Killer whales often live in family groups termed matrilines, which comprise both mature, immature, and dependent individuals. Given FMR is calculated proportionally to mass, smaller juveniles will have a higher mass-specific FMR in comparison to larger adults, as seen across mammalian taxa (Kleiber 1961). Adult male killer whales have a longer body length, and a greater mass than females, resulting in sexual differences in energetic requirements and FMRs in adults. The inclusions of population demographics (e.g., age and sex structure) is therefore important to the development of robust estimates for a given population. Studies taking into account the population demography and presence of discrete killer whale populations have been conducted for fish-eating (Noren 2011) and mammal-eating killer whales (Barrett-Lennard et al. 1995; London 2006; Shields et al. 2018)in the Pacific Northwest, providing population-specific consumption estimates for various prey populations.

5.1.3 Impact of killer whale predation on the study populations of seals

Killer whale predation has been hypothesised as a potential driving factor behind regional declines in harbour seal populations around Scotland. Consumption estimates for killer whales in Scotland are only available from one study (Bolt et al. 2009), which assumed a diet comprising entirely of harbour seal pups with killer whale calorific requirements derived from previously published estimates of Pacific Northwest individuals (Williams et al. 2004). However, for the observed rates of decline in seal abundance to have occurred, or to hinder the population recovering, adult harbour seals must be removed from the population (Hanson et al. 2013; Hanson et al. 2017). Outputs from Chapter 3 provided evidence of predation of both harbour and grey seal adults and pups by killer whales foraging inshore in Shetland. Since the publication of Bolt et al. (2009), citizen science photo-identification and observation efforts have greatly advanced our understanding of the demography and occurrence of killer whales foraging inshore in northern Scotland (Scullion et al. 2021). The study population consists of a number of identifiable individuals and are considered site-faithful to Scottish waters, ranging from the Northern Isles (Shetland and Orkney) to the north coast of mainland Scotland (Scullion et al. 2021). The whales are observed in matriarchal groups, consisting of 3 to 8 individuals (in the chosen year, 2021; Scullion et al. 2021), so understanding the energetic needs on the level of the study population is critical to understanding their role as apex predators and inform decisions regarding the conservation of both the predator and prey populations.

The aim of this chapter is to estimate daily energy expenditure and prey requirements for inshore-feeding killer whales in Shetland, and predict the potential consequences this may have for harbour and grey seal populations trajectories in the Shetland SMA. First, I develop and parameterise a bioenergetic model with input parameters and their associated uncertainties as derived for the study population. Second, to investigate potential population consequences of predation for harbour and grey seals, two common population modelling approaches were taken. (1) Acceptable thresholds set for removal by anthropogenic mortality, termed PBRs (potential for biological removal) (SCOS 2022), are calculated under different assumptions and compared to estimated predation takes. (2) Consumption estimates as derived from the bioenergetic model are incorporated into an existing population model developed as part of the Harbour Seal Decline project under the Marine Mammal Scientific Support Research Programme (MMSS) (Arso Civil et al. 2019). The integrated population model is based around an age and sex-segregated Leslie matrix model incorporating demographic parameters (e.g., fecundity and survival rates) for five life stages of seals: pup (age 0), juveniles aged 1,2,3, and adults aged 4+. Population trajectories are simulated under different realistic scenarios of input parameters (e.g., vital rates, harvest-type consumption estimates) to explore the potential impacts that killer whale predation may have on harbour and grey seals given various assumptions (e.g., composition in killer whale diet).

5.2 Methods

To estimate the potential impacts of killer whales on prey populations, information is required on the following parameters (see Williams et al. 2004 for methodology): 1) The calorific requirements of the killer whale population, taking into account individual requirements based on population demographics (age and sex structure); 2) the composition (proportion) of prey species and age-classes in a killer whale's diet; 3) the calorific values of individual prey, including variation both within (age-class) and between prey species (e.g., harbour vs grey seal); 4) the digestive efficiency of predators, measured as caloric energy assimilation from prey consumption; 5) the number of days killer whales were present in inshore waters of Shetland in a given year. For the purposes of this study, energetic requirements and consumption estimates were derived for the sample year 2021 (1st January to 31st December). This year was chosen for two reasons: Firstly, the latest Scottish Killer Whale Photo Identification Catalogue (Scullion et al., 2021) was published in this year, and thus represents the best and most recent estimate of demography for the study population (see Section 5.2.1b). Secondly, a known individual, juvenile male (#151) from a regularly re-sighted, site-faithful pod (27s), deceased in September of this year, with the necropsy providing a known reference length to estimate body length of associated adults in the 27s and 64s pods, and thus derive body mass for field metabolic rate states, for other killer whale age classes (see section 5.2.1.1c).

5.2.1 Bioenergetic parameter estimates

5.2.1.1 ENERGETIC REQUIREMENTS OF THE PREDATOR POPULATION

a) Field metabolic rates

Two calculations for FMR were explored to estimate the calorific requirements of the predator population (Equation 5.2). In line with current evidence taking into account species-specific difference in estimates, the FMR for bottlenose dolphins is used here as a proxy for the FMR for killer whales, calculated as 4.18 ± 1.68 (standard deviation) times BMR_K (Noren and Rosen 2023) (henceforth termed 'contemporary estimate' or FMRa). Of the species included in this most recent review, bottlenose dolphin was chosen as the most comparable to killer whale given similarities in measured BMRs (killer whale, 1.69 ± 0.78 x BMR_K ; bottlenose dolphin 1.96 ± 0.45 x BMR_K) and the physiology and ecology of the two species as compared to estimates available for other odontocetes (harbour porpoise and beluga whale). However, given the use of a different FMR estimate will likely impact the resulting estimated calorific requirements of killer whales in the present study in comparison to historical studies (e.g., Williams et al., 2004; Noren et al., 2011; Shields et al., 2018), FMR was also calculated as 5-6 times BMR_K (Costa and Williams 1999) (henceforth termed ‘historical estimate’ or FMRb).

Equation 5.1. Predicted BMR for terrestrial mammals (Kleiber 1961)

$$BMR_K = 70M^{3/4}$$

Where BMR_K = predicted basal metabolic rate in kcal per day (kcal d-1), M = body mass in kg (Kleiber 1961)

Equation 5.2. Calculation of proxy field metabolic rate for killer whales (Noren et al., 2023; Costa & Williams, 1999)

$$FMR = \alpha * \ BMR_K$$

Where FMR is the field metabolic rate (kcal d^{-1}), α is the multiplier specified as 4.18 ± 1.68 (Noren and Rosen 2023) for bottlenose dolphin (FMRa) and 5-6 times (Costa and Williams 1999) for marine mammals (FMRb), and BMR_K is the Kleiber-predicted BMR (Equation 1)

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b) Population demographics

Population demographics were derived for the Scottish Killer Whale Photo Identification Catalogue (Scullion et al. 2021). Known individuals were assigned an age-class based on either known or assumed (best estimate) age as of 2021, with classification based on previously published categories for killer whales (Noren 2011; Shields et al. 2018; Grimes et al. 2022) (Table 5.1). Calves were defined as those <3 years old, juveniles aged >3 & < 15, and either adult male or adult female for ≥ 15 years old.

Table 5.1. Demography of inshore-feeding killer whale pods in the year 2021 as derived from Scullion et al., (2021)

Pod	Adult females	Adult males	Juveniles	Calves	Total	Notes
27s	2	2	3	1	8[a]	Northern Isles Community
64s	1	1	1	1	4	Northern Isles Community
65s	1	1	3	1	6	Northern Isles Community
12s	1	2	3	1	6	Scotland – Iceland migrants
169s	3	0	0	0	3	Community unknown
19s	2	1	3	0	6	Scotland – Iceland migrants
15s	2	3	1	0	6	Scotland – Iceland migrants
Bull 018	0	1	0	0	1	Lone bull
27a's	1	1	2	0	4	27s group split
27s&64s	3	3	4	2	12[b]	27s and 64s group join

Notes.

[a] Group size of 8 from January to September. Juvenile 151 stranded in September when group split into two groups of 4 and 3 until rejoining in December. Sightings in December have a total group size of 7.

[b] Group join occurred prior to stranding of 151 when 27s group size was 8.

c) Body length to mass

Given the challenges of accurately measuring the body mass of free-ranging killer whales, an alternative method is to estimate mass from body length(Bigg and Wolman 1975) (Equation 5.3). However, body length varies considerably between killer whale ecotypes globally, and even within the north-east Atlantic, the body length of stranded mature animals is found to range between approximately 5 and 8m (Foote et al. 2009). To accurately estimate the body length of individuals of each age-class within this study, drone-based estimates of body length were made as part of a separate study investigating body condition of inshore-feeding killer whales from citizen science photogrammetry (Isojunno et al., in prep). The length measurement methodology followed Kotik et al. (2023). Body lengths were measured from drone footage collected in the year 2021, which, as previously described, was in part chosen because a known individual (151) stranded in September of this year – thus his known length from necropsy could be used as a known-size reference ('yard stick') to measure other members of the 27s and 64s pods against in drone photogrammetry. From this, upper (the longest individual in the sex age-class) and lower (the shortest individual in the sex age-class) body length estimates for sex specific age-classifications were derived for inshore-feeding killer whales (Table 5.2) and used for mass calculations.

Equation 5.3. Deriving body mass from body length for killer whales (Bigg and Wolman, 1975)

$$M = 0.000208L^{2.577}$$

where M = body mass in kg and L = total body length in cm (Bigg and Wolman 1975)

5.2.2 Killer whale diet composition

Diet composition of inshore-foraging killer whales was based on the results of Chapter 3. Prey species were identified from citizen science imagery with associated confidence from an expert elicitation process, with the probability of consumption given a killer whale encounter modelled by species using a binomial GLM (see Section 3.3.3). Of the 127 events, 87 resulted in observed consumption: harbour seal (n=16/25), grey seal (n=7/20), harbour porpoise (n=5/6), seabird (n=5/2), seal (where harbour vs grey identification could not be confidently discerned) (n=38/52), and unknown mammals (n=15/15). To estimate the composition of species in the inshore-feeding killer whale diet in Shetland, the proportion of seals vs other species of substantial nutritional value, namely harbour porpoise was calculated. Seabirds were assumed unlikely to contribute considerable nutritional value, and otters were not observed as consumed in the dataset. Given unknown mammals could either be seals, porpoises, or other unidentified small cetaceans or mammals, the unidentified species in killer whale diet were allocated an ID in proportion to the number of each of the species consumed in confidently identified events (n=66). That is, out of the 66 consumption events where species were identified, grey seals comprised of 10% (n=7/66), harbour seal 25% (n=16/66), seal 58% (n=38/66), and harbour porpoise 7% (n=5/66). Seals therefore comprised a majority (93%) of observed predation events (n=61/66), and for the purpose of this study it is assumed that 90% of the diet of inshore-feeding killer whales is comprised of seals, given the unknown composition of unknown mammals. Of this 90%, 60% are assumed to be harbour seal and

30% grey seal, representing the higher proportion of harbour seal consumed vs grey seals and taking into account the uncertainty in the seal species composition of the ‘seals’ category.

As observed during the expert elicitation process, estimating the age-class of seals consumed by killer whales for the given data was challenging, and confidence in age-classification of harbour seal pups was low amongst experts (maximum 0.4). Nevertheless, harbour seal pups were identified as most likely prey species in a small number of events (n = 4/37) during the elicitation process on a subset of predation events; however, grey seal pup was never assigned as the most likely prey species. Given the small proportion of harbour seal pups observed in the expert elicitation dataset, only 10% of the harbour seals consumed by killer whales were assumed to be pups, with the remaining 50% split evenly among adults (25%) and juveniles (25%). Given no grey seal pups were identified during the elicitation process, the 30% composition of grey seals in killer whale diet was split evenly amongst juveniles (15%) and adults (15%).

5.2.3 The calorific values of prey & assimilation efficiency

Calorific content of harbour seals has been estimated to be between 2500 kcal/kg and 3800 kcal/kg (Perez 1990), with values obtained from bomb calorimetry of two harbour seal carcasses from Canada falling within this range: 3590 kcal/kg for a 19kg yearling, and 2798 kcal/kg for a 49kg subadult (London 2009). Body mass of UK harbour and grey seals of age-classes pup, juvenile, and adult were obtained from records of individuals captured as part of various research projects carried out at the Sea Mammal Research Unit (SMRU) (years 1988 – 2023). Ranges of calorific content were calculated for each age-class of species using the 95% percentile of seal masses to remove outliers, with the assimilation rate (proportion of ingested prey absorbed and utilised by the predator) for killer whales fixed at 0.85 (Williams et al. 2005).

5.2.4 Killer whale days & pod days

The number of days killer whales were sighted in Shetland was obtained from opportunistic citizen science sightings collated by the Shetland Biological Record Centre (SBRC) coordinated by K. Hall. Sighting records include the date, time, latitude and longitude, group number (best estimate), pod ID (if known), and observer platform (e.g., land, ferry, charter boat, fishing boat), although data were incomplete for some entries (e.g., latitude and longitudes were missing for ~40% of sightings). Given the present study is investigating the energetic requirements and prey consumption of killer whales feeding inshore, only land-based or inshore vessel sightings (e.g., inter-island ferries or charter boats within 2.5km) were included. The number of days killer whales were recorded as present was considered the minimum number of killer whale days (n = 124), as it is likely whales were present in inshore waters on other days but were not observed and recorded.

To estimate the maximum number of days killer whales were present, sightings were interpolated using the following criteria: where a known pod (e.g., 27s) was observed inshore on consecutive days prior (e.g., 1st, 2nd) and post (e.g., 4th, 5th), it was assumed that the pod was present on the missing interim day (3rd) but were not detected and recorded. This approach follows previous methodology to account for days where killer whales may not have been detected by sightings networks (e.g., Houghton et al. 2015; Shields et al. 2018). In Shetland, observer effort varies around the coastline due to geographical constrains on accessibility. That is, certain areas are more challenging to access and thus killer whale detection in these areas is expected to be lower than those that are readily accessible. It was therefore considered plausible that, especially in these areas, killer whales remained inshore on interim days but were not recorded due to the variation in detectability. Whist it is plausible killer whales moved offshore in this time, they would not have been able to travel to Orkney, for example, and back to Shetland within 24 hours. Sightings were therefore only interpolated for single days, as it could not be ruled out that they had travelled to inshore waters to elsewhere before returning to Shetland during periods greater than one day. Based on this criteria, an additional nine days were added across known pods: 1 day to bull 018; 3 days to 27s pod; 4 days to 27s (a); and 1 day to the 64s. Given this reflected a proportional increase of 1.14 days where known pods were present, the number of days unknown pods were present (n=69) was multiplied by 1.14 to account for days where unknown pods may not have been detected.

To estimate daily prey consumption taking into account the demography of different pods, the number of days each pod was present was calculated, termed pod days (d_i where *i* denotes different pods). Only days where there was high confidence in pod ID were assigned as a pod day, with the days that unknown pods were present distributed amongst the known pod days based on the pod's proportional occurrence. Specifically, of the 124 days during which killer whales were known to be present, sightings on 69 of those days were of unknown pods. For example, the 27s pod were known to be present on 31 days, reflecting 48% of the minimum known pod days (31/64), thus 48% (33/69) of the unknown days was assigned to the 27s pod demography. Following this methodology, pod demography was assigned to each killer whale day, allowing for days where multiple pods were present to yield lower, upper, and best estimates for pod days (Table 2), with subsequent consumption estimates reflecting the best estimate for the study population as present in inshore waters in 2021.

Table 5.2. Estimates of killer whale presence and calculated pod days for the year 2021. Where days present represent known lower and interpolated upper days pods were present; proportions of known days represent the proportion of lower and upper known days each pod was present; and best estimate represents the total lower, upper, and best (mean) estimates, calculated as the known days plus the proportionate number of unknown days added for each pod.

		Day present		Proportion of known days		Best estimate of pod days		
		Lower	Upper	Lower	Upper	Lower	Upper	Best
Pods	12s	2	2	0.03	0.03	4.16	4.16	4.16
	15s	1	1	0.02	0.01	2.08	2.08	2.08
	169s	3	3	0.05	0.04	6.23	6.25	6.24
	18	1	2	0.02	0.03	2.08	4.16	3.12
	19s	3	3	0.05	0.04	6.23	6.25	6.24
	27s	31	34	0.48	0.47	64.42	70.79	67.61
	27s_a	10	14	0.16	0.19	20.78	29.15	24.97
	64s	10	11	0.16	0.15	20.78	22.90	21.84
	64s&27s	3	3	0.05	0.04	6.23	6.25	6.24
	Unknown	69	79					
Totals	Known days	64	73					
	Pod days	133	152			133	152	143
	Killer whale days	124	133			124	126	133

5.2.4 Statistical Analysis

5.2.4.1 BIOENERGETIC UNCERTAINTY ANALYSIS

To account for uncertainty in parameter estimates and in the final consumption estimate, Monte Carlo simulations of the bioenergetic calculations (Equations 1-3) were performed. In each iteration, values were chosen from continuous uniform distributions of ranges for the respective parameters (Table 3). The bioenergetic model was re-calculated 10,000 times, with new parameter values chosen from the continuous uniform distribution ranges during each iteration. To investigate the impact the contemporary FMR parameter ranges had on the final consumption estimates, two versions of the bioenergetic model were constructed: one using the contemporary FMRa estimate of 4.18 ± 1.68 times BMR_K, (α_a, Table 3) and one using the historical FMR estimates of five to six times BMR_K (α_b, Table 3). For each model, the calorific requirements of each killer whale age and sex class were estimated as daily calorific (kcal/day) and mass-specific daily calorific requirement (kcal/kg/day). The resulting prey consumption estimates from the uncertainty analyses assumed that killer whales only targeted one age class of one species. Diet composition, as a proportion of each species and age class assumed to be consumed, was not incorporated in the uncertainty analysis. Instead, the output was multiplied by an assumed prey composition as detailed in Section 5.2.1.2 to yield species and age-class specific takes for the year 2021. By doing this, the population consequences of species and age-class specific takes could be explored under different compositions during subsequent Leslie Matrix population modelling (Section 5.2.4.2).

Table 5.3. Input parameters to the Monte Carlo simulation of killer whale energetic requirements and prey consumption in coastal Shetland. Point "best" estimates and ranges were derived for each input parameter from literature. For input parameters with a range of plausible values (all expect assimilation rate which was fixed at 0.85), the range was used to sample alternative values from a uniform distribution at each iteration of the simulation in an uncertainty analysis.

Parameter	Description (units)	Best estimate (range)	Source
ω	Seal caloric content (kcal/kg)	2,650 (2,500 – 2,800)	Perez, 1999
$M_{Pv,a}$	Harbour seal adult mass (kg)	82.2 (54.9 – 111)	SMRU
$M_{Pv,j}$	Harbour seal juvenile mass (kg)	37.8 (19.2 – 59.2)	SMRU
$M_{Pv,p}$	Harbour seal pup mass (kg)	18.2 (10.2 – 44)	SMRU
$M_{Hg,a}$	Grey seal adult mass (kg)	135 (69.4 – 209)	SMRU
$M_{Hg,j}$	Grey seal juvenile mass (kg)	43.8 (30.9 – 94.3)	SMRU
$M_{Hg,p}$	Grey seal pup mass	38.6 (29 – 51.6)	SMRU
L_f	Killer whale adult female body length (cm) (Eq. 3)	516 (510 – 522)	Isojunno et al., (in prep)
L_m	Killer whale adult male body length (cm)	610 (605 – 615)	Isojunno et al., (in prep)
L_j	Killer whale juvenile body length	424.5 (350 – 420) cm	Isojunno et al., (in prep)
α_a	Contemporary field metabolic rate multiplier (kcal d^{-1}) (Eq. 2)	4.18 (2.5 – 5.86)	Noren et al., 2023
α_b	Historical field metabolic rate multiplier (kcal d^{-1}) (Eq. 2)	5.5 (5-6)	Costa & Williams, 1999
λ	Assimilation rate	0.85 (constant)	Williams et al., 2004
d_i	Killer whale days specific to each pod i	143 (133 – 152)	SBRC

5.2.4.2 Population consequences: PBR

Potential for Biological Removal (PBR) estimates are used to calculate whether current levels of anthropogenic mortality may be within reach or exceed a specific target population, taking into account expected population growth rates (Wade 1998; SCOS 2022). PBRs are calculated using the minimum population estimate, the population growth rate (considering population densities), and a recovery factor (between 0.1 and 1) set to account for stochastic effects and overestimation of other parameters.

Equation 5.4. PBR calculation (SCOS 2022; Wade 1998)

$$PBR = N_{min} \times \left(\frac{R_{max}}{2}\right) \times F_R$$

Where PBR is the number of animals permissible to be removed from a population.

N_{min} is the minimum population estimate.

R_{max} is the population growth rate at low densities (default 0.12 for pinnipeds), which is halved to give an estimate of the growth rate at the target population level.

F_R is the recovery factors, ranging between 0.1 and 1. Low factors give some protection from stochastic effects and overestimation of other parameters, and increase the expected equilibrium population size under the PBR.

Of the parameters in Equation 4, the recovery factor (F_R) is considered the most subjective (Lonergan 2011). Official guidance for using PBR recommends a recovery factor of 0.1 for population considered endangered, 0.5 for those that are threatened or depleted, and 1 for those not depleted (Barlow et al. 1995). In Shetland, a low recovery factor (0.1) is recommended to account for prolonged declines and no signs of population recovery or harbour seals (SCOS 2022). Whilst PBR calculations reflect acceptable removals on top of pre-existing removal, as population growth rate is depended on fecundity, survival, and density dependence, it is as yet unknown whether killer whale predation is a contributing factor (and thus already incorporated in) to this slow recovery. Given this, the PBR for both harbour and grey seals were calculated under different recovery factors to explore a range of plausible PBRs for the populations.

5.2.4.2 POPULATION CONSEQUENCES: LESLIE MATRIX MODEL

A pre-existing population model for harbour seals (Arso Civil et al., 2019) was modified to incorporate a harvest-type parameter (with associated killer whale diet composition (to represent the additional h_i) (Table 4.3 c_i) The harvest-type input parameter values were derived directly from the Monte Carlo uncertainty analysis detailed in Section 5.2.4.1 to ensure uncertainty in consumption estimates was propagated through the statistical modelling. The annual consumption estimated for male and females was distributed evenly between the sex specific life-stage (pup, juvenile aged 1-3, and adult).

Table 5.3. Vital rate input parameters included in the Leslie Matrix simulation model with associated sources.

Parameter	Description	Harbour seal sources	Grey seal sources
f	Fecundity per female	Arso Civil et al., 2019; Matthiopolous et al., 2014; Graham et al., 2017	Harwood & King 2017; Thomas et al., 2019
S_0	Pup survival		
S_1	Juvenile survival		
S_{2F}	Adult female survival		
S_{2M}	Adult male survival		
N_P	Starting seal population size	Morris et al., 2021; SCOS; 2022	Morris et al., 2021; SCOS; 2022
N_Y	Number of simulation years	Estimated	Estimated
h_i	Number of seals consumed in a year specific to each species i	Present study	Present study
c_i	Killer whale diet composition proportionate to age class i	Present study	Present study

Default parameters for vital rates already incorporated in the model were derived from an expert elicitation process, with experts providing independent judgements of quantiles of interest for each vital rate as estimated for a declining/depleted harbour seal population (Arso Civil et al, 2019). Alternative vital rates estimated for stable/increasing harbour seal populations, and UK grey seal populations were derived from published literature (Matthiopoulos et al. 2014; Graham et al. 2017; Harwood and King 2017). The simulation was then run under different scenarios (i.e., parameter changes) to explore the consequences of predation for harbour and grey seal population trajectories given certain assumptions (Table 4.4 – 4.5). For each species, harbour and grey, simulations were run for four scenarios (A-D) to address to the following questions:

A) “Consequences of estimated rates” What impact would the predation rates, as estimated in this study, have on Shetland seal populations? This scenario assumes the levels of predation as estimated in the present study is representative of the true rates. To address this the model was constructed using vital rates equal to the median values from the expert elicitation detailed in Arso Civil et al. (2019) as derived for declining / depleted harbour seal populations and Harwood and King (2017) as derived for stable / increasing grey seal populations. Harvest-type predation takes for each life-stage were derived from the Monte Carlo simulation outputs from Section 5.2.4.1.

B) “Required prey population size”. If Scenario A proved unsustainable (i.e., result in extinction) what prey population size would be required to sustain the predation takes as estimated in the present study? If Scenario A proves sustainable, what is the minimum starting population that would sustain the predation takes as estimated in the present study? To address this, the starting population of harbour and grey seals was either increased until predation takes no longer resulted in a simulated population decline or decreased to a minimum sustainable population.

C) “Consequences of diet composition”. What impact would a change in estimated diet composition have on population trajectories? This scenario assumes a misrepresentation of species and/or age-classes in killer whale diet as estimated in the present study. To address this, the proportion of species and/or age-classes comprising killer whale diet was altered to and the resulting population trajectory simulated. For harbour seals, a higher proportion of seal pups vs adults and juveniles was modelling to given the possibility that pups were under-represented in the “consequences of estimated rates” scenario. For grey seals, an age-class proportion equal to that of harbour seals was modelled given the possible under-representation of grey seals in the “consequences of estimates rates” scenario. A C_{max} scenario was modelled to explore the population trajectories for grey seals under the assumption they comprised all seals estimates in a killer whale diet.

D) “Adjusted vital rates”. For harbour seals only, what if the default vital rates derived from declining / depleted populations already accounted for mortality through predation? This scenario assumes seal vital rates already incorporate the effects of predation. To address this, vital rate parameters for harbour seals were set to those as derived from a stable or increasing population, namely Loch Fleet and Moray Firth as detailed in Matthiopolous et al. (2014) and Graham et al. (2017).

Table 5.4. Input parameters for harbour seal Leslie Matrix model population simulations. Grey boxes denote which parameter(s) were modified in each simulation scenario (B-D) in comparison to scenario A.

Scenario	f	S_0	S_1	S_{2F}	S_{2M}	N_P	N_Y	c_i (adult, juvenile, pup)
A	0.88	0.35	0.86	0.94	0.89	3180	35	(0.25, 0.25, 0.1)
B	0.88	0.35	0.86	0.94	0.89	11000	35	(0.25, 0.25, 0.1)
C	0.88	0.35	0.86	0.94	0.89	3180	35	(0.15, 0.15, 0.3)
D	0.9	0.7	0.79	0.97	0.94	3180	35	(0.25, 0.25, 0.1)

Table 5.5. Input parameters for grey seal Leslie Matrix model population simulations. Grey boxes denote which parameter(s) were modified in each simulation scenario (B-C_{max}) in comparison to scenario A.

Scenario	f	S_0	S_1	S_{2F}	S_{2M}	N_P	N_Y	c_i (adult, juvenile, pup)
A	0.9	0.62	0.95	0.95	0.95	3760	35	(0.15, 0.15, 0)
B	0.9	0.62	0.95	0.95	0.95	1350	35	(0.15, 0.15, 0)
C	0.9	0.62	0.95	0.95	0.95	3760	35	(0.25, 0.25, 0.1)
C_{max}	0.9	0.62	0.95	0.95	0.95	3760	35	(0.4, 0.4, 0.1)

5.3 5.3 Results

5.3.1 5.3.1 Bioenergetics uncertainty analysis

5.3.1.1 KILLER WHALE CALORIFIC REQUIREMENT ESTIMATES

Results from the Monte Claro bioenergetic uncertainty analysis yielded ranges of calorific requirements estimates for each killer whale age and sex class, summarised here as the median number of kcal/day and kcal/kg/day with associated 95% ranges calculated as the 95% percentile of the 10,000 simulation values. FMRs calculated using the historical FMRb multiplier resulted in a ~30% increase in calorific requirements across age classes, compare to the estimates obtained using the contemporary FMRa multiplier (Figures 5.1 – 5.2, Table 5.6). FMR calculated using either multiplier estimated the daily caloric requirements for adult females to be 72% of adult males.

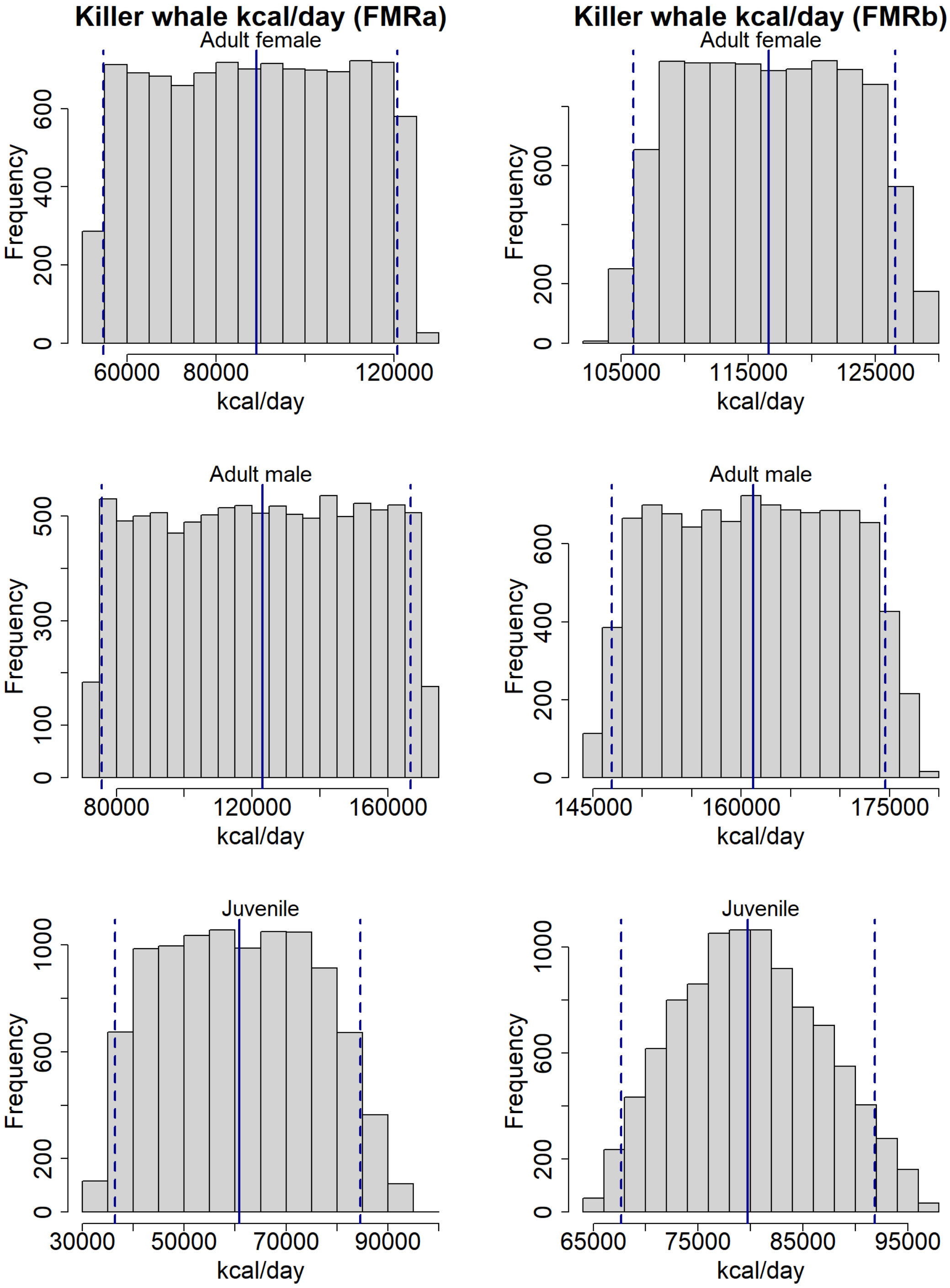

Figure 5.1. Killer whale calories per days (kcal/day) for each age-sex class. Based on 10,000 Monte Carlo simulation, with median (solid line) and 95% CIs (dashed lines) using contemporary FMRa (left) and historical FMRb (right).

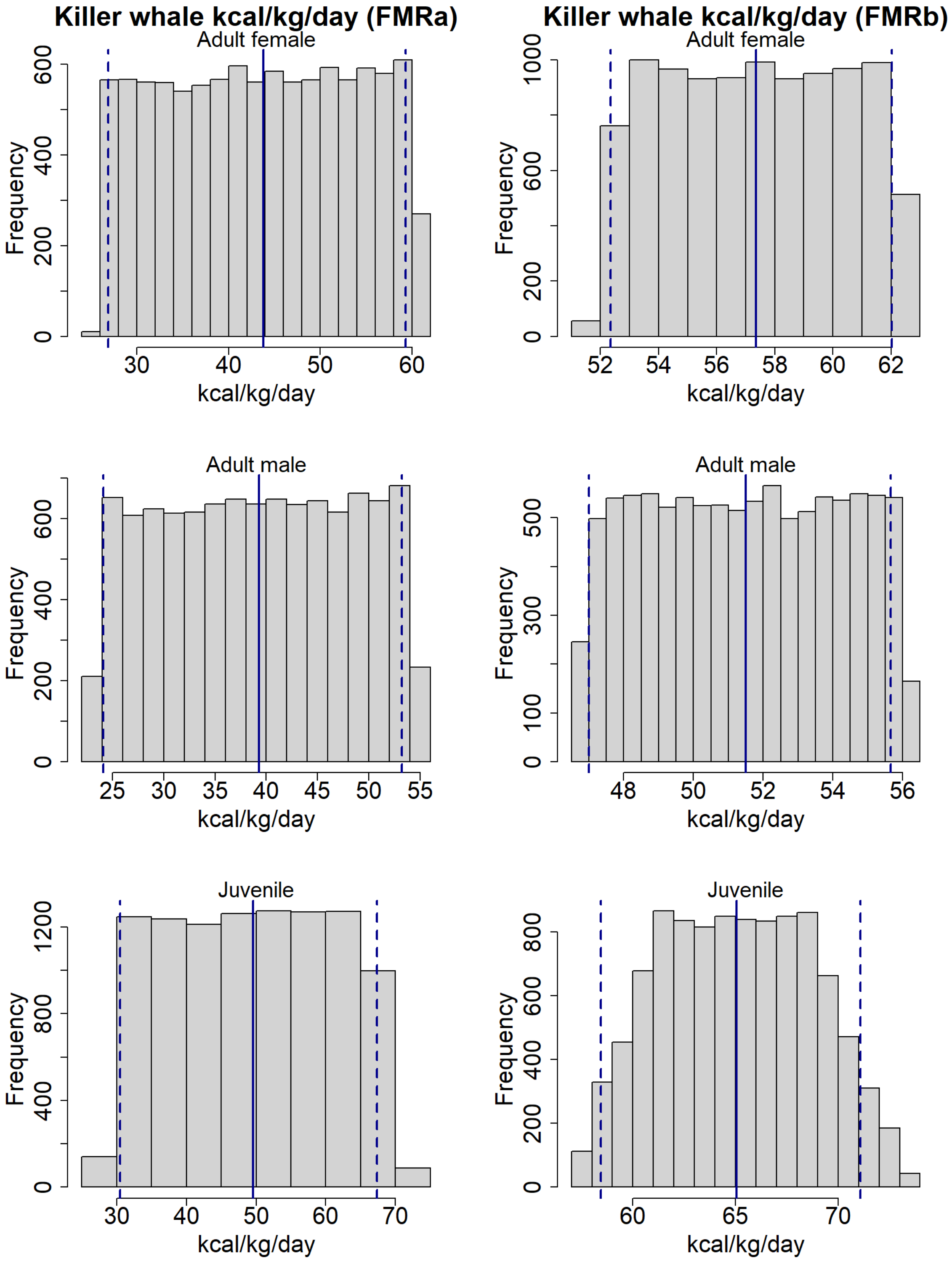

Figure 5.2. Killer whale calories per kilogram mass per day (kcal/kg/day) for each age-sex class. Based on 10,000 Monte Carlo simulations, with median (solid line) and 95% CIs (dashed lines) using contemporary FMRa (left) and historical FMRb (right)

Table 5.6. Ranges (median with 95% CI) of mass and field metabolic rates (FMRs) for sex and age-classes of killer whales.

		FMRa		FMRb	
Age class	Mass (kg)	kcal/day	kcal/kg/day	kcal/day	kcal/kg/day
Adult female	2,036 (1,978 -2093)	89,076 (54,666 – 122,585)	44 (27 – 60)	116,605 (105,954 – 127,560)	57 (52-62)
Adult Male	3,132 (3,070-3,196)	123,116 (75,645 – 169,111)	39 (24 – 54)	161,214 (146,938 – 175,845)	51 (47 – 56)
Juvenile	1,231 (1,058 -1,419)	60,799 (36,405 – 87,833)	50 (31 – 69)	79,741 (67,660 – 93,456)	65 (58 – 72)

Notes

[a] based on 4.18+/-1.68 times Kleiber predicted BMR (Noren and Rosen 2023)

[b] based on 5-6 times Kleiber predicted BMR (Noren 2011)

5.3.1.2 KILLER WHALE PREY CONSUMPTION ESTIMATES

Results from Monte Carlo simulations for the year 2021 are summarized here as the median number of each seal species and age class consumed with associated 95% ranges calculated as the 95% percentiles of the 10,0000 simulated values, assuming a diet composition 60% harbour seals (25% adults, 25% juveniles, 10% pups) and 30% grey seals (15% adults, 15% juveniles) (see Chapter 3). Killer whales were estimated to take a similar number of adults and pup, however the uncertainty around the number of pup taken was considerably higher than that of adults, as demonstrated in the right skew of the estimate distribution (Tables 5.7 – 5.8, Figures 5.3 – 5.4). The highest number of individuals taken was estimated for juvenile seals. Consumption estimates based on the historical FMRb were ~30% higher than consumption estimates from the cotemporary FMRa multiplier, however there was substantial overlap in the 95% ranges for each seal age class.

As expected, the number of individuals estimated to be consumed given FMRa were lower than those for FMRb, given FRMb resulted in higher ranges of daily energetic requirements. Pooling across all harbour seal age classes, the median (400) and 95th percentiles (196 – 916) consumption estimates as derived from FRMa represents 12.4% (65 - 28%) of the latest harbour seal population estimated (3,180) in the Shetland SMA (Morris et al. 2021; SCOS 2022). The median (525) and 95th percentiles (341 – 1004) consumption estimates as derived from FMRb represented 16% (11% - 32%) of the latest harbour seal population estimate. As a percentage of the latest estimated grey seal population in the SMA, 3,760 individuals based on August 2019 aerial survey data corrected for proportion of grey seals expected to be hauled out during harbour seal moult counts (SOCS 2022), the median (105) and 95th percentiles (51 – 234) consumption estimates derived from FMRa represents 3% (1% – 6 %) of the population when pooling all ages classes. Derived from FMRa, the median (139) and 95th percentiles (90 – 267) consumption estimates represent 4% (2% – 7%) of the grey seal population.

Table 5.7. Median and 95th percentiles from Monte Carlo simulations for harbour seal consumption estimates for the year 2021 based on the application of FMRa and FMRb.

Harbour Seal		FMRa			FMRb		
Age class	Proportion in diet	5th percentile	Median	95th percentile	5th percentile	Median	95th percentile
Adult	0.25	49	91	163	87	120	182
Juvenile	0.25	95	197	444	165	258	501
Pup	0.1	52	112	309	89	147	365
Totals	0.6	196	400	916	341	525	1004

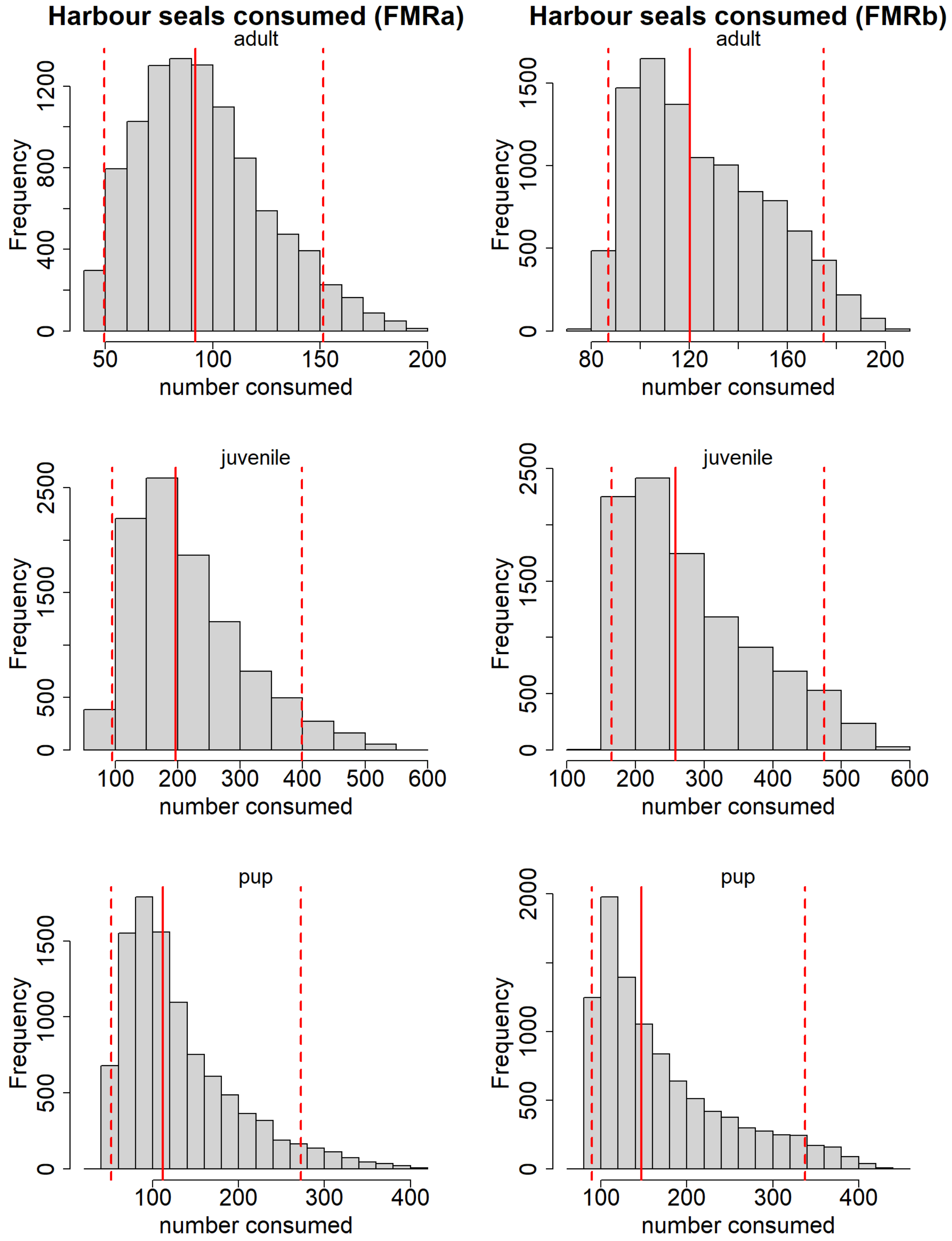

Figure 5.3. Histogram of bioenergetic Monte Carlo simulations for consumption estimates of harbour seal adults, juveniles, and pups using FMRa (left) and FMRb (right)Assuming a proportion of 0.25 adults, 0.25 juveniles, and 0.1 pups, with median (solid red line), and 95th (dashed red lines) percentiles.

Table 5.8. Median and 95th percentiles from Monte Carlo simulations for grey seal consumption estimates for the year 2021 based on FMRa and FMRb.

Grey Seal		FMRa			FMRb		
Age class	Proportion in diet	5th percentile	Median	95th percentile	5th percentile	Median	95th percentile
Adult	0.15	16	32	72	28	43	82
Juvenile	0.15	35	73	162	62	96	185
Pup	0	0	0	0	0	0	0
Totals	0.3	51	105	234	90	139	267

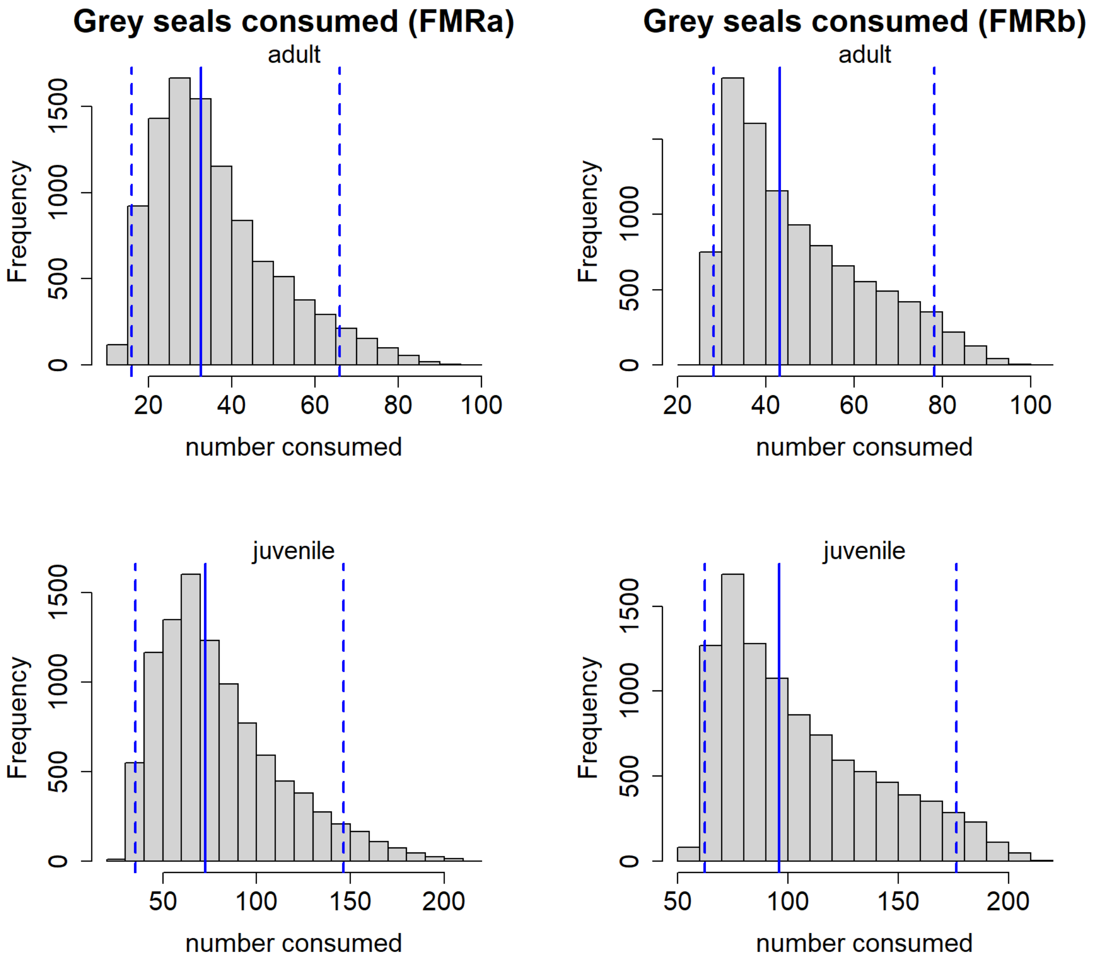

Figure 5.4. Histogram of bioenergetic Monte Carlo simulations for consumption estimates of grey seal adults and juveniles using FMRa (left) and FMRb (right). Assuming a proportion of 0.15 adults, 0.15 juveniles, and 0 pups (not depicted), with median (solid blue line), and 95th (dashed blue lines) percentiles.

5.3.2 Population consequences: PBR

PBR estimates were calculated for harbour and grey seal minimum population estimates in the Shetland SMA region based on a range of population recovery factors, F_R. For harbour seals, a low recovery factor (0.1) resulted in a PBR of 19 individuals; a medium (0.5) in 95 individuals; and a high (1) in 190 individuals (Table 5.8). For grey seals, a low recovery factor (0.1) resulted in a PBR of 22 individuals; medium (0.5) in 112 individuals; and high (1) in 225 individuals (Table 8).

Table 5.8. PBRs calculated for harbour and grey seals in Shetland under different recovery factors ($\mathrm{F_R}$)

			PBRs based on recovery factors F_R of 0.1, 0.5 or 1		
Species	N_{min}	R_{max}	0.1	0.5	1
Harbour	3180	0.12	19	95	190
Grey	3760	0.12	22	112	225

5.3.3 Population consequences: Leslie Matrix model

5.3.3.1 HARBOUR SEALS

Future projected population trajectories for harbour seals were explored under four different scenarios across a 35-year prediction period (Table 5.4). Scenario A, ‘Consequences of estimated rates’, explored the potential consequences of the estimated consumption rates; assuming vital rate parameters were equal to those as derived from a declining / depleted harbour seal population, a starting population equal to the minimum population estimate for harbour seals in the Shetland SMA (3,180), and harvest-type parameter assuming the removal of individuals was equal to that derived from the bioenergetic uncertainty analysis with a diet composition of 0.25 adult, 0.25 juveniles, and 0.1 pups. In this scenario, the population trajectory declined and was completed depleted after 12-20 years (Figure 5.5).

Scenario B, ‘Required prey population size’, explored what prey population size would sustain the estimated consumption rates; assuming the same vital rate and harvest-type parameter as Scenario A, but with the starting population increased until the trajectory did not result in a decline. At a starting parameter of 11,000 harbour seals, the population trajectory remained stabled across the 35-year prediction period (Figure 5.6).

Scenario C, ‘Consequences of diet composition’, explored the potential consequences of the specified diet composition and potential under-estimation of pup consumption, assuming the same vital rate and starting population as Scenario A, with the harvest-type parameter changed to a higher proportion of harbour seal pups, in comparison to juveniles and adults, in the diet composition. Under a diet composition of 0.15 adult, 0.15 juveniles, and 0.3 pups, the population trajectory declined and was completed depleted after 22-32 years (Figure 5.7).

Scenario D, ‘Adjusted vital rates’, explored whether seal prey population might persist with vital rates from a seal population with likely less predation pressure, assuming the same starting population and harvest type-parameter as Scenario A, with the vital rates changed to those as derived from a stable / increasing harbour seal population. In this scenario, population trajectories diverged across simulations and varied between declining until depletion (after 20-35 years) and increasing to over 10,000 individuals (Figure 5.8).

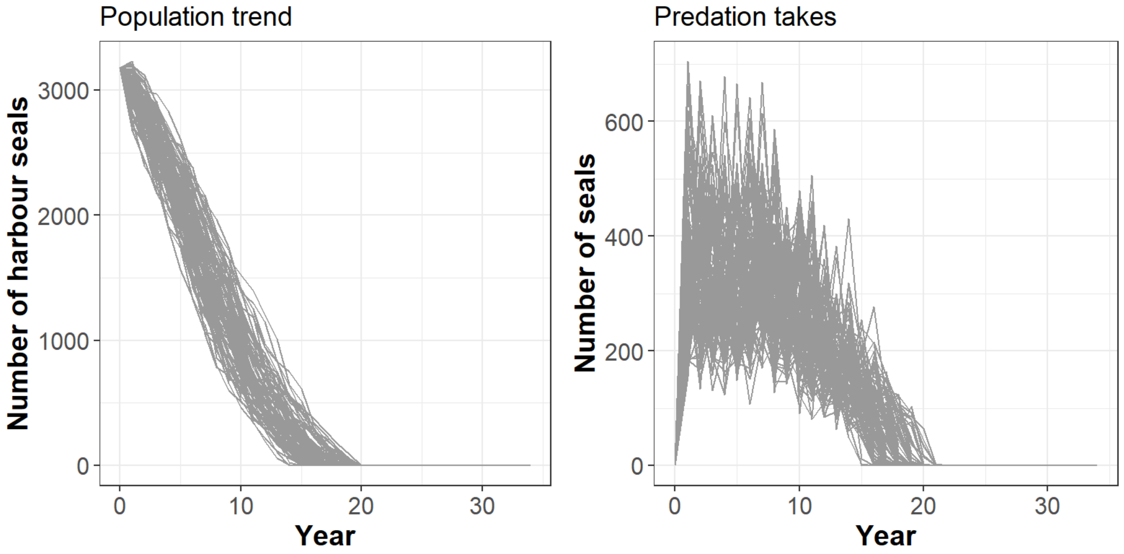

Figure 5.5. Simulated population trajectories (left) and predation takes (right) for harbour seals under input parameters in Scenario A, ‘Consequences of estimated rates’. Where the starting population is equal to the 2021 estimate for harbour seals in Shetland (3180), vital rates are set to that of a declining population, and killer whale diet composition is assumed to be 0.25 adult, 0.25 juveniles, and 0.1 pups.

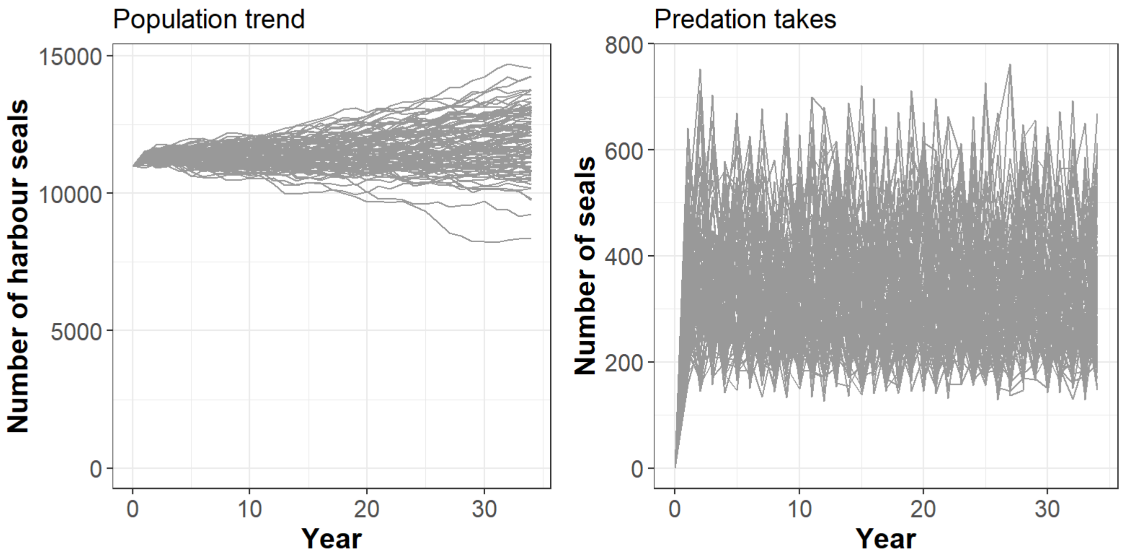

Figure 5.6. Simulated population trajectories (left) and predation takes (right) for harbour seals under input parameters in Scenario B, 'Required prey population size'. Where a starting population of 11,000 harbour seals is required for the population to remain stable given vital rates are set to that of a declining population, and killer whale diet composition is assumed to be 0.25 adult, 0.25 juveniles, and 0.1 pups.

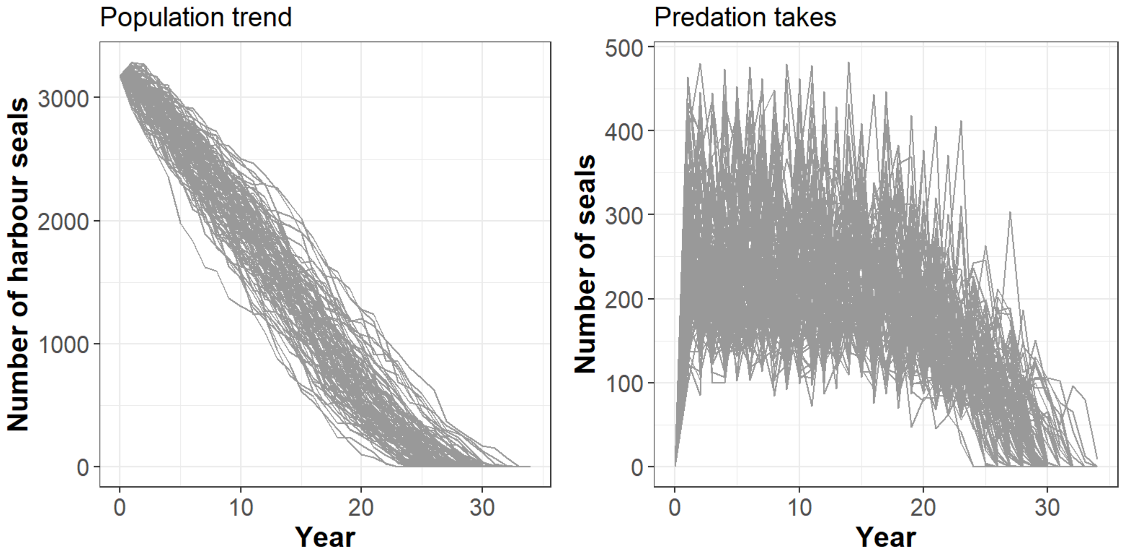

Figure 5.7. Simulated population trajectories (left) and predation takes (right) for harbour seals under input parameters in Scenario C, 'Consequences of diet composition'. Where the starting population is equal to the 2021 estimate for harbour seals in Shetland (3180), vital rates are set to that of a declining population, but killer whale diet composition is assumed to contain a higher proportion of pups vs adult and juveniles: 0.15 adult, 0.15 juveniles, and 0.3 pups.

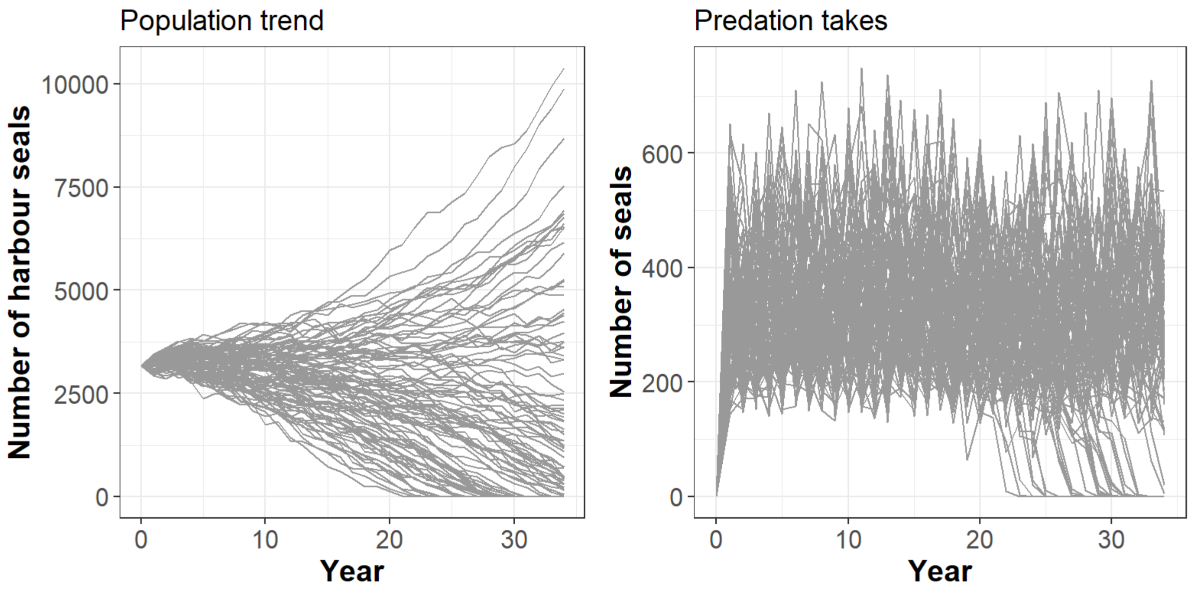

Figure 5.8. Simulated population trajectories (left) and predation takes (right) for harbour seals under input parameters in Scenario D, 'Adjusted vital rates. Where the starting population is equal to the 2021 estimate for harbour seals in Shetland (3180), vital rates are set to that of a stable population, and killer whale diet composition is assumed to be 0.25 adult, 0.25 juveniles, and 0.1 pups.

5.3.3.2 GREY SEALS

Population trajectories for grey seals were explored under four different scenarios across a 35-year prediction period (Table 5.5). Given population vital rates recommended for grey seals are consistent across regions of the UK, the same vital rates were used in Scenarios A – C_{max}. Scenario A, 'Consequences of estimated rates', assumed vital rate parameters were equal to those as derived from UK populations of grey seals, a starting population equal to the minimum population estimate for grey seals in the Shetland SMA (3,760), and harvest-type parameter assuming the removal of individuals was equal to that derived from the bioenergetic uncertainty analysis with a diet composition of 0.15 adult and 0.15 juveniles. In this scenario, the population trajectory increased over the 35 year period (Figure 5.9).

Scenario B, 'Required prey population size', assumed the same vital rate and harvest-type parameter as Scenario A, with the starting population reduced to the minimal viable population to support estimated levels of predation. At a starting population of 1,450 grey seals, the population trajectory remained stable or increase across the 35-year period. Starting populations below this resulted in a decline population decline for some simulations (Figure 5.10).

Scenario C, ‘Consequences of diet composition’, assumed the same vital rate and starting population as Scenario A, with the harvest-type parameter changed to a higher proportion of grey seals in the diet composition. Under a diet composition of 0.25 adult, 0.25 juveniles, and 0.1 pups (i.e., that assumed for harbour seals), the population trajectory increased over the 35-year prediction period (Figure 5.11).

Scenario C_{max} , ‘Consequences of maximum diet composition’, assumed the same vital rate and starting population as Scenario A, with the harvest-type parameter changed to a grey seal only diet composition. Under a diet composition of 0.4 adults, 0.4 juveniles, and 0.1 pup (totalling the 0.9 proportion seals are estimated to comprise in killer whale diet), the population trajectory still increased over the 35-year prediction period (Figure 5.12).

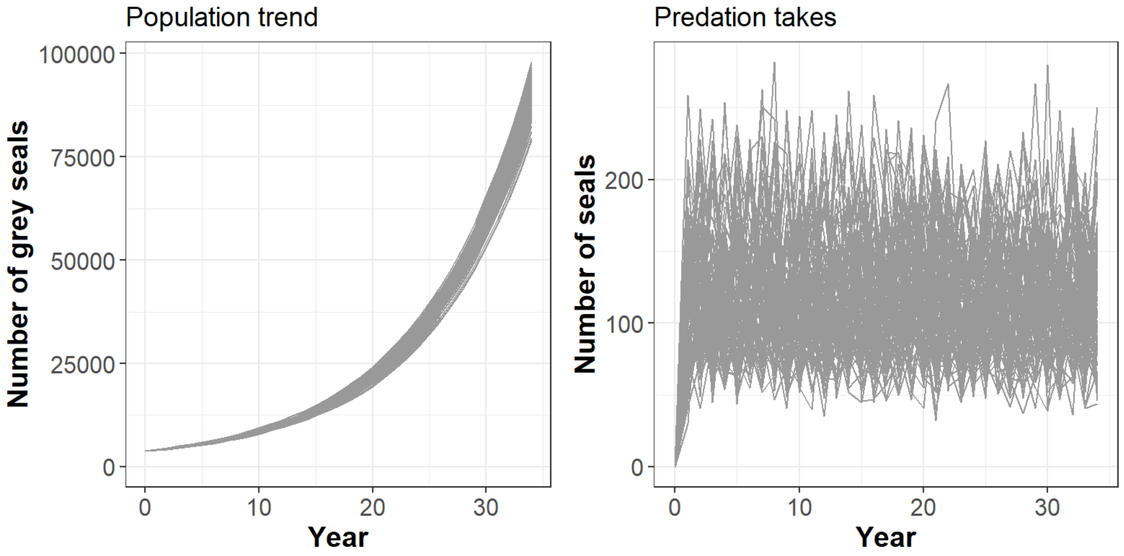

Figure 5.9. Simulated population trajectories (left) and predation takes (right) for grey seals under input parameters in Scenario A, ‘Consequences of estimated rates’. Where the starting population is equal to the 2021 estimate for grey seals in Shetland (3,760), vital rates are set to that of Harwood & Kind 2017, and killer whale diet composition is assumed to be 0.2 adult, 0.2 juveniles, and 0 pups.

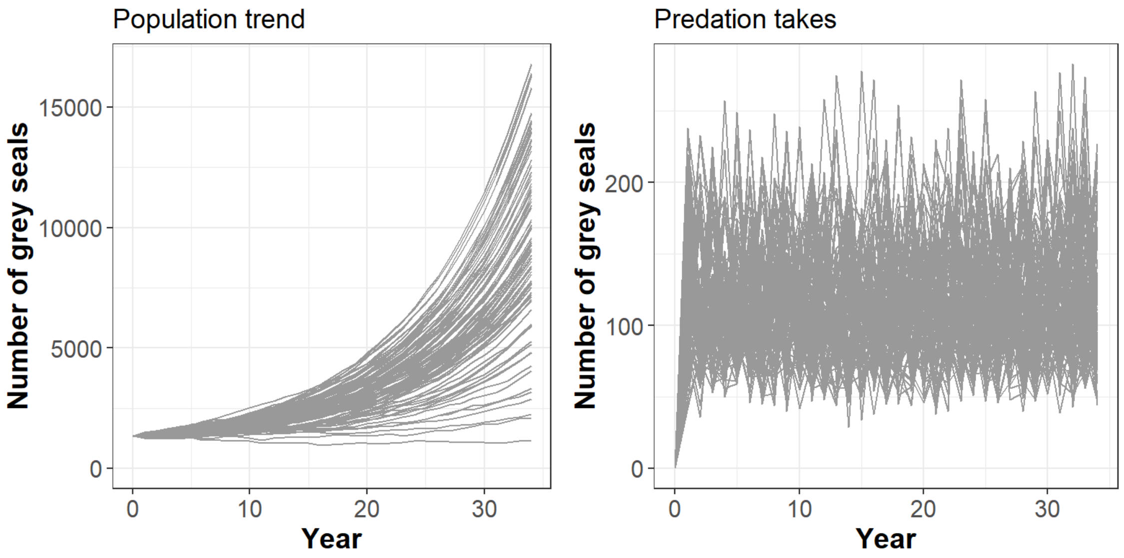

Figure 5.10. Simulated population trajectories (left) and predation takes (right) for grey seals under input parameters in Scenario B, 'Required prey population'. Where a starting population of 1,350 grey seals is required for the population to remain stable given vital rates are set to that of a Harwood & King 2018, and killer whale diet composition is assumed to be 0.2 adult, 0.2 juveniles, and 0 pups.

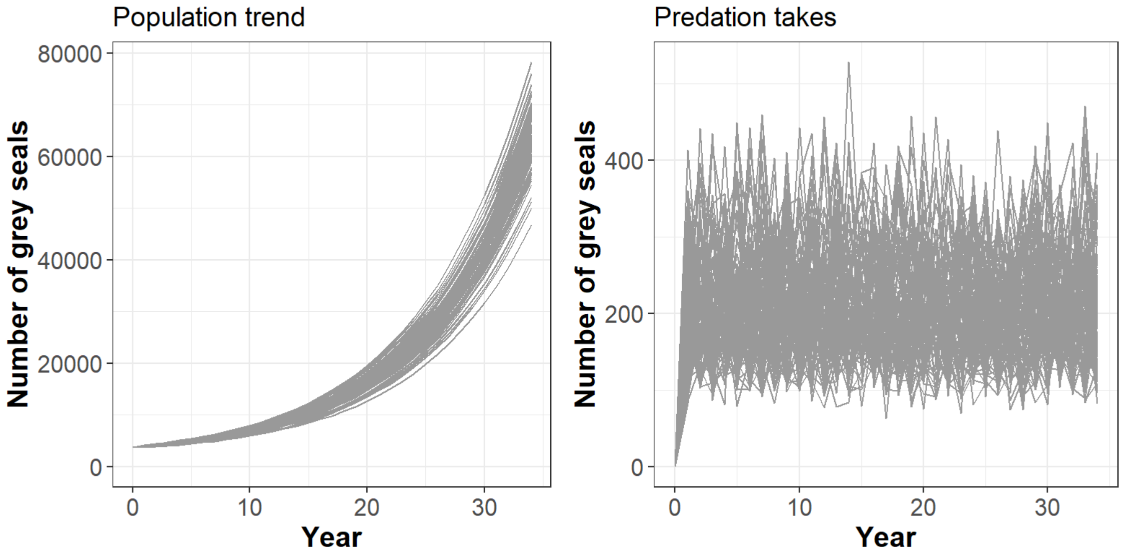

Figure 5.11. Simulated population trajectories (left) and predation takes (right) for grey seals under input parameters in Scenario C, 'Consequences of diet composition'. Where the starting population is equal to the 2021 estimate for grey seals in Shetland (3760), vital rates are set to that of a declining population, but killer whale diet composition is assumed to the same as that of harbour seals: 0.25 adults, 0.25 juveniles, 0.1 pups.

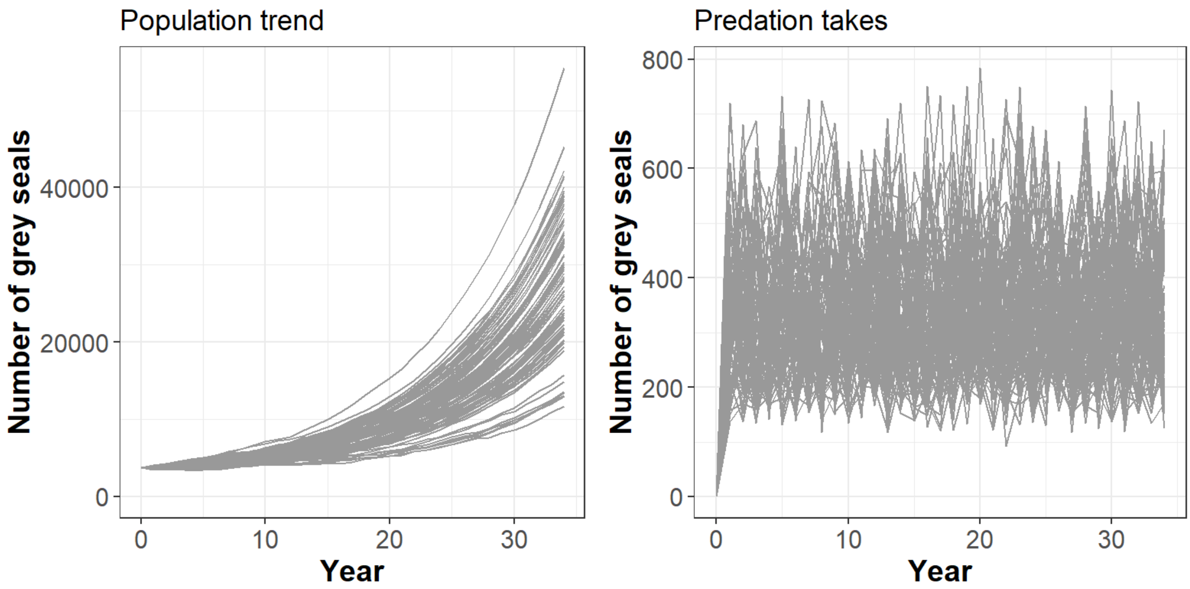

Figure 5.12. Simulated population trajectories (left) and predation takes (right) for grey seals under input parameters in Scenario C_{max}, 'Consequences of maximum diet composition'. Where the starting population is equal to the 2021 estimate for grey seals in Shetland (3760), vital rates are set to that of a declining population, but seals consumed in killer whale diet as assumed to comprise entirely of grey seals: 0.4 adult, 0.4 juveniles, 0.1 pups.

5.4 Discussion

The aim of this chapter was to review and collate information on the daily energy expenditure and prey requirements for inshore-feeding killer whales as present in Shetland in 2021, and estimate, with associated uncertainty, the potential consequences estimated predation may have for harbour and grey seal populations trajectories in the Shetland SMA as simulated across a 35-year period. Given the multitude of uncertainties surrounding input data pertaining to killer whale FMRs and diet composition, an uncertainty analysis was carried out to estimate prey consumption with associated 95% confidence ranges, expressed as the 95% percentile of values in a Monte Carlo simulation. This uncertainty was propagated through the Leslie Matrix models to simulate harbour and grey population trajectories, with uncertainty in parameters influencing population trajectories (e.g., seal vital rates, proportion in killer whale diet) explored under different input scenarios. Here, I discuss the results in relation to factors affecting uncertainty, including bias and errors both incorporated and omitted from the uncertainty analysis, and the implications these uncertainties have for interpreting results in comparison to estimates derived for other populations, and when drawing conclusions in the context of top-down predation pressure on harbour and grey seals.

5.4.1 Factors affecting uncertainty in energetic requirements & prey consumption estimates

FMRs estimate the metabolic costs of physiological processes and activities of wild animals (Nagy 1994). To account for the uncertainties associated with input parameters used to estimate FMR (e.g., body mass in each age-class), a Monte Carlo uncertainty analysis was conducted to estimate a reasonable range of FMRs for the study population. Furthermore, in line with recent advancements in understandings of taxa specific FMR calculations (Noren & Rosen 2023), two versions of the Monte Carlo uncertainty analysis were conducted: one using the contemporary FMRa (4.18 ± 1.68 $x\ BMR_K$) calculation, and one using the historical FMRb (5 - 6 $x\ BMR_K$) calculation.

By calculating energetic requirements using both the contemporary FMRa and historical FMRb multipliers, variation in estimates due to uncertainty in this parameter could be better explored. To account for differences in daily energetic requirements due to body size across killer whale populations, and allow for better comparison between studies, FMRs are compared here per unit of body mass (kcal/kg/day). FMRs as calculated using the contemporary FMRa were ~ 30% lower (Table 5.6) than those derived from FMRb in the present study and were towards the lower limits of previously published estimates. FMR as calculated using the historical FMRb (47-72 kcal/kg/day for adult females and males) were more consistent with previously published estimates: Previous FMRs of adult killer whales used in bioenergetic modelling have included ranges of 46-55 kcal/kg/day for adult females and 34-51 kcal/kg/day for adult males (Noren 2011), and 51-59kcal/kg/day for both adult females and males (Williams et al. 2004). The contemporary FMR multiplier resulted in estimated kcal/kg/day lower than would be expected based on previously published ranges, and consequently median harbour and grey seal consumption estimates based on this were ~30% lower than as calculated using the historical estimate (see Section 5.3.1.1).

FMRa was derived based on bottlenose dolphin measurements (Noren and Rosen 2023) and may better reflect the true FMR of killer whales given the variability in estimated FMR between taxa that may not be captured by the historical FMRb, which was interpolated across marine mammal species (cetaceans and pinnipeds) (Costa and Williams 1999). Whilst uncertainty is further generated when extrapolating measurements from one species to another, the ranges of FMRa (4.18 ± 1.68 x BMR_K) included in the uncertainty analysis capture the range of uncertainty as derived from FMRb (5 – 6 x BMR_K). The range of values for FMRa may therefore better capture the plausible ranges of FMRs for killer whales. However, this conclusion is challenging to evaluate without direct estimates of killer whale FMR as measured in-situ, which is currently unavailable in the literature.

Alternative methods of estimating FMRs have involved the use of cost of transport (COT) curves, respiration rates, daily activity budgets, and average swim speed for each activity state (Noren 2011; Roos et al. 2016). When the metabolic cost of swimming during different activity states was taken into account, Noren (2011) estimated adult females to have an FMR of 5 * BMR_K and males to have 7.4 * BMR_K. It would be useful to explore this method in the present study population and compare it to FMRs derived from calculations used here. Activity budgets are available from Chapter 4; if average swim speed for each activity state could be acquired for the study population, COT curves developed for killer whale (Williams and Noren 2009) could be applied to estimate the metabolic cost of daily activity budgets (Noren 2011). Future research addressing this knowledge gap would provide further insights into the energetic expenditure and prey consumption requirements of killer whales visiting coastal Scotland, and may be a particularly important avenue of research if killer whale activity budgets are impacted by changes in prey availability, changes to their habitats/environment, or human activities such as vessel traffic (Williams et al. 2006; Lusseau et al. 2009).

A further consideration with the biogenetic approach used here is that bioenergetic models assume energy balance; consumption estimates are derived directly from the daily nutritional requirements as estimated from FMR calculations. However, it is plausible that killer whales feed more intensively during certain periods, such as seal breeding seasons, which are then depleted before the next bout of intensive feeding (Durban and Pitman 2012). If killer whales in this study population primarily travel inshore for feeding purposes, then they may consume more than their daily energetic requirements to increase fat stores and thus consumption estimates reflect here may be an underestimate. To explore this, it would be useful to further investigate the movement patterns and associated body condition of killer whales seen foraging inshore in Shetland.

There is inherent uncertainty in prey selection and intake rates which influence the modelling of prey consumption estimates. To reduce this uncertainty, alternative methods could be explored to directly measure prey intake instead. Extended focal follows would provide an estimate of prey intake rates across a given observation period which could be used to calculated hourly or daily prey intake rates (Baird and Dill 1996). Studies have used prey feeding rates to calculated average mass specific energy intakes; such estimates by Baird (1994) yielded energetic intakes of 62kcal/kg/day for transient killer whales feeding on harbour seals, beyond the upper limit of what is typically estimated. Estimating intake rates through visual and drone-based observations for the study population may prove a useful tool to investigate the expected level of consumption (calculated through bioenergetic models) and compare it to the actual level of consumption (calculated through visual observation) to discern whether modelled consumption rates reflect those occurring in-situ.

To explore this in data as presently available, prey intake rates as observed from contributed drone-footage and PhD fieldwork efforts could be organised into a time-series to quantity the number of predation events observed in a given day, correcting for the proportion of time animals are not observed. However, a limitation of the land-based observations used to collect field data in this thesis is animals moving out of sight of the observer (e.g., behind headlands) or being too far from the observer to quantity behavioural state and predator-prey interactions. Whilst drone footage as obtained from land-launched flights available for analysis in this thesis proved valuable for collecting fine-scale behavioural data and prey identification, the relatively low sample size (~14hrs across 7 years) may mean a proportion of predation events are still missed in this data sample, and the data sampled here may not be representative of the population. To overcome this, future research could employ boat-based focal follows with concurrent collection of drone footage to obtained continuous data sampling, or suction-cup attached animal-borne data logger to collect sequential data over a period of days. Boat-based focal follows would help maximise the on-follow time for both visual (e.g., using binoculars and telephotos lens) and done-based data collection by ensuring the whales were in continuous view, maximising opportunities for continuous data collection and minimizing time spent locating focal animals. Foraging behaviour could be inferred from horizonal and underwater movements obtained from animal-borne loggers (Tennessen et al. 2019; Aguilar de Soto et al. 2020). Nevertheless, the ranges of FMRs reported here based on the bioenergetic model and Monte Carlo uncertainty analyses represent a considerable advancement in our understanding of the energetic expenditure of this present study population, with associated uncertainties, and provides a valuable starting point from which to base future research.

In the present study, energetic requirements as estimated based on FMR calculations were used to derive estimates of prey consumption requirements (see Section 5.3.1.2). The digestive efficiency of killer whales is taken into consideration when calculating prey consumption requirements as based on FMRs, with assimilation fixed at 0.85 (Williams et al. 2004). However, it is plausible that assimilation rates may vary between prey species, particularly given variation in the body composition (lipid vs protein) both within and between prey species (MacHovsky & Raubenheimer, 2020). Furthermore, prey consumption requirements may increase to compensate for additional energetic costs associated with gestation and lactation (Noren and Rosen, 2023). Studies on captive killer whales(Kriete 1995; Kastelein et al. 2003a) and bottlenose dolphins (Kastelein et al. 2003b). saw no significant increase in food intake by pregnant females. Food intake rates of captive females of the same species did increase during lactation; however, considerable differences were observed between individuals and in relation to lactation periods (Kriete 1995; Kastelein et al. 2003a; Kastelein et al. 2003b, Noren and Rosen 2003), making it challenging to establish a robust estimate of increased requirements during lactation (Noren 2011). Ideally, direct observations of intake rates of known pregnant or nursing individuals in the wild would provide insights into the additional requirements associated with such states.

An additional source of uncertainty in this analysis surrounds the overall proportion of harbour and grey seals in killer whale diet, and the age-stage composition of seals within these total proportion. In this study, the proportion of harbour seals consumed as part of killer whale diet was derived from prey composition results from Chapter 3. However, there is possibility for over-representation of harbour seal predation events, and thus over-estimate of composition in killer whale diet, due to a bias towards killer whale sightings and collection of drone footage inshore and during the summer months (see Chapter 3). Harbour seals may be better available as prey to killer whales during summer months due to breeding and are more likely to be encountered in close proximity to the shore when travelling (i.e., overlapping with sightings and data collection) (Carter et al., in prep), with adults and pups staying closer to breeding haul-outs during mum-pup weaning and for male-female mating opportunities (Mogren et al. 2010; Aarts et al. 2016; SCOS 2022). With greater observer effort during the summer months, the diet estimates may be more representative of killer whale diet during the summer. As a result, the proportion of harbour seals in killer whale diet (here, 0.6 or 60%) and thus the overall consumption estimates for the species may be an over-estimate. To address this, an increased understanding of killer whale diet composition throughout the year through increased data collection on predation events would undoubtedly reduce uncertainty in overall consumption estimates. Furthermore, increased spatial coverage of data collection, for example to more remote locations of grey seal breeding sites (SCOS 2022), would further inform the extent to which killer whales seasonally predate different species, and thus how their overall energetic needs are met by both harbour and grey seals.

The proportion of pups, juveniles, and adults consumed by killer whales was derived from results from Chapter 3, with an equal split assumed between adults and juveniles which were grouped together during expert elicitation for prey identification (see Chapter 2). However, as discussed in Chapter 3, it is possible the number of predation events on pups is an underestimate due to challenges in detecting and observing predation of smaller animals. That is, if pup predation events are less likely to be detected due to minimal at-surface evidence of predation (e.g., minimal blood, slick, and less prey handling due to smaller body size and mass) it is possible a higher proportion of pups are taken than estimated here, for both harbour and grey seals. Indeed, no grey seal pups were identified during the expert elicitation process and were therefore not included in the killer in the killer whale diet composition explore here. It is likely this does not reflect what is occurring in-situ but is simply a result of challenges associated with identification of prey age-class in the dataset.

An additional source of uncertainty not included in this analysis is the proportion males versus female seals consumed by killer whales, of which females of breeding age and pregnant females are of particular interest for population consequences (Keith 2008). Whilst no direct observation of a pregnant harbour seals was observed during this study, evidence of predation on pregnant grey seals was observed in drone footage and stomach content analysis (conducted by SMASS; see Chapter 3). Removal of breeding-age and pregnant females would have implications for population growth through reduction in fecundity and ultimately recruitment (Wickens et al. 1992). Therefore, even if killer whale predation is not found to be a causal factor in historical declines of harbour seals, predation of pregnant females and females of breeding age may prove significant in hindering population recovery. Whilst further research is required to better estimate killer whale diet composition, to overcome these biases and potential errors in killer whale diet composition within the scope of this Chapter, population trajectories were explored under different assumption of diet composition as part of the Leslie Matrix model simulations.

5.4.2 Population consequences of predation

A primary driver of this study was to explore the potential consequences of killer whale predation on harbour seals in the context of their regionally declining populations, both in terms of potential causation of declines, but also in terms barriers to population recovery. Given this, it is important to consider sources of uncertainty in consumption estimates and how this might influence the overall population level impacts of consumption on harbour seals as estimated in population modelling.

To frame consumption estimates in terms of consequences for the seal populations in Shetland, the number of individuals estimated to be removed by predation were first compared to acceptable thresholds set for removal by anthropogenic mortality (SCOS 2022). PBRs are used by the Scottish Government to estimates permissible anthropogenic takes for each of the SMAs (SCOS 2022). Their application to the population consequences of predation is limited, given the recovery factor of a population is likely influence by the level of predation it is exposed to. Comparisons are not included here to infer a ‘permissible’ take through predation, but more to frame the range of consumption estimates reported here in the context of conservation and management parlance and highlight how assumptions as to population status (e.g., recovered or depleted) can considerably alter estimated acceptable takes.

PBRs for harbour seals based on low (0.1) and high (1) recovery factors were calculated as 19 and 190 individuals respectively. The lower estimates of harbour seals consumed as derived based on both FMRa (196) and FMRb (341) therefore exceeded even the higher PBR estimate here. The recovery factor recommended for the harbour seal population in Shetland was recommended as 0.1 given the population is considered stable at a depleted level after a stepwise decline (SCOS 2022). Given PBR calculations reflect acceptable removals on top of pre-existing removals, as population growth rate is depended on fecundity, survival and density dependence, the number of harbour seals taken through predation in a given year may represent a considerable removal of individuals from the population, even if the recovery factors are higher than that recommended. For grey seals, PBRs based on a low (0.1) and high (1) recovery factor were calculated as 22 and 225 individuals respectively. In Shetland, the recovery factor for the grey seal population was recommended at 1 given the population appears stable (SCOS 2022). Upper estimates of grey seal consumption as derived based on FMRa and FMRb were just below and just above this upper PBR estimate at 234 and 267 grey seals respectively. However, lower estimates of grey seal consumption from FMRa and FMRb were 51 and 90 respectively, exceeding the PBR estimate based on a low recovery factor (0.1). The number of grey seals removed through predation may therefore be substantial for this population if the recovery factor is lower than estimated. However, pooling all age- and sex-classes does not incorporate the demography of the seal populations (i.e., proportion of age-classes and sex ratio in the total population) and associated expected survival regardless of predation (i.e., pup to juvenile, juvenile to adult). To better explore the potential population consequences of predation beyond simple PBR comparison, scenarios were explored for harbour and grey seal populations in a Leslie Matrix model. By incorporating a harvest-type parameter into the age and sex-segregated model, populations trajectories were explored under various assumptions of input parameters such as vital rates and proportions of species and age-classes in killer whale diet.

For the purposes of estimating population-level impacts in the Leslie Matrix model, the consumption estimates as derived from FMRa were used given these were calculated based on the most recent estimates of cetacean FMRs at time of analysis. Uncertainty from these estimates were propagated through the analyses by incorporating the Monte Carlo uncertainty analysis output directly into the harvest-type parameter of the Leslie Matrix model. Additional sources of uncertainty incorporated into the modelled population consequences of predation included species-specific vital rates, and killer whale diet composition.

The overall proportion of harbour seals in killer whale diet, and the demography of prey in this diet both have important implications for quantifying top-down predation pressure. In Scenario A, 'Consequences of estimated rates', of population modelling, seals (harbour and greys) were assumed to comprise a proportion of 0.9 of killer whale diet, with 0.6 being harbour seals (0.25 adults, 0.25 juveniles, and 0.1 pups) and 0.3 being grey seals (0.3 adults and 0.3 juveniles). With regards to population level consequences for harbour seals, the accurate estimation of their proportional representation in killer whale diet is of importance as killer whales could also meet energetic requirements through the consumption of alternate abundant prey resources such as grey seals and harbour porpoise, and thus the impact on the harbour seals may be lower than estimated in this Scenario. Additionally, the implications of age-stage related consumption estimates may have important consequences for population demographics and vital rates, ultimately influencing population trajectories (Pilfold et al. 2012).

With regards to the population consequences for harbour seals, an increase in adult mortality is thought to have led to the regional declines (Hanson et al., 2013). To explore this, Scenario C, 'Consequences of diet composition' was ran with a higher proportion of pups vs adults and juveniles for harbour seals (0.3, 0.15, and 0.15 respectively). However, changing the diet composition in the population model did not markedly affect the simulated population trajectories (Figure 5.7). Even with a higher proportion of pups assumed to be consumed, in comparison to adults and juvenile, the simulated trajectory still resulted in a decline until depletion. Although, it should be noted that the simulated trajectory did not account for prey switching from one prey source to another based on relative abundance. That is, as the harbour seal population declined and neared depletion, killer whales would likely increase consumption of alternative prey sources to meet energetic demands. The rate of decline may therefore not reach extinction at this stimulated time scale.

Modifying the vital rate parameters (Scenario D, ‘Adjusted vital rates) to those derived from stable/increasing harbour seal populations, however, resulted in some stable population trajectories, though there were substantial divergence between projections (Figure 5.8). This highlights the importance of exploring uncertainties surrounding modelling assumptions and raises the question as to whether levels of killer whale predation are already implicitly reflected in the vital rates derived for declining/depleted population. Vital rates as derived for declining/depleted populations were based on estimates for Orkney, where harbour seal populations have undergone declines (Arso Civil et al. 2019) Killer whales are frequently observed around Orkney, with the study population analysed here for Shetland also seen foraging inshore Orkney (Scullion et al. 2021). By contrast, the vital rates as derived for stable/increasing populations were based on estimates from the Moray Firth, where killer whales are less frequently sighted (Scullion et al. 2021). If vital rates as derived for stable/increasing populations do not incorporate mortality due to killer whale predation, then simulated results may suggest that killer whale predation as estimated here could have important consequences for an otherwise stable harbour seal population. Furthermore, even if the estimated level of predation does not result in a dramatic decline, it may hinder the recovery a depleted population such as Shetland.

In comparison to harbour seals, grey seal population trajectories continued to increase under both the assumed diet composition (Scenario A, ‘Consequences of estimated rates’) (Figure 5.9), a diet composition equal to that assumed for harbour seal (Scenario C, ‘Consequences of diet composition’) (Figure 5.11) and even an extreme scenario whereby only grey seal were present in killer whale diet composition (Scenario C_{max}, ‘Consequences of maximum diet composition) (Figure 5.12). This would suggest that killer whale predation may not have the same implications for grey seal populations as it may for harbour seals, as explored in the present study. With regards to understanding potential drivers of the harbour seal decline, if killer whale predation is not affecting the grey seal population, then alternative potential causes such as increased competition with grey seals may result in a culmination of stressors on harbour seals (SCOS 2022). Exploring the potential cumulative impacts and potential non-consumptive effects on harbour seals, including killer whale predation, in a framework such as the iPCOD (Harwood and King 2017) may help to further elucidate the potential drivers of historical declines, and explore factors influencing the recovery of the depleted population.

5.4.3 Conclusion

The energetic requirements and prey consumption estimates presented here represent a considerable advancement in understanding of top-down consumptive effects in the predator-prey study population, and associated uncertainty. As calculated here, the number of harbour seals taken appear to reflect a significant number of the Shetland SMA population and may have implications for population trajectories even under vital rates as derived for a stable/increasing population. While these results represent a range of best estimates based on currently available data, there are caveats associated with modelling assumptions that should be considered when interpreting results as discussed throughout. Further evidence to reduce uncertainty in the model parameters would undoubtedly increase the precision of overall prey consumption estimates and consequent population trajectories. Furthermore, whilst killer whales may impact seal populations through direct consumption, potential non-consumptive impacts should also be considered when estimating the overall top-down pressure elicited by the top predator population.

6 CHAPTER 6. GENERAL DISCUSSION

6.1 Thesis Summary

Predator-prey interactions are mediated by a myriad of behavioural, ecological, and environmental factors. This study aimed to investigate the ecological drivers and consequences of predator-prey interactions of killer whales and seals in inshore Shetland. Quantifying the top-down pressure on the depleted harbour seal population was of particular interest, with killer whale predation hypothesised as one of potential driving factors of the historical decline and hindering the recovery of the present population.

In Chapter 2, the first data chapter, I investigated the co-occurrence of killer whale foraging effort and seal prey availability, as observed during PhD land-based fieldwork (2021-2023). A twofold analysis was conducted to explore common spatiotemporal, environmental, and ecological predictors of seal presence and killer whale foraging effort. Whilst seal counts were found to vary in response to spatiotemporal (e.g., season and SMA subregion) and environmental (e.g., shoreline type and sea state) variables, the only common variable to significantly predict seal counts and probability of killer whale foraging effort was sea-state. Although biological explanations may be applicable, observational and detectability biases associated with land-based field data collection should be considered when drawing conclusion based on this finding alone.

Following the relatively limited seasonal coverage and sample size afforded by dedicated field work, community-led monitoring efforts were incorporated into methodological approaches to quantity killer whale predation in inshore Shetland. In Chapter 3, I investigated prey consumption by killer whales as observed from PhD fieldwork, drone-based observations, and citizen science contributions. Uncertainty in prey species and age-class identification in predation events was explored through an expert elicitation process. Killer whale predation success, as observed in the data sample, was found to vary as a function of distance to shore, between SMA subregions, and between prey species. Predation attempts further from the shoreline (max ~800m) were found to have a higher probability of success than those closer to the shoreline, and those occurring in the S&E SMA subregion had a higher probability of success in comparison to the intercept of the W SMA subregion. Harbour seals were over twice as likely to be consumed given an encounter with a killer whale in comparison to grey seals. Findings here reveal insights into how probability of capture given an encounter is variable across spatial contexts, with important implications for species-specific predation risk from inshore-foraging killer whales as experienced by harbour and grey seals.

In Chapter 4, drone footage from community-led monitoring efforts was used to develop a comprehensive ethogram for inshore-foraging killer whales, with application to the quantification of activity budgets. Killer whale behaviour was found to vary as a function of distance to shore, with 'foraging' only occurring when the shoreline was visible. Overall, the most frequently observed behaviour was 'transit', which primarily occurred at an unknown distance to shore. This Chapter, in conjunction with Chapter 3, highlights the value of community-led monitoring efforts to facilitate year-round data collection to inform research objectives.

In Chapter 5, I investigated the consumptive impact of inshore-foraging killer whales on harbour and grey seal populations in Shetland. A bioenergetic approach was applied to estimate field metabolic rates (FMRs) and energetic requirements of the killer whale population, with associated parameter uncertainties, as observed in inshore Shetland in the year 2021. Species and age-class specific consumption estimates were derived from Monte Carlo uncertainty simulations, with prey composition as estimated by output from Chapter 3. Population consequences of killer whale predation were explored under different assumptions in Leslie Matrix population models. By incorporating a harvest-type parameter in the population model, population trajectories for harbour and grey seals were explored under different input parameters (e.g., population vital rates and composition in killer whale diet). The only scenario in which the harbour seal population trajectory did not decline over the 35-year simulation was under vital rates derived from stable and increasing harbour seal populations. Grey seal population trajectories did not decline in any scenario, even under a maximum scenario whereby all killer whale energetic requirements were met by grey seal consumption. Results from this Chapter represent a range of best estimates based for and consequences of prey consumption on currently available data.

6.2 Predation Sequence: From spatiotemporal overlap to capture and consumption

To explore the factors mediating the top-down predation pressure elicited by killer whales, predator-prey interactions were explored across the predation sequence, from spatiotemporal overlap to capture and consumption. Here, I will discuss findings from this study in relation to their associated limitations and considerations. Alternative approaches and methodology to address research objectives outwith the scope of the present study are discussed throughout, along with recommendations of future avenues for research.

A fundamental aspect of predator-prey foraging interactions is that both parties must co-occur spatially (Lima and Dill 1990). A general assumption of the ‘predator-prey space race’ (Sih 1984) is that predators should seek to increase spatial overlap with prey, and prey should seek to minimize spatial overlap with predators (Luttbeg et al. 2020). As such, spatial overlap has been used a proxy to quantity predator-prey interactions (Hurlbert 1978), particularly for free-ranging animals where interactions are challenging to observe directly (Suraci et al. 2022). However, as discussed in this thesis (Chapter 1 and Chapter 2) spatial overlap alone does not dictate encounter rates, as the scale of spatiotemporal overlap probability of encounter can be mediated by both predator and prey functional traits (Schmitz 2017).

In the context of the current study, the inshore waters of Shetland could be considered and area of spatial overlap, given both predator and prey are known to occur at this scale. Prior to this thesis, data were available on harbour and grey seal distribution and abundance from SMRU aerial surveys (SCOS, 2023; Morris et al., 2021) and at-sea movements (Carter et al. 2020), and killer whale presence from various data sources (e.g., Sea Watch, OMMRI, and SBRC). However, the disconnect in the spatiotemporal scale at which these data were collected made it challenging to explore predator-prey interactions beyond rudimentary spatial overlap. To address this within the scope of the present study, I established surveys of seal haul-outs and conducted focal-follows of killer whale during PhD fieldwork (Chapter 2). The purpose of the seal surveys was to capture spatiotemporal variability in prey presence at the same scale at which killer whale focal follows could be conducted, i.e., to quantify patterns of predator-prey area use in both space and time and in relation to environmental and ecological variables. A key consideration with the seal surveys here is that counts were conducted at haul-outs, where seals were both resting on land and in the water. Given killer whales in this study population are not known to temporarily strand to capture seals, these survey counts are not intended to represent the prey field experienced by inshore-feeding killer whales. More, surveys were aimed to capture the predictability of, and variation in, seal species in relation to environmental and life-history covariates using feasible methods available, and at a finer scale than what was available in other existing datasets.

Predators are capable of tracking, detecting, and locating prey across various spatiotemporal scales: at larger scales, predators may use experience and memory to locate prey patches patch (Bradshaw et al. 2004; Biuw et al. 2009; Iorio-Merlo et al. 2022). At smaller scales, predators may also use sensory information and environmental cues to detect and locate prey within this patch (Hansen et al. 2010; Lawson et al. 2019). In the present study, it was hypothesized that if seals were found to be predictable around inshore haul-outs in relation to ecological and environmental variables, then killer whales may be able to increase foraging opportunities by focusing foraging efforts concurrently (Chapter 2). However, the only common significant variable to predict seal counts and probability of killer whale foraging (versus other behaviours) was sea state, which could in part be due to detectability biases associated with land-based visual observations (see Section 2.4). To overcome the limitations of data collection methods employed within the scope of this study, both in terms of the inshore sample area and biases associated with land-based visual observations, alternative methodologies would be worth considering.

To fully explore the factors influencing spatiotemporal overlap and encounter rates, concurrent quantification of killer whale foraging effort and the associated experienced prey field (i.e., number and species of seals within detection range of killer whales) would be optimal. Predator-prey encounter rates and realized prey field structure of killer whales at-sea could be obtained using animal-borne cameras (Hooker et al. 2002; Kuhn et al. 2022). Alternatively, GPS-tracking of both predator and prey concurrently would provide valuable data on the fine-scale movements of both parties, from which location data could be compared in unison (Davis et al. 2007; Breed et al. 2017). Data derived from GPS tags could inform co-occurrence occupancy models, or Kernal density overlap coefficients (Waddle et al.

2010; Rota et al. 2016). In addition, percentage spatiotemporal overlap between predator and prey could be calculated to identify 'hot spots' of overlap, and intersection between movement paths detected to inform encounter rates (Courbin et al. 2013; Middleton et al. 2013; Winner et al. 2018). The resolution of data collected from GPS tags would allow for fine-scale spatiotemporal analysis of predator and prey movement in relation to habitat and environmental data, and sample areas outwith those available from visual observation (e.g., at depth or further offshore). Fine-scale data may be of particular importance if seals utilize microhabitats or adjust the timing of their activities to reduce chances of encountering killer whales within an area of overall high spatiotemporal overlap.

Initial results from previous deployments of GPS tags on harbour and grey seals around Shetland showed that both species generally remained relatively close to the shore, harbour seals observed to spent at least half their time at sea within 240m of land and greys 1.2km (Carter et al., in prep). Killer whale foraging success, as observed in this study, increased as a function of distance to shore (Chapter 4). Seals remaining closer to the shoreline may be safer than those at-sea where predation risk may be greater, leading to fear-based microhabitat selection (Brown et al., 1994). Exploring how harbour and grey seal behaviour (e.g., distance to shore, proportion of time spent hauled out; Russell 2016) varies in response to the presence and absence of killer whales would provide further insights into the risk allocation by seals (Lima and Bednekoff 1999; Mukherjee and Heithaus 2013). For example, if seals remain close to the shore regardless of killer whale presence, it may suggest a "seascape of fear" effect whereby the threat of predation persists in the long term (Wirsing et al. 2008), although other potential causes should not be discounted. If tagged seals' distance to shore varied as a function of killer whale presence / absence, it may suggest seals are capable of detecting the variability in killer whale presence and alter their behaviour accordingly (Wcisel et al. 2015). Playback experiments in the northeast Pacific have shown harbour seals are capable of detecting and responding to killer whale vocalisations, with different responses observed to mammal-feeding 'Transients' and fish-feeding 'Resident' (Deecke et al. 2002). Conducting playback experiments in northern Scotland, and between seal populations subject to high- and low- predation pressure from killer whales, could be used to investigate plasticity in such anti-predator responses.

Predation risk depends not only on the probability of encountering a predator, but also the probability of being captured and killed by a predator given an encounter (Suraci et al. 2022). Probability of capture can be mediated by both predator and prey functional traits, as well as environmental features that influence predator capture and prey escape (Schmitz 2017). To explore whether a predator-prey encounter poses direct lethal threat, factors including predator hunting state, predatory dietary preference, and predator lethality given environmental conditions and prey traits should be considered (Suraci et al. 2020).

In Chapter 3, I investigated context and species-specific variability in predator success as observed from community-led monitoring efforts and PhD fieldwork. Here, I found that predator success varied as a function of distance to shore, with predators having a higher probability of successfully capturing and consuming prey further from the shoreline (max ~800m). Given the propensity of prey species to escape to the shoreline, results here would suggest shallow refuges are an important habitat feature for harbour and grey seals. Whilst shoreline type, as included in the present study and with the available sample size, was not found to be a significant predictor of capture probability, it would be useful to explore other environmental variables that potentially influence the probability of escape. For example, shoreline type included in the present analysis focused on substrate and littoral characteristics, such as sand/gravel beaches and rocky cliffs and bedrock. Data on shoreline gradient and seabed geomorphology would be useful to investigate how localised refuge may influence the probability of capture given an encounter with a killer whale. Linking back to predator-prey overlap and encounter probability, fine-scale analysis of individual seal movements using GPS tags in relation to habitat variables conducive to escape would further disentangle the extent to which predator-prey overlap is mediated by prey fear-based microhabitat selection.

Probability of capture given an encounter will be mediated by prey functional traits; characteristics that the determine the vulnerability of prey to predator capture and consumption (Schmitz 2017). In Chapter 3, I found that harbour seals were more likely to be consumed, given an observed encounter with a killer whale, in comparison to grey seals. However, when drawing conclusions as to whether this means harbour seals are more vulnerable to killer whale predation given an encounter, potential sampling biases must be considered with regards to their implications for prey traits (Mukherjee and Heithaus 2013). For example, killer whale predation events, as collated in this thesis, came from inshore sightings during PhD fieldwork, citizen science contributions, and drone-based observations. The strong peak in predation observations in the summer months is therefore likely a function of increased observer effort and detection probability as a result of longer daylight hours. The small sample size here precluded an interaction term of season and species, and thus it is unclear whether species-specific vulnerability depended on species-specific traits, such as breeding seasons. In addition, challenges in identifying age-classes of seals prevented conclusions about age-specific vulnerabilities to be drawn. This is an important consideration with regards to prey vulnerability traits. That is, if predation success does vary temporally and between age classes, then the finding that harbour seals were more vulnerable to predation may be driven more by intraspecific as opposed to interspecific variation.

Harbour seal adults, particularly females, may be more vulnerable to predation immediately prior to- and post-partum if their locomotive capabilities are compromised when pregnant, and their depleted body-fat storage means a change in risk balancing (predator escape vs foraging) due to the energetic demands of pregnancy and lactation. Furthermore, naïve pups foraging for their first time post-weaning may be more susceptible to predation than other age classes. Exploring the temporal aspect of species-specific variability in predation would provide valuable insights into prey selection, and how this may vary in response to seal breeding cycles, as theoretically the same should hold true for grey seals in autumn/winter months. Furthermore, more accurate identification of prey age-classes in killer whale diet would yield understanding into intraspecies variability in predation rates, which is important to inform stage-specific survival for prey population modelling. To address the limitations of and sampling biases in the current data, additional analytical approaches could be employed in future research. In the current data, the majority of predator-prey encounters involving seals were not identified to the species level; correcting this through a two-stage Delphi elicitation process (Mukherjee et al. 2015; Hemming et al. 2018) would likely greatly increase the value of the present data. In addition, effort data could be sourced from drone meta-data to explore spatial and temporal trends in observed predation events.

Probability of capture will also be mediated by predator functional traits; characteristics that the determine the foraging ability of predators and their probability of capturing and consuming prey (Schmitz 2017). Of these traits, two facets would be particularly useful to explore in the present study population: predator motivation and predator hunting tactics. Motivation is likely a key determinant of whether a predator chooses to attack prey upon encounter (Stephen and Krebs 1986). This would be useful to explore with regards to predator satiation across spatiotemporal scales. At a broader scale, measurement of predator body condition would prove a useful avenue of research to explore with regards to variation in foraging rates and nutritional condition (Fearnbach et al. 2018; Stewart et al. 2021; Kotik et al. 2023). Foraging activity as observed in drone footage (Chater 4) only occurred at a known distance to shore. If killer whales utilize the inshore waters primarily for foraging purpose and feed less elsewhere (i.e., when offshore), this may be reflected in their relative body conditions when they 'arrive' and 'leave' the inshore waters. Preliminary research has shown that killer whale body condition can be effectively measured using opportunistic drone footage on the present study population (Isojunno et al., in prep). Identifying variability in body condition between sighting periods would prove a worthwhile avenue of research to explore this hypothesis. On a finer-scale, more continuous and a longer-term time-series of behaviour as obtained from suction-cup attached data loggers would likely be an effective method to explore foraging effort sequentially over a period of a day or two. For example, foraging behaviour could be inferred from horizontal and underwater movements (dive depth, tri-axis accelerometery) using animal-borne data loggers (Tennessen et al. 2019; Aguilar de Soto et al. 2020). The use of such methods would provide fine-scale data on foraging effort and prey capture attempts across broader spatiotemporal scale, including behaviour further offshore, irrespective of sighting conditions (e.g., high sea states, night-time) than explored in the present study. Such future research could provide valuable insights as to how predators may distribute foraging effort within their wider range.

Predator hunting tactics would be useful to explore with regards to characteristics that influence predation success. For instance, group size in killer whales is thought to vary based on targeted prey, and is likely to be a balance between individual foraging effort and nutritional reward (Lopez & Lopez 1985; Bird & Dill 1996; Deecke et al. 2011; Reisinger et al., 2011; Beck et al. 2012). Furthermore, individuals within pods are hypothesised to adopt consistent individual roles (Guinet 1991; Baird 2000; Weiss et al. 2023), with adult females having been shown to lead hunting efforts and provision other pod members in some populations (Weiss et al. 2023). Drone footage has proved a valuable resource to facilitate the quantification of fine-scale behaviour and social associations in killer whales. Utilising datasets presently available, focal follows at the individual level could be conducted for hunting sequences captured in drone footage. Comparisons could them be made between individual pod members of known sex and age-class to explore individual roles in relation to capture success and prey-sharing. Exploring hunting tactics in the present study population would not only provide insights into their foraging ecology (Reisch et al. 2012), but also how predation pressure may vary with pod size and composition.

6.3 Population Consequences & Implications for Conservation

A key driver of this PhD research was to explore the potential role that killer whale predation plays in the regional decline of harbour seal populations. As previously discussed, observations of predation events included in the present study found harbour seals to be more likely capture and consumed given an observed encounter with a killer whale. Whilst these findings should be viewed in light of their associated caveats, Leslie Matrix population modelling included in this thesis aimed to explore the potential population level consequences of estimated predation takes with due consideration for associated uncertainties in killer whale diet composition. To expand on the bioenergetic and Leslie Matrix population modelling explored in this thesis, further data on killer whale diet composition and nutritional requirements would be valuable.

As discussed throughout, it is plausible that diet composition estimates obtained from observations of predation events in this study may under- or over-represent certain age classes and species due to data collection biases. In particular, the inshore nature of the data collection in this study may only reflect the inshore diet composition of killer whales. Whether all energetic requirements are met through the consumption of marine mammals, or whether alternative prey resources such as fish are taken but have been missed in the sampling methodology here, is still unknown (Jourdain et al., 2020; Bowen et al., 2013). A change in estimated diet composition can have important implications for predicting prey population trajectories (Chapter 5); expanded data collection outside of seal breeding seasons and to areas not sampled in this study would facilitate understanding of diet composition across spatial and temporal scales. Alternative methodologies outwith the scope of this study would also be a valuable avenue of research for broader quantification of killer whale diet composition. For example, stomach content and blubber analysis of stranded specimens (e.g., Foote et al. 2009), and biopsy sampling may also glean valuable insights as to the trophic levels targeted by inshore-foraging killer whales (Remili et al. 2023), and whether they solely feed on marine mammals or exhibit a more flexible diet (Jourdain et al. 2020). Analysis of stable isotopes and fatty acids as obtained from blubber biopsies can provide information on the trophic level at which an animal has fed in the weeks prior to sampling (Choy et al. 2019). Because adipose tissue in cetacean blubber can integrate information about diet over longer periods (Iverson 2009) collecting biopsy samples from animals inshore would help address the question as to whether they feed on fish elsewhere (Teixeira et al. 2022).

Alternative effort to quantify killer whale foraging effort (e.g., through GPS tagging and paired accelerometer) within their broader range, as discussed throughout Section 6.2, would further understanding as to the importance of inshore-foraging areas for killer whales. This has important implications for quantifying their predation impact, as the bioenergetic modelling approach used in this study assumed balance in estimated energetic expenditure and nutritional requirements. If killer whales are found to visit inshore-foraging areas primarily for foraging, and feed less when elsewhere, then their inshore consumption may be greater than estimated in the current approach. A key objective of future research should be to address this knowledge gap, given its implication for predator requirements and the strength of top-down predation pressure exerted by inshore-foraging killer whales.

With regards to conservation implications, the predicted effects of killer whale predation on prey populations should not be viewed in isolation. Even if killer whale predation is sustainable for a given population, the cumulative impact of killer whale predation in addition to other pressures may still have the potential to result in population-level impacts (Pirotta et al. 2018; Simmonds 2018; Booth et al. 2020). As part of on-going research into the regional declines of harbour seals, numerous potential ultimate causes are proposed. Examples include interspecific interactions with grey seals (e.g., competition for prey resources), declines in prey quality and availability, indirect effects of climate change, and exposure to toxins from harmful algae (Arso Civil et al. 2019). If other ultimate causes are found to contribute to the observed declines in harbour seals, then the additional pressure of killer whale predation may influence the recovery of harbour seal populations through exposure to multiple stressors.

Whilst not explored in the present study, non-consumptive interactions of killer whale predation should be considered when exploring population consequences and implications for conservation. One avenue which has already been alluded to is whether seals exhibit anti-predator behaviour in their fine-scale movements. Anti-predator behaviour must be balanced with other fitness-enhancing behaviours, such as foraging; if seals are excluded from foraging grounds due to predation risk from killer whales, missed foraging opportunities or reduced foraging efficiency could lead to population-level fitness consequences. GPS-tagging methodology, as discussed above, could be used to explore this question, particularly with regards to identifying important foraging areas for seal species and whether their usage of these areas varies in the relation to killer whale presence.

6.4 Future research & recommendations

The results present here demonstrate the complexities and challenges in investigating the causes and consequences of an apex predator-prey interaction. Further research is required to disentangle how interactions are mediated by the nature and strength of the functional traits of both predators and prey, how these may very across ecological contexts, and the consequences they may have for shaping predator and prey fitness. Results above are discussed in terms of their strengths and limitations, with knowledge gaps and future research avenues discussed throughout. Here, I summarise future research and recommendation as a series of research topics with their associated aims, objectives, and possible approaches. This thesis has demonstrated the strengths of collaborating with citizen scientists and longer-term community-led monitoring efforts, from inter-annual and seasonal coverage to longitudinal life history data. Future research should seek to continue this engagement and collaboration across research topics.

I. Spatial and temporal patterns of predator-prey interactions

Future research should look to develop a spatially explicit model of predator-prey encounter probability throughout their overlapping range. Concurrent GPS-tagging of predator and prey species would facilitate the collection of fine-scale movement data from which percent overlap and conditional encounter probabilities could be quantified. Co-occurrence occupancy models and joint species distribution models could provide insights into areas of high-use and interaction rates, and where cross-referenced with environmental and behavioural data, important habitats for both predator and prey could be identified across spatiotemporal scales. Continued citizen science and engagement with community-led monitoring, such as the collection of drone footage and photo-identification, will be critical to address these objectives.

II. Killer whale diet composition

Further understanding of killer whale diet composition should be investigated across spatial and temporal scales. At the broadest level, stable isotope and fatty acid analysis from blubber biopsy samples could be used to investigate the trophic level at which killer whales forage, and whether they feed primarily on marine mammals or also other trophic levels such as fish. Sampling across seasons and locations (e.g., around Scotland) would glean insights into how prey composition may vary throughout the year and in relation to killer whale movements. At the finest level, continued community-led monitoring and recording of predation events throughout the year to increase sample size across different seasons, and identification of prey consumed in visual observations (e.g., through a two-stage Delphi expert elicitation process), would further understanding of species- and age-class specific composition of prey in killer whale diet. This would have important consequences of bioenergetic estimates of prey consumption requirements, and potential impact on prey populations.

III. Non-consumptive interactions of killer whales and seals

With regards to the top-down impacts on seal population, non-consumptive interactions should be explored. Particularly, whether seals exhibit anti-predator behaviour in their movements, and how predator avoidance is balanced with other fitness-enhancing behaviour such as foraging and resting. Data obtained from GPS-tags on harbour and grey seals could be used to explore their fine-scale movements and infer behaviour both in the presence and absence of killer whales, as identified from sightings data. Playback experiments to investigate how seals respond to killer whale vocalisations, in comparison to a control stimulus, would further understanding of the capacity of prey to detect and respond to killer whale presence. Quantifying the non-consumptive impacts would help quantify the overall top-down predation pressure elicited by killer whales, if fitness-enhancing behaviour of seals is affected by killer whale presence (e.g., reduced foraging).

7 REFERENCES

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APPENDIX A2. SUPPLEMENTARY MATERIAL FOR CHAPTER 2

A2.1. ECOPREDS GUIDELINES FOR RETROSPECTIVE DRONE OPERATIONS.

ECOPredS guidelines for retrospective footage

To contribute drone footage that was shot prior to 1st April 2021, we ask that the flights that you carried out adhered to the following guidelines:

- Civil aviation law: all drone pilots must have adhered to the law, recommended flying parameters and operating procedures (such as minimum distance to non-involved people and residential areas) set out within the flight class they were legally permitted by the Civil Aviation Authority (CAA).
    - Please note that the law changed in January 2021 and flying even a small drone with a camera now requires registration with CAA (https://register-drones.caa.co.uk/registration-requirements).
- Animal welfare: animals must not have been intentionally disturbed during the process of collecting footage.
    - All drone pilots must have adhered to guidelines and laws set out in *A Guide to Best Practice for Watching Marine Wildlife* and *The Scottish Marine Wildlife Watching Code* published by Nature Scot, applying to both on the ground and airborne activities. Where flights were conducted from boats, vessels must have adhered to best practice guidance for boat-based wildlife watching as outlined in the wildlife watching codes.
    - Animal welfare is not exclusive to the target species and consideration must have been made for colonies of breeding birds (e.g. Arctic Terns), seal haul outs and any other species that could be disturbed by a drone (e.g. Oystercatchers, gulls etc.).
    - We may request for additional details about the flight, such as altitude or whether footage was cropped.
- Using areas of operation: all drone pilots must follow the Scottish Outdoor Access code at all times.

For best practice for future flights contributing to research, please see the ECOPredS standard operating procedures (SOP) for drone flights.

Further reading

- CAA Drone and Model aircraft code https://register-drones.caa.co.uk/drone-code/flying-safely-and-responsibly
- A Guide to Best Practice for Watching Marine Wildlife https://www.nature.scot/guide-best-practice-watching-marine-wildlife-smwwc-part-2

- The Scottish Marine Wildlife Watching Code https://www.nature.scot/professional-advice/land-and-sea-management/managing-coasts-and-seas/scottish-marine-wildlife-watching-code
- The Scottish Outdoor Access Code https://www.outdooraccess-scotland.scot/
- ECOPredS community science project https://ecopreds.com/citizen-science and Facebook page www.facebook.com/ecopreds

Submitting images/footage

To contribute data to the project, please email ecopreds@st-andrews.ac.uk. If this is your first time contributing to the project, we will send you participant information that will explain how the data would be used, and a consent check list. If you agree to participate, we can then proceed with the image/footage contributions in way that is convenient to you.

A2.2. ECOPredS Standard Operating Procedure (SOP) for PROSPECTIVE DRONE OPERATIONS.

ECOPredS Standard Operating Procedure (SOP) for drone flights

To participate in the ECOPredS study, we ask drone pilots to adhere to the following:

1. All drone pilots and equipment must be registered and validated with the UK DMARES (Drone & Model Aircraft Registration and Education Scheme).
2. Adhere to the law, recommended flying parameters and operating procedures set out within the flight class they are legally permitted by the CAA (Civil Aviation Authority).
3. Submit a copy of your CAA qualification (e.g. A2CofC, PfCO, GVC etc) to the ECOPredS coordinator. The minimum requirement is A2 certificate of competency (A2CofC), which allows you to fly in the A2 open category ('close to' people).
4. Consider animal welfare at all times and agree to adhere to guidelines and laws set out in *A Guide to Best Practice for Watching Marine Wildlife* and *The Scottish Marine Wildlife Watching Code* published by Nature Scot. This is applicable to both ground and airborne activities travelling to, within and on departure from operating sites. Animal welfare is not exclusive to the target species and consideration must be made for colonies of breeding birds (e.g. Arctic terns), seal haul outs and any other species that could be disturbed by an operational drone (e.g. oystercatchers, gulls flying near whales etc).
5. Follow the Scottish Outdoor Access code at all times.

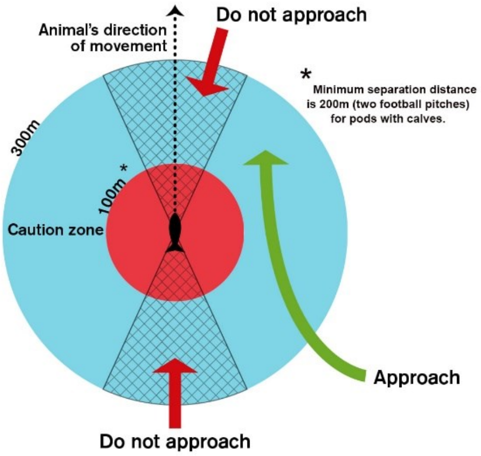
Flights contributing to research must:

1. Use a drone less than 2 kg in weight. No modifications (e.g. GoPro cameras attached to the main chassis or cameras suspended from chassis) are permitted.
2. Use a 2.7K/60fps or 4k/30 or 60 fps video setting.
3. Have all flight sensors enabled.
4. Keep your drone a minimum 30 m (90 ft) above any marine mammals, at all times
5. Maintain a safe, steady speed during approach.
6. The direction of travel of the drone should match those of the animals and the pilot should not undertake aerial manoeuvres that moves the drone ahead of the animals.

7. More than one drone over animals causes a heightened collision risk and the welfare of the animals must come first. Where possible communicate with the drone owner and continue the flight only when it is safe to do so. If you feel you will not have enough battery to complete the flight and secure intended footage, fly back to the launch site and reassess.
8. When ready to RTH (return to home), hold your position and vertical height for one minute where possible so that the animals beneath you have swam further away, and then fly back.

Boat-based flights:

1. Please read carefully and follow the Best Practice for Watching Marine Wildlife (links provided below)
2. The vessel <u>must not</u> approach the animals from ahead or behind their direction of movement when within 300 m (see figure to the right)
3. Aim to keep 400 m distance between the vessel and the animals, and never stay closer than 200 m to groups with calves ***
4. Avoid sudden unpredictable changes in speed, direction and engine noise



*** Groups/pods with calves, those actively hunting, feeding or in transit (moderate to fast swimming in a single direction) should be given a minimum separation distance of 200 metres – preferably 400 metres. Most groups of inshore killer whales will contain calves and juveniles. It should therefore be assumed that a minimum separation distance of 200 metres, preferably 400 metres, should be maintained.

Further reading

- A Guide to Best Practice for Watching Marine Wildlife https://www.nature.scot/guide-best-practice-watching-marine-wildlife-smwwc-part-2
- The Scottish Marine Wildlife Watching Code https://www.nature.scot/professional-advice/land-and-sea-management/managing-coasts-and-seas/scottish-marine-wildlife-watching-code
- ECOPredS community science project https://ecopreds.com/citizen-science and Facebook page www.facebook.com/ecopreds

Submitting images/video

To contribute data to the project, please email ecopreds@st-andrews.ac.uk. If this is your first time contributing to the project, we will send you participant information that will explain how the data would be used, and a consent check list. If you agree to participate, we can then proceed with the image/footage contributions in a way that is convenient to you (e.g., email, memory stick by post).

Please note: these guidelines were updated in May 2023, raising the minimum recommended drone altitude above all marine mammals to 30 metres. Earlier footage contributed to the project (1st April 2021 - 25th May 2023) followed our SOP established in 2021. To contribute older footage (shot prior to 1st April 2021), please see our guidelines for retrospective footage.

A2.3. DRONE HEIGHT CALIBRATION FLIGHTS

A DJI Mavic 2 Pro was flown over a 7m reference at different height and orientations: 10m, 15m, 30m, both horizontal and vertical (Figure A1). The drone was set to full HD (1920 x 1088 pixel dimensions) and multiple photos and video stills were taken over the reference object. The images were opened in Image J and the pixel scale set to the known distance of 700cm as measured from the reference object. From this, lines of length 100cm, 600cm, 700cm, 800cm, and 900cm were drawn on the image to represent killer whales of different body lengths (tail notch to rostrum tip) (Figure A2). Measurements of known lengths were taken at each height and orientation in pixels per cm. To calculate the proportion whales of different lengths would occupy in a horizontal and vertical frame, the whale body length was multiplied by the pixels were cm, divided by the total frame pixel dimensions, and multiplied by 100 to give a percentage. Multiple independent measurements were taken over photos and video stills, with the mean percentage for each height and orientation taken as the best-estimate proportion a whale would appear in a frame (Table A2.1, Figure A2.3).

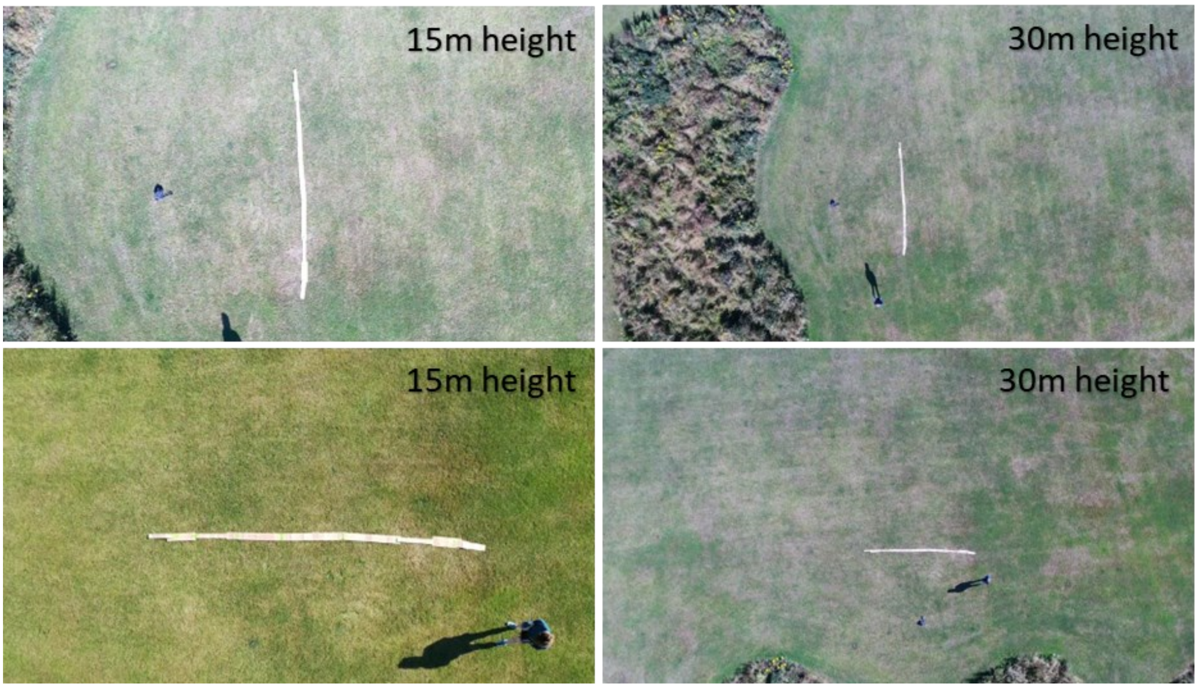


Figure A2.1. Images from drone calibration flights using a DJI Mavic Pro 2. The white line represents an object of known length, here a 700cm 'killer whale'. Images were taken at 10m, 15m and 30m flight heights, with the object in horizontal and vertical orientation to calculate the proportion an animal would occupy of an HD frame at different flight heights and orientations.

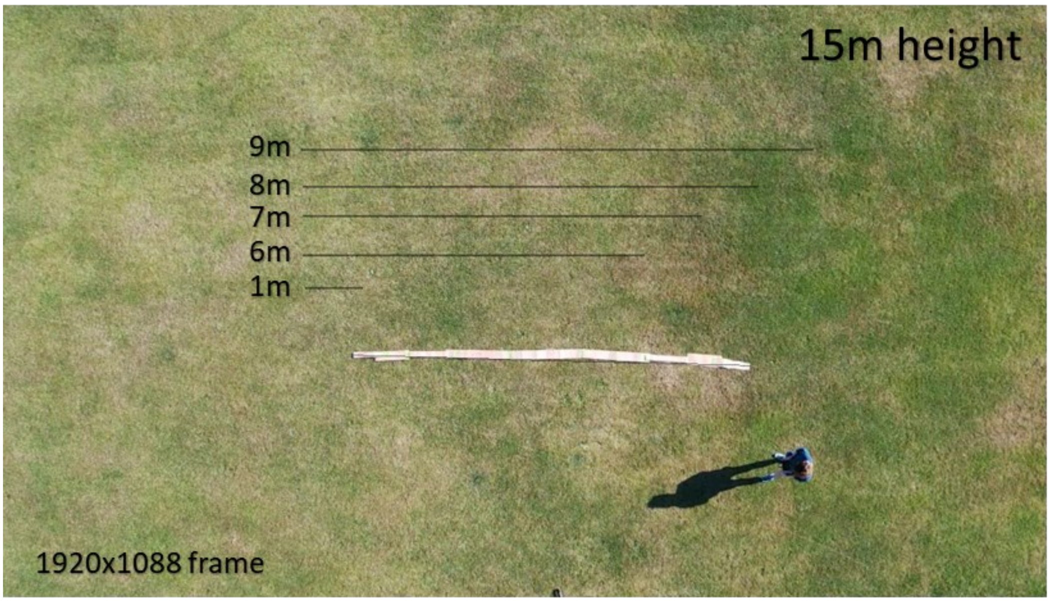


Figure A2.2. Drone image and lines of known length as drawn in Image J, after calibrating the image using the known reference size of the 7m object.

Table A2.1. Calculations for killer whale body length in pixel/cm at different drone heights in vertical orientation.

Height (m)	KW length (cm)	Pixel/cm	Length*pixel/cm	% vertical	Mean % vertical**
10*	700	1.55	1088.29	100.02	100.03
15	700	1.07	750.26	68.96	69.5
30	700	0.52	365.33	33.58	33.7

*7m whale filled vertical from so pixel/cm and measurements not accurate.

** mean calculated across repeated measurements from video and stills.

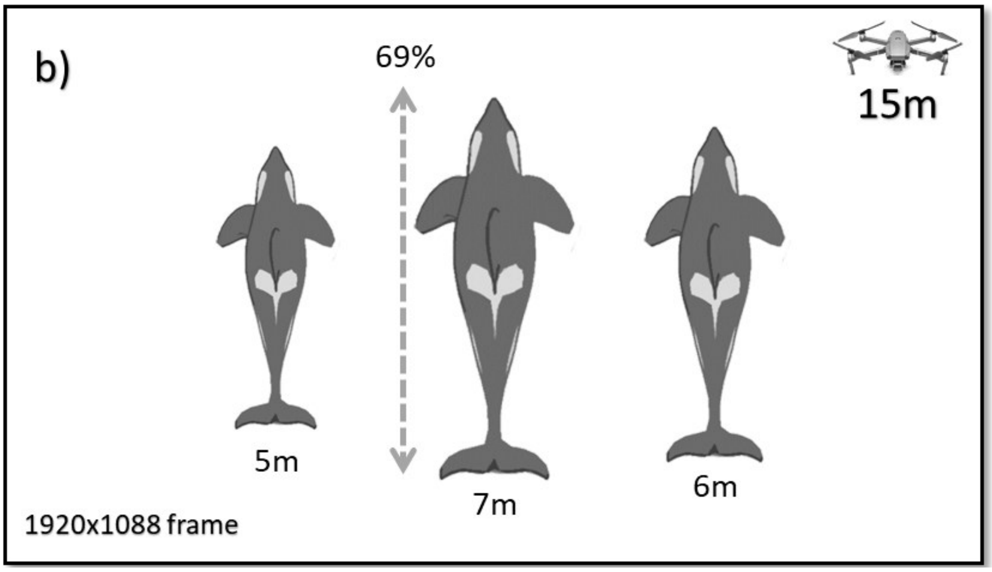


Figure A2.3. Calculated proportions of whale lengths 5m, 7m, and 6m in an HD frame at flight height 15m. At 15m, a whale of body length 7m was calculated to occupy 69% of the vertical frame.

A2.4. ECOPREDS QUALITY AND CONTENT SCORING PROTOCOL

ECOPredS Image / Video Analysis Protocol

Photo credit to R. Shucksmith & N. McCaffrey

Metadata

1. List Metadata – Run “import_video_data_.R” in R
    a. Full path: full file path (standardised across hard drives)
    b. File name: name of media file
    c. File type
    d. Duration
    e. Width: frame height in pixels
    f. Height frame width in pixels
    g. Frames: total number of frames
    h. Frame rate: frames per second
2. Associate metadata with sightings information – R & Excel
    a. Associated sighting / focal follow reference ID (where possible)
    b. Pod ID / composition

Manual Quality and Content Scoring

View footage in VLC, enter data in Excel

- Open VLC > Open File
- Playback speed
    - Normal
- Set up zoom function:
    - Tools > Video effects > Geometry > tick ‘interactive zoom’

1. Drone “on-follow” time

   a. Start_follow: Start of drone 'on_follow' time (mm:ss): when the drone has arrived at the whales' location and keeps whales in the middle of the frame from there onwards
   b. End_follow: End of drone ‘on_follow’ time (mm:ss): when the drone is no longer following the whales, e.g., whales have moved out of the frame, or the drone is flying back to the pilot.
      - The main idea is to exclude the initial period where the drone is looking for the whales, rather than following them, and exclude time where footage is not focusing on whales but either on scenery or flying back to the home location (pilot).

Note: The following points are scored in categories labelled 1,2,3 as defined for each.

2. Score video quality.

Note width and heigh from R metadata gives footage resolution in pixels:

- *SD = 640 x 480*
- *HD = 1920 x 1080*
- *UHD = 3840 x 2160*
- *4K = 4096 x 2160*

Although we have the video resolution from the metadata, it is still important to manually score image quality. The grainy vs fair examples below are both 1920x1088 (HD) but the grainy image is noticeability grainier/more pixelated (although framerate/datarate are different though 27.89, 10555kps vs 29.97,5752kps). Other things might influence how clear the image is too, e.g. height (how much the image is needed to be zoomed in) or weather condition (e.g. a clear day vs misty).

Manually assess video quality in VLC.

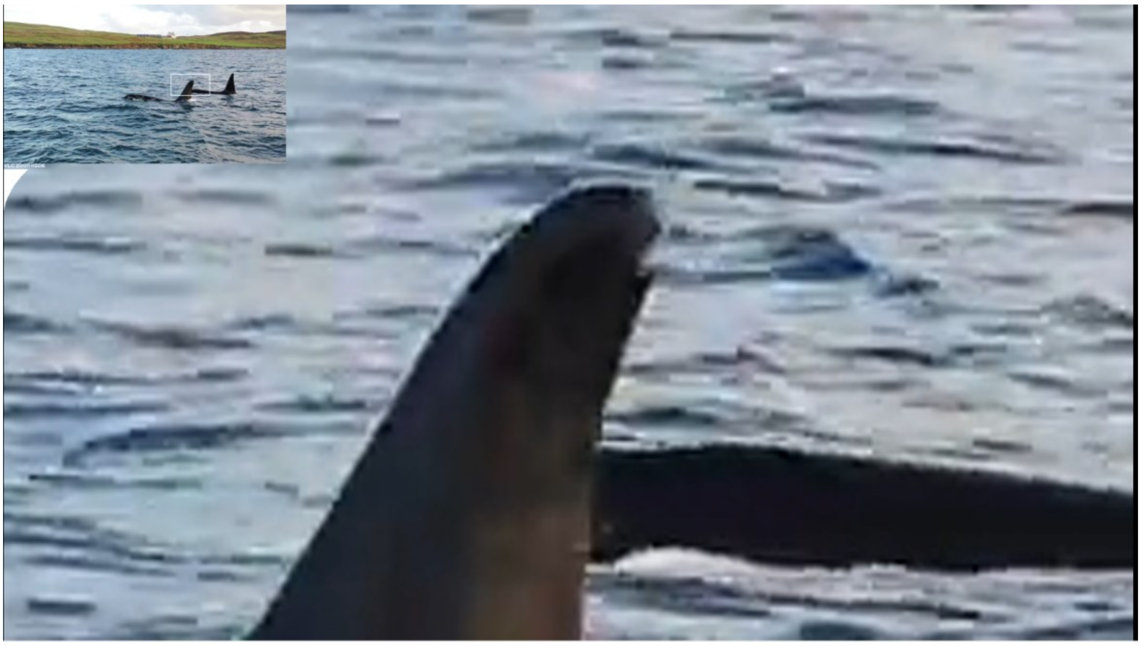
- Pause footage when animal(s) is/are at minimum distance during drone on-follow
- Measure quality on full screen and full zoom in VLC.
- Categorize video quality as 1, 2 or 3 based on following definitions:
  – *Ticks indicate what the footage could be used for in terms of data collection, crosses what it would likely not be good enough quality for.*
   a. Grainy (1) – on full screen image is pixelated, on full zoom image is very grain/pixelated.
      - ✓ Number of animals in shot
      - ✓ Breathing / surfacing intervals
      - ✓ distance to shore
      - ✗ ID individuals
      - ✗ ID prey items
      - ✗ Habitat qualities
   b. Fair (2) – on full screen image is clear, on full zoom image is slightly grainy/pixelated
      - ✓ Habitat qualities
      - ✓ Distinct dorsal marks e.g., nicks
   c. Clear (3) – on full screen image is very clear, on full zoom image has slight grain/minimal pixilation

- ✓ Distinct dorsal marks e.g., nicks
- ✓ Clear eye patches
- ✓ Clear prey outline

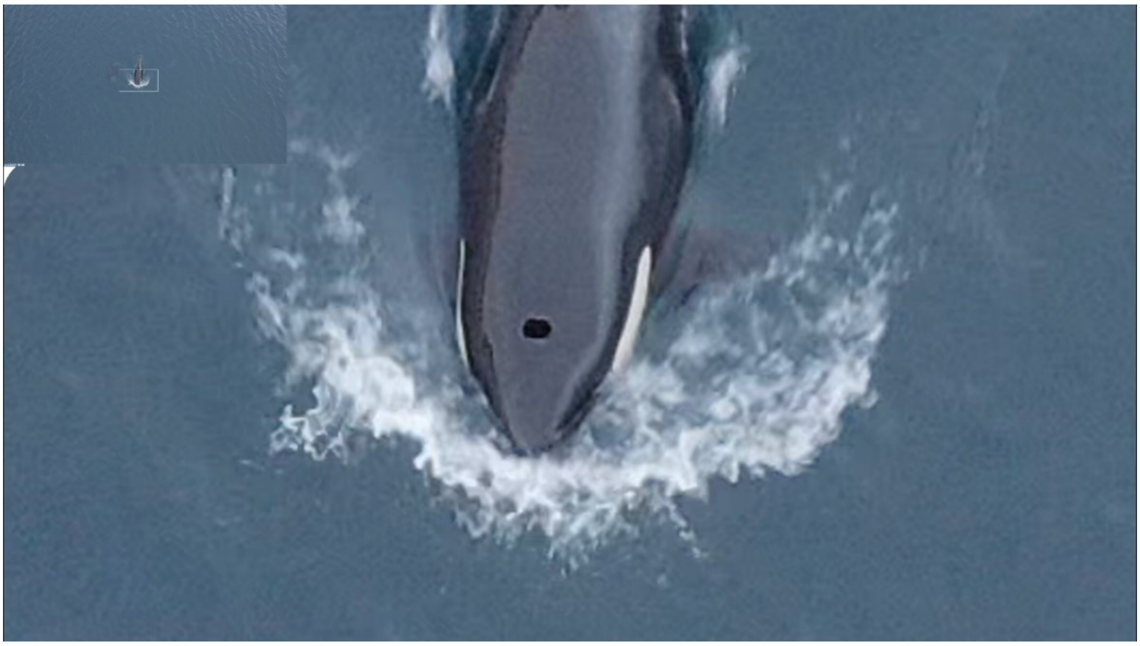
Example of grainy (1):

Examples of fair (2):

Example of fair (2):



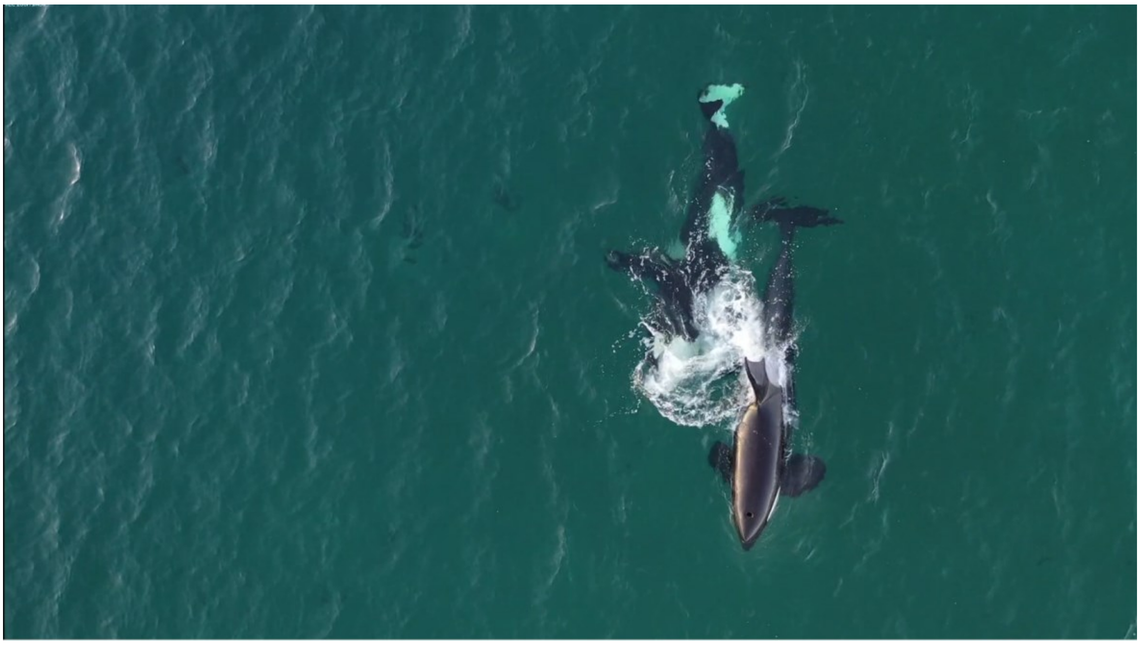
Example of good (3):



Example of good (3):

3. Minimum distance during drone on-follow.
   - Measure as body length (BL) in frame height (top-bottom of screen/image).
   - Pause footage when animal(s) is/are at minimum distance during drone on-follow
   - Categorize minimum distance from 1-3 based on following definitions:
     a. Close (1) – frame high <2BL
     b. Medium (2) – frame height <3-6BL
     c. Far (3) – frame height 7BL+

Example of close (1):

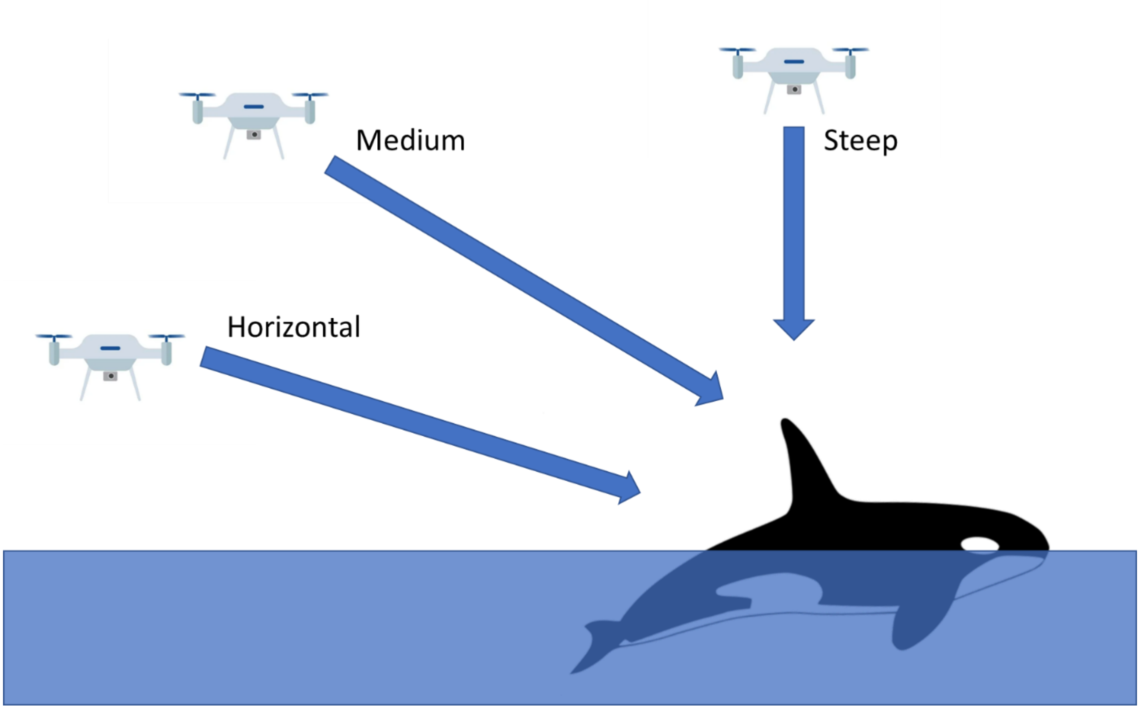


Example of medium (2):

Example of far (3):

4. Viewing angle while drone on-follow. If the drone changes angle, choose the most prominent angle (i.e., what angle the drone is at for the majority of the on-follow)
   - Categorize angle as 1, 2 or 3 based on the following definitions:
   - *Ticks indicate what would likely be visible from the angle, crosses what would likely not be visible.*
   a. Horizontal (1) –viewing side-on from land
      - ✓ Dorsal fin silhouette
      - ✓ Eye patch shape
      - ✓ Surface glare
      - ✗ Habitat/bottom substrate
   b. Medium (2) – viewing from height
      - ✓ Dorsal fin silhouette
      - ✓ Less surface glare
      - ✓ Potential to see habitat/bottom substrate (if sea is clear enough)
      - ✗ Eye patch
   c. Steep (3) –viewing from birds-eye angle
      - ✓ Relative body size measurements
      - ✓ Habitat/bottom substrate (if sea is clear enough)
      - ✗ Dorsal fin silhouette
      - ✗ Eye patch

Rough guide/visualisation of drone angle:



Example of horizontal (1):

Example of medium (2):

Example of medium (2):

Example of steep (3):

Note: The following points are coded as NO (0) and YES (1).

5. Any snapshot(s) in footage potentially useful for photogrammetry (e.g. body condition): No (0); Yes (1)

These should have steep viewing angle and animals central to the frame, but if you are unsure, it is best to mark Yes (1) rather than discard (0). Examples of snapshots with potential for photogrammetry:

6. Initial prey presence scoring
    a. Prey species (seal sp., porpoise, otters) are present in footage: No (0); Yes (1)
        - Not prey species ID not required at this stage, simply where any prey item is present in the footage at any point
        - Feel free to comment on potential prey species and any association with birds in the comments
    b. Predator and prey in same shot (i.e., could be used for relative size measurements): No (0); Yes (1)
        - As before, prey ID not required

Examples of predator & prey in footage (white arrows point to prey):

7. Shoreline (including skerries) visible: No (0); Yes (1)
8. Do animals come close to shoreline (<100m): No (0); Yes (1)
9. Presence of anthropogenic items
    a. Boats: No (0); Yes (1)
    b. Fish / shellfish farms: No (0); Yes (1)
10. Comments and additional notes
    a. Make notes on presence of other drones, presence/interactions with fishing gear (e.g., creel pot ropes, buoys), presence/interactions with seabirds

A2.5. EXPERT ELICITATION PROTOCOL AND EXAMPLE

Expert Elicitation for Killer Whale Prey Identification
Protocol and notes

Steps

Please read the following protocol and predator-prey size guide before starting the assessment

- Save the assessment excel sheet to your desktop/laptop before filling in
    - The “sp_total” column cells fill with green by up to 100%
    - If it is over 100%, it will turn red (alerting you that the total is too high)

Access the predation images shared on the OneDrive

- Media for each predation event is saved in one folder, with the name corresponding to the “Event_Id” in the assessment sheet. Predation events may contain multiple media, either from the same or different sources (photographers).
- Please do not share these images

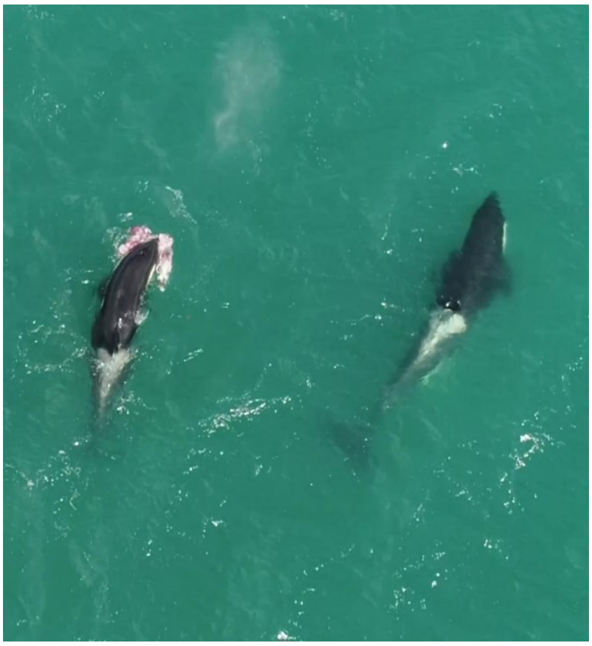
Fill and then return the excel sheet via email to

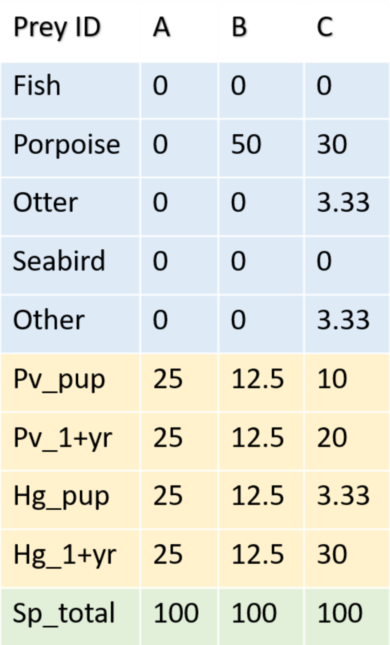
- Please do not upload your assessment sheet to the OneDrive, otherwise other participants well be able to see your judgments

Protocol

- We are asking for your judgment about the subjective probability (0-100%) that the prey could be any of the listed species.
- Please assign a probability (0-100) for each prey species so the total species probability for the predation event equals 100.
- Please think realistically about the plausibility that the prey could be a given species.
    - At the lower limit, assigning 0 to a species would imply it is implausible for the prey to be this species
    - At the upper limit, assigning 100 to a species would imply it is implausible for it to be any other species (listed or “other”)
- As much as possible, try to be an impartial observer of these images: please do not use your prior expectation of killer whale diet composition in Scotland to inform your answers. Only use the images to make your judgement.
    - To consider prey size relative to the predator size, please feel to use additional literature and examples, provided below.
    - If you have additional literature suggestions, please share them with us – we will aim for everyone to have the same background material

Example





Prey ID	A	B	C
Fish	0	0	0
Porpoise	0	50	30
Otter	0	0	3.33
Seabird	0	0	0
Other	0	0	3.33
Pv_pup	25	12.5	10
Pv_1+yr	25	12.5	20
Hg_pup	25	12.5	3.33
Hg_1+yr	25	12.5	30
Sp_total	100	100	100

Person A judges that the prey could only be a seal, not any other type of prey, and it was equally as likely to be any one of the 4 seal sp categories

Person B judges that the prey remains are blubber, so realistically it could be either a seal or a porpoise. They judge that is equally as likely to be a porpoise (50%) as it is a seal, and that is equally as likely to be any one of the 4 seal sp categories (12.5% x 4 = 50%).

Person C judges that the prey is quite large, so it is most likely to be an adult seal or porpoise (80%), but there is still a possibility it could be a pup, otter, or something not listed (e.g., another small cetacean). C judges that the prey has more than a random chance to be either a porpoise or an adult grey seal (60%), but thinks both are equally likely (60/2 = 30%). They judge the prey less likely to be an adult harbour seal (20%), followed by a harbour seal pup (10%), and allocates the remaining probability (10%) equally between grey seal pup, otter, or another unlisted species. Importantly, person C still judges the prey to be so large that it could not realistically be a bird or fish. In other words, if person C was later told the prey was actually a bird species, then the person C would seriously doubt that information – thinking perhaps there was a confusion about what images they were looking at, for example.

THE ROULETTE METHOD

In the roulette method, you create a physical representation of your probability distribution for X by placing probs on a grid.

The expert's allocation of probs in our example

MAKING THE JUDGEMENTS

Identify the bins that you think X is most likely to lie in and place 2 probs in each. Place 1 prob in each of the other bins where you judge there to be at least enough probability to warrant placing a prob. Use the remaining probs to build up the bins until you are happy with the allocation.

TESTING THE JUDGEMENTS

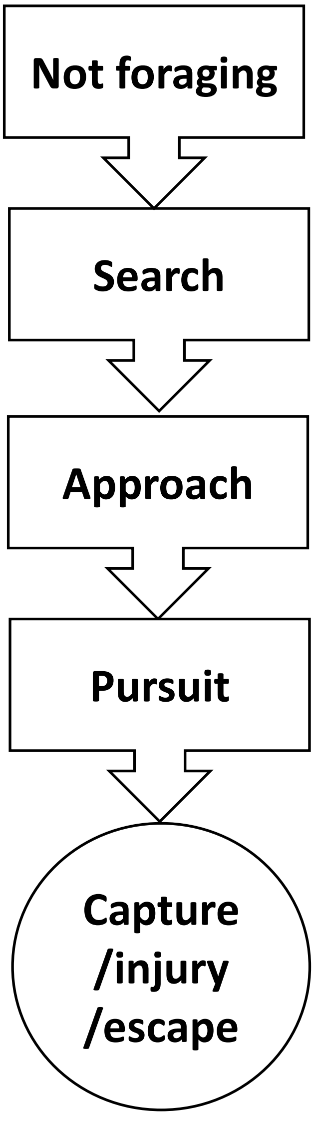
Essentially, we are asking you to create a representation of the probability distribution for prey ID – similar to the example on the left. We have created the 'bins' (possible species) and we are asking you, as experts, to put your 'probs' (percentage) in the bins reflecting the subjective probability of species ID. The screenshot included is from an e-learning course on probabilistic judgement, available here: http://www.tonyohagan.co.uk/shelf/ecourse.html

APPENDIX A4. SUPPLEMENTARY MATERIAL FOR CHAPTER 4

A4.1 ECOPREDS EFFORT AND FOCAL FOLLOW PROTOCOL (2020)

Effort and focal follow protocol

Phases of orca predation on seals: figuring out the orca time budget



Not foraging for seals: not a single member of the orca group is seen searching, approaching, or pursuing seals – they may instead be foraging for fish, socializing, or resting.

Search: one or more member(s) of the orca group are seen **actively searching** in areas where seals are either present or expected to be present (=near a known seal haulout). Circling around land/rocks/shallow waters, spy-hopping to look for seals.

Approach: directed movement towards seals, by one or several members of the orca group**. Seals are not yet escaping/ avoiding** the orca, although may have seen them and be more vigilant (=head up, frequent gaze around).

Pursuit: fast directed movement towards seal(s), by one or several members of the orca group. **Seal(s) show escape/ avoidance** response.

Capture: orcas are seen killing a seal, or remains of a seal are seen following a pursuit. Report *injury* if seal is seen to escape but with visible damage/ blood. Report escape if seal was confirmed to be alive and seemingly uninjured after the pursuit. Please record **'unknown' if you are unsure** what happened to the seal.

Effort form: please make a new record when conditions change or there is a break in the effort

Start, End	Start and end time of your watch. Please use local UK time, and please make a note if the start or end time was determined by your ability to track animals!
Sea state	0 = mirror calm; 1 = slight ripples, no foam crests; 2 = small wavelets, glassy crests, but no whitecaps; 3 = large wavelets, crests begin to break, few whitecaps; 4 = longer waves, many whitecaps; 5 = moderate waves of longer form, some spray; 6 = large waves, whitecaps everywhere, frequent spray; 7 = sea heaps up, white foam blows in streaks; 8 = long, high waves edges breaking, foam blows in streaks; 9 = high waves, sea begins to roll, dense foam streaks.
Swell height	Light = <1m; Moderate = 1-2 m; Heavy = >2 m
Visibility	Visibility: < 1 km; 1-5 km; 6-10 km; >10 km
Number of seals (best estimate; zero if none seen)	<u>Total</u> – total number of seals, including harbour/grey/unknown species <u>Harbour</u> – number of harbour seals present (leave empty if unknown) <u>Grey</u> – number of grey seals (leave empty if unknown) <u>Pups</u> – number of pups (<5 months old)
Num. of boats	<u>W motor</u> – motor boats, RIBS, yachts <u>No motor</u> – kayaks, dinghies, rowing boats, rafts
Num. of people	If seals present, number of people on foot within seals' vicinity (<500m)
Fish & fishing	Any fish seen to jump out of water, presence of anglers, fishing boats, etc. Mackerel, herring, sprat, lumpsuckers are potential fish prey to killer whales.
Other prey	Presence of other potential prey such as porpoises, otters, swimming seabirds
Additional notes	Additional notes such as any other sources of disturbance for the seals than killer whales, grey-harbour seal interactions, species ID confidence, tide state, habitat description (rocky/sandy, sea weed, water colour, SAC?)

Focal follow observations: if you can, please track an individual orca and its associated group, adding a new row when behaviour (esp. seal foraging phase) or group composition changes.

Start, End	Start and end time of each behaviour (local UK time). If you didn't see the behaviour start/end, indicate it e.g. "Start: Before 14:55, End: After 16:10".
Focal ID	Please label the individual you are tracking for this watch with a number. Change the number and make a new record if you lose track of it. If focal follow is not possible, leave this empty and focus on group behaviour instead.
Focal whale behaviour	Dive duration (min) – typical/average dive duration of focal whale, in minutes Inter-breath-interval (s) – typical/av. time interval between breaths, in seconds
Number of orca (circle the number that includes focal whale)	<u>Total</u> – total number of whales associated with focal, include males/calves/other <u>Male</u> – number of males seen (clearly taller fin) <u>Calves</u> – number of calves (small body, foetal folds, yellow, close to mother) Please indicate to which of the three categories the focal tracked whale belongs by circling the appropriate number.
Distance	Min distance of the orca to shore in metres (100 m= 109 yards= 328 feet; 1000 m=0.6 mi)
Orca behaviour	Any behaviours displayed *by the group*: Surfacing; Normal Swim; Fast Swim; Feeding; Leap/Breach; Tail Slap; Bow-ride; Rest/Milling; Sexual; Aggression

Foraging for seals phase	Choose one: None/ Search/ Approach/ Pursuit/ Capture/ Injury/ Escape. Please see overleaf for definitions. If individual orcas in the group are in different phase, choose the later phase (e.g., select pursuit rather than approach).
Number of seals affected	Number of seals approached, pursued, captured, injured, escaped, as defined in previous column. Leave empty if whales are searching for seals, or not foraging. Total – total number of seals, including harbour/grey/unknown species Harbour – number of harbour seals, all ages (leave empty if unknown) Pups – number of pups (<5 months old)
Notes	Additional info such as known orca individuals, and seal species ID confidence.

Never disturb wildlife keep your distance, use binoculars, minimize noise, and leave at the first sign of disturbance. Know the signs; seals can be vulnerable while resting on land. More info: Scottish Marine Wildlife Watching Code.