INVESTIGATING MONITORING OPTIONS FOR HARBOUR SEALS IN SPECIAL AREAS OF CONSERVATION IN SCOTLAND

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ABSTRACT

Managing a wild population effectively requires knowledge of the abundance and behaviour of the species. Harbour seals (*Phoca vitulina)* are usually counted when they come ashore at haul-out sites, and so it is important to understand how the number of seals counted at this time relates to total population size. Satellite telemetry studies confirmed that harbour seals on the west coast of Scotland showed a degree of site fidelity and coastal foraging. Most trips taken by tagged animals involved travelling only 10-30 km from haul-outs and lasted less than a day (mean 21.07 hours, SE = 0.54), although some seals travelled over 100 km. Eighteen percent of the time these tagged seals spent hauled out was in the Special Area of Conservation where they were caught.

Individual seals can be recognised from their unique pelage patterns using computer-assisted photo-identification. Capture histories for adult harbour seals at a site in north-west Scotland indicated that the number of seals using the study area between April and October was 3.4 times higher than the number counted during an aerial survey made during the August moult. In the UK, aerial surveys of harbour seals are usually conducted during the first three weeks of August, when seals are moulting. These counts have a coefficient of variation of around 15%. Land-based counts made at study sites on the north-west coast of Scotland indicated that the number of seals hauled out was most consistent during the moult, but highest counts were from the pupping period. Analysis of moult counts indicated that starting surveys one week earlier (on 7th August) and surveying 1½ hours earlier in the tidal cycle would reduce the count variation. There was spatial, seasonal, diurnal and sex-related variation in the proportion of time harbour seals hauled out. Thus the relationship between counts and total population size is likely to vary spatially and temporally. This variation should be included in the estimates of the CV of correction factors.

A 5% annual change in harbour seal population size was predicted to take around 14 years to detect based on annual surveys and a CV = 0.15. This detection period increases when monitoring methods with lower precision are used, or surveys are made less frequently. Trends in seal abundance at pairs of haul-out sites were not synchronous and so it is unlikely that counts from small land-based protected areas, such as Special Areas of Conservation, can be used to monitor overall population status.

RECOMMENDATIONS

The following recommendations should be considered for inclusion in future harbour seal conservation programmes in Scotland:

1. An appropriate monitoring method should be selected for each study. There should be consistency in data collection methods, and the precision of abundance estimates should be maintained (or improved).
2. The extent to which the moult period varies spatially and temporally should be investigated further to determine if the timing of surveys ought to be reconsidered. Confidence intervals for the correction factor used to account for the number of seals in the water at the time of the survey should be determined for different areas.
3. Harbour seal abundance should be surveyed during both the pupping and the moulting periods to improve our understanding of the relationship between these periods of high seal abundance ashore, and to provide additional information on the conservation status of harbour seals.
4. Alternative monitoring methods that are not limited to single counts of seals on land should be considered. Capture-recapture techniques are an obvious alternative for estimating the number of animals using a specific area. Data collected using these techniques should be analysed using models that account for movement between haul-out sites and individual heterogeneity in capture probability.
5. Satellite telemetry should be used to identify haul-out sites to which seals exhibit high site-fidelity. These sites can then be used for photo-identification and capture-recapture studies that use closed-population models to estimate abundance.

6. The underlying reason for any changes in abundance that are detected through monitoring should be investigated. In addition, potential threats to the seals or to their habitat should be identified and, where possible, monitored.
7. Monitoring harbour seal abundance should take place on the widest possible scale to detect regional as well as local changes in population size.
8. Population monitoring should be conducted annually, where possible. Minimum acceptable changes in abundance should be agreed so that timely responses to any change in abundance can be initiated.
9. The current boundaries of land-based Special Areas of Conservation should be extended seaward by 25 km as a first step towards designating a marine component to protected areas for harbour seals.
10. Measures of the ecological and socio-political effectiveness of SACs should be developed, and an integrated management approach adopted.

CHAPTER ONE

GENERAL INTRODUCTION

There is a long history of interactions occurring between marine mammals and man. These range from commercial exploitation at one extreme, to a more recent move towards eco-tourism funded conservation at the other. These multiple interests require monitoring programmes and management plans to be based on the best available information, which has fuelled considerable marine mammal research efforts. Despite this interest, marine mammals are difficult to study due to their association with the sea. Consequently estimates of marine mammal abundance, and many aspects of their behaviour and movements, remain uncertain. It is therefore crucial to improve upon and expand our current knowledge of these animals.

Pinnipeds are constrained to terrestrial breeding sites and so spend part of their time on land. Despite being more visible than some of the more 'elusive' marine mammals, this association with land raises a number of issues that must be addressed, including both the probability of animals being ashore and the spatial relationship between the terrestrial and marine components of the animals' lifecycle.

The harbour seal, *Phoca vitulina*, Linnaeus 1758

The harbour (or common) seal is a member of the pinniped family Phocidae, called 'true' or 'earless' seals because they lack external ear flaps. Members of this family include 19 species (one, the Caribbean Monk Seal *Monachus tropicalis,* now extinct) in 13 genera. The species name is derived from the Latin words *vitula*, meaning 'calf', and *innus* meaning '-like'. Unlike otariids ('eared' seals) and walruses, phocids use their foreflippers to pull themselves along on land; in water they move their hind

flippers from side to side, spreading their digits widely for propulsion and use their foreflippers to steer and maintain their position in the water column.

General characteristics

The harbour seal is a relatively small species, with adult females and males weighing 85 kg and 110 kg respectively (Coltman *et al.*, 1998). Maturation occurs at between two and six years of age, with most females maturing at three or four, and most males by five years (Bigg, 1969). Pups generally shed their lanugo pelage *in utero* and are therefore born with juvenile pelage allowing them to enter the water within a few hours of birth (Reeves *et al.*, 2002).

Harbour seal pelage pattern varies substantially with latitude (Kelly, 1981; Reeves *et al.*, 2002), and this has led to five subspecies being recognised (see *Distribution* below). As with other phocids, the function of the spotted pattern in harbour seals may have evolved as camouflage for concealment from prey and/or predators.

In addition to time spent reproducing and moulting, pinnipeds spend a significant amount of time hauling out onto a variety of habitats, including beaches, sandbanks and rocks (see *Distribution* below). The benefits of this behaviour that compensate for the costs of travel and reduced foraging time are not clear (Watts, 1996). Possible reasons include thermal regulation (Boulva & McLaren, 1979), predator avoidance (da Silva & Terhune, 1988), rest (Schneider & Payne, 1983), social interaction and parasite reduction (Stevick *et al.*, 2002). It is also possible that the raised temperature of peripheral tissues promotes skin growth and maintenance when seals are hauled out (Hayward *et al.*, 2005).

Haul-out behaviour in harbour seals varies with a range of factors including tidal cycles (Schneider & Payne, 1983; Simpkins *et al.*, 2003; Chapter 2), time of day (Thompson *et al.*, 1989; Frost *et al.*, 1999; Boveng *et al.*, 2003; Chapter 2), photoperiod (Watts, 1996) and levels of disturbance (Allen *et al.*, 1984). Studies in Canada showed that seals were less likely to haul out in temperatures below -15°C (Boulva & McLaren, 1979), but the effect of temperature on haul-out patterns was not

so apparent in places with less extreme weather conditions (Schneider & Payne, 1983; Grellier *et al.*, 1996). Precipitation (Godsell, 1988) and high wind speed (Kovacs *et al.*, 1990) may also reduce the numbers of seals hauled out.

Harbour seals use several different haul-out sites throughout the year (Simpkins *et al.*, 2003), the importance of which varies seasonally and as a result of individual changes in site use (Brown & Mate, 1983; Thompson *et al.*, 1996; Chapter 2). Females may choose specific haul-out sites for pupping and lactation, or the change in the use of haul-out sites may depend on local variation in food availability (Thompson, 1989). Nevertheless, several studies suggest that harbour seals, particularly older females, do show site-fidelity (Yochem *et al.*, 1987; Thompson, 1989; Härkönen & Harding, 2001; Chapter 2), particularly in older females (Härkönen & Harding, 2001).

Distribution

Harbour seals are generalist predators and forage in most types of coastal habitat including deep fjords, coastal lagoons and estuaries, and high-energy, rocky coastal areas (e.g. Brown & Mate, 1983; Allen *et al.*, 1984; Mathews & Pendleton, 2006). Sometimes harbour seals forage at the mouths of freshwater rivers and streams (SCOS, 2005), occasionally travelling hundreds of kilometres upstream (Reeves *et al.*, 2002). They haul out in a variety of habitats including sandy and pebble beaches, intertidal rocks and ledges, sandbanks, mud bars and occasionally on ice floes (Bigg, 1981; Stewart, 1984; Stevick *et al.*, 2002). Thus harbour seals are widely distributed, inhabiting a broad latitudinal range that encompasses temperate and subarctic coastal areas on both sides of the North Atlantic and North Pacific Oceans (Figure 1.1)

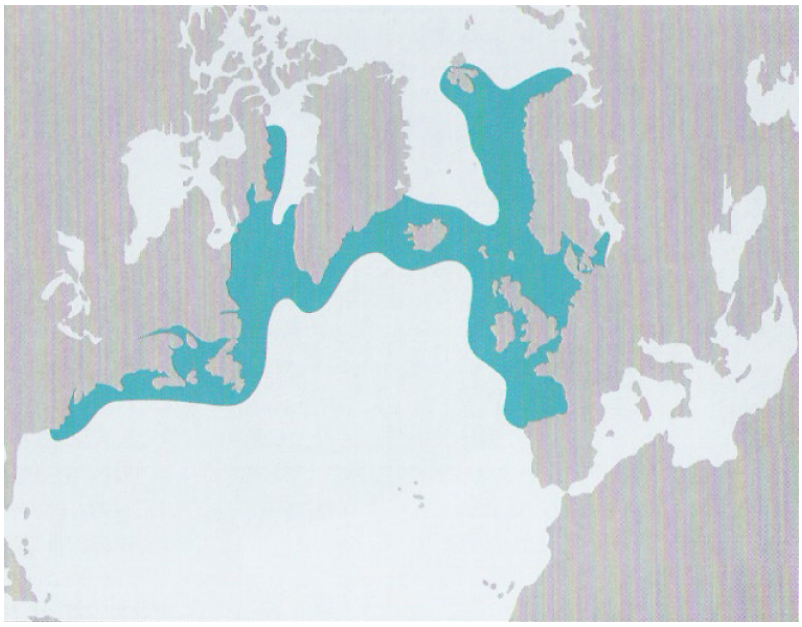

Figure 1.1: Map of the distribution of the harbour seal in the North Atlantic, taken from Kinze (2002).

There are five recognised subspecies of harbour seal, distinguished principally by minor morphological differences and geographical distribution: *Phoca vitulina stejnegeri* (western Aleutian Islands & western North Pacific), *P.v.richardii* (eastern Aleutian Islands & eastern North Pacific), *P.v.concolor* (western North Atlantic), *P.v.mellonae* (freshwater lakes and rivers in north-eastern Canada) and *P.v.vitulina* (Barents Sea, southern Baltic Sea & eastern North Atlantic). There appears to be virtually no movement among these subspecies (Reeves *et al.*, 2002). Despite considerable uncertainty with regards to population estimates, it is thought that 40% of the European population of harbour seals (*P. v.vitulina*), the focus of this study, is found in Scotland (SCOS, 2005).

Genetics

Genetic data can be used to make inferences about levels of gene flow between populations and hence about movement. For example, Goodman (1998) was able to identify six genetically-distinct harbour seal populations in the North Sea and suggested that most dispersal was among neighbouring subpopulations. Goodman's work further suggests that not all harbour seal dispersal results in recruitment. Harbour seals separated by relatively short distances in the north Pacific may also have significant genetic differences (Westlake & O'Corry-Crowe, 2002).

Age structure

Knowledge of the age structure of the Scottish population of harbour seals is sparse (Mackey, 2004), yet this information is of vital importance because it affects the relationship between counts of seals hauled out and the total population size (Härkönen *et al.*, 1999). As a result, the numbers of seals hauled-out at particular sites may change over time as a consequence of changes in the population's age and sex structure rather than its actual size (Härkönen *et al.*, 1999). Age structure also influences the way in which total population size may change over time. For example, if a large number of young animals are present in the population then the population will increase rapidly in subsequent generations (provided the sex ratio is not heavily skewed towards males), because of a high average life expectancy (and therefore reproductive output). A detailed knowledge of the age and sex structure of a population therefore aids in the management of the population. In the absense of such information, it is important to remember that counts of harbour seals at haul-out sites are not necessarily a robust indicator of changes in population size.

Although the sex ratio among pups is 1:1, females become relatively more numerous with age (Boulva & McLaren, 1979; Härkönen & Heide-Jørgensen, 1990). Little is known about harbour seal pregnancy rates in the UK, but studies in the Kattegat-Skagerrak region suggest that around 90% of mature female seals produce a pup each year, with lowered success before the age of eight years or after 25 years (Härkönen & Heide-Jørgensen, 1990). Thus the mean pregnancy rate within a population will be affected by its age structure. Haul-out behaviour differs among age and sex classes (Härkönen *et al.*, 1999), and harbour seals show age and sex segregation at haul-out sites (Härkönen & Harding, 2001). For example, due to a strong bond between harbour seal mothers and their pups, pups are generally found with females (Thompson, 1989; Kovacs *et al.*, 1990). Consequently, surveys that are biased towards haul-out sites favoured by mature females will overestimate the recruitment rate for the population as a whole. Previous work has estimated that harbour seal pups comprise 18.6% of the total population in Shetland (Venables & Venables, 1955), 20.8% in Ireland (Summers *et al.*, 1980), 19.9 - 23.8% in Atlantic Canada (Boulva & McLaren, 1979) and 20.4% in Pacific Canada (Bigg, 1969).

Life history

Between January and early May, harbour seals in Scotland spend much of their time foraging at sea. Most foraging trips last between 12 and 24 hours (Chapter 2), with some trips of up to 21 days occurring (Thompson *et al.*, 1989). Females give birth to a single pup on land between June and early July (Venables & Venables, 1955) and they nurse for an average of 24 days (Bowen *et al.*, 2002). As they are frequently born below the high water mark, pups have to be able to swim within a few hours of birth (Summers & Mountford, 1975) and spend much of the lactation period in the water (Thompson *et al.*, 1994). After fasting for about one week, females begin to undertake regular foraging trips (Boness *et al.*, 1994) each lasting up to six days (Thompson & Miller, 1990). Although lactating females mobilise considerable amounts of fat stored in blubber, unlike the larger-bodied phocid species harbour seal females also forage intensively during lactation to support the energetic costs of lactation (Bowen *et al.*, 2001). Mating is thought to occur in the water (Van Parijs *et al.*, 1997; Coltman *et al.*, 1998) at the end of the lactation period (Thompson, 1988).

Prompted by hormonal changes, old skin and hair are moulted once a year; in Scotland this moult period occurs between late July and early September. Yearlings are the first to start moulting (Thompson & Rothery, 1987) and females are thought to moult before males (Thompson *et al.*, 1989). The distribution of harbour seals in Orkney during the moult was more concentrated than during the breeding season, and numbers ashore were at their greatest and most consistent at this time (Thompson, 1989; Thompson *et al.*, 1989, but see Thompson *et al.*, 1997). From October through to the end of the year harbour seals are predominantly at sea (Chapter 2), most probably replenishing the reserves used during the breeding and moulting seasons.

Prey

Harbour seals forage in inshore waters (Thompson & Miller, 1990) and appear to consume prey roughly in proportion to their abundance in the sea (Tollit *et al.*, 1997). Studies of harbour seals on Northern European coasts indicate that they are largely piscivorous (Pierce *et al.*, 1991), feeding on a variety of prey including sandeels, whitefish, flatfish, herring, sprat, octopus and squid (e.g. Härkönen, 1987; Tollit,

1996; Hall *et al.*, 1998; Härkönen & Heide-Jorgensen, 1991; Wilson *et al.*, 2002; Pierce & Santos, 2003). Many of these species are commercially important (Rae, 1968; Rae, 1973), though their removal does not necessarily have negative consequences for the fishing industry (Bjørge *et al.*, 2002a). Although seals are capable of changing their diet in accordance with a change in availability of prey species (Bjørge *et al.*, 2002a), their diet is often dominated by just a few key species (Tollit & Thompson, 1996). However, there is a wide variation in the reported importance of different prey species, reflecting the diverse geographical and seasonal origins of samples, different sampling methods and, probably, changes in diets over the years (SCOS, 2004).

Natural and anthropogenic threats

Killer whales (*Orcinus orca)* are the only natural predator of harbour seals in Scottish waters, yet the frequency with which they enter Scottish waters is unknown. However with increasing concern over the last decade about the growing problem of overfishing of marine ecosystems (and the associated threat to global food security, biodiversity preservation and general ecosystem function), some fishermen have speculated on the role of seals in the drastic decline of fish stocks. Thus the relatively large numbers of harbour seals, together with between 90,000 and 150,000 grey seals (SCOS, 2005), have been blamed for the decline in Scottish fish catches and subsequent economic loss to fishermen, leading many to favour local culls (Moore, 2003). Despite the interest in researching the interactions between seals and fisheries (Bjørge *et al.*, 2002a), due to the complexity of the marine food web it is not easy to calculate the extent to which seals actually compete with commercial fisheries (Harwood & Greenwood, 1985).

Seals often remove, or attempt to remove, fish from nets or fish farms (Harwood & Greenwood, 1985). In doing so they may damage fishing gear and allow fish to escape or to be damaged, thus lowering their market price and causing potentially substantial economic loss to fishermen (Rae & Shearer, 1965; Bonner, 1982; Lunneryd, 2001; Moore, 2003). The presence of seals around nets may also drive fish away (Harwood & Greenwood, 1985). The fish-based diet of harbour seals means that some fishermen

shoot seals in an attempt to boost fisheries yield (Jennings *et al.*, 2001). This is particularly the case for some coastal salmon fisheries, which may be more affected by harbour seals than grey seals.

Marine mammals are also victims of bycatch, the unintentional catching of non-target species due to unselective fishing nets (Tegner & Dayton, 1999). Bottom set gillnets (Bjørge *et al.*, 2002b) and nets lost at sea that continue to catch and kill marine life unintentionally for many years (Gislasson, 1994) are particularly problematic. Many untargeted fishery species have their remains thrown overboard (Safina, 1998), causing the proliferation of scavenger species (Wassenberg & Hill, 1987) which may alter the abundance of predators like seals. The full extent of these impacts on harbour seals is still not known (Woodley & Lavigne, 1991).

Some fishing gear directly affects the habitat in which it is used (Kaiser, 1988). Trawling, for example, increases turbidity and alters sediment characteristics, causing pollutants to re-suspend and thus altering benthic communities (Dayton *et al.*, 1995). This could potentially alter the availability of prey for seals as fast breeding species, such as polychaete worms, become increasingly prevalent over slow-growing, late-reproducing species such as molluscs, crustaceans and fish (Thrust *et al.*, 1991). Many fisheries also focus their efforts on harvesting top predators (Vitousek *et al.*, 1997; Goñi, 1998), thus directly removing food from marine mammals (Nightingale, 2001).

More than 18,000 harbour seals were found dead in Northern Europe in 1988 due to an outbreak of phocine distempter virus (PDV - Dietz et al., 1989), reducing the harbour seal population by up to 60% in some parts of Europe (Reijnders *et al.*, 1997; Heide-Jørgensen *et al.*, 1992). A second epidemic occurred in 2002 (Jensen *et al.*, 2002; Harding *et al.*, 2002). Previously unidentified, PDV is a morbillivirus that is closely related to canine distemper virus and measles (Osterhaus & Vedder, 1988; Kennedy, 1990). Although the origin of the disease remains unknown, the disease may have been introduced by Arctic harp seals (*Pagophilus groenlandicus*) migrating from the Barents and Norwegian Seas (Heide-Jørgensen *et al.,* 1992).

International movements of livestock and marine disposal of waste have probably resulted in marine mammals being exposed to a much wider range of disease agents than was the case in the past (Reijnders *et al.*, 1993). Thus episodic mass mortalities, such as those caused by PDV, may occur more frequently in the future, either in response to an expanding population or resulting from anthropogenic threats.

Pollutants tend to bioaccumulate in the tissue of seals because they feed at the top of the food chain. Thus many toxins have been found in seals, and some have been implicated in suppression of the immune system (Reijnders *et al.*, 1993) and lowered reproductive success (Reijnders, 1986). Levels in Scottish seals are comparatively low. Organochlorine pollution has been recorded in Scottish seals since the 1960s (Hall *et al.*, 1992) and shows significant differences between sample sites.

Managing harbour seal populations

The protection afforded to seals found in Scottish waters has changed historically in response to pressure from fishermen, hunters and environmentalists. Outlined below, the history of British and European legislation for protecting seals is summarised in Table 1.1.

Commercial hunting of seals for their oil-rich blubber started in the Stone Age (Bonner, 1982) and decreased the Scottish seal population to such an extent that in 1914 the Grey Seals Protection Act was passed, forbidding capture or killing of grey seals (*Halichoerus grypus*) between 1st October and 15th December. Although Hickling (1972) claimed the Act was largely ignored, the Scottish grey seal population was reported to have increased to an estimated 4,000 or 5,000 animals within 14 years (Rae, 1962). Despite the population no longer being threatened with extinction (Hickling, 1972), the Grey Seals Protection Act was amended in 1932, extending the 'close season' by six weeks.

In response to increased protection of grey seals and the higher value of harbour seal skins, hunting pressure shifted towards targeting harbour seals. Exploited commercially for their skin and blubber (Tickell, 1970; Bonner *et al.,* 1973) harbour seals were also killed under the assumption that commercially important fish species formed a major dietary component. Thus the 1970 Conservation of Seals Act was passed to regulate the hunting of both grey and harbour seals through restricted methods of culling and close seasons. In order to placate fishermen, the government gave permission to kill seals if they were a threat through, for example, damaging fishing equipment. This was the so-called "Fishermen's Defence". The Conservation of Seals Act remains one of the most stringent protective measures for any non-endangered species in Britain (Scottish Executive, *pers. comm.*).

Sealing continued until 1973 when a complete ban on hunting harbour seals was put in place in certain areas such as Shetland. In response to continued concern about the condition of the stock (Brown & Pierce, 1997), harbour seals remained protected in Shetland till 1998, despite an increase in numbers (Hiby *et al.*, 1993).

Complete protection of harbour seals around the British coast was put in place for a period of two years following an outbreak of phocine distemper virus (PDV) in 1988 (see *Natural and anthropogenic threats* above). With the return of PDV in 2002, the 'close season' was extended under a Conservation Order (2002), restricting the taking or killing of grey and harbour seals in Scotland for a period of two years.

At present there is no commercial harvest of seals in the waters of the European Union and the most recent minimum population count of about 34,000 harbour seals in the UK, 90% of which were counted in Scotland, is likely to indicate a total population of around 50,000 – 60,000 harbour seals (SCOS, 2005). Nevertheless, although harbour seals are not listed as endangered or vulnerable at the global level (according to the IUCN World Conservation Union red list, 2006), many human activities influence harbour seal populations and their habitats (see *Natural and anthropogenic threats* above). Further, the current legislation for marine species is both limited and flawed, principally due to the wording and an inability to give any real effect to measures

through enforcement (Laffoley & Bines, 2000). Three principle statutory measures are currently available to deliver marine conservation in the UK:

- Marine Nature Reserves (MNRs), which offer limited protection to habitats and species in just a few small scattered areas. Largely seen to have failed, MNRs require 100% agreement before being put in place;
- Schedule 5 of the Wildlife and Countryside Act provides a mechanism to afford protection to specified marine species (though it excludes seals);
- The 1992 Council Directive on the Conservation of Habitats and of Wild Fauna and Flora, commonly known as the Habitats Directive, has measures for some wide ranging marine species and requires the development of protected sites, known as Special Areas of Conservation (SACs), for species of European importance. Thus under certain circumstances more widespread protection is offered.

At a European level, both grey and harbour seals have been protected since the 1979 Berne Convention on the Conservation of European Wildlife and Natural Habitats, which lists both species on Appendix III; this requires exploitation to be regulated and the use of 'close seasons' to maintain the population at a level corresponding to "ecological, scientific and cultural requirements, while taking account of economic and recreational requirements". Further, they are protected under the 1992 Habitats Directive (Appendix I), which aims to maintain or restore listed species, including the harbour seal, to "favourable conservation status" within the European Union. The conservation status of a species is defined as "the sum of the influences acting on the species concerned that may affect the long-term distribution and abundance of its population within the territory". Thus the conservation status will be taken as favourable when data indicate that the population is "maintaining itself on a long-term basis as a viable component of its natural habitats and the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future and there is, and probably will continue to be, a sufficiently large habitat to maintain its populations on a long-term basis". Grey and harbour seals are also protected in the Baltic and Wadden Seas under Appendix II of the Bonn Convention on Migratory Species (1979).

Table 1.1: National and European legislation affecting seals inside the seaward limits of Scottish territorial waters.

Year	Legislation	Duration	Seal	Area	PROTECTION/ REQUIREMENTS
1914	Grey Seals Protection Act	5 years, extended	*H.grypus*	Scotland	Prohibition of killing, injuring or capturing seals during the close season of 1st October to 15th December.
1932	Grey Seals Protection Act		*H.grypus*	Scotland	Close season extended to 1st September to 31st December.
1970	Conservation of Seals Act	Indefinite	*H.grypus* *P.vitulina*	England, Wales & Scotland	Close season for greys: 1st September to 31st December; Close season for harbours: 1st June to 31st August; Restricted methods of killing; A licence to kill may be granted for scientific or educational purposes, to prevent damage to fisheries or to reduce population surplus for management purposes.
1973	Conservation of Seals (Scotland) Order	Indefinite	*P.vitulina*	Shetland Islands	Year-round close season within the seaward limits of territorial waters.
1979	Convention on the Conservation of European Wildlife and Natural Habitats (Berne Convention)	Indefinite	*H.grypus* *P.vitulina*	Europe *	Use of close seasons and/or other procedures regulating exploitation; Temporary local prohibition of exploitation in order to restore satisfactory population levels.
1988	Conservation of Seals (Common Seals) Order	2 years	*P.vitulina*	England, Wales & Scotland	Year-round close season in Great Britain and within the seaward limits of the adjacent territorial waters.
1990	Conservation of Seals (Common Seals) (Shetland Islands Area) Order	1 year	*P.vitulina*	Shetland Islands	Year-round close season within the seaward limits of territorial waters.
1991	Conservation of Seals (Common Seals) (Shetland Islands Area) Order	Indefinite, lifted 1998	*P.vitulina*	Shetland Islands	Year-round close season within the seaward limits of territorial waters.
1992	Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (Habitats Directive)	Indefinite	*H.grypus* *P.vitulina*	European Union †	Network of Special Areas of Conservation should be set up to allow species' habitats to be maintained or restored to a favourable conservation status such that the natural range is not reduced; Monitoring of conservation status of species.
2002	Conservation of Seals (Scotland) Order	2 years	*H.grypus* *P.vitulina*	Scotland	Year-round close season for grey seals in the Moray Firth; Year-round close season for harbour seals in the adjacent territorial waters of Scotland.
2004	Conservation of Seals (Scotland) Order	Indefinite	*H.grypus* *P.vitulina*	Scotland	Year-round close season for grey and harbour seals in the Moray Firth;

* Signatories: Albania, Andorra, Austria, Azerbaijan, Belgium, Bulgaria, Burkina Faso, Croatia, Cyprus, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Iceland, Ireland, Italy, Latvia, Liechtenstein, Lithuania, Luxembourg, Malta, Moldova, Monaco, the Netherlands, Norway, Poland, Portugal, Romania, Senegal, Slovakia, Slovenia, Spain, Sweden, Switzerland, the former Yugoslav Republic of Macedonia, Tunisia, Turkey, Ukraine, United Kingdom.

† Austria, Belgium, Cyprus, the Czech Republic, Denmark, Estonia Finland, France, Germany, Greece, Hungary, Ireland, Italy, Latvia, Lithuania, Luxembourg, Malta, the Netherlands, Poland, Portugal, the Slovak Republic, Slovenia Spain, Sweden and the United Kingdom.

The Habitats Directive requires countries within the European Union to set up a "coherent ecological network" of sites of European importance, known as *Natura 2000*, comprising:

- Special Protection Areas (SPAs) for birds, according to the Council Directive on the Conservation of Wild Birds (1979), and
- Special Areas of Conservation (SACs) for habitat types listed in Annex I of the Habitats Directive, and plants and animals, including the harbour seal, listed in Annex II of the Directive.

Member states must report to the European Commission every six years on the conservation status of each site designated under the Habitats Directive and, if they "deem it necessary", can restrict the wild capture and exploitation of listed species, including harbour seals and subject them to "management measures".

At present there are eight SACs for harbour seals in Scotland (Figure 1.2, Table 1.2), and one in England. A further area in the Sound of Barra is still under consideration. In due course these SACs will have conservation objectives designed to protect seals from disturbance, and their habitats from deterioration (Scottish Executive, *pers. comm.*).

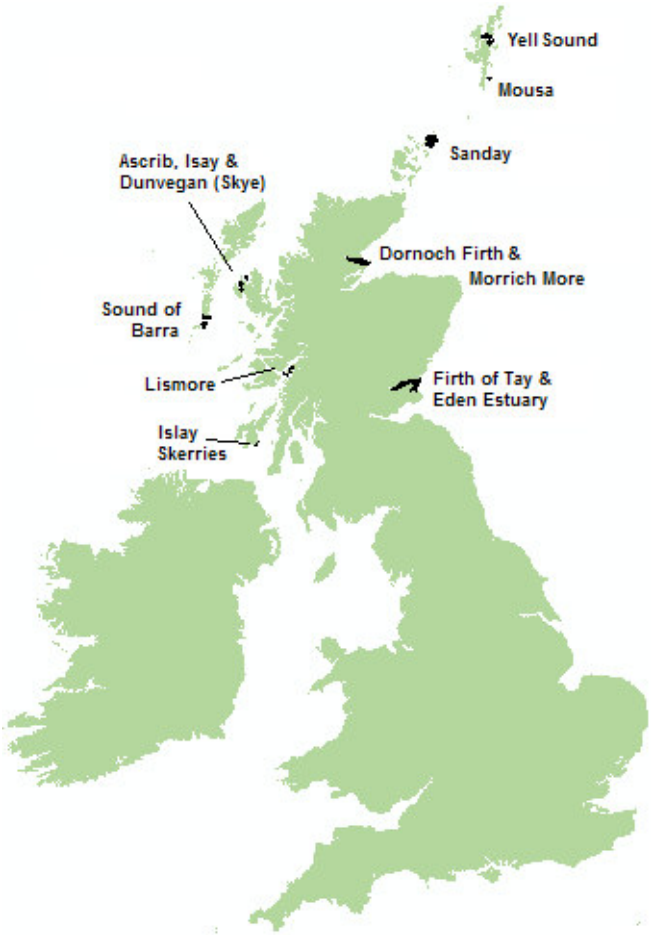

Figure 1.2: Location of Special Areas of Conservation (SACs) for harbour seals in Scotland.

Adequate monitoring of the seal population is required to aid decisions over whether or not control measures need to be put in place in certain areas. Current control measures include scaring animals away from fish farms (Yurk & Trites, 2000; Terhune *et al.*, 2002) or culling seals directly (UNEP., 1999). However, as with their conservation, the removal of seals is a controversial issue with a number of socio-political, economic and ecological components.

Table 1.2: Details of Special Areas of Conservation (SACs) for harbour seals in Scotland, as designated in compliance with the Habitats Directive.

SAC	Description	Population (% of UK)	Area (km^2)
Yell Sound, Shetland	Although primarily designated for otters, the rocky shores and uninhabited islands and skerries support harbour seals in the most northerly selected site in the UK.	> 1%	15.4
Mousa, Shetland	The large rocky tidal pools on the island situated off the south-east mainland are of particular importance for pupping, breeding and moulting, as well as providing shelter from the exposed conditions on the open coast.	> 1%	5.3
Sanday, Orkney	Breeding groups of harbour seals are found on intertidal haul-out sites, whilst the surrounding nearshore kelp beds are important foraging areas. The colony is also linked to a very large surrounding population.	> 4%	109.7
Ascrib, Isay & Dunvegan, Skye	A complex of skerries, islets, undisturbed mainland shores and offshore islands, this site represents one of the larger discrete colonies of harbour seals in the UK that consistently supports a breeding colony.	≈ 2%	25.9
Sound of Barra, Western Isles	Haul-out sites are dispersed over a wide area but this site is still under consideration.		
Lismore, Loch Linnhe	The low-lying island is composed of the largest expanse of coastal limestone in western Scotland and provides sheltered and enclosed haul-out sites on offshore islands and skerries.	≈ 2%	11.4
Islay, Inner Hebrides	The skerries, islands and rugged coastline of the island are extensively used as pupping and moulting haul-out sites. The surrounding sandbanks, reefs and dense kelp forests provide an important food supply.	1.5 - 2%	15.0
Dornoch Firth & Morrich More	The seals that utilise the sandbars and shores at the mouth of the estuary as haul-out and breeding sites are the most northerly population to utilise sandbanks.	≈ 2%	87.0
Firth of Tay & Eden Estuary	A nationally important breeding colony of harbour seals utilising sandbanks to rest, pup and moult.	≈ 2%	154.1

Monitoring harbour seal abundance

Harbour seals spend much of their lives at sea where they are difficult to count; it is easier to count them when they haul ashore and most surveys are of hauled out animals (Boveng *et al.*, 2003). Although there are temporal differences in the numbers of harbour seals found ashore (see *General characteristics* above), in most areas the greatest numbers of seals are hauled ashore during the annual moult (Thompson & Harwood, 1990; Boveng *et al.*, 2003; Harris *et al.*, 2003). However, all demographic components of the population do not moult at the same time, as a consequence the overall timing of the moult may vary spatially and temporally (Thompson & Rothery, 1987; Härkönen *et al.*, 1999; Daniel *et al.*, 2003).

The greatest number of harbour seals is seen ashore during the early afternoon or two hours either side of low tide (Allen *et al.*, 1984; Yochem *et al.*, 1987; Thompson *et al.*, 1989; Watts, 1996; Simpkins *et al.*, 2003). However, haul-out behaviour is affected by many environmental covariates, which make it difficult to compare counts from different surveys. Statistical methodologies are therefore being developed to estimate the effects of covariates, such as weather, on the number of animals seen, thus improving monitoring accuracy and precision, and improving estimates of abundance (Frost *et al.*, 1999; Small *et al.*, 2003; Ver Hoef & Frost, 2003; Chapter 4).

The minimum size of the Scottish population is estimated to be 29,500 animals (SCOS, 2005), and some authors have reported an overall increase in harbour seal abundance since the 1988 phocine distemper virus outbreak (e.g. Hiby, 1996). However, Lonergan *et al.* (2007) found that there was strong evidence for a major decline in most of the major British harbour seal colonies on the east coast (e.g. Shetland, Orkney, the Moray Firth and the Wash) since 2001. Harbour seal populations on the west coast of Scotland, including those that haul out on the Isles of Islay and Skye where parts of this study were carried out, have remained relatively constant over the last 18 years (SCOS, 2005).

The Habitats Directive requires that the harbour seal populations are monitored to determine trends in abundance and current status. A number of different techniques

are currently used to survey harbour seals in order to estimate regional abundance. These are described briefly below.

Land-based counts

Land-based counts provide detailed information for specific sites and, as well as being relatively cheap, they provide a good opportunity to obtain a prolonged series of counts from the same site. Consequently a number of studies have used land-based counts to look at trends in abundance of harbour seals and the factors influencing haul-out behaviour (e.g. Brown & Mate, 1983; Grellier *et al.*, 1996; Hayward *et al.*, 2005; Chapter 4). However there is a potential to miss seals hidden by others if the vantage point is not sufficiently high up or where some animals are hauled out on the far side of a rocky skerry. In addition, it is difficult to maintain the same effort at different sites, and there are potential access problems to some sites.

Boat counts

Counts of harbour seals conducted from small boats may provide information on size classes, and potentially the health status, of the seals being counted. The precise location can be obtained and there is good access to a number of coastal and island haul-out sites. However, as with land-based counts, some seals may be missed (Chapter 3) and using boats is heavily weather dependent.

Aerial surveys

Aerial surveys overcome some of the limitations of land- and boat-based counts. Surveys can be conducted from a fixed-wing aircraft (using binoculars [e.g. Frost *et al.*, 1999], hand-held 35mm cameras [e.g. Boveng *et al.*, 2003] or a large vertical camera mounted in the floor [e.g. Thompson *et al.*, 2005]), or from a helicopter using a hand-held camera or a thermal imager with a telescope (e.g. Chapter 4; SCOS, 2005). These surveys provide repeatable, consistent and complete coverage of haul-out sites with accurate counts of all the groups of seals in a short period of time without disturbance (Duck, 2003). However, groups of seals may be missed, and a large amount of post-processing is necessary. Although they provide rapid access to haul-out sites, helicopter surveys are expensive due to costly transit time between surveyed areas. Moreover they are constrained by weather conditions.

All of the survey methods described above involve counting seals when they are hauled out and thus visible (Reijnders, 1978; Payne & Selzer, 1989; Boveng *et al*., 2003). Although high-speed colour film can be used to distinguish seals from a rocky shore background (Thompson & Harwood, 1990), counts made using thermal imaging are up to 40% higher than those made from fixed wing aircraft (Hiby *et al.,* 1996). Thermal imaging is therefore likely to be the most accurate monitoring method at present for harbour seal populations in most parts of Scotland.

Telemetry

Like land- and boat-based counts, aerial surveys only produce a minimum estimate of the population and a correction factor is required to account for the animals that are not hauled out at the time of the survey (Huber *et al.*, 2001). Because little is known about the extent to which hauled out seals are representative of the population (Härkönen *et al.*, 1999), it is necessary to either estimate the proportion of seals that are in the water at the time of survey, or to assume that this proportion does not vary temporally or spatially in order to assess long-term trends (Thompson & Harwood, 1990).

Several studies have used telemetry to estimate the proportion of seals hauled out at a given time (Pitcher & McAllister, 1981; Stewart & Yochem, 1983; Yochem *et al.,* 1987; Sharples, 2005; Chapter 2). This assumes that the age and sex composition of the tagged sample is representative and that the proportion of the population hauled out is consistent over time. Estimates of the number of harbour seals ashore during peak haul-out times vary between 50 - 74% (Huber *et al.*, 2001) and 79 - 88% (Olesiuk *et al.*, 1990). These differences are presumably due to regional variations in haul-out behaviour. During the rest of the year, individuals spend between 10 - 30% of their time hauled out (Thompson *et al.*, 1998; Chapter 2).

In addition to their use for determining correction factors, a number of datalogging devices have been used to investigate movements, physiology and behaviour of animals at sea:

(a) Many marine studies have used time-depth recorders (TDR) that record data (e.g. depth, velocity, temperature, light levels) at user-defined intervals until the tag is recovered or until its memory is full (Hooker & Baird, 2001). These tags are also known as archival recorders because individuals must be recaptured to retrieve data (e.g. Kooyman, 1965; Naito *et al.*, 1990; Boyd & Arnbom, 1991; McCafferty *et al.*, 1998);

(b) Short-term studies on grey seals have benefited from ultrasonic telemetry (Thompson *et al.*, 1991). However these studies are limited because signals transmitted from acoustic tags can only be received within two kilometres of the tagged animal (Goodyear, 1993). Lowering the frequency of the transmissions to increase range is unlikely to be effective because the resulting transmissions are likely to be within the hearing range of the animal and therefore to affect its behaviour (Hooker & Baird, 2001);

(c) Tags can transmit data remotely via VHF signals to a nearby receiver or by UHF signals to a satellite whenever an antenna comes above the water surface (see below);

(d) Advances in miniaturised imaging technology have seen a number of marine studies using cameras to record behaviour (e.g. Marshall, 1998; Hooker *et al.*, 2002; Davis *et al.*, 2003; Takahashi *et al.*, 2004);

(e) GSM (Global System for Mobile Communications) mobile phone technology has recently been tested for use in survivorship studies (McConnell *et al.*, 2004). The signals from these phone-tags, which automatically attempt to send a Short Message Service (SMS) text message once every two days, can only be received when animals are relatively close to the shore. However, archived information can be transmitted at these times, so at-sea behaviour can be monitored when a Global Position Service receiver is combined with the tag;

(f) The Life History Transmitter (Horning & Hill, 2005) is an implantable tag designed to collect data from marine vertebrates for up to a decade. Data are transmitted to orbiting satellites after the tagged animal dies and its body has decayed.

VHF transmitters have been used on a number of species of seal despite their limited range (20 – 30 km, depending on the power of the transmitter and the height of the

transmitting and receiving antennas – Antonelis *et al.*, 1990; Thompson *et al.*, 1996). As a consequence, most harbour seal studies using VHF radio-tracking techniques have concentrated on near-shore behaviour (Pitcher & McAllister, 1981; Brown & Mate, 1983; Thompson, 1989). Some (e.g Thompson & Miller, 1990) have looked at foraging range and feeding areas, but studies using this approach have been limited in duration and it is only applicablein locations where foraging occurs in inshore waters.

Satellite tracking transmitters relay data to orbiting satellites. Unlike traditional VHF telemetry this means that foraging range does not affect the ability to obtain positional information. Satellite tracking has been used to track long-distance movements of seabirds (Jouventin & Weimerskirch, 1990), turtles (Hays *et al.*, 2001), seals (Le Boeuf *et al.*, 2000) and whales (Mate *et al.*, 1995). Although the number of transmissions is limited by the amount of time seals spend above water, and the reliability of the uplink depends on whether environmental and atmospheric factors degrade the transmitter signal, the transmitters have provided information on the at-sea distribution and movements of grey seals (McConnell *et al.*, 1992; Thompson *et al.*, 1991) and of harbour seals (Stewart *et al.*, 1989; Sharples, 2005; Chapter 2). When combined with a wet-dry sensor, satellite transmitters also provide information on the duration and proportion of time individual seals spend hauled out (Chapter 2).

Satellite telemetry has the major advantage of rendering ship-based tracking and tag recovery unnecessary whilst potentially increasing sampling time. It therefore provides a comparatively large amount of information from each study animal (Hooker & Baird, 2001). However increased sampling time, likely to increase the probability of detecting long-term variation and extremes within the data (Link & Sauer, 1996), is not equivalent to increased sample size, which may be constrained due to the costs associated with this method. Despite major technological advances since the first deployment of mechanical depth recording devices on diving seals (Kooyman, 1965), a number of limitations still remain. In particular, device attachment and battery life have restricted the duration of many telemetry studies.

Several studies have compared the accuracy of satellite positions determined under field conditions with those reported by ARGOS (e.g. Vincent *et al.*, 2002; White &

Sjöberg, 2002). Although these inaccuracies can mask small-scale and/or short-duration movements, satellite transmitters provide insight into the biology of animals when they cannot otherwise be seen. To reduce tag size and power consumption, the number of transmissions by the tag is often limited and the amount of data per transmission is constrained by the bandwidth available. Nevertheless, satellite telemetry provides information on animals over a relatively long time period. As a result, they are particularly useful for conservation and management oriented studies.

Capture-recapture methods

Capture-recapture analysis uses data on the number of marked animals, and the proportion of marked animals seen in subsequent surveys, to estimate population size and demographic rates. Studies using capture-recapture often rely on adding artificial tags or marks to individuals specifically for recognition (White *et al.*, 1987; Hindell, 1991; Hastings *et al.*, 1999; Hall *et al.*, 2001), or on removing or altering part of the animal itself (e.g. toe clipping: Parris & McCarthy, 2001). However harbour seals have unique and permanent pelage patterns allowing individuals to be recognised from photographs of their natural markings (Middlemas, 2003; Mackey, 2004; Chapter 3).

Recognising individuals from natural markings has been widely used in mammal (e.g. Kelly, 2001; Heilbrun *et al.*, 2003), bird (Bretagnolle *et al.*, 1994) and reptile (Sheldon & Bradley, 1989) studies. It is, however, harder to recognise individuals from their natural markings than from an artificial tag (Hammond, 1986). This may lead to false positive recoveries (in which one individual is mistaken for another) or false negatives (if markings are indistinct or so similar that several individuals are indistinguishable). In the case of seals, marks may be harder to determine at certain times of year and may appear different according to how wet or dry the individual is during the survey. Natural markings may also change with time or become unrecognisable through extensive scarring.

Accessibility and visibility of the seals are crucial to the application of this technique and may not be available at all sites. Weather conditions, photographer experience, and the proximity of seals are factors that may limit the ability to produce high quality

photographs consistently. Nevertheless, the indirect nature of photo-identification techniques mean that all 'captures' are non-invasive, instead relying on identifying individuals from natural markings. It is therefore particularly useful in situations where there is concern about disturbance of endangered or protected species, and/or where capturing individuals is difficult. Using natural markings has the ethical advantage of not putting the animal in any discomfort and also ensures that the 'capture' will not affect the animal's behaviour and thus influence the probabilities of capture or survival.

Capture-recapture studies are usually limited in spatial extent (but see Stevick *et al.*, 2003) and the derived abundance estimates are dependent on a number of assumptions, which are discussed extensively by Seber (1982), Hammond (1986) and Pollock *et al.* (1990). There are a number of different capture-recapture models, each with its own strengths and weaknesses. There are two main types: closed and open population models, where the term 'population' refers to the number of individually identifiable animals within the study area for the duration of the study.

1. Closed population models

Many capture-recapture models assume that the population is closed, i.e. that the population size is constant with neither additions (immigration or births) nor losses (emigration or death) to the population between surveys. This is rarely the case in natural populations and consequently population closure is defined as meaning there are no unknown changes to the initial population (Otis *et al.*, 1978). Thus it is only a reasonable assumption when the study is of relatively short duration (Wilson *et al.*, 1999) and intervals between capture and recapture are kept short (Abt *et al.*, 2002).

A number of studies suggest that harbour seals are site-faithful (Chapter 2; Anderson, 1981; Yochem *et al.*, 1987; Thompson, 1989; Härkönen & Harding, 2001) and therefore that migratory movements can be ignored. However some individuals may use different haul-out sites throughout the year (Brown & Mate, 1983; Thompson, 1989; Thompson *et al.*, 1996; Simpkins *et al.*, 2003) and it is possible that there is both permanent and temporary immigration and emigration.

For estimates based only on two surveys (an initial capture, and one subsequent recapture), the conventional approach is to use the Lincoln-Petersen estimator:

$$N = \frac{n_1 n_2}{m}$$

where N = estimate of total population size,

n_1 = total number of animals captured on first visit,

n_2 = total number of animals captured on second visit,

m = number of animals on the first visit recaptured on the second visit.

When more surveys are conducted it is possible to fit a number of different models, that examine behavioural and temporal variation in recapture probability, as well as individual capture heterogeneity (e.g. Otis *et al.*, 1978; Chapter 3).

2. Open population models

Open population models are applicable where immigration, emigration and re-immigration occur either within or between field seasons, e.g. in sperm whales (Childerhouse *et al.*, 1995). Population estimates from these models are usually less precise than those estimated from closed population models and do not allow for heterogeneity of capture probabilities (Pollock *et al.*, 1990; Wilson *et al.*, 1999).

Remote photography

Remote photography has been used for a wide range of applications, including denning behaviour in bears (Bridges *et al.*, 2004), nesting in birds (e.g. Booms & Fuller, 2003) and abundance estimates of jaguars (Silver *et al.*, 2004). Remote photography can be less time consuming, less costly, and less invasive than traditional research methods (Cutler & Swann, 1999), and provides information on harbour seal abundance and disturbance factors throughout the tide, day and season (Allen *et al.*, 1984; Thompson & Harwood, 1990). Abundance estimates can therefore be based on several counts at no additional cost. However, the restricted field of view of the camera limits the extent of the site being monitored, potentially missing animals that have moved only short distances along the shore, thus requiring the use of several cameras to cover each group of haul-out sites. There is a potential difficulty in finding suitable vantage points and a number of maintenance and housing issues need to be addressed (Boveng *et al.*, 2004). Camera security is also an issue in many locations.

Thesis structure

The past 15 years show little evidence of significant trends in the overall harbour seal population on the west coast of Scotland (where some of the studies reported in this thesis were conducted), but uncertain estimates must be improved given the legal conservation status of seals and the current potential decline in harbour seals on the east coast of Britain (Lonergan *et al.*, 2007). Improving our knowledge of harbour seal abundance and seasonal variability will allow the status of the population to be monitored more precisely and will assist in determining the role of SACs for harbour seals in Scotland. In addition, the effectiveness of such a policy for mobile marine animals is still debatable, and management measures encompassing a wide range of priorities remain to be devised. This thesis uses a number of the methods outlined above to address the key questions outlined in Table 1.3, with the overall aims of:

i) Improving the monitoring of harbour seal (*Phoca vitulina*) populations in Scotland, especially within Special Areas of Conservation; and

ii) Determining the effectiveness of land-based protected areas, such as Special Areas of Conservation for harbour seals.

Table 1.3: The methods used to answer the key questions in this study.

	Key question	**Satellite telemetry**	**Photo-ID**	**Ground counts**	**Aerial surveys**
1.	What proportion of time is spent at haul-out sites and what factors affect the frequency with which individual harbour seals haul out?	√			
2.	With what frequency do seals move between nearby haul-out sites?	√	√		
3.	How important are haul-out sites within land-based protected areas relative to those elsewhere?	√	√		
4.	Are haul-out sites closely linked geographically to foraging locations?	√			
5.	What is the trend in harbour seal abundance at haul-out sites?		√	√	√
6.	Can monitoring 'trend sites' be representative of the wider trends in harbour seal abundance?			√	√
7.	Do numbers of seals plateau during the moult? If so, can the timing and duration of this plateau be predicted for future surveys?			√	
8.	What coefficient of variation should be used to compare counts of seals?		√	√	√

Understanding the geographical relationship between where harbour seals haul out, and consequently are counted, and their movements is crucial to understanding the usefulness of land-based protected areas, such as SACs. Chapter 2 therefore looks at the movements of individual harbour seals, tracked using satellite telemetry, and the location and time spent hauled out. Spatial, temporal and sex-related variation in the proportion of time harbour seals spent hauled out were apparent and so it is likely that variation also occurs during the moult, when harbour seal abundance is currently surveyed. Chapter 3 therefore tests the use of photo-identification and capture-recapture techniques as a monitoring method that accounts for heterogeneity in the proportion of time individual seals spend hauled out, and chapter 4 accounts for the variation in current survey methods in order to determine the conservation status of harbour seals. Chapter 5 examines whether monitoring SACs is sufficient to determine the conservation status of the population as a whole, and assesses the predicted length of time to detect a change in harbour seal abundance at different levels of monitoring precision and frequency. The results and their implications are discussed within the context of the literature throughout the thesis and more broadly in chapter 6.

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CHAPTER TWO

USING SATELLITE TELEMETRY TO DETERMINE HARBOUR SEAL MOVEMENTS AND HAUL-OUT PATTERNS

ABSTRACT

This study used satellite transmitters deployed on 10 harbour seals in south-west Scotland and 14 in north-west Scotland to examine movements and haul-out patterns. Two geographical scales of movement were apparent. Generally seals made short trips to within 25 km of a haul-out site, often (40% of the time) returning to the haul-out site they last used. Thus a degree of site-fidelity and coastal foraging was apparent. However some individuals occasionally undertook longer distance movements of over 100 km, indicating that there was at least some mixing between regions. Around half of the trips lasted between 12 and 24 hours, with the longest recorded trip lasting over nine days (217 hours). The proportion of time harbour seals were hauled out (daily means of between 11 and 27%) varied spatially, temporally and according to sex. The mean haul-out duration was five hours, with a maximum of over 24 hours. Of the time seals spent hauled out, 18% occurred within the harbour seal Special Areas of Conservation where the transmitters were deployed.

INTRODUCTION

Like many other pinnipeds, harbour seals spend a significant amount of time hauled out on beaches, sandbanks and rocks (Stevick *et al.*, 2002), especially during the breeding and moulting seasons. Consequently most information on the abundance and distribution of harbour seals is based on observations at haul-out sites (e.g. Bonner, 1972; Boveng *et al.*, 2003) and these sites have therefore been the focus of legislative protection. Because seals spend a proportion of their time at sea, counting seals at haul-out sites provides a minimum population estimate. However little is known about the extent to which hauled out seals are representative of the population of seals within any specified region (Härkönen *et al.*, 1999). To assess long-term trends in abundance it is therefore necessary to either estimate the proportion of seals that are in the water at the time of survey, or to assume that this proportion does not vary temporally or spatially (Thompson & Harwood, 1990).

Increasingly studies have used radio telemetry methods to obtain information about the proportion of time animals spend at sea, which can be used to correct the counts of animals hauled out to provide an estimate of the absolute abundance (Eberhardt *et al.*, 1979; Pitcher & McAllister, 1981; Yochem *et al.*, 1987; Thompson & Harwood, 1990; Thompson *et al.*, 1997; Huber *et al.*, 2001; Sharples, 2005). Telemetric devices, such as satellite transmitters, have also been used to investigate movements, physiology and behaviour of harbour seals (Stewart *et al.*, 1989; Sharples, 2005), grey seals Thompson *et al.*, 1991a; McConnell *et al.*, 1992, seabirds (Jouventin & Weimerskirch, 1990), cetaceans (Mate *et al.*, 1995), turtles (Hays *et al.*, 2001) and polar bears (Mauritzen *et al.*, 2002). Unlike traditional VHF telemetry which uses ground-based receiving stations (e.g. Brown & Mate, 1983; Thompson, 1989), satellite transmitters relay data to orbiting satellites, and as a result foraging range does not affect their ability to obtain positional information.

Telemetry studies have shown that harbour seals in north-east Scotland make relatively local movements around their breeding sites throughout the year (Thompson & Miller, 1990; Thompson *et al.*, 1991b), and suggest that harbour seals show a

degree of site-fidelity (Thompson, 1989). VHF radio-telemetry also has shown that juvenile harbour seals remain in the area of birth for at least three to four months (Corpe, 1996). However, other marking studies have shown that some harbour seals disperse widely from their natal sites in the post-weaning period (e.g. Bonner & Witthames, 1974; Thompson *et al.*, 1994a; Härkönen & Harding, 2001) and that seals use different haul-out sites throughout the year (Brown & Mate, 1983; Thompson, 1989; Thompson *et al.*, 1996; Simpkins *et al.*, 2003).

The significance of abundance trends depends on the variability in harbour seal haul-out behaviour, including the effect of tidal cycles (Schneider & Payne, 1983; Watts, 1996; Simpkins *et al.*, 2003), time of day (Thompson, 1989; Frost *et al.*, 1999; Boveng *et al.*, 2003), season (Thompson, 1989) and weather conditions (Godsell, 1988; Kovacs *et al.*, 1990; Grellier *et al.*, 1996). Many previous studies of haul-out behaviour have examined changes in the number of seals hauled out in relation to these factors (Boulva & McLaren, 1979; Stewart, 1984; Chapter 4), but their influence on the haul-out behaviour of individual seals will also determine the extent to which counts of hauled out animals are representative of the population.

The Habitats Directive[1] provides a framework within which Special Areas of Conservation (SACs) have been designated for harbour seals with the aim of maintaining the "favourable conservation status" of harbour seal populations in Europe. To determine the usefulness of harbour seal SACs, and to manage these areas effectively, it is important to understand the extent to which they are used by individual seals. High site-fidelity may lead to SACs protecting a distinct group within the harbour seal population as a whole, whereas longer distance movements of seals would indicate that a larger proportion of the harbour seal population uses the SAC and may receive some level of protection from the legislation. In addition, to determine the conservation status of harbour seals, abundance estimates must account for variation in haul-out behaviour.

[1] The 1992 Council Directive on the Conservation of Habitats and of Wild Fauna and Flora (Appendix I)

Satellite telemetry provides information on animals over a relatively long temporal scale, which is ideal for understanding more about the conservation status of harbour seals and for guidance on the management of SACs. A number of studies have used telemetry to study harbour seal ecology in the North Sea (e.g. Thompson *et al.*, 1997; Ries *et al.*, 1998; SCOS, 2004; Sharples, 2005). However, whilst harbour seals have been tagged at most of the major haul-out sites on the east coast of Britain, no movement or distribution information is available for animals using haul-out sites on the west coast. This study deployed tags in SACs in north-west and south-west Scotland, to provide information on the appropriateness of these areas for harbour seals. The influence of temporal, spatial and endogenous factors on the proportion of time harbour seals were hauled out was investigated, and whether spatio-temporal variables and/or individual characteristics could explain the observed duration of haul-out events and the inter-haul-out interval. The usage of haul-out sites, particularly within SACs, and the duration and extent of trips were also examined.

METHODS

Study locations

Satellite relay data loggers (SRDLs) were deployed on 24 harbour seals in north-west and south-west Scotland between September 2003 and March 2005 (Figure 2.1). In 2003/2004 eight animals were tagged in the SAC in south-east Islay (55°39' N, 6°3'W; Ardbeg Bay and Plod Sgeirean) and two on Jura (Lowlandmans Bay), approximately 25 km further north (Figure 2.1b). A further 14 SRDLs were deployed on harbour seals caught in the SAC on the Isle of Skye (57°29' N, 6°37' W; Eilean Dubh, Sgeir Nam Biast and Mingay) in 2004/2005 (Figure 2.1a). To maximise seasonal coverage, approximately half the deployments occurred after the annual moult (September), and the rest in the spring (March or April).

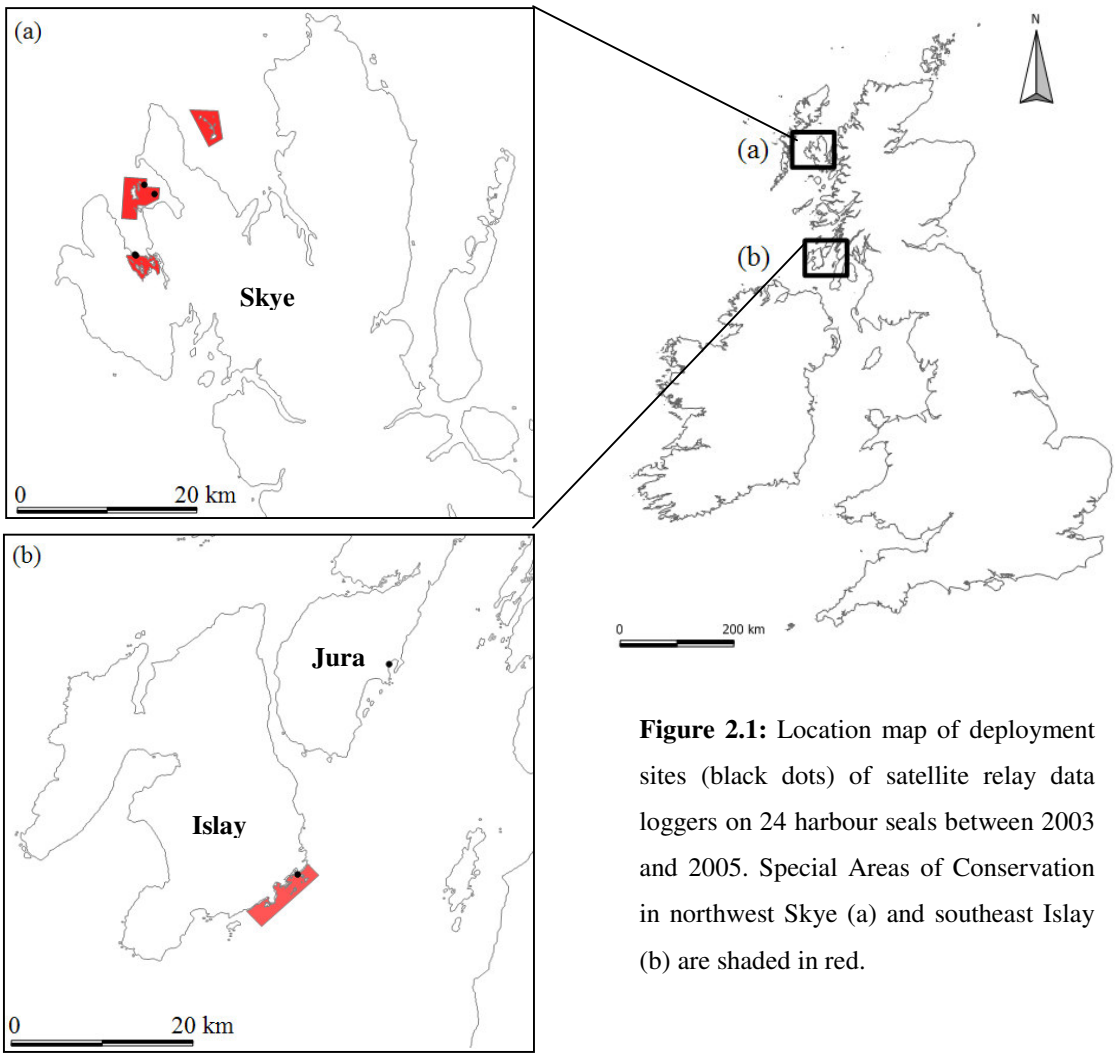


Figure 2.1: Location map of deployment sites (black dots) of satellite relay data loggers on 24 harbour seals between 2003 and 2005. Special Areas of Conservation in northwest Skye (a) and southeast Islay (b) are shaded in red.

Animal selection and capture

Animals were either captured on land or in the water near haul-out sites. A rubber boat (Zodiac, Mark III) was used to approach groups of animals on land. From a distance of approximately 50 m, it was driven onto the shore adjacent to the seals and nets, consisting of a funnel of 10 mm mesh netting attached to a plastic hoop approximately one metre in diameter, were used to capture the seals. Catching animals in the water involved using a six metre rigid inflatable boat (RIB). This was driven alongside a haul-out and a 60 m long by two metre deep tangle net was set close to the shoreline to catch seals as they swam away from the land. This method was only used in shallow water without strong currents that could drag the net down. Adult seals were selected for tagging according to their sex, to maintain a roughly equal sex ratio, and only if they had finished moulting. All other seals were released from the nets.

Using a dose rate of approximately 0.05 mg/kg, the seals selected for tagging were anaesthetised with an intravenous injection of Zoletil (Virbac, France) delivered to the extradural vein using a 18 or 19-gauge needle. Body mass was measured using a 100 kg Salter spring balance (accuracy circa 0.5 kg). Body length, from nose-tip to the end of the tail, and axial girth, at the base of the fore flippers during exhalation were measured to nearest 5 mm. The seal fur at the dorsal base of the skull was then dried with paper towels and methylated spirit, and then cleaned to remove grease with acetone to ensure the glue bonded to the fur. A SRDL was attached to the fur, with two-part rapid setting epoxy resin (Fedak *et al.*, 1983), in a way that allowed the aerial to emerge when the seal surfaced (Figure 2.2). Total handling time was usually less than 20 minutes. All capture and handling procedures were performed under Home Office project licences 60/2589 and 60/3303 and conformed to the Animals (Scientific Procedures) Act 1986.

Figure 2.2: Position of a SRDL attached to the back of the neck of a harbour seal shown hauled out on land and when at the sea surface.

Telemetry system

The SRDLs (Sea Mammal Research Unit, University of St Andrews, Scotland), consisting of a data logger interfaced to an ARGOS transmitter unit, measured 100 x 70 x 45 mm (excluding a 150 mm antenna) and weighed 305 grams in air. These transmitters were well below the maximum 5% of body weight recommended for telemetry studies (Cuthill, 1991). McConnell *et al.* (1999) provide further details of the telemetry system used.

Data from a depth sensor and a wet-dry sensor were used to classify the 'activity' of the seal into one of three categories: 'diving' when deeper than two metres for at least sixteen seconds, 'hauled out' when the sensor remained dry for at least 10 minutes, or 'at surface'. A 'haul-out event' was defined as beginning when the wet/dry sensor remained continuously dry for a 10 minute period and ended when the sensor was wet for a 40 second period. The wet-dry sensor ensured no transmission was attempted whilst the tag was underwater. Records were therefore temporarily stored before transmission by a pseudo-random process such that all times of day were adequately represented, irrespective of diurnal satellite availability and animal behaviour. The distance swum was determined by a turbine odometer mounted on the top of the tag.

Daily and monthly mean proportions of time hauled out were derived from six-hourly summary activity data transmitted by the SRDLs (Fedak *et al.*, 2002). Using the statistical package SPSS, version 12, seasonal (monthly) variation in the proportion of time hauled out was examined with a Kruskal-Wallis test and a Spearman's rank order correlation was used to look at the relationship between the proportion of time hauled out and body mass.

Data processing

The accuracy of location fixes was calculated at the ARGOS ground station and assigned an index, termed Location Quality (LQ). LQ varies from three (highest accuracy) to zero (unguaranteed accuracy) and is primarily dependent upon the number of uplinks to the satellite within a pass (McConnell *et al.*, 1999). Locations with a large degree of error were excluded using an iterative forward/backward averaging filter that rejected locations that required unrealistic rates of travel (McConnell *et al.*, 1992).

The data sets were run through a LQ-weighted smoothing algorithm (M. Lonergan, *pers.comm.*) treating longitude and latitude separately. The resulting locations were not equally distributed through time. To avoid biasing the temporal and spatial distribution of seal activity, new locations were estimated at hourly intervals by interpolation. Using the date and time records, haul-out events were assigned a location from the filtered and smoothed tracks. The nearest secondary tidal port was assigned to each haul-out event and, using POLTIPS version 3, tidal height and phase were estimated every hour for each event.

Haul-out events were automatically allocated an incrementing number. Occasionally information on haul-out events was not transmitted by ARGOS. In this case the gap in numbers was used to detect that a haul-out event had occurred but there was no information about its location, timing or duration. These data were not used for analyses. Haul-out events separated by 15 minutes or less were concatenated together as it was assumed that these were likely to result from brief disturbance of the animal.

Seal movements

'Haul-out sites' and 'haul-out clusters'

Haul-out sites were identified from the locations of harbour seals counted during aerial surveys carried out in 1988 (July & August), 1989 (August), 1990 (August), 1992 (July & August), 1996 (June, July & August), 2000 (July & August), 2003 (August), 2004 (August) and 2005 (August) (C. Duck, *pers. comm.*). Every location on the west coast of Scotland where a harbour seal was observed hauled out during these surveys qualified as a 'haul-out site' (Figure 2.3). Harbour seals appear to use the same haul-out sites consistently from year to year (Anderson, 1981; Thompson, 1989), so it was assumed that these sites were representative of the actual haul-out sites available during the study period. The numbers of haul-out events at haul-out sites within and outwith SACs were compared.

SRDL location accuracy was less than the accuracy with which the haul-out sites were identified during aerial surveys, so haul-out sites that were within five kilometres of each other were grouped into 529 'haul-out clusters' (Figure 2.4). The location of a haul-out cluster was defined as the mean of the location of all the haul-out sites occurring within each grid-cell of a five-kilometre grid projected in GIS package Manifold, version 6.5, using the British Grid projection. Haul-out cluster locations were checked visually to ensure that none were far inland as a result of the clustering process. Each haul-out site and haul-out cluster was given a unique three-letter code. Seasonal patterns in haul-out cluster use were checked visually using MamVis (Fedak *et al.*, 1996), which allowed seal behaviour, including time and location, to be visualised in three dimensions. A Spearman's rank order correlation was used to test for the presence of a correlation between the number of haul-out clusters used by individual seals and the tracking duration.

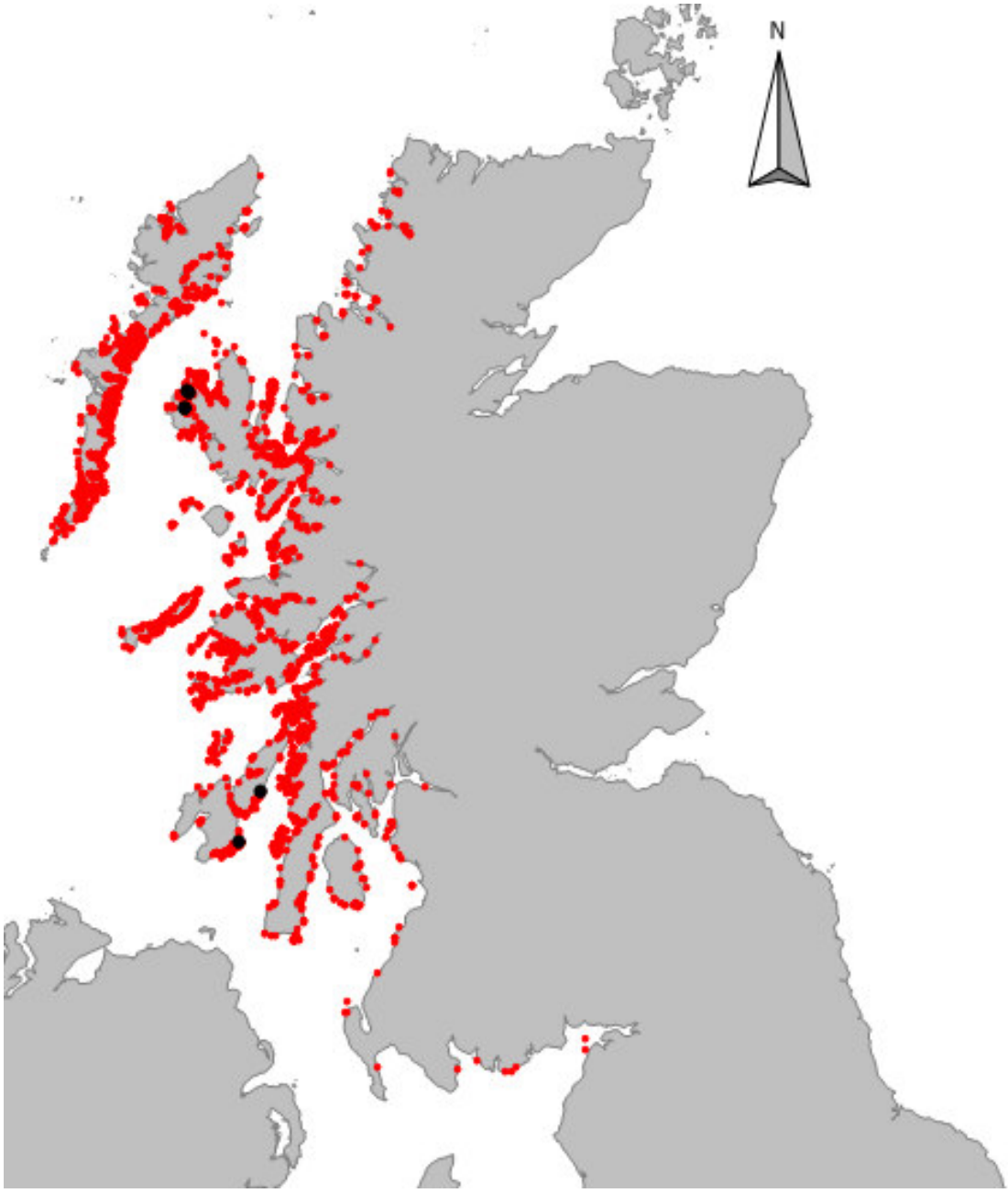


Figure 2.3: Harbour seal 'haul-out sites' identified from aerial surveys of the west coast of Scotland between 1988 and 2005. Deployment sites of SRDLs are illustrated in black.

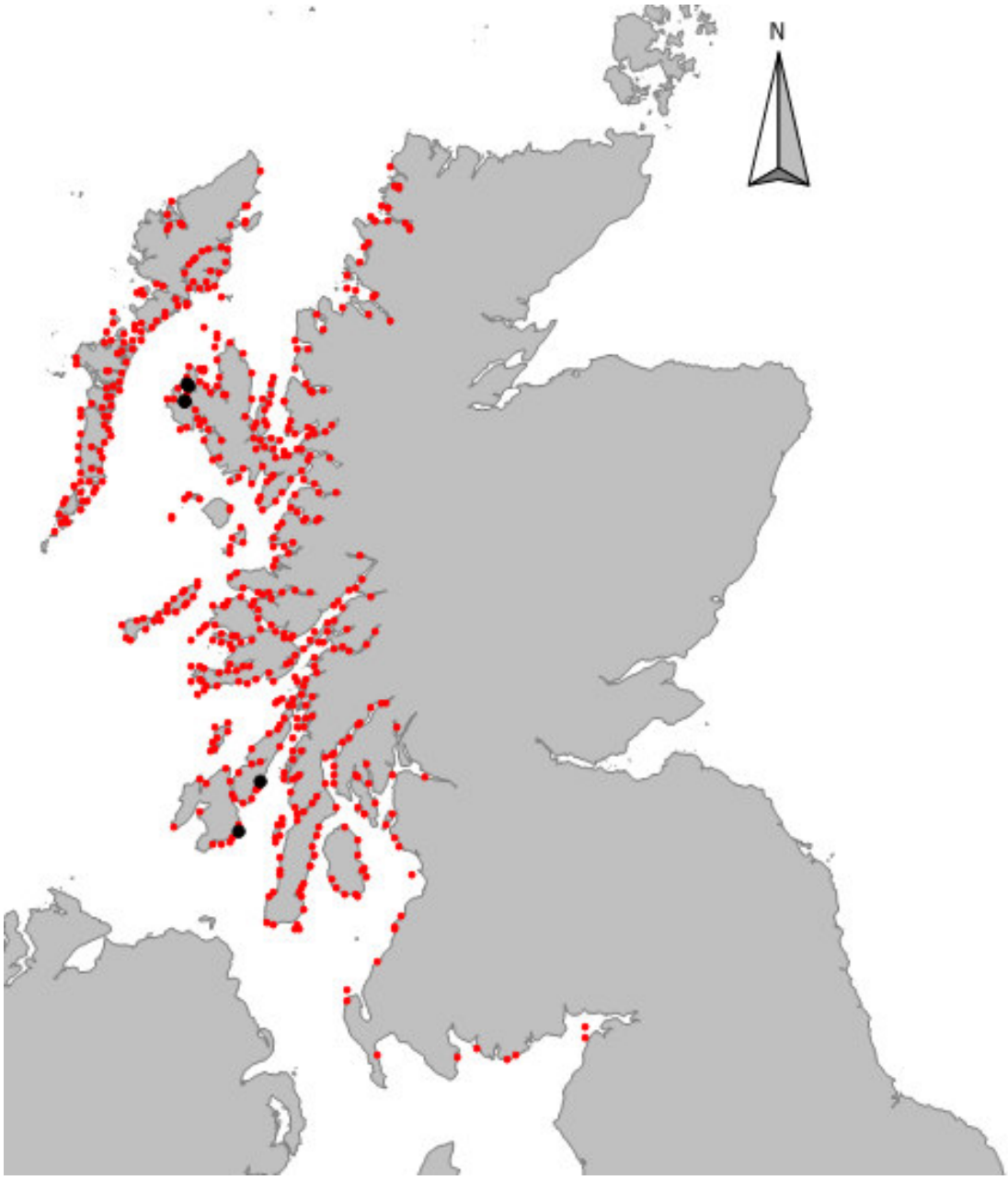


Figure 2.4: Harbour seal 'haul-out clusters' identified from aerial surveys of the west coast of Scotland. Deployment sites of SRDLs are illustrated in black.

The locations of haul-out events provided by the telemetry data were not always on land due to ARGOS location error. Locations were therefore 'snapped' to the nearest known haul-out cluster (B. McConnell, *pers.comm.*). A maximum snapping distance of 15 km was chosen, on the basis that snapping beyond this threshold implied too much uncertainty about the actual location of the haul-out event. Haul-out events that occurred over 15 km from haul-out sites could have taken place in locations not

identified from aerial surveys, could have been the result of a seal remaining motionless at the sea surface such that the wet/dry sensor was dry for the required period of time (10 minutes), or could have been the as a result of particularly large ARGOS location error.

'Travel trips' and 'return-trips'

The frequency and duration of all trips made by tagged harbour seals were recorded. The start and end of a trip was determined when the seal was a pre-specificed distance from a haul-out cluster and when the seal was not classified as being hauled out. This was to avoid inflating the number of trips by including occasions when animals entered the water following disturbance events. Trips specified by distances of 1 and 10 km from haul-out clusters had almost identical durations, and so for the purpose of this study trips were defined as movements of greater than one hour in duration that were more than one kilometre from a haul-out cluster. A 'travel-trip' was defined as a trip in which a seal travelled to a different haul-out cluster from its starting point. A 'return-trip' was defined as one in which the seal returned to the same haul-out cluster. Note that the distinction between travel-trips and return-trips is dependent on the five-kilometre grid used to identify haul-out clusters.

'Trip extent'

'Trip extent' (measured to the nearest one kilometre) was defined as the distance from the centre of a haul-out cluster to the furthest at-sea location. For travel-trips it is therefore the longest of the two possible trip extents.

Association tests were used to examine the presence of any spatial and temporal variation in trip duration and extent. A Mann-Whitney U test was used to look at differences between deployment location (north-west or south-west Scotland) and differences according to the sex of the seals. A Spearman's rank order correlation was used to examine the relationship between trip duration and trip extent, and between body mass and trip duration and body mass and trip extent.

Modelling haul-out behaviour

Model specification

Generalized Linear Mixed Models (GLMM) were constructed (a) to attempt to describe what factors affect the duration of harbour seal haul-out events, and (b) to examine the inter-haul-out interval (IHI) of harbour seals on the west coast of Scotland. The duration of haul-out events can be used to ascertain whether seal surveys are independent events, which is particularly important for designing monitoring protocols. The models used a non-symmetric Gamma distribution and were fitted using penalised quasi-likelihood in software package R, version 2.1, using function glmmPQL(MASS).

Mixed effects models contain a mixture of fixed effects, which are unknown constants to be estimated from the data, and random effects, which can be thought of as coming from a population of effects. The models are therefore particularly useful for individuals that are repeatedly measured through time, as in this study. GLMMs take the general form:

$$f(Y_j) = (\beta_0 + b_{0j}) + (\beta_1 + b_{1j}) \cdot X_{1j} + \ldots$$

where j = the jth individual,

β = the fixed effect: i.e. valid for the whole population,

b_j = the random effect: i.e. individual specific.

The following fixed effect explanatory variables, and their interactions, defined the upper limit of the multivariate regression models: Julian date (from September to mid-August), maximum dive depth since previous haul-out event (in metres), total dive duration since previous haul-out event (in decimal hours) and tidal height at the mid-point of the haul-out event (in metres). The time of the haul-out event and tidal phase at the mid-point of the haul-out event were converted into angles (where one 24 hour cycle = 360º; high water = 0º and 360º, low water = 180º) to allow for their circular nature. For the haul-out duration model the IHI prior to the haul-out event (in decimal hours) was also included, and for the IHI model the duration of the previous haul-out event (in decimal hours) was also included. The individual seal reference code was

used as a random effect, allowing the intercept for haul-out duration or IHI to vary for each seal.

Model selection

A combination of forward and backward stepwise selection (Venables & Ripley, 2002) was used to determine the best-fitting model. Starting with a full model the effect of deleting variables was evaluated, with those variables not contributing significantly to the fit of the model being placed into a pool of candidate variables from where they could be reselected. When comparing models, the number of parameters used should be taken into consideration, such that models with more parameters should be penalised (Hayward *et al.*, 2005). Akaike's information criterion (AIC - Akaike, 1973) is an information-theoretic model selection index designed to select the model closest to the 'truth' from a suite of alternative models (Burnham & Anderson, 2002). Thus the importance of each deleted or added term was evaluated using AIC. Model comparison is based on relative rather than raw AIC values, and so models are ranked according to AIC differences, with the best model having ΔAIC = 0. When models had ΔAIC of less than two the most parsimonious model was chosen (Burnham & Anderson, 2002). The best fitting correlation structure was also determined using AIC. Model selection was carried out in software package R.

Model validation

The model residuals were visually inspected and checked for non-randomness using function acf(stats) in software package R. The explained deviance of the model, *D*, was calculated as:

$$D = \frac{-2\ln L(M_B) + 2\ln L(M_N)}{-2\ln L(M_N)}$$

where $\ln L$ = the log likelihood, M_B = the best fitting model and M_N = the intercept only model.

The models were built to test whether spatio-temporal variables and/or individual characteristics could explain the observed duration of haul-out events. Therefore there was no need to assess the predictive performance of the models by means of cross-

validation, a tool used to assess whether the model captures a persisting biological relationship (Burnham & Anderson, 2002; Olden *et al.*, 2002). Instead, the goodness-of-fit of the final model was investigated using a chi-squared test on model deviance relative to the full model. This test, using the ratio of the likelihoods, assumes that the variance estimated from the residuals of the candidate model reflects the underlying uncertainty in the process and consequently is a measure of discrepancy of the model (McCullagh & Nelder, 1989). The model has an adequate fit if the chi-square goodness-of-fit is not significant (i.e. H_0 = correct model; H_A = model not correct). Goodness-of-fit was estimated in statistical package SPSS.

RESULTS

Data obtained

Each SRDL operated for about four months (range = 31 to 243 days, mean = 126 days), providing information in every month of the year except August when the seals were moulting (Table 2.1, overleaf). However data coverage was not equal for all months (Figure 2.5).

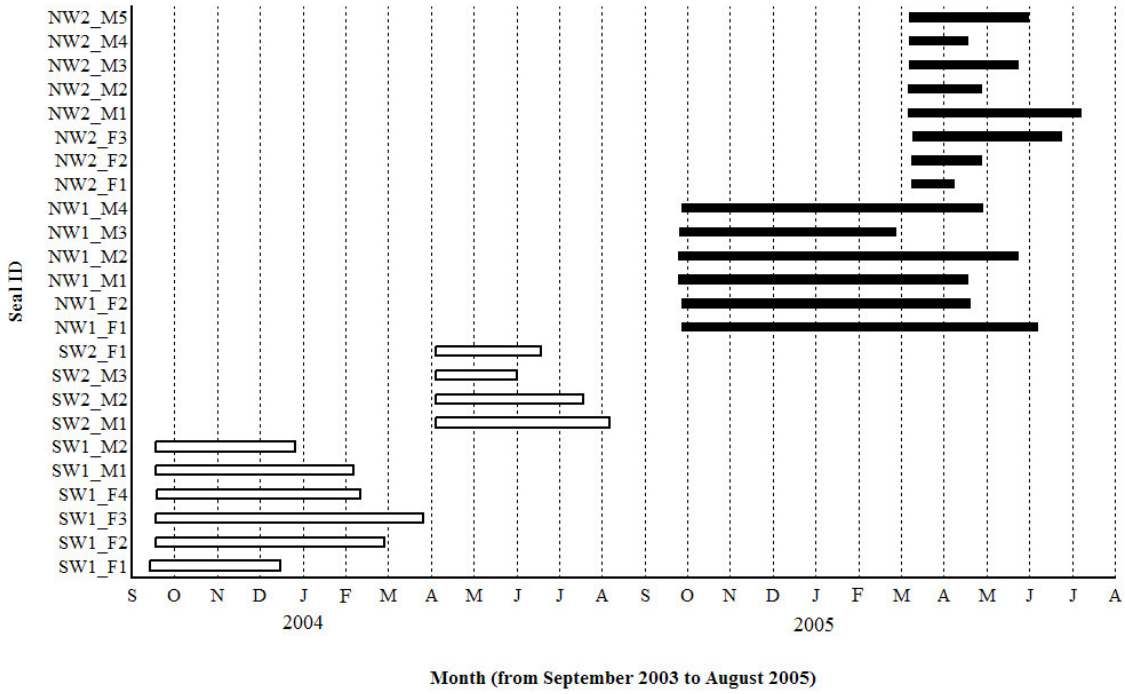


Figure 2.5: Operating duration of SRDLs deployed on harbour seals in south-west (□) and north-west (■) Scotland. Individual seals are represented by a code indicating the location of deployment (SW = south-west or NW = north-west Scotland), the season of deployment (1 = autumn or 2 = spring) and the sex (F = female, M = male).

A total of 1,195 days of data were collected from 10 harbour seals (five females, five males) captured in south-west Scotland in September 2003 and April 2004. In north-west Scotland, 1,854 days of data were collected from 14 harbour seals (five females, nine males) captured in September 2004 and March 2005. Walker and Bowen (1993) suggest that only male harbour seals weighing more than 80 kg are reproductively

active. Although it was not possible to ascertain if they were actively breeding, all seals in this study appeared to be physically mature and weighed over 80 kg. Details of the seals captured and tagged are given in Table 2.1.

Table 2.1: Details of harbour seals fitted with ARGOS Satellite Relay Data Loggers (SRDLs). One SRDL did not work due to configuration error (*). One SRDL failed to transmit any data from the date of deployment (†). Data from these seals (*,†) were therefore not included in analyses.

ID code	Capture location	Sex	Length (cm)	Girth (cm)	Weight (kg)	Date of capture	Transmission days
SW1_F1	Jura	F	137	91	62	14-Sep-03	93
SW1_F2	Islay	F	121	82	40	18-Sep-03	163
SW1_F3	Islay	F	149	100	72	18-Sep-03	191
SW1_F4	Jura	F	144	89	60	19-Sep-03	145
SW1_M1	Islay	M	138	93	56	18-Sep-03	141
SW1_M2	Islay	M	143	101	74	18-Sep-03	100
SW2_F1	Islay	F	142	115	87	05-Apr-04	75
SW2_M1	Islay	M	152	113	95	05-Apr-04	124
SW2_M2	Islay	M	149	118	102	05-Apr-04	105
SW2_M3	Islay	M	155	115	100	05-Apr-04	58
SW2_M4	Islay	M	158	116	103	05-Apr-04	0*
SW2_M5	Islay	M	167	104	78	05-Apr-04	0†
NW1_F1	Skye	F	113	90	48	27-Sep-04	255
NW1_F2	Skye	F	119	80	40	27-Sep-04	207
NW1_M1	Skye	M	157	102	84	25-Sep-04	207
NW1_M2	Skye	M	139	99	74	25-Sep-04	243
NW1_M3	Skye	M	146	107	90	26-Sep-04	155
NW1_M4	Skye	M	152	103	90	27-Sep-04	216
NW2_F1	Skye	F	145	100	81	10-Mar-05	31
NW2_F2	Skye	F	149	101	83	10-Mar-05	51
NW2_F3	Skye	F	144	108	86	11-Mar-05	107
NW2_M1	Skye	M	148	118	97	08-Mar-05	124
NW2_M2	Skye	M	137	102	69	08-Mar-05	53
NW2_M3	Skye	M	135	96	60	09-Mar-05	78
NW2_M4	Skye	M	159	104	85	09-Mar-05	42
NW2_M5	Skye	M	153	111	85	09-Mar-05	85

Following filtering 6,868 locations were extracted from seals tagged in south-west Scotland and 11,306 from seals in north-west Scotland (overall mean = 5.96 locations/day). Of these, 4.7 % were assigned the highest location quality index (Table 2.2).

Table 2.2: Total number of locations for all seals, grouped by ARGOS location quality index (LQ) and predicted accuracy of positions (Argos., 2000). 'Accuracy' is the distance that 68% of locations will be from the true location (with latitude and longitude treated separately).

LQ	Number of locations(%)	ARGOS predicted 'accuracy' (m)	Real 'accuracy' (Vincent *et al.* 02)
3	861 (4.7)	150	226
2	1063 (5.8)	350	372
1	1483 (8.2)	1000	757
0	795 (4.4)	> 1000	
-1	5013 (27.6)	un-guaranteed	
-2	8959 (49.3)	un-guaranteed	

Seal movements

In total 1,254 trips were identified from the movement data, of which 39.15% were return trips.

Trip extent

About half (51.75%) the travel-trips extended no further than 25 km (mean = 10.48, SE = 10.23) from the haul-out cluster from whence the seals came (Figure 2.6). However, travel-trips of up to 144 km were recorded (Table 2.3). The maximum return trip observed was 46.2 km (mean = 7.25, SE = 5.75). Return-trips to haul-out clusters were not significantly different from the average (mean = 4.57, SE = 5.15). Neither travel-trip nor return-trip distances were correlated with individual body mass (Spearman's rank order correlation for travel-trips: $r_s = 0.231$, $p = 0.290$ and return-trips $r_s = -0.187$, $p = 0.404$).

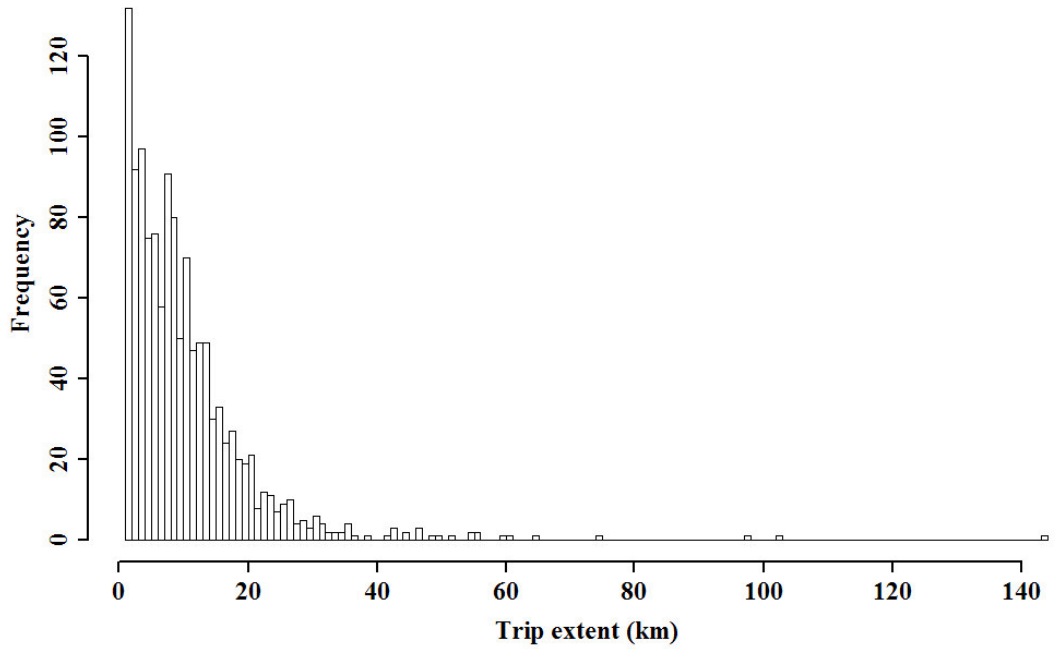


Figure 2.6: Frequency distribution of the extent (in kilometres) of trips made by 24 satellite-tagged harbour seals on the west coast of Scotland between September 2003 and July 2005. A 'trip' was defined as being > 1 hour in length and started when the individual was > 1 km from the haul-out cluster.

Table 2.3: Data for harbour seal 'travel-trips' and 'return-trips', where a trip was defined as being > 1 hour in length and started when the individual was > 1 km from the haul-out cluster. A return-trip occurred when the individual hauled out at the same haul-out cluster at the start and end of the trip.

	N	Trip extent (km)			Trip duration (hours)		
		Mean	Max.	SE	Mean	Max.	SE
Travel-trips	1254	10.48	144	10.23	31.06	217	27.32
Return-trips	491	7.25	46.2	5.75	28.14	185	23.60

Trip duration

About half (48.48%) the travel-trips in this study lasted between 12 and 24 hours (Figure 2.7 and Table 2.3). However some lasted several days, with the longest being over nine days in duration (217 hours). A similar pattern was seen in the duration of return-trips (Table 2.3), with the longest return-trip lasting 7.7 days (mean = 28.14 hours, SE = 23.60). The maximum duration of a return-trip to a haul-out cluster within a SAC was 63 hours (mean = 22.66, SE = 14.28). A multimodal pattern was also apparent in the duration of both return- and travel-trips, with peaks at 18, 43 and 69 hours (Figure 2.7).

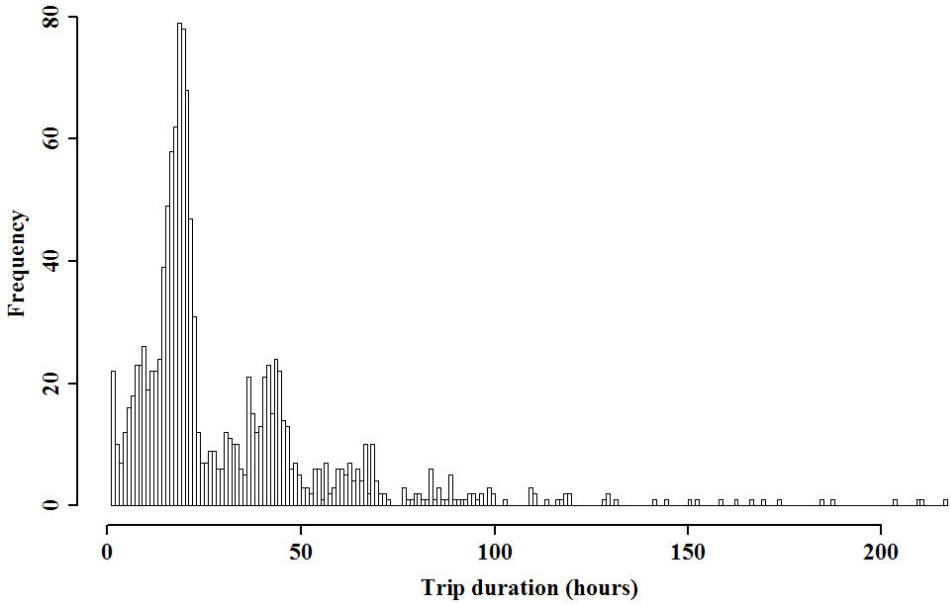


Figure 2.7: Frequency distribution of the duration (in hours) of travel-trips made by 24 satellite-tagged harbour seals on the west coast of Scotland between September 2003 and July 2005. A 'trip' was defined as being > 1 hour in length and started when the individual was > 1 km from the haul-out cluster.

Trip-duration was correlated with trip-extent (Figure 2.8, Spearman's rank order correlation $r_s = 0.397$, $p < 0.001$ and return-trips $r_s = 0368$, $p < 0.001$).

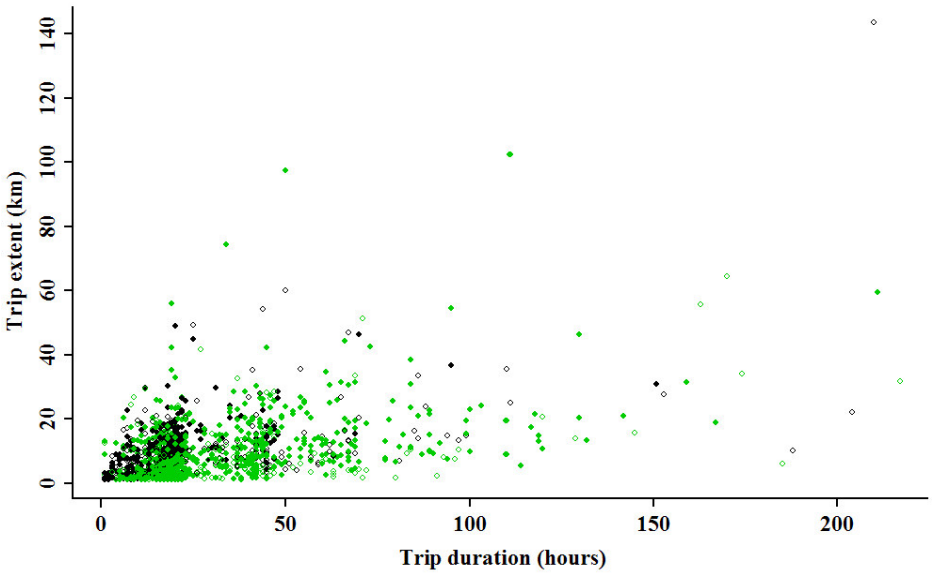


Figure 2.8: Travel-trip duration (hours) plotted against maximum trip extent (km) for trips > 1 hour in length and 1 km in extent for female (○) and male (●) harbour seals caught in north-west (green, $r_s = 0.500$, $p < 0.001$) and south-west (black, $r_s = 0.402$, $p < 0.001$) Scotland.

Spatial, seasonal and sexual variation

The duration and extent of trips differed between those animals tagged in south-west Scotland and those in north-west Scotland (Mann Whitney, z = -7.823, p < 0.001; z = -3.251, p = 0.001 respectively). There was a gradual increase in travel-trip duration in south-west Scotland from September until May and a decrease in north-west Scotland (Figure 2.9). Mean travel-trips were longer in north-west Scotland until March, after which they were shorter than travel-trips in south-west Scotland. Overall mean travel-trip duration was 24.9 hours (SE = 24.1) in south-west Scotland and 35.0 hours (SE = 28.6) in north-west Scotland (Table 2.4).

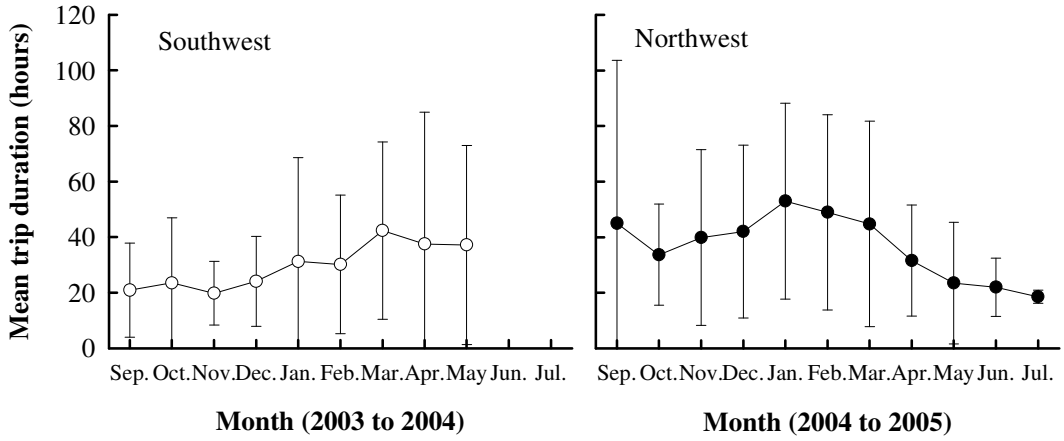


Figure 2.9: Mean travel-trip duration (with standard errors) in hours of 10 harbour seals tagged in south-west Scotland in 2003/2004 (-○-) and 14 seals in north-west Scotland in 2004/2005 (-●-). A trip was defined as lasting > 1 hour and > 1 km from the starting haul-out cluster.

Table 2.4: Summary statistics of trip extent (kilometres) and duration (hours) during different months of the year: 2003-2004 for seals caught in south-west Scotland and 2004-2005 for those caught in north-west Scotland. Return-trips are when the seal returned to the haul-out cluster it had just left.

Month (2003- 2005)	N seals		N travel-trips		N return- trips		Max extent (km)				Trip duration (hours)			
							Mean		SE		Mean		SE	
	SW	NW	SW	NW	SW	NW	SW	NW	SW	NW	SW	NW	SW	NW
September	6	6	46	4	25	1	9.3	7.9	5.9	7.5	20.9	45	16.9	58.6
October	6	6	110	60	60	14	11.6	10.4	7.8	10.4	23.5	33.7	23.5	18.2
November	6	6	112	68	68	23	8.9	10.4	5.7	10.0	19.8	39.9	11.4	31.6
December	6	6	99	58	63	25	10.9	10.7	9.0	10.5	24.1	42.1	16.2	31.1
January	4	6	63	52	49	11	12.1	12.8	18.4	10.0	31.2	53.0	37.4	35.2
February	4	6	28	34	20	17	11.1	9.8	9.9	8.3	30.2	49.0	24.9	35.1
March	1	13	11	116	5	24	10.3	10.5	8.8	9.0	42.4	44.8	31.9	37.0
April	4	13	18	147	5	36	16.8	10.7	14.5	11.3	37.5	31.6	47.5	20.0
May	4	6	6	138	2	29	14.5	9.6	12.6	13.0	37.2	23.5	35.8	21.9
June	3	2	0	70	-	13	-	7.8	-	5.2	-	22.0	-	10.5
July	2	1	0	14	-	1	-	8.6	-	5.4	-	18.6	-	2.4
Total	*10*	*14*	*493*	*761*	*297*	*194*	*10.9*	*10.2*	*10.1*	*10.3*	*24.9*	*35.0*	*24.1*	*28.6*

There was no apparent seasonal variation in mean trip extent across the seasons in north-west Scotland, or in south-west Scotland only April and May had increased trip extents (Figure 2.10). Overall, mean travel-trip extent was 10.9 km (SE = 10.1) in south-west Scotland and 10.2 km (SE = 10.3) in north-west Scotland (Table 2.4).

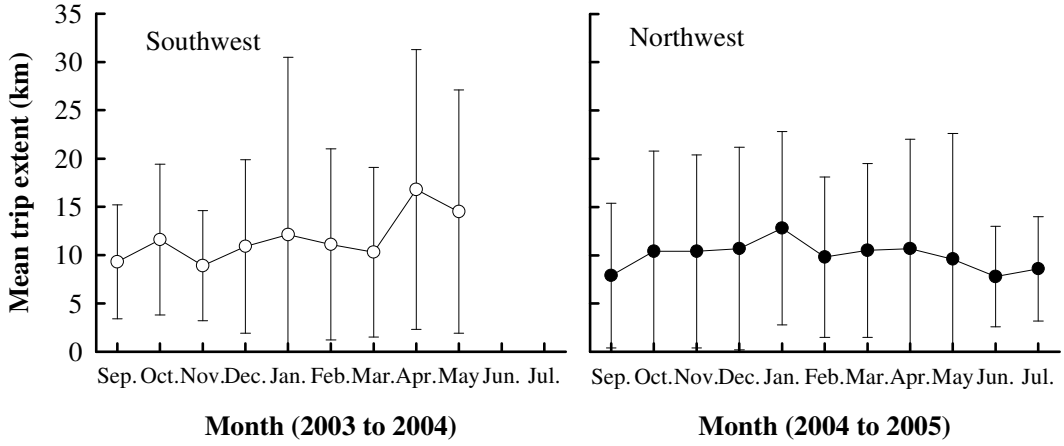


Figure 2.10: Mean travel-trip extent in kilometres (with standard errors) of 10 harbour seals tagged in south-west Scotland in 2003/2004 (-○-) and 14 seals tagged in north-west Scotland in 2004/2005 (-●-). A travel-trip was defined as lasting > 1 hour and > 1 km from the starting haul-out cluster.

The statistical significance of sex differences in the duration and extent of travel-trips and return-trips differed according to which definition of trip was used. Statistical significance at the 0.05 level was only obtained for trip extent (Mann Whitney U: $z = -5.180$, $p < 0.001$), where females travelled further than males.

Usage of haul-out clusters

Of the 491 return-trips, 35 (7.1%) were made to and from a haul-out cluster within an SAC. Although haul-out clusters around the SRDL deployment locations were frequently used, some individuals also used other haul-out clusters (Figure 2.11). Over 40% of consecutive haul-out events were separated by less than 2 km (mean = 5.21, 95% CI = 4.94 – 5.49; Figure 2.12).

Most long-distance movements followed direct routes from one haul-out cluster to another. For example NW2_M2 travelled approximately 120 km from Skye to Tiree twice. The trip took just over two days in each direction (mean = 56.23 hours, SE =

6.47) with 33 days spent on Tiree on the first occasion and just three days on the second.

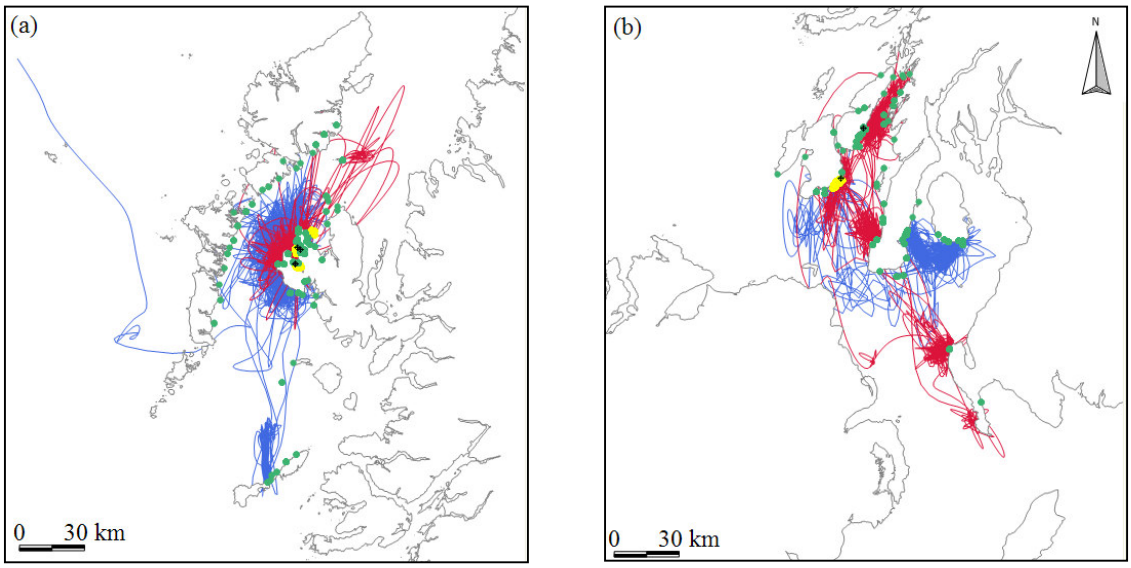


Figure 2.11: Individual tracks of male (blue) and female (red) harbour seals tagged off the Isles of Skye (a), and Islay and Jura (b). ♦ = SRDL deployment locations. Locations of haul-out events, interpolated from smoothed track data and 'snapped' to the nearest known haul-out clusters, are shown in green, with those inside SACs in yellow.

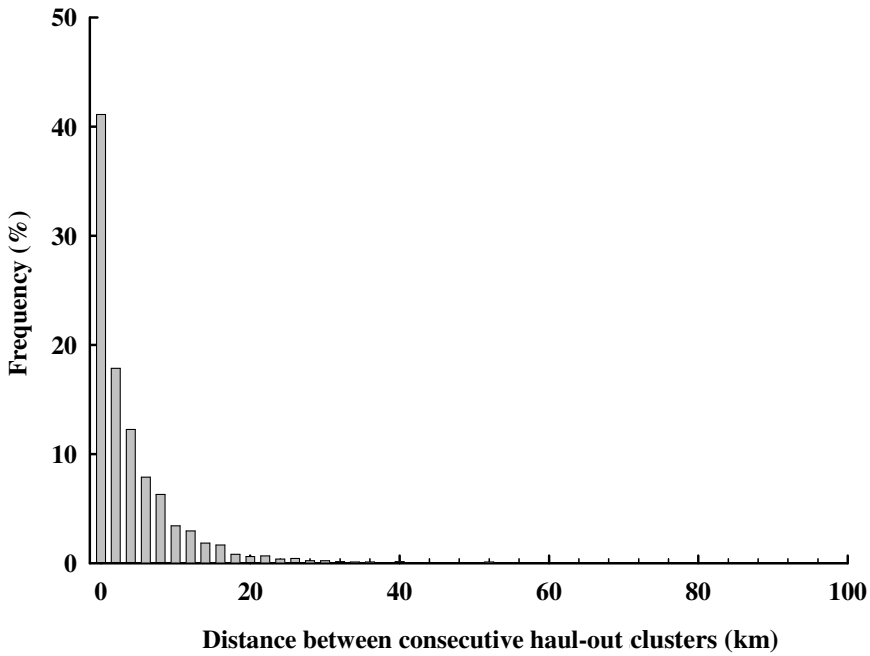


Figure 2.12: Frequency of distance (in kilometres) between consecutive haul-out events of 24 harbour seals tagged in south-west (2003/2004) and north-west (2004/2005) Scotland.

Harbour seals used 50 haul-out clusters in south-west Scotland and 60 in north-west Scotland (Figure 2.13) during the tagging period. Individual seals used a mean of 13 haul-out clusters (range = 6 to 29, SE = 6.07, Figure 2.14). Individuals tagged in north-west Scotland that used over 20 haul-out clusters also hauled out in the Shiants (NW1_F1), South Uist (NW1_M2) and Tiree (NW2_M2); SW1_F4 tagged in south-west Scotland used over 20 haul-out clusters including the Rhins of Galloway. The number of haul-out clusters used showed a positive association with the tracking period (Figure 2.15, Spearman's rank order correlation: $r_s = 0.435$, $p = 0.038$).

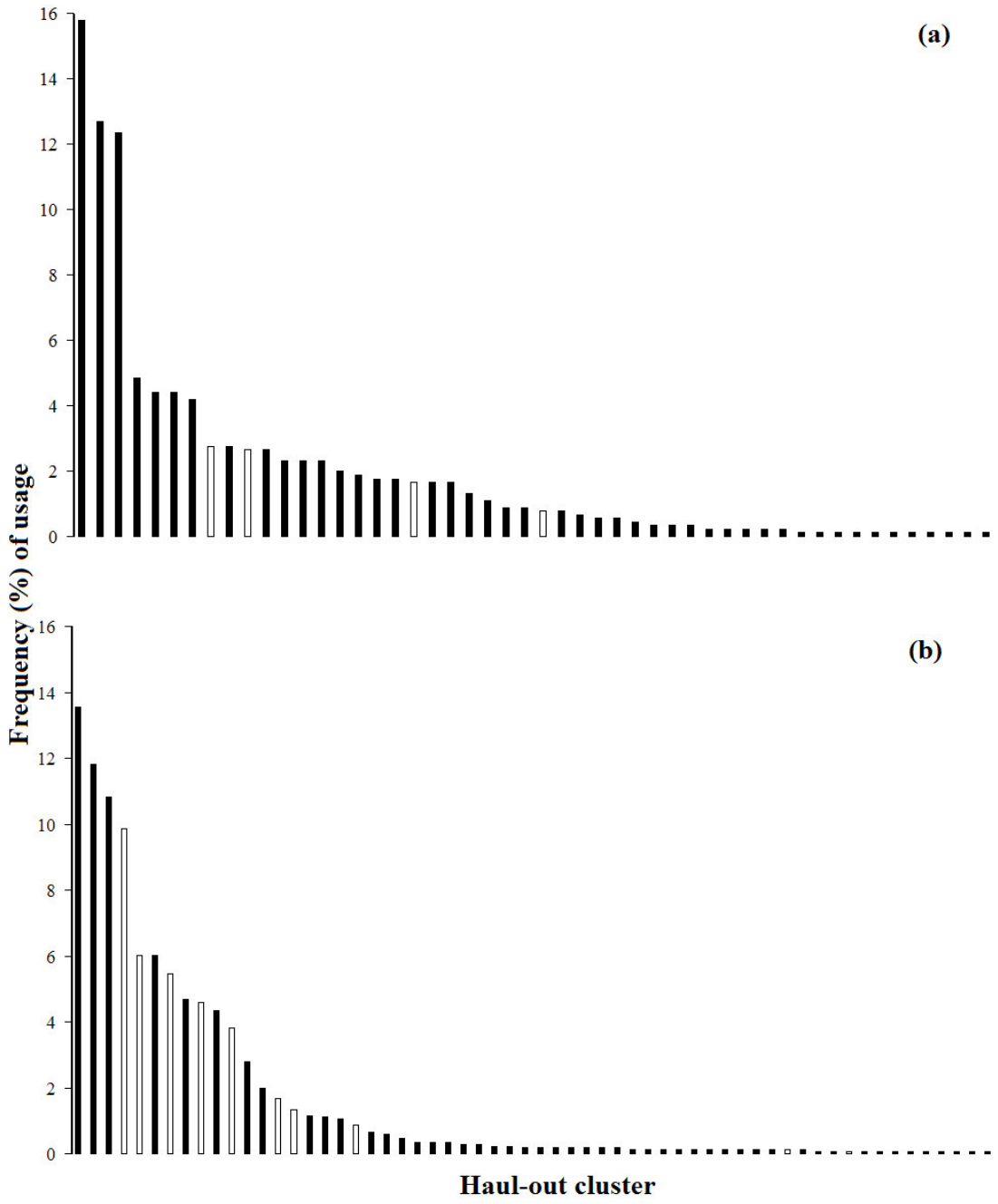


Figure 2.13: Frequency distribution of the proportion of haul-out clusters used by individual tagged harbour seals in south-west Scotland (a) and north-west Scotland (b). Haul-out clusters in SACs are shown in white.

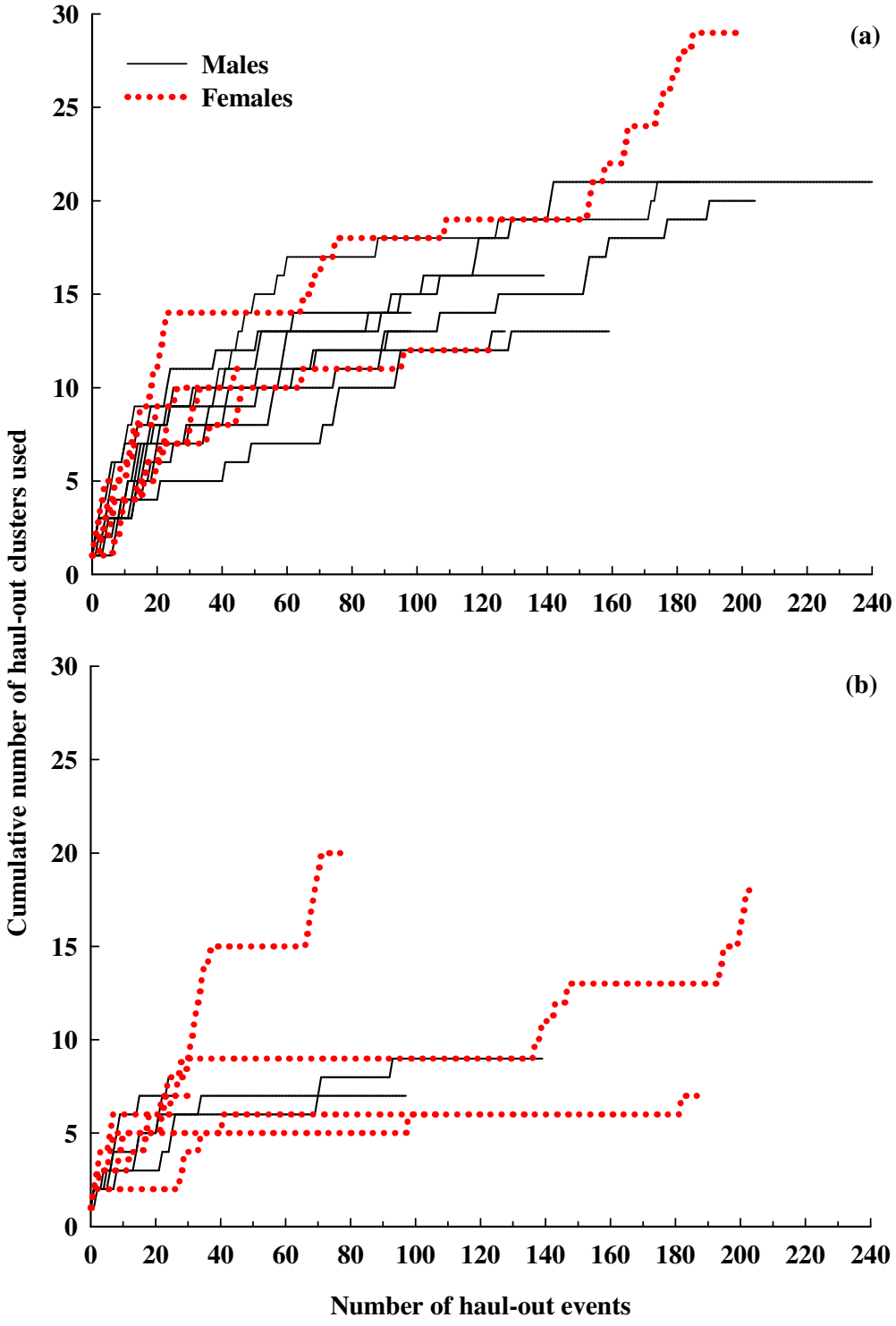


Figure 2.14: Cumulative use of new haul-out clusters used with the number of haul-out events for male (solid black lines) and female (dotted red lines) harbour seals in north-west (a) and south-west (b) Scotland.

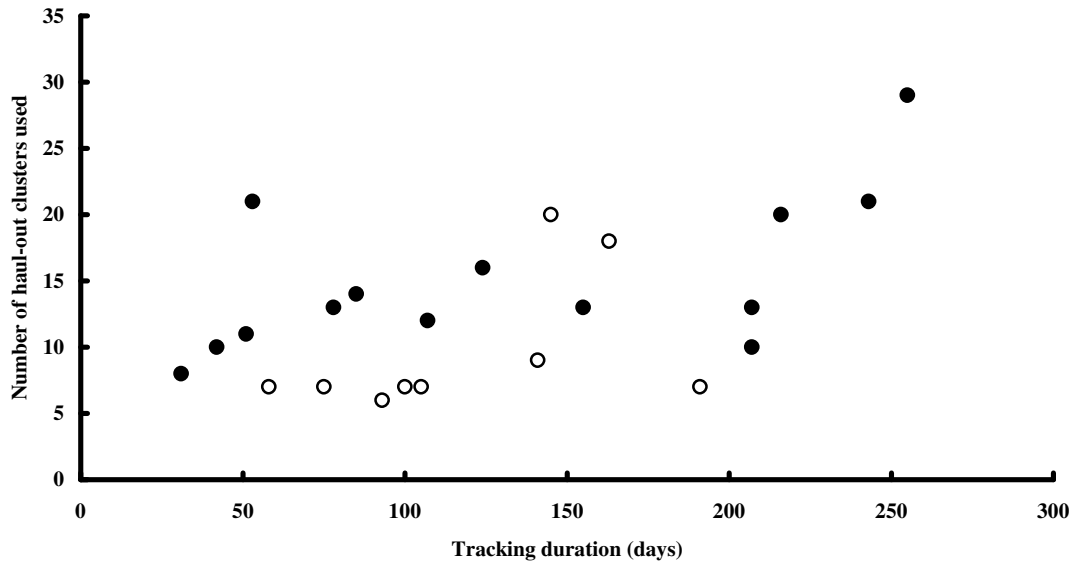


Figure 2.15: Correlation between the number of haul-out clusters used per individual and the transmission length of the SRDL. ○ = seals tagged in south-west Scotland (Isles of Islay and Jura in 2003/2004), ● = animals tagged in north-west Scotland (Isle of Skye in 2004/2005).

Most individuals switched between two main haul-out clusters occasionally using additional haul-out clusters when travelling between these (e.g. Figure 2.11a, NW2_M2 hauled out on Canna whilst *en route* to Tiree). Visual inspection of haul-out clusters used by individual seals gave some evidence for seasonal changes in south-west Scotland, but none were apparent in north-west Scotland. Two seals appeared to disperse from the deployment location: SW1_M2 went to Arran from Islay immediately after SRDL deployment in mid-September and NW2_M4 left Skye in April, one month after being tagged, passed through the Sound of Barra and continued beyond St Kilda, where the transmissions ended (Figure 2.16).

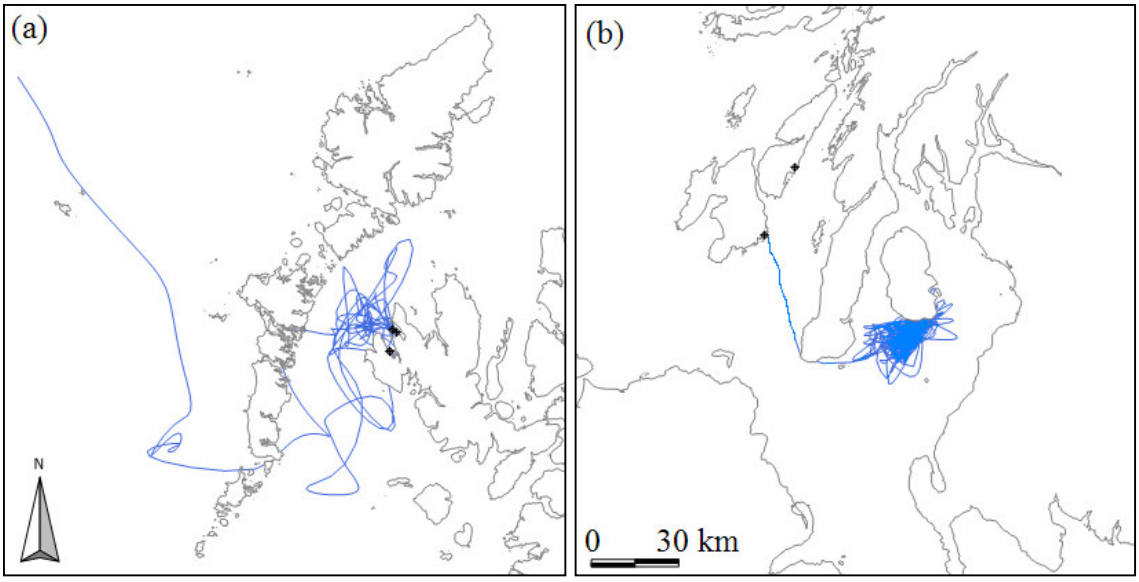


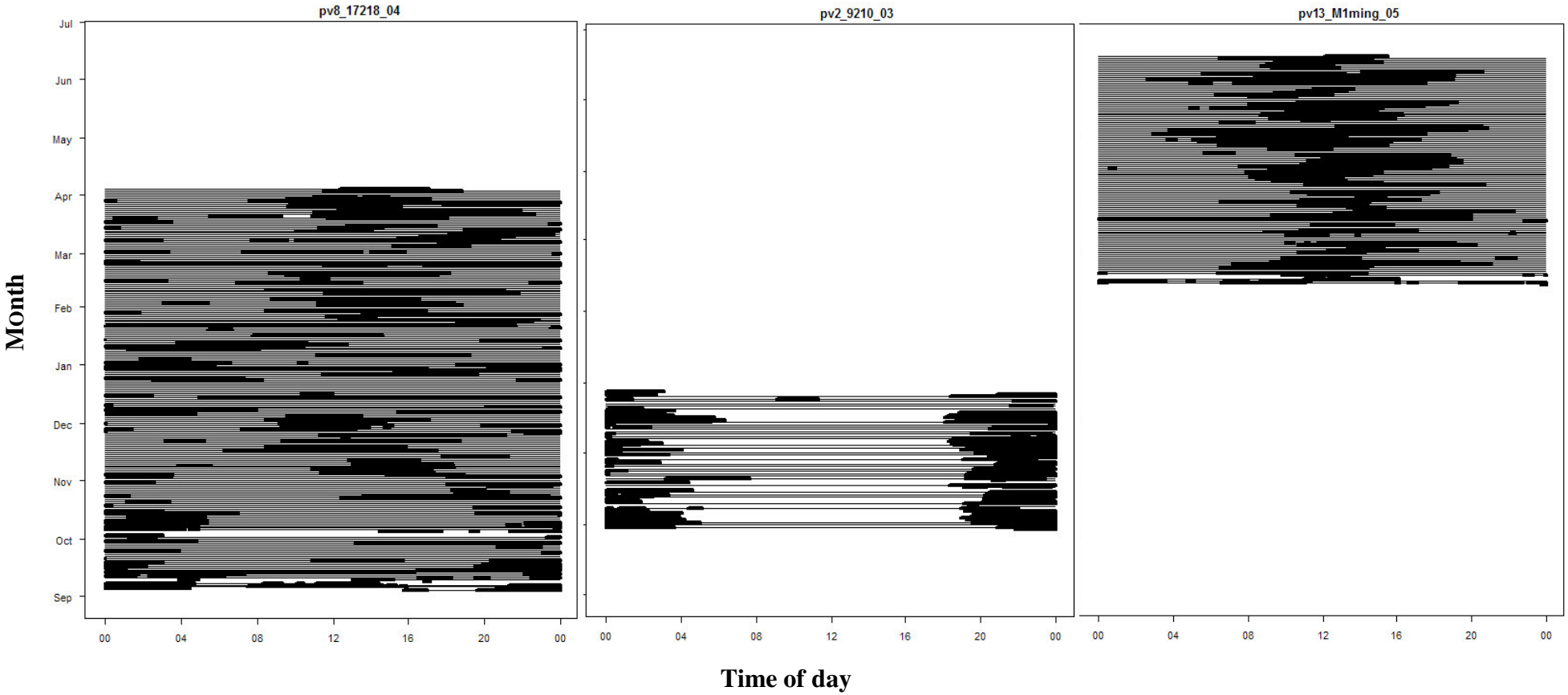
Figure 2.16: Smoothed tracks of dispersal movements of males NW2_M4, caught on Skye in March 2005 (a) and SW1_M2, caught on Islay in September 2003 (b). ♦ = SRDL deployment locations.

Haul-out patterns

Proportion of time hauled out and duration of haul-out events

The observed haul-out patterns showed considerable individual variation (Figure 2.17). Seals spent between 11 and 27% of their time hauled-out. Individual daily mean time hauled out (mean = 4.39 hours, 95% CI = 4.13 – 4.52) varied by location (Mann Whitney U: $z = -4.13$, $p = 0.04$), sex (Mann Whitney U: $z = -2.02$, $p < 0.001$) and season (Kruskal-Wallis: $\chi^2 = 121.75$, df = 10, $p < 0.001$), but was not correlated with individual body mass (Spearman's rank order correlation: $r_s = 0.275$, $p = 0.194$).

Figure 2.17: Examples of three individual haul-out patterns indicating the variability between seals and in the quality and quantity of data obtained. Thick black lines represent haul-out events and are joined together by a thin line if the seal was definitely not hauled out during this time. White indicates missing data during which time the seal could either have been hauled out or at sea.



In north-west Scotland females spent less time hauled out than males between October and May but more time in June and September (Figure 2.18 and Appendix II: Table II.i). The pattern was less clear in south-west Scotland. In both areas, a higher proportion of time was spent hauled out during the spring months (February to June) than in the winter (October to January; Mann Whitney U: $z = -6.654$, $p < 0.001$).

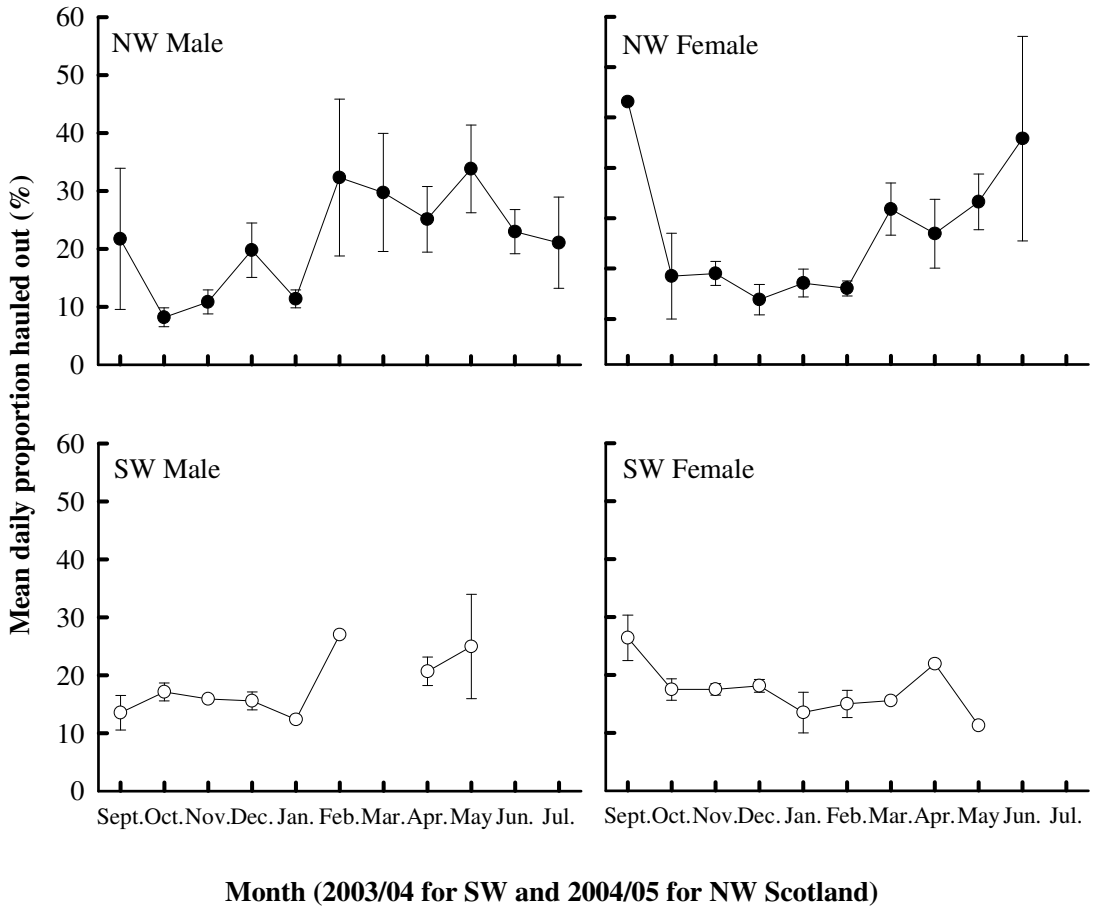


Figure 2.18: Individual daily percentage of time hauled out by month (with standard errors) for 10 seals in south-west Scotland in 2003/2004 (-○-) and 14 seals in north-west Scotland in 2004/2005 (-●-).

Harbour seals did not haul-out every day, spending less than one hour hauled out on over 66% of days in this study. The mean duration of a haul-out event was 4.77 hours (SE = 3.63), with about 30% of all haul-out events longer than six hours (roughly equivalent to a tidal cycle; Figure 2.19). Occasionally haul-out events lasted over 20

hours, with a maximum haul-out duration of 24.63 hours, approximating a full tidal cycle.

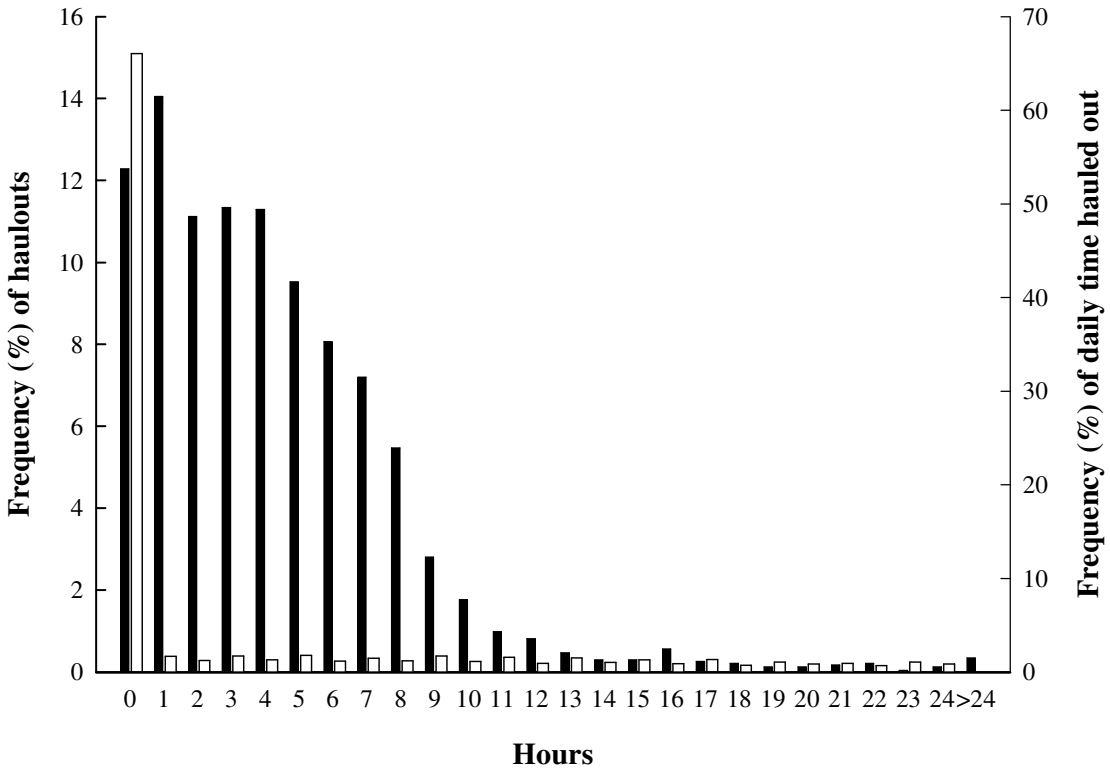


Figure 2.19: Frequency distribution of haul-out duration (black) and the mean daily percentage of time spent hauled out each day (white). Data are from 24 SRDLs fitted to harbour seals caught on the west coast of Scotland between September 2003 and July 2005.

The probability of a seal being hauled out around midday, when aerial surveys are often conducted, showed strong seasonal patterns, particularly in north-west Scotland (Figure 2.20, cf. Chapter 4). Between March and July, the highest probability of hauling-out did occur around midday, but between September and February, the probability of being hauled out around midday was either the same as, or lower than, that at other times of day. This diurnal pattern was particularly strong between May and July when there was an 80% chance that a seal would be hauled out around midday and less than 10% chance that it would haul-out between18:00 and 08.00.

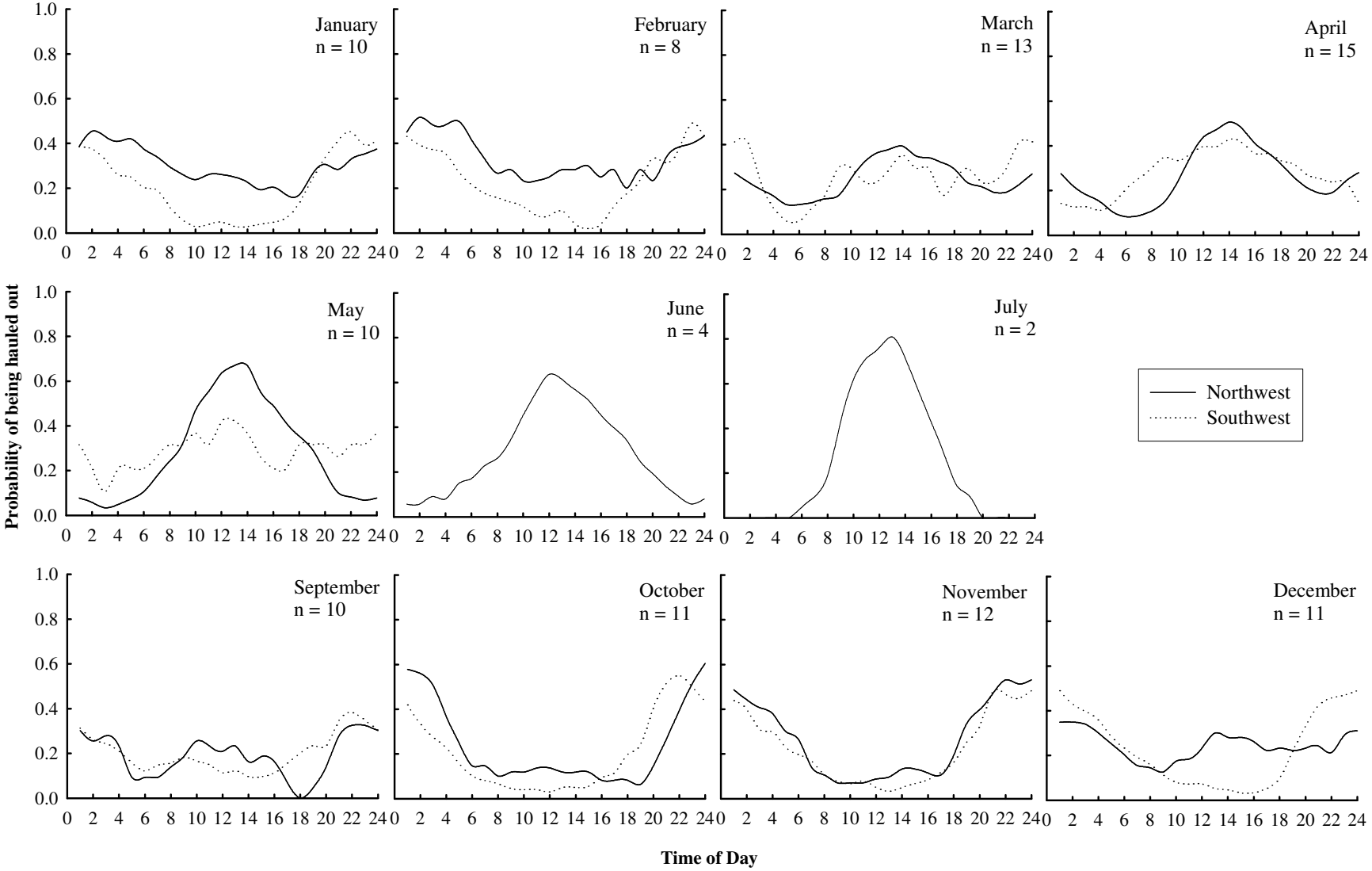


Figure 2.20: Diurnal and seasonal variation in the probability of a seal being hauled out in northwest and southwest Scotland. n = total sample size for both locations of animals with haul-out records.

Duration of haul-out events

The haul-out duration analysis indicated some relationship with the duration of the previous observed haul-out. To eliminate the complications associated with serial correlation in the data, and so that each haul-out event could be considered independently, only alternate records were used for the GLMM. Variables affecting haul-out duration included in the final model (AIC = 2134.86, Table 2.5) were Julian date and cosine-converted time of day with individual seal reference code as a random effect. No interaction terms improved the model fit.

Table 2.5: Results of the 'best' candidate GLMM model (with Gamma error structure and log link function) relating behavioural and temporal variables to the duration of harbour seal haul-out events.

Term	log β	SE	t-value	p-value	
Intercept	0.763	0.210	3.624	< 0.001	**
Julian date	0.001	< 0.001	3.494	< 0.001	**
Time of day	0.341	0.171	1.994	0.047	*

* significant at p = 0.05, ** significant at p < 0.001

Although visual inspection of the autocovariance estimates gave no reason to suspect non-randomness in the data (Figure 2.21a), the deviance residuals suggested that the assumption of normality of errors was violated (Figure 2.21b) and that the model variance was not sufficiently accounted for by the GLMM. The fit of the model was also deemed inadequate (χ^2: $p < 0.001$, df = 921), explaining less than 1% of the variance.

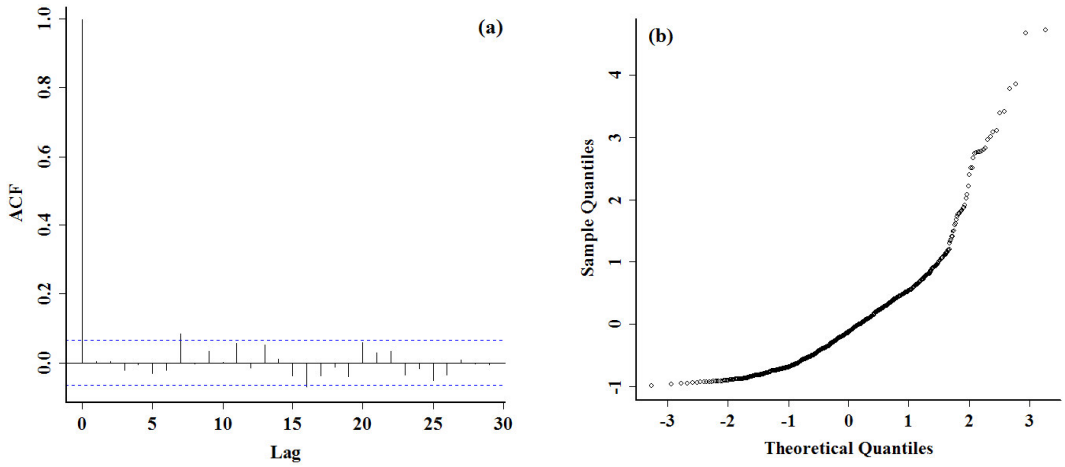


Figure 2.21: The autocorrelation function at varying time lags for the haul-out duration GLMM (a) and a normal QQ plot showing deviance residuals for the best-fitting GLMM of factors affecting harbour seal haul-out duration (b). Calculated autocorrelations should be near zero for all time-lag separations if data are random. If non-random, one or more of the autocorrelations will be significantly non-zero. Dotted blue lines represent 95% confidence intervals. The closer the deviance is to a straight oblique line, the lower the variance unaccounted for by the model.

Inter-haul-out interval (IHI)

Variables affecting the IHI included in the final model (AIC = 5528.35, ΔAIC = 9141.90, Table 2.6) were maximum depth of dive within the IHI and sine-converted time of day, with individual seal reference code as a random effect. As with the haul-out duration GLMM no interaction terms improved the model fit, visual inspection of the autocovariance estimates gave no reason to suspect non-randomness in the data (Figure 2.22a), and the deviance residuals suggested that the model variance was not sufficiently accounted for by the model (Figure 2.22b). The fit of the model was also deemed inadequate based on a goodness-of-fit test (χ^2: $p < 0.001$, df = 1843), explaining less than 1% of the variance.

Table 2.6: Results of the 'best' GLMM model (with Gamma error structure and log link function) relating endogenous and temporal variables to the IHI duration.

Term	log β	SE	t-value	p-value	
Intercept	3.093	0.088	35.336	< 0.001	**
Dive depth	< - 0.001	0.001	-0.227	0.821	
Time of day	- 0.091	0.095	-0.956	0.339	

**significant at p < 0.001.

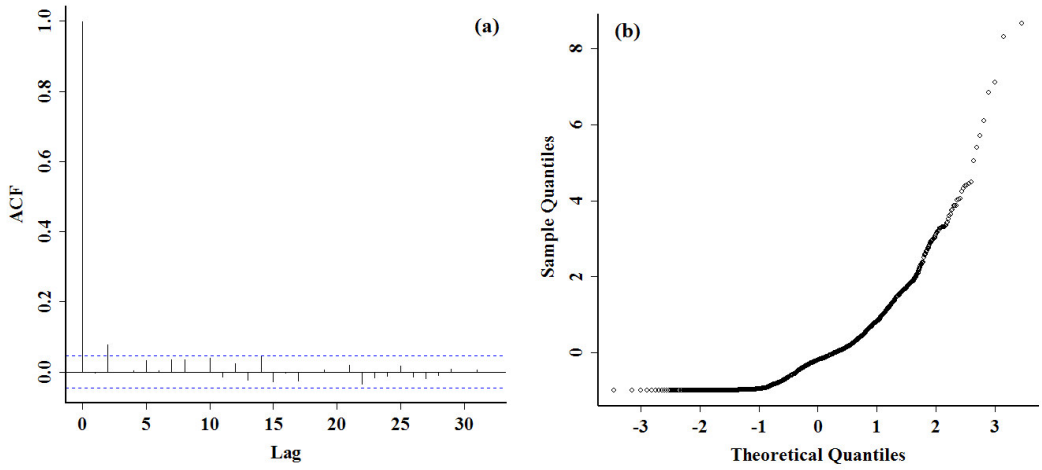


Figure 2.22: The autocorrelation function at varying time lags for the IHI GLMM (a) and a normal QQ plot showing deviance residuals for the best-fitting GLMM of IHI duration (b).

DISCUSSION

Haul-out behaviour

Harbour seal aerial surveys only provide a minimum estimate of the population because they do not account for seals in the water at the time of survey. Thus it is necessary either to estimate the proportion of seals that are in the water at the time of survey, or to assume that this proportion does not vary temporally or spatially in order to assess long-term trends in abundance. These alternatives are considered below.

Proportion of seals in the water

Harbour seals in this study hauled out for less than an hour on 66% of the days studied. The mean daily time an individual was in the water ranged from 70 - 90% during the tracking period (September to July). The highest proportions of seals hauled out are thought to coincide with important life-cycle events, such as pupping, mating and moulting (Thompson *et al.* 1998). However there is a gap in the telemetry data during the moult as tags, attached to the fur, are lost at this time. Previous estimates of the number of harbour seals ashore during peak haul-out times vary from 50 - 70% (Yochem *et al.*, 1987; Härkönen & Heide-Jørgensen, 1990; Ries *et al.*, 1998; Thompson & Harwood, 1990; Thompson *et al.*, 1997; Huber *et al.*, 2001) to 79 - 88% (Olesiuk *et al.*, 1990). In this study the peaks in daily proportion of time individuals spent hauled out were 36% in June, when animals were pupping, and 43% in September, towards the end of the moult. In the months prior to the survey period (i.e. May to July) there was a strong diurnal influence on the probability of a seal being hauled out, such that there was an 80% chance that a seal would be hauled out around midday, but less than 10% chance at night (18.00 – 08.00). In contrast there was no clear diurnal pattern in September, with the probability of being hauled out fluctuating around 20%.

Variation in the proportion of animals ashore

It is likely that there are regional variations in haul-out behaviour; for example seals may haul out less frequently in areas of low food abundance or high disturbance (Huber *et al.*, 2001). However the seasonal change in diurnal haul-out behaviour was simiilarin north-west and south-west Scotland. However, there was a change in the diurnal pattern of hauling out with season. During the winter months haul-out events were more likely at night than during the summer, whereas the opposite was true in the summer. This is probably a result of the need to spend time ashore when pupping, suckling and moulting in the summer.

In the absence of data from August, when seals are typically surveyed, the proportion of time harbour seals are in the water at this time remains unknown. It is essential that haul-out patterns for this time are measured if the true seal population size is to be estimated accurately from aerial survey data. Thus alternative attachment methods that collect information during this period must be considered, e.g. attaching telemetry devices to the flipper (Huber *et al.*, 2001; Simpkins *et al.*, 2003) or by means of an implantable tag (Horning & Hill, 2005; Lander *et al.*, 2005).

Female harbour seals are thought to moult before males (Thompson *et al.*, 1989), yet in this study the mean proportion of time hauled out in September, towards the end of the moulting period, was higher in females than in males. This suggests that either there are regional differences in the order in which the sexes moult, or that females take longer than males to complete their moult. Mating is thought to occur in the water (Van Parijs *et al.*, 1997) at the end of the lactation period (Thompson, 1988) and hence the decrease in the proportion of time hauled out by males in July may be a result of males spending more time in the water to increase their chances of encountering females. However, as the animals tagged in this study were selected as having completed or almost completed the moult, the patterns observed in September may not be representative of the population. The consequences of the way in which animals were selected for telemetry are discussed further below (see **Method evaluation**).

Haul-out patterns and site-usage

In addition to investigating the probability of hauling out, the duration of haul-out events is also important for designing monitoring protocols. Longer haul-out events (and therefore potentially shorter periods in the water) were observed in the spring compared to the winter months. The haul-out habitat on the west coast of Scotland, where this study was conducted, comprises numerous rocky skerries, which remain available for hauling out throughout the tidal cycle. Nevertheless, most (85%) haul-out events in this study were less than eight hours in duration (mean = 4.77). This is comparable with results from similar studies conducted in the Moray Firth, north-east Scotland (Thompson & Miller, 1990), despite the differences in haul-out habitat (estuarine sandbanks) and availability (strongly influenced by the tide). It is therefore possible that haul-out duration is governed by physiological factors and food availability, rather than habitat characteristics, and consequently it may show little spatial variation. Occasionally individual seals hauled out for over 24 hours as observed in other locations where haul-out sites are available throughout the tidal cycle (Yochem *et al.*, 1987). These rare events were not limited to one individual, they may occur when a seal is unwell, needing extra time to rest and with a reduced appetite. Visual inspection of data showed no correlation between probability of hauling out and tidal phase.

Of the total time spent hauled out, 18% occurred within harbour seal SACs. It is, however, important to note that the study animals were caught in SACs and consequently may have a higher association with these areas than the rest of the population. Moreover, this value is dependent on the five-kilometre scale used to cluster haul-out sites. Härkönen & Harding (2001) used a coarser scale to examine site-fidelity and found that harbour seals in the Skagerrak and the Kattegat, particularly females, have a high association with specific haul-out sites. This illustrates that harbour seals show a degree of site-fidelity and consequently could benefit from legislative protection of terrestrial sites.

On average harbour seals used 13 haul-out clusters, though the number of clusters used by an individual was positively correlated with the tracking period. Nevertheless, 40% of consecutive haul-out events occurred at sites separated by less than two

kilometres. Seasonal switches in haul-out site usage have been reported in harbour seals in other areas (e.g. Brown & Mate, 1983; Thompson *et al.*, 1994b; Lowry *et al.*, 2001). Some seasonality was apparent in movements from one haul-out cluster to another in this study, but this did not appear to be sufficient to explain the observed patterns. Site-switching is likely to be related to prey availability, with seals changing haul-out site to minimise the distance to prime foraging areas (Thompson, 1988). The timing of a change in haul-out site is therefore likely to be influenced by a range of factors including prey preferences and availability and the movements of other seals.

Seal movements

This study showed that harbour seals generally remained within a 25 km radius of haul-out sites: only one seal (NW2_M4) travelled more than 30 km from land. Although some trips were several days in duration (maximum = nine days) almost 50% of trips made by harbour seals in this study lasted between 12 and 24 hours (mean = 31.06 hours). Previous studies have also suggested that harbour seals haul out and feed locally (e.g. Brown & Mate, 1983; Suryan & Harvey, 1998; Thompson *et al.*, 1996; Lowry *et al.*, 2001). Most of these studies either relied on VHF technology, which could potentially have missed longer distance movements, or studied harbour seals that utilise a different habitat from that considered in the present study (for example sandbanks, estuaries or glaciers). Satellite telemetry has shown that the majority of harbour seal trips in this study were to coastal waters and that animals often remained within fairly restricted areas, presumably because sufficient prey are available in these areas. This gives support to the suggestion that these areas could be considered as 'management units' for harbour seals (Thompson *et al.*, 1996; cf. Chapter 6).

Not all movements in this study were short, small-scale return-trips to sea. The directed travel to known harbour seal haul-out clusters (e.g. NW2_M2 trips to and from Tiree) and Thompson and Miller's (1990) suggestion that harbour seals swim directly to and from their feeding areas suggest that harbour seals show bipolarity in their centres of activity, with a land and a sea component. Although travel in this

study was not as far-ranging as in grey seals (McConnell *et al.*, 1992; Thompson *et al.*, 1996; McConnell *et al.*, 1999), adult harbour seals, which occasionally travel over 100 km, do not move over large areas. Pacific harbour seals have also been reported to show inter-annual or inter-seasonal use of haul-out sites over 200 km apart (e.g. Brown & Mate, 1983; Yochem *et al.*, 1987). The relatively low proportion of return trips (40%) further suggests that there is a degree of mixing between local harbour seal populations on the west coast of Scotland. This could be a consequence of the arbitrary definition of haul-out clusters and trips and the error associated with ARGOS locations. However, increasing the scale of the grid used to cluster haul-outs to ten kilometres decreased the number of retrun trips, as did increasing the minimum duration of a trip to ten hours. Hence even if these definitions are changed, harbour seal dispersal was still observed.

During the breeding season dispersal facilitates gene flow, enabling a species to spread its range, repopulate vacant habitat, or respond to environmental change (Howard, 1960). Consequently dispersal is important from a conservation perspective. In this study, two males (one weighing 74 kg on capture, the other 85 kg) showed what appeared to be temporary emigration movements (although their transmitters may have failed before they returned to the haul-out cluster where they were initially captured). This suggests that dispersal may not be exclusively limited to young animals and/or the mating season in adult males, as suggested by some authors (Bonner & Witthames, 1974; Thompson, 1989; Lowry *et al.*, 2001; Härkönen & Harding, 2001).

Some previous work suggests that the duration and extent of trips varies with body size, sex (Thompson *et al.*, 1998) and season (Lowry *et al.*, 2001). Except for females travelling further than males, these relationships were not apparent in this study. One explanation for this is that all of the individuals in this study could meet their requirement within 25 km of a haul-out clusters. The observed difference in the duration and extent of trip between harbour seals in north-west and south-west Scotland may have been a result of the differences in the distance from haul-out sites to prime foraging areas. The multimodal pattern observed in the duration of trips (with

peaks at 18, 42 and 66 hours) may be the result of synchronisation with tidal cycles, because they represent one and a half, three and a half and five and a half tidal cycles. This could correspond with a seal leaving a haul-out site on a rising tide, as observed in harbour seals elsewhere (Chapter 4), and returning on the ebbing tide, also frequently observed in harbour seals. The apparent lack of a peak at six, 30 and 54 hours, which would correspond to half, two and a half and four and a half tidal cycles, may be the result of a preference for foraging or hauling out at night. Indeed telemetry data elsewhere in this chapter has pointed to the importance of diurnal influences, particularly during the summer months (Figure 2.20).

Method evaluation

A number of assumptions have been made in this study, the validity of which will affect the results and possibly the overall conclusions. In particular, the behaviour of tagged individuals was assumed to be representative of those in the population at large, and that the tagging procedure did not adversely affect the animals' behaviour (Gauthier-Clerc *et al.*, 2004; Moorhouse & Macdonald, 2005). No teeth were taken for reliable ageing, and due to the difficulty in catching animals no stringent selection procedure was implemented. Most of the study animals were captured when they were onland, and this may have resulted in a bias towards individuals that spend more-than-average amounts of time hauled out. Furthermore, SRDLs could only be attached to animals that had finished moulting (in order to ensure that the tag would remain attached to the fur for as long as possible) so only animals that had completed their moult by early September were selected for the autumn deployment. It is therefore probable that the haul-out patterns shown by these individuals were not representative of the whole population, because many captured individuals were rejected because they were still moulting. It is also likely that, due to the time taken to recover fully from the anaesthetic and sampling procedures involved during the tagging procedure, the seals did not show characterisic haul-out behaviour immediately after SRDL deployment. Consequently, care should be taken when extrapolating from observed haul-out behaviour during September and shortly after SRDLs were deployed in the

spring in order to draw up monitoring recommendations. It is possible that the timing of events within an individual seal's life are related to the timing of the previous life-cycle event (e.g. the timing of the moult in female seals may occur a certain number of days after they pup). As a result the haul-out behaviour of early-pupping seals may differ from that of seals which pup later, or, as in this study, there may be differences between early (tagged) and late (not tagged) moulting seals. This should not be a problem for animals that were tagged in the spring, because the sampling process should have selected early- and late-moulting seals at random. However, it might mean that the haul-out patterns observed during the autumn and winter months in this study were those of only part of the population. Without information from branded or otherwise marked individuals (cf. Chapter 3) it is difficult to see how the presence or absense of this potential influence on haul-out behaviour can be determined.

Some seals tagged with large data recorders have shown adverse behaviour as a result of additional drag (Gentry & Kooyman, 1986; Walker & Boveng, 1995). The SRDLs in this study weighed less than 5% of individual seal body mass. By studying size increase, stomach contents, filmed behaviour and external appearance Dietz *et al.* (2003) concluded that satellite tags, attached to the head of harbour seals, have no negative effect on feeding behaviour. Thus it is deemed unlikely that there was a sufficient increase in drag from the SRDLs to raise energetic costs, and therefore foraging demand, of tagged individuals in this study and thus reduce their haul-out time.

Yochem *et al.* (1987) suggest that disturbance during capture and tagging may prompt some seals to relocate to new sites. This is considered to be unlikely in the present study because individuals only rarely moved away from the capture site immediately after catching and almost all (96%) of the seals tagged in this study returned to the haul-out cluster where they were caught. When harbour seals are disturbed they usually haul-out at neighbouring sites whereas in this study seals travelled large distances passing other known harbour seal haul-out clusters on the way. Moreover, visual comparison of the movements and haul-out behaviour showed no difference between the days immediately after capture and a few months later.

One problem with using telemetry to study seal haul-out patterns, as mentioned above, is that if tags are attached to the fur they are lost during the moult. In this study some SRDLs lasted until the annual harbour seal summer moult, but many stopped earlier. There was no apparent difference in tag duration between the sexes in this study. Other harbour seal telemetry studies using SRDLs (e.g. Lowry *et al.*, 2001; Sharples, 2005) have typically lasted for a similar period of approximately four months (Appendix II; Table II.ii). Some SRDLs may suffer technical errors causing batteries to fail early. It was assumed that damage to the antenna would cause intermittent transmissions. Most transmissions ended abruptly, suggesting that few SRDLs in the present study failed due to antenna wear and tear. Instead it is likely that the fur of tagged harbour seals loosened, either as a mini-moult roughly half-way between annual summer moults, or due to shedding of the fur at the site of SRDL attachment, in a similar way to skin shedding to eliminate barnacles/parasites.

Possibly as a result of the relatively small sample of tagged seals, neither the haul-out duration nor the inter-haul-out interval (IHI) GLMMs provided a good fit to the observed data. Generalized Additive Mixed Models (GAMM), an extension of GLMMs that use non-linear functions to model covariate effects, were also used to attempt to model haul-out duration and IHI. However, these models performed as poorly as the GLMMs, suggesting that an inappropriate combination of explanatory variables had been chosen for the models, or that the wrong dependent variable was used. It is possible that, due to the location error associated with the SRDLs, the actual location of a haul-out event occurred closer to a different secondary tidal port and that the estimated tidal height was therefore incorrect in the model. However this is unlikely to have such a strong influence on the power of the models as observed in this study. The probability of hauling out may have been a more appropriate dependent variable than the duration of the haul-out events.

Whilst every effort was made to justify the criteria used to define activities in this study (e.g. haul-out events, trips), from a biological point of view they remain subjective. However despite this arbitrariness there was no difference in the

conclusions drawn using a range of different thresholds that were deemed biologically plausible. Inevitably there was a substantial degree of individual variation in this study and so some consideration should be given to the small sample of tagged animals in this study. The individual variation suggests that the number of tags used in this study were insufficient to capture the full extent of the variability in the study population. As mentioned above, this study assumed that the tagged individuals were representative of the adult population; yet at times only one seal provided data for that sex in the deployment region. Future studies should therefore consider how many tags to use to provide an appropriate characterisation of the behaviour of the study population, for example by using bootstrapping methods to simulate the effects of using a larger sample. Other, larger, telemetry datasets have been collected from harbour seals in the UK (e.g. Sharples, 2005; SCOS, 2005). These data could be used to investigate the extent to which conclusions drawn vary as a result of the number of individual seals used in the analysis. Comparing results between a subset of data and the full dataset may then allow predictions to be made as to how many individual harbour seals should be tagged to overcome the effects of variation observed in the present study.

Conclusions

The Habitats Directive protects harbour seals in Special Areas of Conservation (SACs). The Directive requires that these SACs be monitored to ensure that harbour seal populations remain in 'favourable conservation status'. No at-sea information was used to designate SACs, thus understanding the geographical relationship between where harbour seals haul out, and consequently are counted, and their movements is crucial to understanding the usefulness of SACs. To manage SACs effectively, and to ascertain their value, it is important to determine how faithful harbour seals are to one site.

There was spatial, temporal (seasonal and diurnal) and sex-related variation in the proportion of time harbour seals spent hauled out. Thus it is likely that variation also

occurs during the moult, when harbour seal abundance is currently surveyed. Seals made return trips 40% of the time (mean trip duration = 25 to 35 hours). Of the time spent hauled out, 18% occurred within harbour seal SACs with 50% of trips within 25 km of the haul-out cluster used. Thus although a degree of site-fidelity and coastal foraging was apparent, the extent to which individual seals, tagged in SACs, subsequently used the protected areas was limited. Some movements of over 100 km also occurred, indicating the presence of mixing between populations.

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CHAPTER THREE

USING PHOTO-IDENTIFICATION TECHNIQUES AND CAPTURE-RECAPTURE METHODS TO MONITOR THE CONSERVATION STATUS OF HARBOUR SEALS

ABSTRACT

Harbour seals have unique pelage patterns providing the potential for reliable photo-identification of individuals from their natural markings. Around 700 photographs of harbour seals were taken each month between April and October 2005 on the Isle of Skye, north-west Scotland. Each seal was photographed several times from both sides and at different angles. Different pattern cells or combinations of pattern cells (ventral, flank, shoulder and side of head) were used for computerised selection of potential matching pairs and those pairs were then checked visually. Using capture-recapture methods population estimates showed monthly variation, with highest numbers of adult harbour seals in May. In September 4% of the seals that used the sampling area between April and October were seen hauled out elsewhere (within a 30 km radius). Around three times more individuals used the sampling area between April and October (268, CV = 0.04) than were observed in a single aerial count in August (83, CV = 0.15) or were estimated per month using capture-recapture methods (mean = 86, CV = 0.07). With increasingly affordable camera equipment combined with digital technology, photo-identification techniques and capture-recapture methods provide both an additional method for monitoring harbour seals and important management information for the conservation of the population.

INTRODUCTION

Animal populations are dynamic and consequently effective population management requires abundance to be estimated regularly. A number of methods have been used to count harbour seals (Chapter 1), of which the preferred method in Britain consists of conducting aerial surveys (Chapters 4 & 5). However temporal and financial limitations restrict the frequency of these surveys and, as a result, large sections of the Scottish coast are surveyed comprehensively on average only once every four to five years (SCOS, 2005). In addition, because only the animals hauled out at the time of survey are counted, aerial surveys provide an estimate of the minimum population size, which does not include animals at-sea at the time of the survey. The objective of this study was to investigate if computer-assisted photo-identification techniques and capture-recapture methods could be used to estimate the absolute abundance of a local harbour seal population.

Capture-recapture is a common technique that can be used to estimate a number of demographic parameters, including abundance (e.g. Gormley *et al.*, 2005), movement (e.g. Calambokidis *et al.*, 1996) and survival (e.g. Langtimm *et al.*, 2004). By using data on the number of marked animals and their proportion in subsequent surveys, capture-recapture methods can be used whenever animals in a population can be individually marked, or otherwise identified, and then re-sighted later. Studies using capture-recapture often rely on adding artificial tags or marks to individuals specifically for recognition (White *et al.*, 1987; Hindell, 1991; Hastings *et al.*, 1999; Hall *et al.*, 2001), or on removing or altering part of the animal itself (e.g. toe clipping: Parris & McCarthy, 2001). Flipper tags have been used for a number of pinniped studies (e.g. Bowen & Sergeant, 1983; Shaughnessy, 1994; Baker *et al.*, 1995), but due to unknown tag loss rates (Seber & Felton, 1981; McConkey, 1999) they are usually unsuitable for long-term identification (but see Testa & Siniff, 1987 and Boyd *et al.*, 1995). In some studies of pinnipeds, branding has been used to provide a permanent mark (Harwood *et al.*, 1976; Hindell, 1991; Schwartz & Stobo, 2000; Härkönen & Harding, 2001). However, inherent in these techniques are a number of obstacles and potential sources of bias: capturing the seals, being able to

read the tags when re-sighted, and the possible effects that capture and handling may have on the animals' behaviour and their recapture probability.

Photo-identification has been used with many marine mammal species, including grey seals (Hiby & Lovell, 1990; Vincent *et al.*, 2001; Abt *et al.*, 2002), Mediterranean monk seals (Forcada & Aguilar, 2000), New Zealand sea lions (McConkey, 1999), Florida manatees (Langtimm *et al.*, 1998), bottlenose dolphins (Wilson *et al.,* 1999), killer whales (Bigg *et al.*, 1990), humpback whales (Mizroch *et al.,* 1990), sperm whales (Dufault & Whitehead, 1995), right whales (Caswell *et al.,* 1999) and bowhead whales (Zeh *et al.,* 2002). The pelage patterns of individual harbour seals are unique and are thought to remain constant throughout their lifetime (Yochem *et al.*, 1990; Olesiuk *et al.*, 1996), and photo-identification has been used to identify individual harbour seals in British Columbia (Olesiuk *et al.,* 1996), California (Yochem *et al.,* 1990), Alaska (Crowley *et al.*, 2001; Hastings *et al.*, 2001) and the Moray Firth, north-east Scotland (Middlemas, 2003; Mackey, 2004).

Matching photographs is a time-consuming and skilled procedure (Hammond, 1986). As the number of animals identified rises it becomes increasingly necessary to use a system that reduces both the time spent matching photographs and the risk of introducing identification errors (Katona & Beard, 1990). Thus, there has been a rise in the use of computer-aided matching systems that aim to reduce the number of images needing visual matching. For example Hiby & Lovell (1990) describe a system for grey seals, Whitehead (1990) for sperm whales, Kreho *et al.* (1999) for bottlenose dolphins, Arzoumanian *et al.* (2005) for whale sharks and Gope *et al.* (2005) for sea lions.

In compliance with the Habitats Directive[1], Special Areas of Conservation (SACs) have been designated in each Member State of the European Union to maintain populations listed on Annex II, including the harbour seal, in 'favourable conservation status'. Some of the SACs designated for harbour seals in Scotland offer high potential for eco-tourist ventures. For example, commercial seal-watching trips have

[1] The 1992 Council Directive on the Conservation of Habitats and of Wild Fauna and Flora (Appendix I)

been running in Loch Dunvegan, which forms part of a SAC, since 1989; the boats run daily, according to demand, from Easter until the end of October. Because the animals are habituated to their presence, boats can approach to within five to ten metres of the seals without causing disturbance. The tourist boats in Loch Dunvegan therefore provided an ideal study platform to test the use of computer-assisted photo-identification techniques and mark-recapture methods for monitoring harbour seals and estimating the absolute number of animals using a protected area.

METHODS

Field procedures

Harbour seals were photographed in approximately 0.5 km^2 of south-eastern Loch Dunvegan (59°27' N, 6°36' W), which is part of the harbour seal SAC on the Isle of Skye, north-west Scotland (Figure 3.1). A pilot study was conducted in October 2004, followed by monthly sighting trips from April to October 2005. Each 'trip' consisted of three repeat surveys of haul-out sites in East Dunvegan on consecutive days, except in September when only one survey was conducted in the eastern part of the loch. On each survey the time of day, tidal height, state of tide and general weather conditions were recorded. Surveys took place between 7:45 and 14:30 GMT, within four hours of low tide, and were not conducted in strong winds or heavy precipitation. The survey route was chosen according to weather conditions and the presence of other boats in order to equalise coverage of the study area, minimise disturbance to individual seals and reduce potential heterogeneity resulting from individual preference for particular haul-out sites. Previous knowledge of harbour seal behaviour (e.g. Chapter 2) suggested that the intervals between daily surveys and monthly trips were long enough to allow a remixing of the population prior to re-sampling, but short enough to reduce the risk of migration, mortality or seasonal demographic shifts.

Photographs were taken using a Canon EOS 20D digital camera with an image-stabilised lens (70 – 300mm f4.5 – 5.6), recorded onto a 2GB CompactFlashcard type II and subsequently downloaded onto DVDs. Shutter speeds were around 1/400 second depending on light conditions. At the end of the survey the route was transcribed onto a 1:50,000 map with details of the location and size of the haul-out groups encountered.

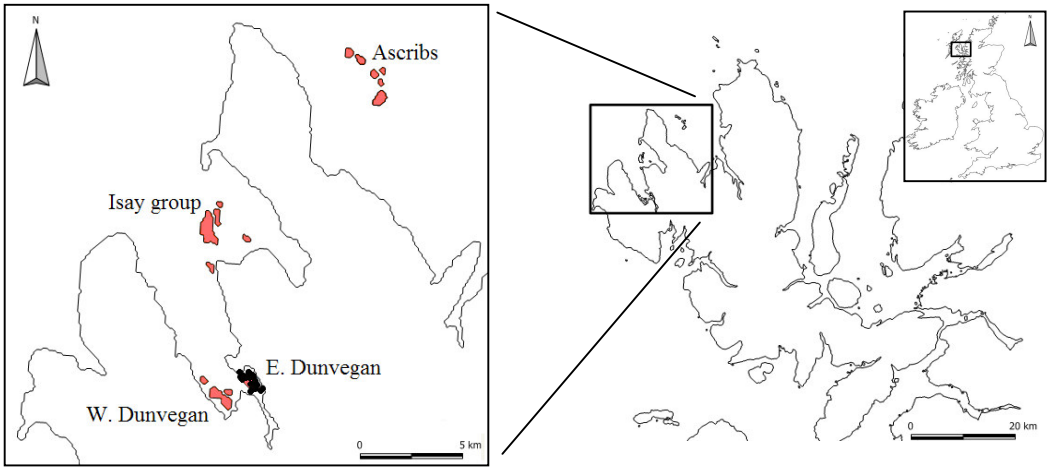

Figure 3.1: The study area in Loch Dunvegan, north-west Skye. Photographic surveys were conducted of harbour seal haul-out sites (●) in East Dunvegan, every month from April to October 2005, using small boats involved in commercial seal-watching. The islands highlighted in red (Ascribs, Isay group and East and West Dunvegan) comprise the harbour seal SAC and were surveyed once as part of a wider survey of the area.

Almost all identification photographs (99%) were taken of seals hauled out on land. The animals were approached in traditional three-metre clinker boats that are used daily from Easter to October for seal-watching trips. The location and size of each haul-out was photographed and recorded. In order not to scare the seals into the water the engine was kept running and the boat cruised slowly past the haul-outs. Seals that were between two and 15 metres from the boat were repeatedly photographed from different angles and both sides, where possible, in order to obtain good quality images for recognition. Seals were photographed regardless of the extent of pelage marking. The position of an animal on the haul-out had some influence on whether a sufficient number of satisfactory photographs could be taken. The animals on each haul-out site were photographed systematically, from one side of the haul-out to the other, in order to reduce the possibility of heterogeneity in capture probability, for example by favouring easily identified seals. Once enough photographs had been taken to ensure that good-quality images of different sides of the animal had been obtained, a 'blank' (e.g. of the sky or sea) was taken to separate the sequences of photographs from individual seals. No adverse behavioural responses to survey aircraft or boats were observed during the study.

A wider photographic survey was conducted in September 2005 (covering all haul-out sites within the SAC on the Isle of Skye, i.e. the Ascribs, Isay Group and East & West Loch Dunvegan, Figure 3.1) to obtain information on harbour seal movement between neighbouring haul-out sites and to start a database for future monitoring. Identification photographs were also taken of 14 seals captured within the SAC and fitted with Satellite Relay Data Loggers (Chapter 2). Because capture-recapture analysis requires at least one recapture survey, individual capture histories were only constructed from the seven trips to East Dunvegan (April to October 2005) and not from animals seen during the wider survey.

Matching procedure

Seals were allocated to three age classes according to size: adults, sub-adults and pups. When the penile aperture was clearly observed in adult seals the sex was noted as male; where clearly absent, or a suckling pup was seen, the sex was noted as female. If neither the genitalia nor a suckling pup was observed the sex remained unknown. Additional information on the general health status of the seals was noted, including the presence of open wounds, distinctive scars, laboured breathing and eye problems.

Individual capture histories were only constructed for adults. All adults had individually distinct markings and so, provided the quality of the photograph was sufficient, all individuals could be identified. Poor quality images, due to the angle of the seal, lack of focus or bad light, were excluded from the matching process along with unnecessary duplicates. Remaining photographs were then assigned a quality rating from one (poor) to five (excellent) based on the focus and resolution of the image, the angle of the seal, and the proportion of the pattern cell (see below) visible within the frame (Figure 3.2). Only photographs with a quality value of three, four or five were considered sufficiently good to ensure certainty of identification. Consequently images rated two or less were not matched to avoid potential biases created by individuals having different recapture probabilities.

Figure 3.2: Example identification photographs of different qualities. Grades were given according to overall image quality, for example based on the angle of the seal.

To compensate for the orientation of the head, which alters the appearance of the pelage pattern, Conservation Research Ltd adapted Hiby & Lovell's (1990) grey seal model for use with harbour seals by including a shape-matching and a dot-matching algorithm. Automated matching occurs by describing an area numerically and then calculating similarity scores between pairs of images. In some species the area described, known as the 'pattern cell', is broadly consistent in shape and location, for example in animals with dorsal fins or tail flukes. Harbour seals do not have a comparable distinctive area and so the pattern cell was described in relation to morphological features such as the position of the eyes, ears and nose. For each digital image, the coordinates of these features were determined using the cursor and then translated by the program to build a three-dimensional projection.

As in Hiby and Lovell (1990), the computer program located the pattern cell, or combinations of pattern cells (ventral, flank, shoulder or side of head – Figure 3.3), within each photograph and extracted a numerical description from the grey-scale intensities. These extracts, called 'identifier arrays', were compared by the computer program with all other identifier arrays of the same side and pattern cell. Each comparison generated a 'similarity score', defined as the correlation coefficient between corresponding elements in the identifier array (Hiby & Lovell, 1990). Similarity scores were calculated from several sub-regions within the identifier arrays and the mean was taken to reduce the effect of gradual shifts in lighting conditions (Hiby & Lovell, 1990). The program accounted for alignment errors by stretching one identifier array over the other to determine the maximum correlation coefficient.

The probability that two identifier arrays were of the same individual, p_m, was calculated as $p_m = \frac{s_1}{s_2}$

where s_1 = the smaller similarity score from the two identifier arrays,

s_2 = the larger similarity score.

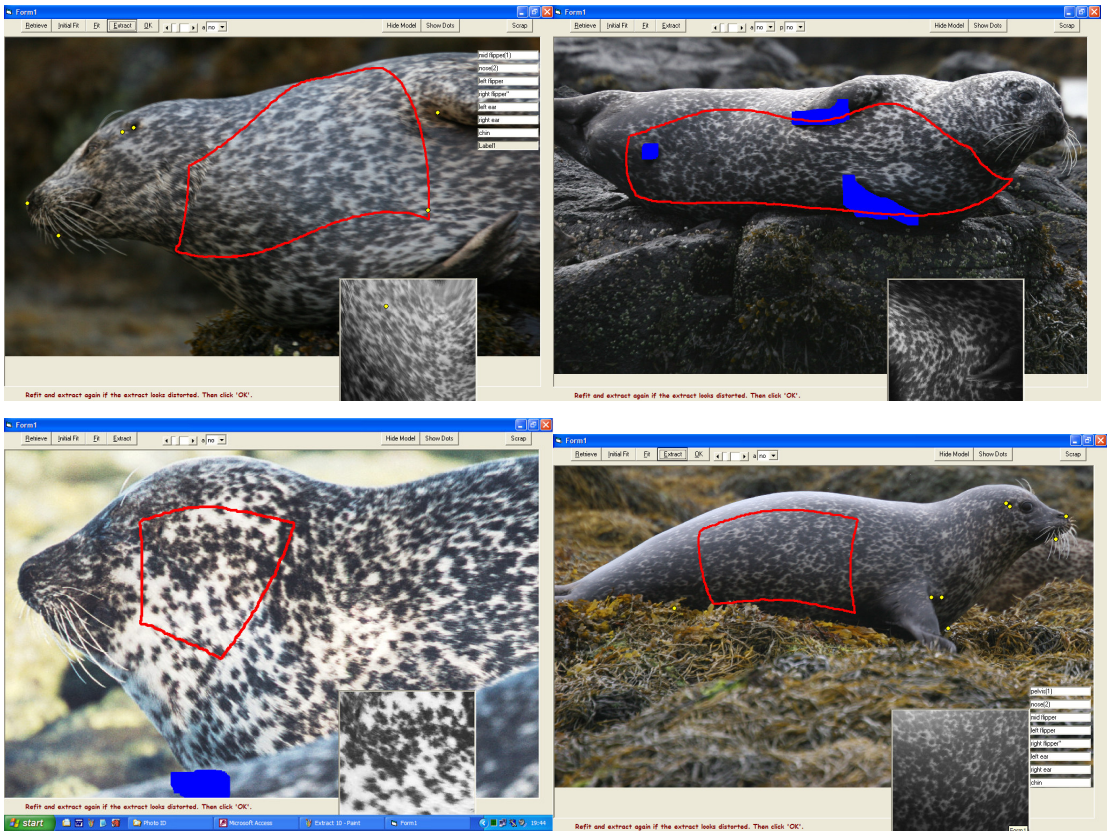

Figure 3.3: Example shoulder, dorso-ventral, flank and head pattern cells (clockwise from top left), outlined in red.

The computer program standardised similarity scores by taking the mean score obtained from the pattern cell compared with all the others in the database. The standardised score was expressed as its position, in number of standard deviations, above the mean score. All matches that generated standardised scores over a critical level of 1.9 standard deviations above the mean score were checked visually to confirm matches. The critical level was the same value used in grey seal matching, where it was chosen as a result of extensive experience with the software (Hiby & Lovell, 1990).

Potential matches were visually compared using as many features as possible and images were only matched if the observer was certain that pairs of photographs were of the same individual. This removed the possibility of false positives (the matching of different individuals, also known as a Type II error) and so any error would only result

from two images of the same individual not being matched (false negative, also known as a Type I error).

Data analysis

Although satellite telemetry has shown that harbour seals in north-west Scotland occasionally travel long distances, these movements were generally only temporary and individuals showed a relatively high degree of site-fidelity (Chapter 2), particularly on a short temporal scale (i.e. several months). It was therefore assumed that there was no permanent immigration or emigration during this study. Although pups were born during the survey period, they did not count as additions to the population because only adults were photographed. Sampling occasions were deemed sufficiently close in time to assume that negligible mortality occurred during the study. Thus the adult harbour seals using haul-out sites in East Dunvegan were considered to belong to a population that was demographically and geographically closed for the duration of the study. All assumptions outlined in Table 3.1 were also considered to be valid. The effects of mark loss and animals insufficiently well-marked to be included in the sample were considered negligible in this study and so it was deemed unnecessary to rescale estimates to take account of $\hat{\theta}$, the proportion of animals with long-lasting marks in the population (Wilson *et al.*, 1999).

Table 3.1: Summary of assumptions made in capture-recapture analysis, and the causes and consequences of violating them, ↑ = population size overestimated, and ↓ = underestimated.

Assumption	Causes of violation	Effect
Every individual is identified correctly	Poor quality photos or lack of distinct markings.	↑ Abundance
	Tag loss or changing visible features.	↑ Abundance
Equal probability of capture	Inherent behavioural differences.	↓ Abundance
	Non-randomised survey route.	↓ Abundance
	Scaring seals during first survey causing 'trap shy' response.	↑ Abundance
Equal probability of survival	Sex or age-biased proportion of population captured.	↓ Abundance
Independent capture events	Haul-outs dominated by one sex or age group.	↓ Variance

Capture-recapture models were constructed using program MARK, version 4.1 (White & Burnham, 1999), to (i) estimate the monthly abundance of adult harbour seals in East Dunvegan and (ii) to calculate the size of the local adult population using East Dunvegan between April and October. Heterogeneity was modelled in MARK at two fixed levels (high and low), to account for the possibility that sex- and age-related variation in haul-out probabilities affected the probability of recapture (Thompson *et al.*, 1997; Härkönen *et al.*, 1999). Multiple samplings of the same individual within a sampling period were ignored to reduce biases from unequal capture probabilities (Calambokidis *et al.*, 1990). For the monthly abundance estimates a jack-knife estimator was used, which assumes that each animal has a unique and constant capture probability. This estimator was chosen for its robustness (Boulanger & Krebs, 1996). Capture probabilities were allowed to vary with time, including heterogeneity and a combination of variation by time and heterogeneity. Models were selected using Aikaike's Information Criterion corrected for small sample size (AIC_c), as recommended by Burnham and Anderson (2002) for situations where the sample size divided by the number of variables is less than 40.

Abundance estimates

Data were available to calculate estimates of abundance from left- and right-side photographs, but both left- and right-sides were not known for all animals. Separate estimates were therefore calculated for left- and right-side data and combined as a weighted mean. Because variance is correlated with the mean, rather than using the inverse variance (Wilson *et al.*, 1999), the inverse of the squared coefficient of variance was used to weight the abundance estimates (Larsen & Hammond, 2004). Left- and right-side encounter histories were compared using a Mann-Whitney U test in SPSS, version 12.

Log-normal 95% confidence intervals, used to prevent an unrealistic lower limit of zero being calculated (Burnham *et al.*, 1987), were determined where the lower limit was $\widehat{N}/c$ and the upper limit $\widehat{N}*c$, as:

$$c = \exp\left(1.96\sqrt{\ln(1+CV^2(\widehat{N}_{Total}))}\right)$$

where $1+CV^2(\widehat{N}_{Total})$ is an approximation of $\mathrm{var}(\ln \widehat{N}_{Total})$ and $\widehat{N}$ is an estimation of population size.

Monthly abundance estimates of adult seals were compared with a minimum estimate of the number of seals of all ages from an aerial survey flown on 8th August 2005, using a thermal imaging camera from a helicopter as described in Chapter 4.

RESULTS

Individual identification

A total of 20 days were spent collecting observations in East Dunvegan between April and October 2005. In general seals lay perpendicular to the shoreline, and so their position severely limited the quality of photographs taken from the confines of a small boat. In addition, rocks or other individuals often obscured the flank and most seals lay on their bellies, thus hiding the dorso-ventral pattern cell. Extracting information from the shoulder cell aided matching of some individuals. However the increased flexibility of the shoulder area, with respect to the side of the head, reduced both the quality and number of photographs taken of the shoulder (Table 3.2). The head pattern cell was consistently the easiest to photograph and the close proximity of the pattern cell to a number of easily identified morphological features helped the visual comparison procedure.

Table 3.2: The total number of images of each quality grade and pattern cell for left- and right-side images that were entered into the database. Only the highest quality image for each side of an individual at each encounter was entered into the database to avoid unnecessary duplicates.

Grade	Dorso-ventral extract		Flank extract		Shoulder extract		Head extract		Total images captured	
	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right
1	0	0	0	0	1	1	31	25	32	26
2	1	1	0	0	16	27	77	104	94	132
3	0	0	0	0	31	31	104	91	135	122
4	1	1	0	1	11	12	88	124	100	138
5	0	0	0	0	2	2	45	52	47	54
Total	*2*	*2*	*0*	*1*	*61*	*73*	*345*	*396*	*408*	*472*

To prevent overestimating the number of individuals, images with extracts of shoulder, flank and dorso-ventral pattern cells were not used in the analysis. Out of the 741 head photographs, 237 and 267 images of the left- and right-side respectively were of quality grade three or more (Table 3.2).

There was no significant difference between the distributions of left- and right-side encounter histories (Mann-Whitney U test: W = 35376, p = 0.682). Right-side head images allowed identification of 187 individuals, of which 84 (48%) were seen more than once. Left-side head extracts allowed identification of 175 individuals, of which 84 (45%) were seen more than once (Figure 3.4). In most cases the sex of the seal remained undetermined with only 34 identified males and 24 identified females (i.e. 16% of identified individuals). The frequency with which individuals were re-sighted is summarised in Figure 3.5 and detailed in Appendix III: Table III.i.

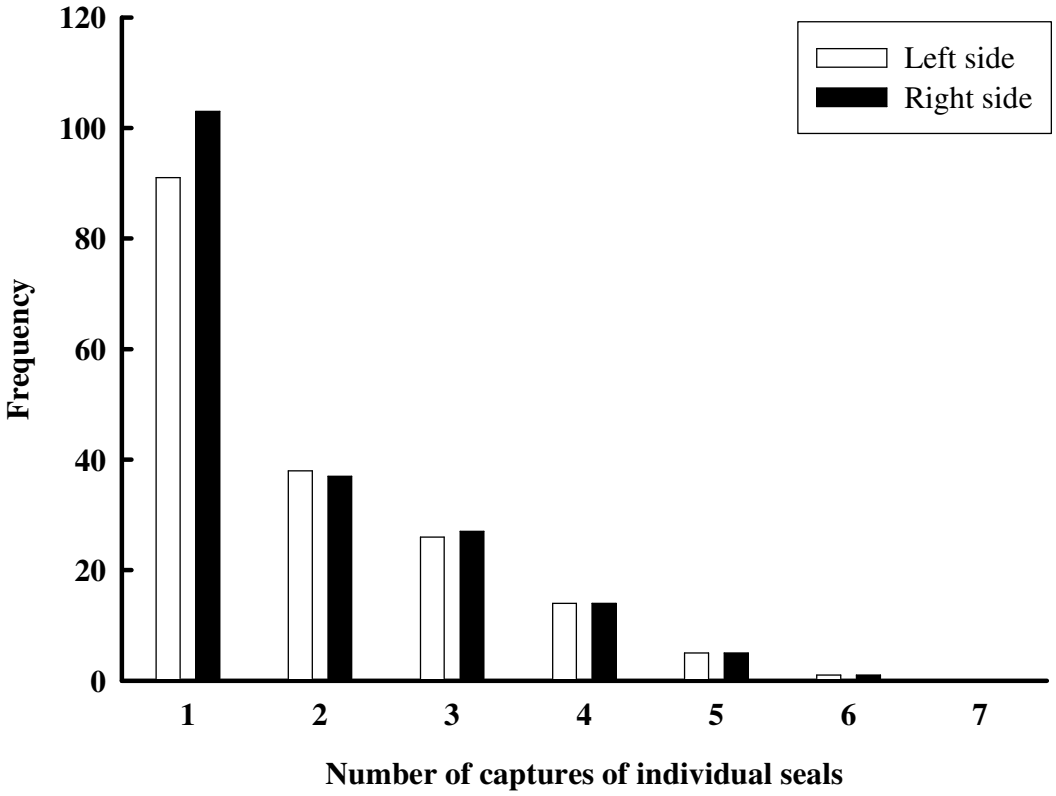

Figure 3.4: Re-sighting frequencies of individually identified harbour seals in East Dunvegan for left- and right-side head pattern cells.

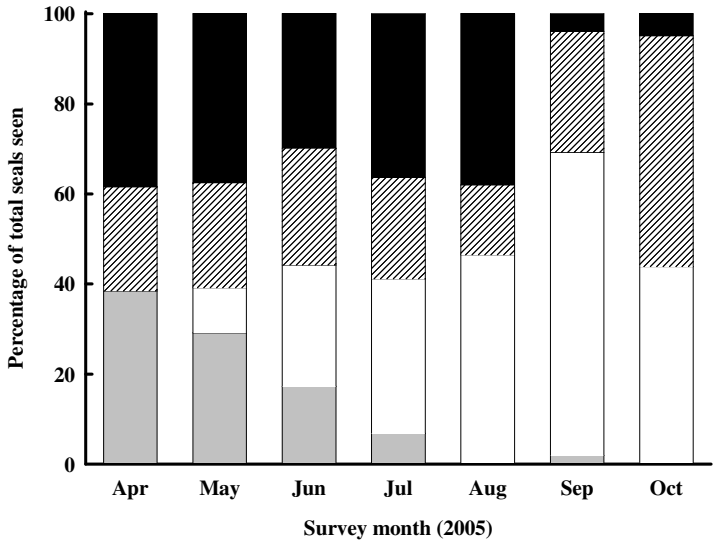

Figure 3.5: Summary of the frequency of encounters of individual seals sighted during the study, including those counted but not photographed, where ▢ = photographed first of several times, □ = previously photographed, ▨ = only seen on that occasion and ■ = not photographed (just counted).

Abundance estimates

Monthly estimates of adult harbour seal abundance in East Dunvegan in 2005 ranged from 62 in April to 117 in May (Figure 3.6). The August estimate of 71 adult harbour seals (CV = 0.08) was similar to the minimum population estimate (83, CV = 0.15), from the aerial survey, which was made four days later. The boat count was lower than both capture-recapture and aerial population estimates (52, CV = 0.23, Table 3.3).

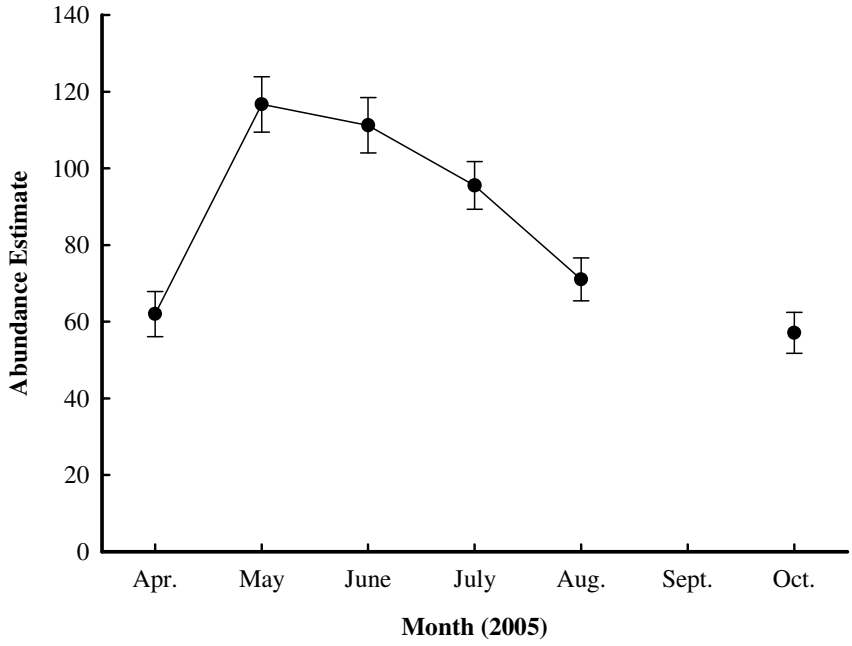

Figure 3.6: Monthly abundance estimates (with standard errors) of adult harbour seals in East Dunvegan calculated using photo-identification techniques and capture-recapture methods.

Table 3.3: Harbour seal abundance estimates for East Dunvegan in August. The boat count and CV are calculated from the number of harbour seals seen during the photographic surveys (in East Dunvegan) on three consecutive days in August 2005. The aerial count was conducted on 8th August 2005 under standard survey conditions; the CV is calculated from five repeat surveys in 2004 (Chapter 4). The photo-ID estimates were calculated using capture-recapture methods, which modelled for individual heterogeneity in capture probabilities.

	Estimated number of adults	**Coefficient of variation (CV)**	**95% confidence intervals (CI)**
Boat count	52	0.23	34 - 82
Aerial counts	83	0.15	62 - 111
Photo-ID: Left-side	72	0.11	60 - 91
Photo-ID: Right-side	70	0.11	59 - 90
Photo-ID: Weighted mean	*71*	*0.08*	*61 - 83*

The estimated number of adult seals using haul-out sites in East Dunvegan between April and October 2005 was 245 for left-side photographs and 297 individuals for right-side photographs. When combined, using the method outlined above, these gave a best estimate of 268 adult harbour seals (Table 3.4).

Table 3.4: Harbour seal population data from capture-recapture analysis modelled for time variation and individual heterogeneity in capture probabilities (Chao *et al.*, 1992). Italicised values were calculated without photographs taken during the August moult.

	Estimated number of adults		**Coefficient of variation (CV)**		**95% confidence intervals (CI)**	
Left-side (Apr. – Oct.)	245	*252*	0.06	*0.06*	223 – 278	*227 - 288*
Right-side (Apr. – Oct.)	297	*270*	0.06	*0.06*	266 – 341	*243 - 309*
Weighted Mean	268	*261*	0.04	*0.04*	247 – 291	*240 - 285*

All harbour seals in this study had distinctive pelage patterns. However, although pelage patterns were the same both before and after the moult, during the annual moult the old fur becomes a uniform brown and patches are lost over a period of a few weeks. Thus the old fur occasionally masked the pelage pattern to such an extent that individuals were no longer identifiable. During the August survey 19% of photographs taken were of unidentifiable seals. This compares with a minimum of 2.1% in October and a maximum of 10.1% in June. Although the model used to estimate local abundance in this study accounted for heterogeneity of capture, abundance was also estimated without the data collected during the August survey; the level of precision was maintained (CV = 0.04) but the abundance estimate decreased by 2.7% to 261 animals with a 95% confidence interval of 240 – 285 (Table 3.4).

The model selection criterion within MARK, AIC_c, confirmed that the model allowing for heterogeneity of capture probabilities (Chao *et al.*, 1992) was the most appropriate closed population model for analysis of the number of seals using haul-out sites in East Dunvegan between April and October. This allowed the probability of capture to either be high or low for each individual, but did not allow the probability of capture to vary over time. However, a discovery curve (Williams *et al.*, 1993), showed that an asymptote was not reached within the survey period, as would be expected if the population was closed and most of the individuals already identified (Figure 3.7). Thus, even during the short time frame of this study, the population was not closed.

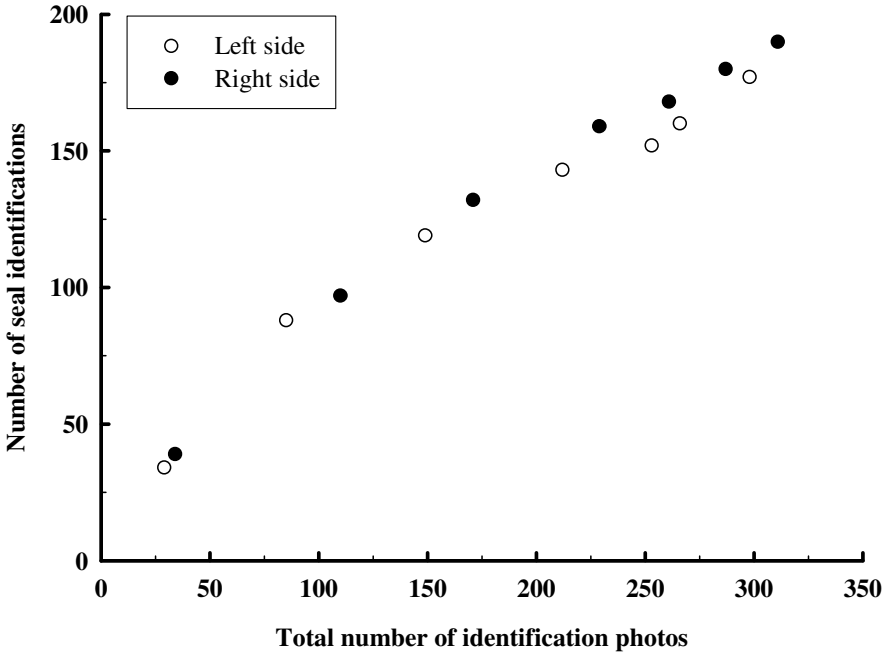

Figure 3.7: A discovery curve showing the number of photographs taken of both left- and right-sides and the corresponding number of new seal identifications.

In September 2005, during a wider survey of Loch Dunvegan (comprising West Dunvegan, the Isay group and the Ascribs), 102 head photographs of grade three or better were taken. Of 52 harbour seals identified in the Ascribs, five (10%) had also been seen in East Dunvegan on one or more days between April and October 2005 (Appendix III: Table III.ii); in West Dunvegan six of the 50 individuals (12%) were also seen in East Dunvegan (Appendix III: Table III.iii). No photographs of sufficient grading were obtained from the Isay group.

Certainty of matching

To determine the effectiveness of the similarity algorithms used in computer-assisted matching methods, identifier arrays (the numerical description of grey-scale intensities of each pattern cell) from matched images were classified into ranks according to their position, when ordered by decreasing similarity scores. The majority of matches ranked very highly (58.9% were rank one and 67.3% rank ten or above). Occasional

disparities from high ranks occurred when multiple, poor quality photographs of the same individual were entered into the database (Figure 3.8). The quality of these photographs was not always sufficient for matching and instead matching was based on prior knowledge obtained from the field (for example, photographs taken of the same individual from different distances). Identifier arrays based on shoulder cells were ranked higher more frequently than those based on head cells, with 71% rank one and 77.4% rank ten or above.

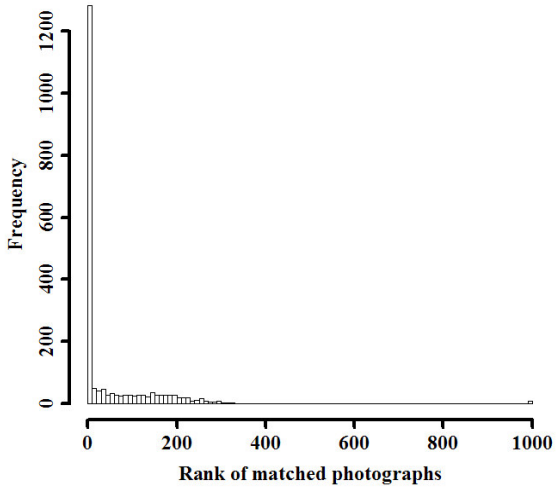

Figure 3.8: Frequency distribution of the ranking of identifier arrays of photographs (of quality grade three or above) of the same individual, irrespective of the pattern cell, or combination of pattern cells, used.

The probability that identifier arrays were taken from photographs of the same seal is shown in Figure 3.9. There is a clear division between those identifier arrays that are very unlikely to be of the same individuals (i.e. close to zero) and those that are almost certain matches (i.e. close to one). Overall there was a 38% chance that two identifier arrays were taken from photographs of the same animal. The probability of a Type II error (i.e. falsely matching identifier arrays of different individuals) was considered negligible in this study due to the rigorous matching procedure.

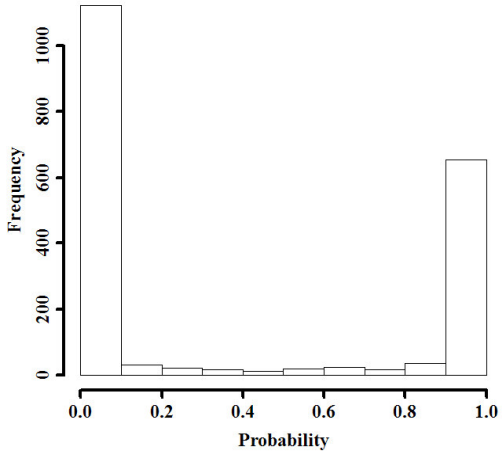

Figure 3.9: Frequency distribution of the probability that identifier arrays from head extracts of quality grade ≥ 3 are taken from photographs showing the same seal.

DISCUSSION

Harbour seals are protected under European legislation and consequently it is important to be able to detect trends in their abundance. This study showed that there was monthly variation in the number of adult harbour seals using haul-out sites in East Dunvegan, estimated using capture-recapture methods between April and October 2005. The highest numbers occurred at the start of the pupping period in May (cf. Chapter 4). Although this could have resulted from seasonal changes in the probability of seals being hauled out, the capture-recapture estimate of the local population of adult harbour seals that used haul-out sites in East Dunvegan between April and October (268, 95% CI = 240 - 285) was 3.1 times more than the estimated monthly mean number of adult harbour seals (86, 95% CI = 74 - 99), and 3.2 times more than the August aerial survey count (83, 95% CI = 62 - 111). Thus this study showed that around three times more adult harbour seals use the haul-out sites in East Dunvegan over a seven-month period than are observed in a single aerial count or monthly capture-recapture estimate.

Similar numbers of seals that had previously been photographed in East Dunvegan were recognised in West Dunvegan and the Ascribs despite the difference in distance from East Dunvegan (2 km and 30 km respectively). This suggests that the adult harbour seal population mixes freely within Loch Dunvegan, with at least 4% of harbour seals using the haul-out sites in the study area hauling out in different parts of the north-west Skye SAC in September. Consequently, at least some of the harbour seals estimated within the local capture-recapture population estimate (i.e. seals using haul-out sites in East Dunvegan between April and October) were likely to be hauled out at neighbouring haul-out sites during the aerial survey in August. Because of the problem of defining the extent of the population being estimated using capture-recapture methods, it is difficult to make a direct comparison between abundance estimates obtained using the different methodologies.

This study was designed to minimise bias and maximise precision in population estimates by considering the assumptions made and the consequences of violating them. These are considered in turn below:

1. Mark recognition

Capture-recapture analyses assume that every individual is identified correctly such that a marked animal will be recognised with certainty if recaptured. Violation of this assumption will increase abundance estimates (Stevick *et al.*, 2001). Although errors in identifying animals are possible in any study, they are more likely to happen when looking at photographs of natural markings (Hammond, 1986). Mismatching may occur where poor quality photographs are used, or due to a lack of distinctive individual markings (Friday *et al.*, 2000). Consequently only high quality photographs (of at least quality grade three) were used in the analysis and it was assumed that all animals were sufficiently marked to be identified with certainty from a good photograph.

Incorrect identification may involve either falsely identifying two sightings of the same individual as different, or identifying two sightings of different individuals as the same. Two similarity algorithms were used in this study: the shape-matching algorithm worked successfully on head pattern cells whereas the dot-matching algorithm was better when used on larger areas (e.g. the shoulder). Using a combination of pattern cells and algorithms allowed over 67% of matching identifier arrays to be highly ranked ($\geq$ rank ten). Most pairs of identifier arrays were deemed either very similar or very different thus minimising the probability of both Type I and Type II errors. The probability of both Type I and Type II errors were therefore considered to be negligible, with any error present being of Type I. In large populations there is also the possibility that two or more individuals are so similarly marked that they are effectively indistinguishable from each other (Pennycuick, 1978).

2. Mark loss

In studies using tags, animals losing their marks (i.e. tags) can cause substantial bias to estimates (e.g. Arnason & Mills, 1981), increasing estimates of abundance. Some identification errors are similar to tag loss, for example where visible features change

considerably over time (e.g. Bretagnolle *et al.*, 1994), rendering an individual unrecognisable. Thus, in order for individuals to be identified correctly, the natural markings used to recognise individuals within a population must be permanent and invariant for the duration of the study. In some individuals in this study the pelage pattern was temporarily obscured during the annual moult. However individuals were recognised during subsequent surveys, indicating that there was no permanent change in pelage pattern; thus mark loss was deemed negligible.

3. Probability of capture

To prevent underestimating abundance all individuals in the population should have the same probability of capture. This assumption is violated if individual preferences for certain areas affect the probability of encountering an animal, which may result from inherent behavioural differences in haul-out patterns. Randomised surveys reduce potential heterogeneity resulting from individual preference for particular haul-out sites. Animals lying high up on the rocks were harder to photograph than inquisitive animals closer to the shore, which may have negatively biased the abundance estimates in the present study. Individuals should also have the same probability of survival between capture occasions. Because photo-identification does not require an initial physical capture of the seals there is no risk of reducing their probability of survival or of accidentally killing them during the marking procedure. The timing of the moult differs by sex (females first, then males) and age-class (young seals before adults - Thompson & Rothery, 1987; Daniel *et al.*, 2003), and so surveys conducted around the moult could be biased as a result of unequal probability of capture. Capture probability will also be affected by the increased length of time that harbour seals spend hauled out when moulting (Daniel *et al.*, 2003).

The overall local population estimate increased by 2.7% when data from August were included. This difference is negligible given the overlap of the confidence intervals (247 - 291 vs. 240 - 285), suggesting that the model adequately accounted for heterogeneity in capture probabilities. However future photo-identification studies of harbour seals should not survey exclusively during the annual moult, and the potential increase in unidentifiable seals during this period should be taken into consideration.

If the action of capturing an individual alters the probability of its recapture then population estimates will be biased (e.g. McCarthy & Parris, 2004). 'Trap shy' behaviour, which reduces the probability of recapture, will lead to an overestimate of population size whereas 'trap happy' behaviour, which increases the probability of recapture, will underestimate abundance. Photo-identification avoids these behavioural responses, since there is no physical interaction to 'capture' individuals, provided animals are photographed regardless of the extent of their pattern. An exception might occur if, whilst taking photographs, an aircraft or boat scared seals thus causing the animals to be more frightened during subsequent surveys (Hammond, 1986). No such adverse reactions were observed in the present study. Another potential limitation is that most (99%) of the animals photographed in this study were hauled out, yet little is known about the extent to which hauled out seals are representative of the population (Härkönen *et al.*, 1999).

4. Independence

Capture events of individuals are assumed to be independent. Violation of this assumption, for example in the case of socially cohesive groups of cetaceans, should not bias abundance estimates but may lead to an underestimate of variance and a false sense of precision (Wilson *et al.*, 1999). Some harbour seal haul-out sites are dominated by one sex or age group, which is likely to have caused the variance in this study to be underestimated (Kovacs *et al.*, 1990; Härkönen *et al.*, 1999). Furthermore, if social conhesion increases capture heterogeneity then abundance estimates will be underestimated.

5. Closed population

Satellite-tagged harbour seals showed some movement out of Loch Dunvegan (Chapter 2), but the majority animals returned to haul-out sites within Loch Dunvegan (Chapter 2). Whilst these movements are unlikely to bias monthly population estimates, they may influence the monthly estimates of local population size. The shape of the discovery curve suggested that the population was not closed, and that new individuals continued to become available to be photographed over the course of the study. This suggests that a proportion of the population remained unavailable for photographic capture throughout the study, and that the overall estimate of adult

population size (268) is biased downwards to an unknown extent. Kendall (1999) found that the Lincoln-Peterson estimator of population size is unbiased if there is random movement into or out of the study population, provided that there is no heterogeneity among animals in capture probabilities. However, there was evidence of such heterogeneity in this study. On the other hand, Kendall (1999) concluded that where there is only immigration during the study period (which appears to be the case here), an unbiased estimate of population size can be obtained by pooling all but the last period. When this was done, an estimate of 294 (95% CI = 279 – 310) was obtained, weighting left- and right-side estimates as previously described.

Method evaluation

In this study 32% of all photographs and 68% of pictures of the head were of quality grade three or above. Low quality pictures were rejected to reduce the probability of marks going unrecognised at recapture. Low light intensity, the position of the animals and/or a lack of focus were the most common problems. There was a noticeable improvement in the quality of photographs taken by the author as this study progressed, so using an experienced photographer and ensuring appropriate training could reduce the proportion of low quality images. In addition, light conditions could be optimised by greater flexibility in the timing of surveys, and blur could be minimised by restricting survey activity to calm sea states.

For the few high-quality dorso-ventral and flank photographs obtained, successful visual comparison was limited by a lack of distinctive morphological features close to the pattern cell. Consequently these pattern cells were not appropriate for individual identification of harbour seals on the west coast of Scotland. However the photographs did provide valuable information on the sex and general health (e.g. presence of scars and wounds, see also Appendix III) of the individuals. To reduce the possibility of false negatives only individuals with head extracts were used for analysis. However, using a combination of shoulder and head pattern cells helped to match some individuals. As many marks as possible were used to confirm each

identification and thus reduce the possibility of false matches. Although helpful for visual matching, these scars and wounds were not always permanent and so, unlike for some species (e.g. porpoises - Würsig & Würsig, 1977; manatees - Reid *et al.*, 1991), were not sufficient to identify individuals reliably.

In this study the capture-recapture estimate for adult seals in August was 17% lower than the aerial count, suggesting that underestimation may be a problem in studies with only a few recapture events. Visual surveys of the study area during August (conducted by boat) showed that there were insufficient young seals to account for the 17% difference between the August aerial count, which included juvenile seals, and the capture-recapture estimate, which did not. The mean monthly estimate of the number of adult seals, calculated from the capture-recapture study, was similar to the aerial count of all seals and so it is believed that photographing seals over a longer period (e.g. seven months versus one) to obtain a local population estimate will overcome some of the negative bias that results from the small sample size of only using the capture-recapture estimate from a single month (e.g. August). In addition, technological advances in the quality of camera equipment now permit photographic capture-recapture surveys to occur in sub-optimal conditions (e.g. heavy cloud and unstable small boats), and this is likely to result in further expansion of an already well-developed methodology. However, consideration still needs to be given to the problem of population closure. For example, future work should consider adopting open-population multi-site models (e.g. Harrison *et al.* 2006), which can estimate migration and recapture heterogeneity. As the name implies, this method requires several study sites; the scattered distribution of harbour seal haul-out sites around Scotland, and the composite nature of the SAC on the Isle of Skye, would permit suitable survey areas to be defined. Alternatively, to comply with the assumption of a closed population, the study area could be expanded to include the surrounding area and/or the duration of the capture-recapture study could be increased.

Conclusions

The similarity between the aerial count and the monthly mean capture-recapture estimate suggests that, like the aerial surveys of harbour seals, the capture-recapture method is only estimating the number of adult animals hauled out at the time of the survey (i.e. not including animals in the water or those hauled out elsewhere). Thus capture-recapture is not a suitable method for estimating local absolute abundance based on three surveys per month on consecutive days. However, this study has shown that photo-identification techniques and computer-assisted capture-recapture methods can be used to determine the number of harbour seals that use an individual haul-out site, or localised group of haul-out sites, over a period of several months. Thus capture-recapture methods can provide an estimate of the number of animals using a specific haul-out site or area without requiring all the haul-out sites used by the individuals in that population to be sampled, or the use of a correction factor to account for individuals in the water at the time of survey. This may be the only way of getting a measure of how many animals use a site. Clearly it also has important implications for determining the number of animals using designated protected areas and will influence any subsequent management actions, including the size of possible management units. Furthermore, photo-identification and capture-recapture studies still provide minimum abundance estimates whilst also potentially providing additional information on the distribution and general health status of individuals, and adult and pup survival.

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CHAPTER FOUR

ESTIMATING HARBOUR SEAL NUMBERS USING AERIAL SURVEYS

ABSTRACT

Aerial surveys of harbour seals are designed to reduce the potential effects that date, time of day, tide and weather might have on population estimates. The current survey window for these counts is limited to a three-week period during the annual moult when, in most areas, the greatest numbers of seals are thought to be hauled out. In order for long-term trends to be determined from these counts it is assumed that the mean number of seals at a particular site does not vary during this survey window and that the start and duration of the window does not vary with location or between years. This study used a combination of repeat land-based and aerial surveys to compare harbour seal abundance at haul-out sites around the Isle of Skye in north-west Scotland. Land-based counts were used to examine the effect of covariates on seal numbers using Generalised Additive Modelling, which suggested that the highest numbers of seals were hauled out during the pupping period but that numbers of seals hauled out during the moult were most consistent. The model also predicted that the current aerial survey window, within the moult period, is about a week too early and that count variation could be reduced by surveying 1½ hours earlier in the tidal cycle. The coefficient of variation in these counts was estimated to be 15%, based on repeat aerial surveys, thus allowing inter-annual comparisons between counts and providing a baseline minimum abundance estimate (579 - 783 harbour seals in the Special Area of Conservation) to aid future monitoring and management of harbour seals as required by the Habitats Directive.

INTRODUCTION

Understanding the status of a population is a fundamental requisite for the effective management and conservation of marine mammals (Small *et al.*, 2003). There has been considerable interest in the status of European harbour seals due to fluctuations in population size resulting from disease (e.g. Tougaard, 1989; Reijnders *et al.*, 1997; Thompson *et al.*, 2005). A number of other factors also drive the dynamics of seal populations including immigration and dispersal (Bowen *et al.*, 2003) and environmental variability, which influences individual reproductive success and survival (e.g. Lunn *et al.*, 1994; Trillmich & Ono, 1991). The relative importance of these factors for population size is not always clear. Moreover, although detecting changes in populations is often a requirement of conservation legislation, it can present considerable challenges.

Harbour seals spend much of their lives at sea and so are easiest to count when hauled out ashore (Summers & Mountford, 1975; Jemison *et al.*, 2006). However at no point in the annual cycle are all the animals in a population hauled out. Thus surveys do not provide an absolute abundance estimate, as some animals will always be missed. Instead an index of abundance, the minimum population estimate, is determined from the number of seals observed on land. Additional information on haul-out behaviour is required to adjust this index and provide an estimate of total population size.

In order to detect trends in abundance it is essential that the mean number of seals counted provides a consistent index of the number of animals in the survey area (Thompson *et al.*, 1997); unaffected by any changes in population structure, it must remain constant over time (Thompson *et al.*, 2005). Thus aerial surveys of harbour seals only take place during a three-week survey window (31st July to 23rd August) within the annual moult when, in most areas, the greatest numbers of seals are hauled ashore (Thompson & Harwood, 1990; Boveng *et al.*, 2003; Harris *et al.*, 2003). The survey window is further restricted to within two hours of low tide when the greatest numbers of harbour seals are thought to be ashore (Allen *et al.*, 1984; Yochem *et al.*, 1987; Thompson *et al.*, 1989; Watts, 1996; Simpkins *et al.*, 2003). Poor weather can

reduce the number of seals hauled out on a given day (e.g. Godsell, 1988; Kovacs *et al.*, 1990; Grellier *et al.*, 1996), especially during the moult when animals probably haul out to increase their skin temperature (Boily, 1995). Therefore aerial surveys only take place in dry weather.

It is assumed that the number of seals hauled out reaches a plateau during the aerial survey window, and that the start and end of this plateau does not vary spatially or between years. However different demographic components of the population differ in the timing of the moult and it is likely that the timing and duration of the moult plateau will alter if there are changes in the demographic structure of a population (Härkönen *et al.*, 1999; Daniel *et al.*, 2003). Some variation in the numbers of harbour seals hauled out, such as that resulting from disturbance (Allen *et al.*, 1984) or changes in food availability (Brown & Mate, 1983), is harder to account for when surveying. It is therefore important to estimate the daily variation in the number of seals hauled out during the survey period.

Financial and temporal constraints limit the frequency and repeatability of aerial surveys. This study therefore modelled land-based counts from a single haul-out site on the Isle of Skye, north-west Scotland, obtained between May and September 2004 and 2005, in order (i) to gain a better understanding of how temporal, tidal and environmental covariates affect the numbers of seals hauled out, (ii) to determine whether numbers of animals remain stable during the moult, and (iii) to assess whether this period coincides with the aerial survey window. Five repeat aerial surveys of haul-out sites around the Isle of Skye, conducted in August 2004, were used to calculate a coefficient of variation (CV) and determine a minimum abundance estimate that could be used as a baseline in the management of this harbour seal population.

METHODS

Land-based counts

Kyle Rhea is a seawater channel located between the Isle of Skye and the north-west coast of mainland Scotland (57°14' N, 5°39' W, Figure 4.1). The channel is busy with boat traffic, especially a ferry that crosses the channel. Seals haul out near the ferry, which runs several times each day from April to October. The number of harbour seals hauled out was observed from both sides of the haul-out site between May and September in 2004 and 2005. All observations took place at distances no greater than one kilometre from the seals and were made using 7 x 50 binoculars. To reduce the potential effects of any observer bias, all counters were trained by the author. Environmental variables (wind strength and direction, cloud cover (%), precipitation, water flow direction and speed), chosen for their potential influence on seal numbers and their measurability, were approximated by sight. Data on the predicted time and height of the tides were taken from POLTIPS, version 2, using Glenelg Bay as the reference port.

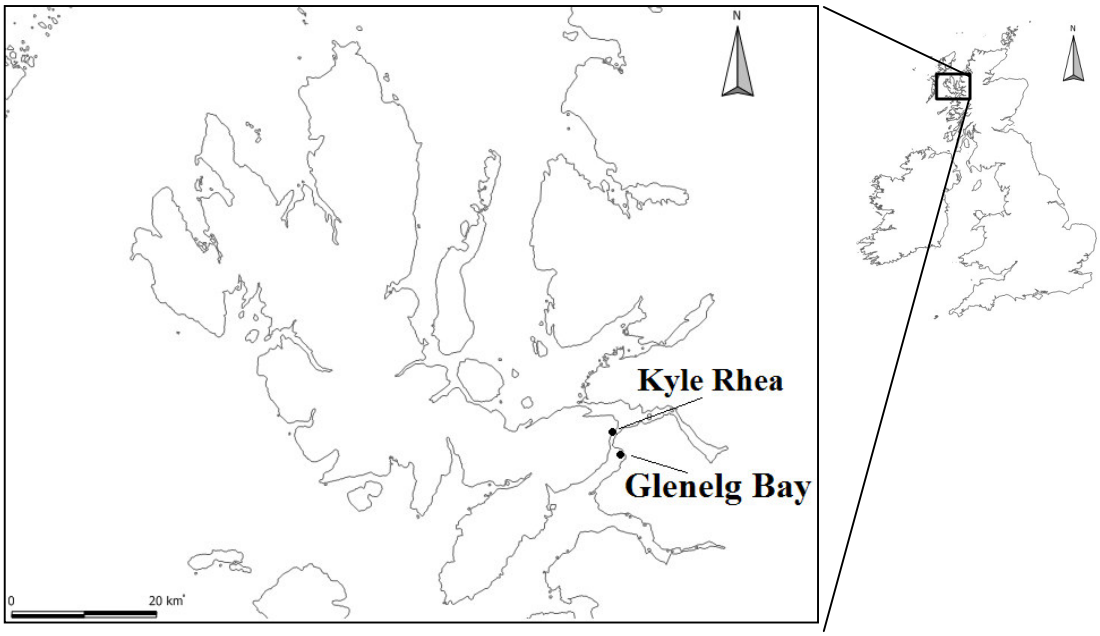

Figure 4.1: Location map of the tidal port, Glenelg Bay, and the Kyle Rhea haul-out site on the Isle of Skye, north-west Scotland. The seals hauled out were counted from both sides of the channel.

Modelling land-based counts

To investigate the effects of temporal, tidal and environmental covariates on harbour seal behaviour it was assumed that the haul-out patterns shown in Kyle Rhea were representative of the broader region. The data collected during 2004 were used to fit the model (calibration data set), and data collected in 2005 constituted an independent validation data set. Environmental variables were compared between the model fitting and validation data sets using Mann-Whitney tests in software package R, version 2.1, to ensure that general environmental conditions were comparable between years. All variables were also examined for co-linearity using Pearson product-moment correlation tests in SPSS, version 12.

Model specification

Over-dispersion, which occurs when the sampling variance exceeds the model-based variance, is often observed in count data as a result of a lack of independence (Burnham & Anderson, 2002). Although the estimators of model parameters often remain unbiased in the presence of over-dispersion (Burnham & Anderson, 2002), over-dispersion should be modelled using quasi-likelihood theory (Wedderburn, 1974). Thus a quasi-Poisson distribution was used with a Generalized Additive Model (GAM) to attempt to describe the factors that may affect the number of seals hauled out, and thus available to be counted, during aerial surveys. GAMs share many of the statistical properties of generalized linear models (McCullagh & Nelder, 1989) but do not require any prior assumptions about the underlying relationships between predictor and response variables.

The following explanatory variables, and their interactions, defined the upper limit of the multivariate regression model: time of day, time since low tide, time of nearest low tide (all in decimal hours), tide height, height of nearest low tide (in metres) and Julian date were modelled as smooth non-metric functions; tide state (high, ebbing, low, flooding or slack), precipitation (absent, mist, drizzle, light rain, heavy rain, hail, sleet or snow), cloud cover (to nearest 25%), wind strength (calm, gentle breeze, light wind, strong wind, gale force winds), wind direction and water flow speed (slow,

medium or fast) were modelled as categorical factors. The direction of water flow was highly correlated with the state of the tide (Pearson's product r = -0.781, $p < 0.001$) and so was not included in the full model.

Model selection

A combination of backward and forward stepwise selection was used to determine the best-fitting model. Starting with a model containing all the covariates, the effect of deleting variables was evaluated at each step, with those variables not contributing significantly to the fit of the model being placed into a pool of candidate variables from where they could be reselected.

Candidate models were specified in R using function gam(mgcv). The mgcv package (Wood, 2001) uses Generalized Cross Validation (GCV) for model selection; the procedure automates a training and cross-validation approach for choosing a statistically defensible degree of smoothing, with penalties for unnecessary flexibility. Model selection consisted of minimising the GCV criterion:

$$GCV = \frac{nD}{(n - df)^2}$$

where D = deviance, n = the number of data and df = the effective degrees of freedom (Wood, 2001).

A circular smooth was used to account for the circularity of the tidal state, but was not needed for 'time of day' as no counting took place at night. Because individual seals could have been hauled out during consecutive counts (Chapter 2) the residuals were checked visually for non-randomness in the data. Some positive correlation with the previous count, rather than the mean number of seals hauled out, was apparent. Consequently, to eliminate the complications associated with serial correlation in the data and so that each count could be considered independently, only alternate records were used for the model. The predicted number of harbour seals hauled out was obtained using the best-fitting model and function predict.gam(mgcv) in R.

The daily mean number of harbour seals predicted to be hauled out was calculated at five-minute intervals within a four-hour tidal window because the probability of surveying was considered to be equal within this four-hour period.

Model validation

An important step in the modelling process is to quantify the confidence in the predictions produced (Olden *et al.*, 2002). Thus cross-validation was used to assess whether the best-fitting model, selected using GCV, captured a persisting biological relationship between temporal, tidal and environmental variables and the observed numbers of harbour seals hauled out (Burnham & Anderson, 2002; Olden *et al.*, 2002). This process estimates the error by using the prediction model on the validation data set and comparing the variation explained for the two data sets and the variance of errors in the predictions. Residuals were examined and the errors were checked to ensure that they were from the same distribution as the calibration data set.

Although GAMs are flexible, the models can still be sensitive to the position of break points. These break points, where the polynomial functions join, are called knots, and the number of knots specified can influence the final shape of the the GAM. Thus the effect of increasing the number of knots from three to seven was observed to ensure that the best-fitting GAM was robust.

Aerial surveys

Harbour seals on the south-east and north-west coasts of the Isle of Skye (Figure 4.2) were counted on five consecutive days during the summer moult (2nd – 6th August 2004) using a thermal imaging camera mounted in a helicopter. This survey method is believed to be the most effective method of estimating harbour seal abundance on rocky coasts, such as those found on the west coast of Scotland, spotting groups of seals up to three kilometres away (SCOS, 2004).

The thermal imaging camera had a dual telescope with x 2.5 and x 9 magnifications and was mounted alongside a Hi8 camcorder, recording onto VHS and Hi8 tapes respectively. Flying at around 180 metres height, the coast was scanned at low magnification, groups of seals were counted in real time using high magnification when they were detected. Species identity was determined using the thermal profile of the seals, the real image from the camcorder, or using binoculars. The size and location of each group were recorded onto 1:50,000 Ordnance Survey maps and later transcribed into a database.

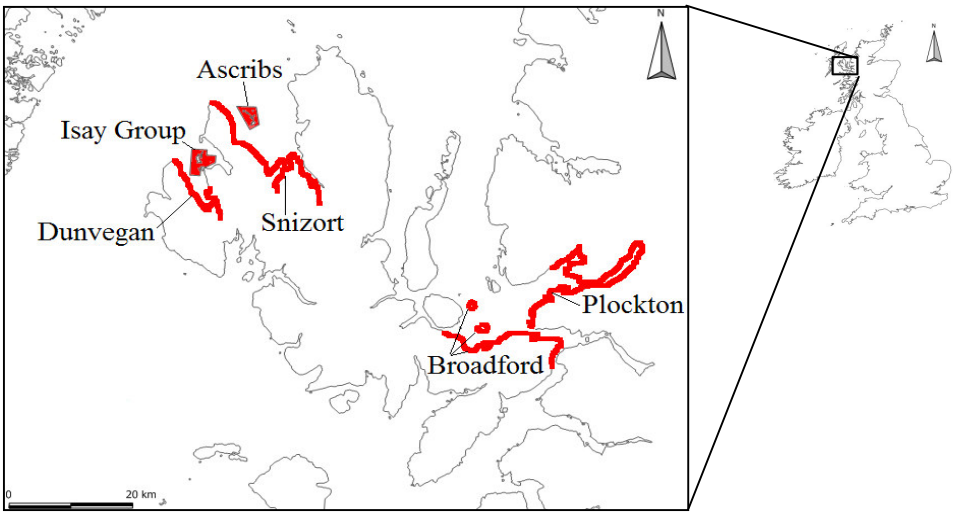

Figure 4.2: Location of repeat aerial survey tracks around the Isle of Skye, north-west Scotland. Northern sub-areas: Dunvegan, Isay Group, Ascribs and Snizort; southern: Plockton and Broadford.

Aerial counts were only carried out during the early afternoon, within two hours of low tide and only in dry weather in order to reduce the potential effects that date, time of day, tide and weather might have on the counts. One survey (3rd August) was conducted in light to moderate drizzle when aerial counts would not usually have taken place.

Data analysis

The aerial survey route was divided into sub-areas (Dunvegan, Isay Group, Ascribs and Snizort in the North; Plockton and Broadford in the South, Figure 4.2) to allow similarly sized groups to be compared. Although care was taken to divide the overall survey area in places where few seals were found, the sub-areas do not represent distinct populations. The mean abundance estimate for each sub-area was calculated

from the replicate counts and a CV was determined for each sub-area and for the survey area as a whole. A regression line with 95% confidence intervals was run in R and a Wilcoxon Signed Ranks test was used to determine which days showed significant change in abundance. All analyses were compared between 'all surveys' (which included the wet-weather count when counts would not usually occur) and 'dry surveys' (which discounted data from 3rd August).

RESULTS

Data obtained

Data for harbour seals hauled out in Kyle Rhea were collected over 45 days in 2004 and 36 days in 2005, producing a total of 406 observations. The maximum number of seals, excluding pups, observed each month varied from 23 in September to 85 in June (Table 4.1).

Table 4.1: Data collected from land-based counts of harbour seals hauled out in Kyle Rhea. Hourly observations were conducted to capture tidal, temporal and environmental variation in the number of harbour seals counted on each survey day.

	Monthly	**Survey days**		**Number of observations**	
	Maximum	**2004**	**2005**	**2004**	**2005**
April	42	0	3	-	12
May	82	9	6	53	31
June	85	10	1	47	8
July	57	11	3	68	14
August	65	10	23	35	111
September	23	5	0	27	-
Overall	-	*45*	*36*	*230*	*176*

Count variability

Model selection

Environmental variables were compared between the model calibration and validation data sets to ensure that general environmental conditions were comparable between years. Only wind strength had a slightly higher median value in 2005 compared to 2004 (Mann-Whitney U: $z = -3.334$, $p = 0.001$). A number of variables were significantly correlated (Table 4.2) but these correlations were weak (all $r < 0.3$, except precipitation and cloud cover where $r = 0.42$) and were probably a result of the categorisation of the variables.

Table 4.2: Correlation matrix for the variables used in this study (*n* = 203 observations) obtained from Pearson product-moment correlation tests.

	Tide state	**Precip.**	**Cloud cover**	**Wind strength**	**Wind direction**
Tide state	-				
Precipitation	0.070	-			
Cloud cover	-0.015	**0.419****	-		
Wind strength	0.026	**0.148***	**0.182****	-	
Wind direction	**0.147***	0.038	0.038	**0.300****	-
Water speed	0.126	-0.042	0.041	-0.022	0.127

* significant at p = 0.05, ** significant at p = 0.01

From the full model the time of day, time of nearest tide, tide height, tide state, precipitation, cloud cover, wind strength, wind direction, water flow speed and height of the nearest low tide were removed. The time of the nearest low tide was highly correlated with time since low tide and so was also dropped from the model. With a log link function and a quasi-Poisson distribution the final GAM took the form:

$$\log(\mathrm{E}_{(\mathrm{PV})}) = \beta_0 + s(\beta_{1(jdate)}) + \mathrm{s}(\beta_{2(time\_\mathrm{since})})$$

where $\log(\mathrm{E}_{(PV)})$ is the log link function of the independent response variable (numbers of harbour seals hauled out), β_0 is the intercept and β_1 and β_2 are the estimated coefficients of the respective variables (*jdate* = Julian date; *time_since* = time since low tide) and *s* is a circular smooth function of covariates β_1 *and* β_2. No interactions improved the model fit. Visual inspection of the deviance residuals gave no reason to suspect non-randomness in the data (Figure 4.3).

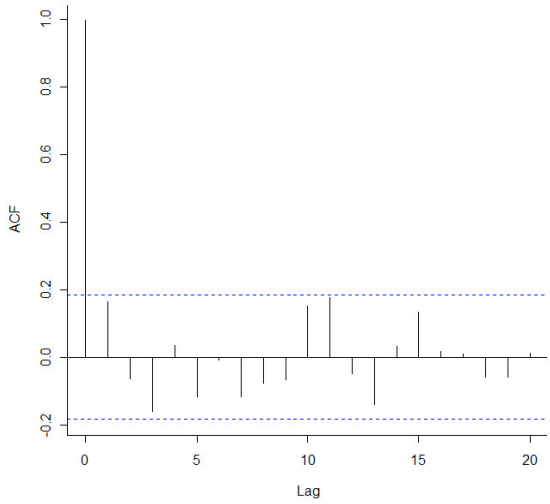

Figure 4.3: The autocorrelation function at varying time lags. Calculated autocorrelations should be near zero for all time-lag separations if data are random. If non-random, one or more of the autocorrelations will be significantly non-zero. Dotted blue lines represent 95% confidence intervals.

Model fit

As for the calibration data set, the deviance residuals of the prediction model using the validation data set were examined and gave no reason to suspect non-randomness in the data. The fit of the model using the calibration data set (collected in 2004, n = 115) explained 62.5% of the variance (R-squared = 0.56), compared with 38% of the variance (R-squared = 0.31) for the validation data set (collected in 2005, n = 88). The variances of errors in the prediction models were 8.27 for the calibration data set and 7.52 for the validation data set.

The prediction model, determined as the best-fitting model from the calibration data set, was not the best-fitting model for the validation data set when using the same model selection procedure. However the ΔGCV between the best-fitting model for the validation data and the prediction model was only -1.410. Thus the difference between candidate model proposed by the validation data set and the prediction was deemed sufficiently small (Burnham & Anderson, 2002), and the more parsimonious prediction model was selected. Increasing the number of knots (Figures 4.4 & 4.5) had little effect on the predicted relationship between numbers hauled out and time of year and time since low tide. Using more knots in the model resulted in a prediction of a slightly higher count of harbour seals during the pupping season (July), and a more sudden increase in harbour seals during the ebbing tide.

Effect of the covariates

Temporal variation

Between May and September there were three periods of particularly high seal counts. Both the first period, with the overall highest numbers of adult seals, and the second occurred during the pupping season. Highest counts during this pupping period were predicted to occur on 27th May (86 seals). The third and longest period of high seal counts occurred during the August moult and coincided with the aerial survey window. During this period the mean predicted numbers of seals, from two hours before until two hours after low tide, was lower than at the peak's zenith on 17th August at both the start and the end of the normal survey window (Table 4.3).

Table 4.3: Mean predicted number of harbour seals hauled ashore calculated from five-minute intervals during a four-hour tidal period, from two hours before until two hours after low tide, and shown for the start, zenith and end of the normal three-week aerial survey window in dry weather. The predicted number of harbour seals one week later is also shown. SE = standard error of the mean.

Time in survey window	Mean	SE
Start (31st July)	13.08	4.60
Start + 1 week (7th Aug)	18.53	6.51
Zenith (17th Aug)	25.27	8.88
End (23rd Aug)	22.76	8.00
End + 1 week (30th Aug)	18.42	6.47

Due to the nature of the GAM, and a relatively small land-based count data set, seal numbers appeared to peak rather than plateau within the normal survey window (Figure 4.4). Few counts were done in early May or in September, and so the predicted effect of early and late season on seal counts is imprecise. Nevertheless, although the normal aerial survey window coincided with the predicted peak in numbers of harbour seals during the moult, delaying surveys by a period of one week would reduce the variability between seals counted at the start and end of the survey period in Kyle Rhea (Table 4.3).

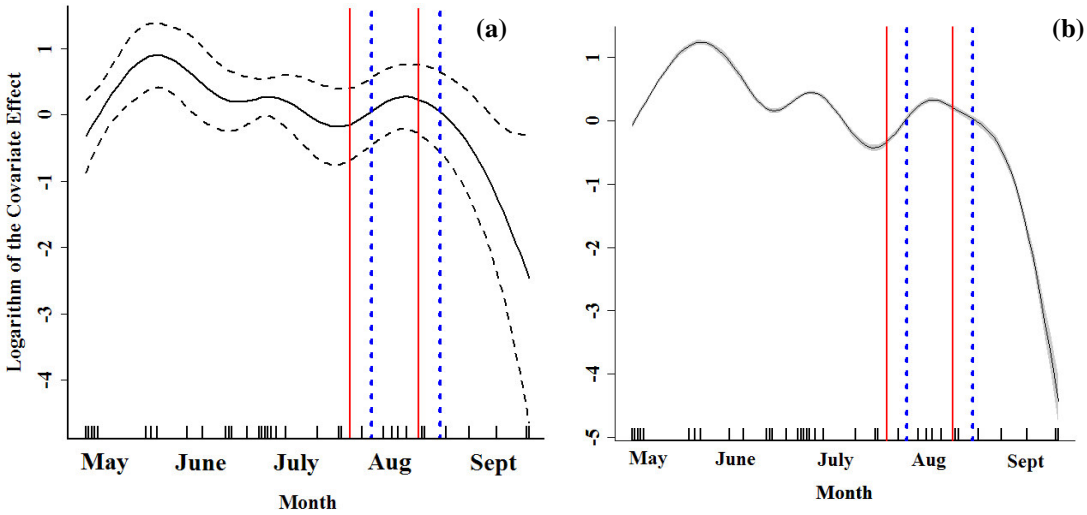

Figure 4.4: The effect of date, a smooth term component of the GAM, for land-based counts of harbour seals in south-east Skye where the default number of three knots was used (a) and where the number of knots was increased to seven (b). Upper and lower curves represent two standard errors above and below the estimate (approximate 95% confidence intervals). Red solid lines represent the start and finish of the normal survey window and blue dashed lines show the start and finish of a survey window delayed by one week. The y-axis is the logarithm of the covariate effect. The rug plots at the foot of the graphs shows when counts were actually made.

Tidal effects

Seal numbers increased during the ebbing tide, with highest numbers observed from about 3½ hours before low tide until half an hour after. Numbers of harbour seals ashore decreased rapidly during the flooding tide, with approximately six times fewer animals hauled out two hours after low tide, compared with the peak at around one hour before low tide (Figure 4.5).

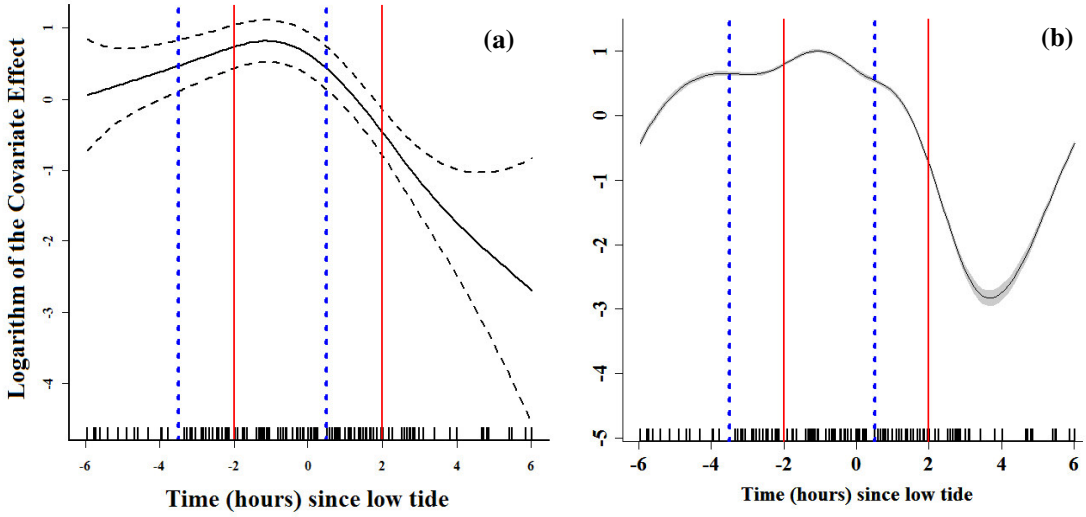

Figure 4.5: The effect of time since low tide, on numbers of seals hauled out, using three knots (a) and seven knots (b). A peak in numbers of harbour seals was predicted at one hour before low tide (mean predicted number of seals = 29.58, SE = 6.02). Red solid lines represent the start and finish of the normal survey window, from two hours before until two hours after low tide, and blue dashed lines show 3½ hours before to ½ hour after low tide (21.4 seals, SE = 6.02; 18.88 seals, SE = 3.84 predicted respectively).

Surveying harbour seals 1½ hours earlier in the tide, from 3½ hours before to ½ hour after low tide, increased the mean daily predicted number of seals and reduced the variance by about half (Table 4.4 and Figure 4.6).

Table 4.4: Mean predicted number of harbour seals hauled ashore calculated at five-minute intervals during a four-hour tidal period, from 3½ hours before to half an hour after low tide, and shown for the start, zenith and end of the three-week normal aerial survey period in dry weather. The predicted number of harbour seals one week later is also shown. SE = standard error of the mean.

Time in survey window	Mean	SE
Start (31st July)	15.09	2.17
Start + 1 week (7th Aug)	21.38	3.07
Zenith (17th Aug)	29.15	4.19
End (23rd Aug)	26.25	3.77
End + 1 week (30th Aug)	21.25	3.05

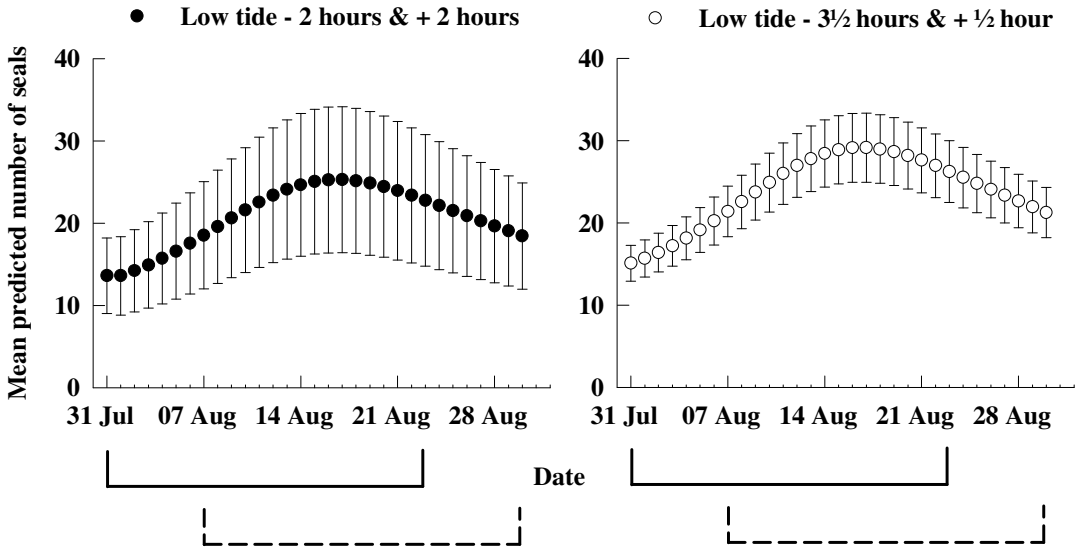

Figure 4.6: Daily mean number of harbour seals (with standard error) predicted to be hauled out in Kyle Rhea, north-west Scotland, from two hours before until two hours after low tide (●) and from 3½ hours before until half and hour after low tide (○). Solid lines represent the start and finish of the normal survey window, from 31st July until 23rd August, and dashed lines show a three-week survey period starting one week later (7th – 30th August).

Repeat aerial surveys

As predicted by the GAM, seal counts did not remain constant during the repeat aerial surveys conducted over five consecutive days at the beginning of the normal survey window. Counts increased significantly between the start and finish of the study period (2nd to 6th August, Wilcoxon Signed Ranks: $Z = -1.99$, $p = 0.046$), and the increase between 3rd - 4th and 4th - 5th August was significant at the 0.05 level ($Z = -1.99$, $p = 0.046$ and $Z = -2.20$, $p = 0.028$ respectively).

Coefficient of variation (CV)

In most cases the CV (defined as the standard error of the mean expressed as a proportion of the mean) around the mean of the counts, obtained using a thermal imager from a helicopter, was reduced when calculated without the wet survey. The mean of the individual CVs, and the CV of the total counts was 15% (Table 4.5).

Table 4.5: Mean counts and coefficient of variations (CV) of harbour seals in different sub-areas around the Isle of Skye calculated from repeat dry-weather aerial surveys ('dry surveys') and from all aerial surveys including one wet-weather count ('all surveys'). The effect of including data from wet-weather surveys is determined by the percentage change in the mean count from 'dry surveys' to 'all surveys'.

	All surveys		**Dry surveys**		**Effect of rain on**
	Mean count	**% CV**	**Mean count**	**% CV**	**mean count**
Dunvegan	295.40	18.99	314.00	13.84	- 6.30%
Isay Group	170.60	13.72	174.25	14.54	- 2.14%
Ascribs	223.20	9.64	226.00	10.51	- 1.25%
Snizort	104.40	18.48	112.75	4.98	- 8.00%
Broadford	358.80	28.71	389.75	22.61	- 8.63%
Plockton	237.60	32.88	260.50	26.16	- 9.64%
Overall	*1390*	*19.68*	*1477.25*	*14.99*	*- 6.28%*

Counts of harbour seals were lower on the wet day (3rd August) than the dry days (2nd & 4 - 6th August). The mean count was therefore lower when calculated using data from all five surveys, but the effect varied considerably from a 1.3% decline in the Ascribs, to an over 9.5% decline in the Plockton area (Table 4.5). The overall mean harbour seal count decreased by 6.3% when the count obtained during the wet weather survey was included.

Spatial variability

The proportion of seals in each area remained roughly constant throughout the survey period; sub-areas Dunvegan, Isay Group and the Ascribs, which comprise a Special Area of Conservation for harbour seals under the Habitats Directive[1], contributed around 50% of seals counted each day (Figure 4.7).

[1] The 1992 Council Directive on the Conservation of Habitats and of Wild Fauna and Flora (Appendix I)

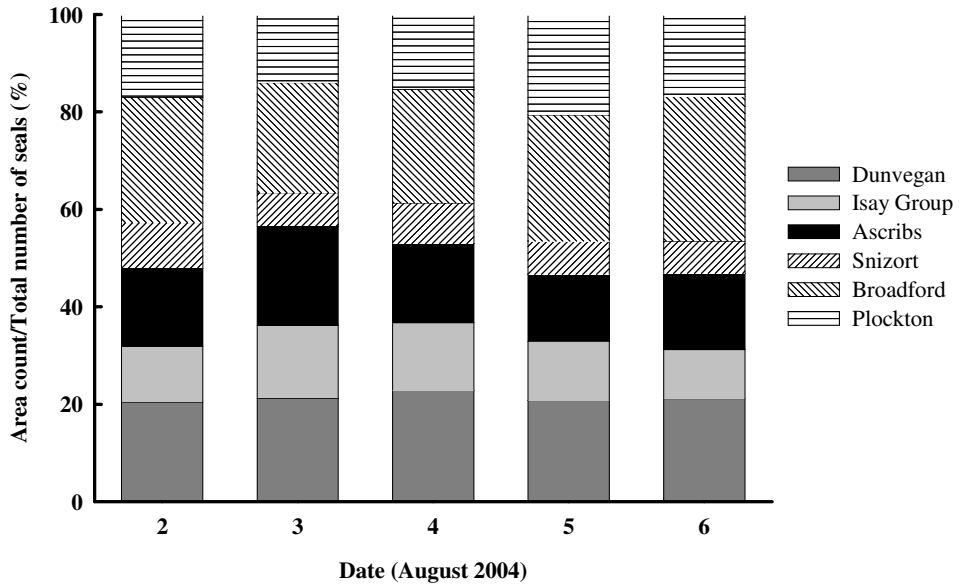

Figure 4.7: Breakdown of the percentage of harbour seals counted in each sub-area compared over five consecutive days. Sub-areas Dunvegan, the Isay Group and the Ascribs comprised the north-west Skye harbour seal Special Area of Conservation, designated under the Habitats Directive.

The synchronicity of counts of harbour seals was compared between sub-areas (Figure 4.8). Harbour seals in Dunvegan decreased on 3rd August before increasing to a peak on 5th August and subsequently remaining relatively stable. Numbers of seals within the Isay Group increased towards a peak on 5th August and then declined, whereas those in the Ascribs were highest on the last count on 6th August. Snizort showed little variability other than a decline on 3rd August, whilst Plockton was much more variable, peaking on 5th August.

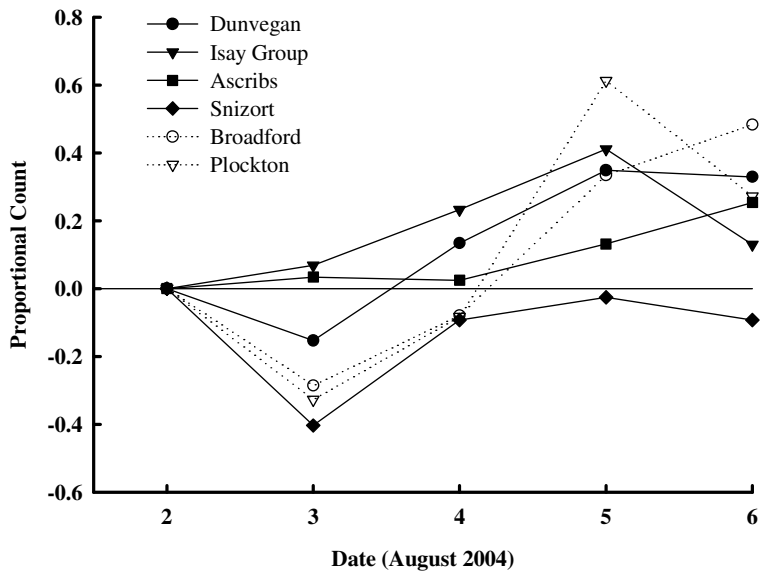

Figure 4.8: Daily count per sub-area, standardished to the 2nd August 2004 count. Usually surveys would not have taken place under the wet conditions of the 3rd August.

A linear regression of the dry counts showed no trend in the South (Broadford and Plockton sub-areas; $r^2 = 0.58$, $p = 0.24$). However in the North (Dunvegan, Isay Group, Ascribs & Snizort) a significant positive trend was apparent when data from an additional count on 1st August were included ($r^2 = 0.89$, $p = 0.02$).

Abundance estimates

The baseline minimum abundance estimate for harbour seals in the study area, with associated 95% confidence limits, was calculated based on the dry-weather counts for each sub-area. The actual dry counts obtained fit within these estimates in all cases except for some Isay Group and Snizort area counts where there were fewer than 200 animals (Figure 4.9). The baseline minimum abundance estimate for the north-west Skye Special Area of Conservation (SAC) was 579 - 783 harbour seals.

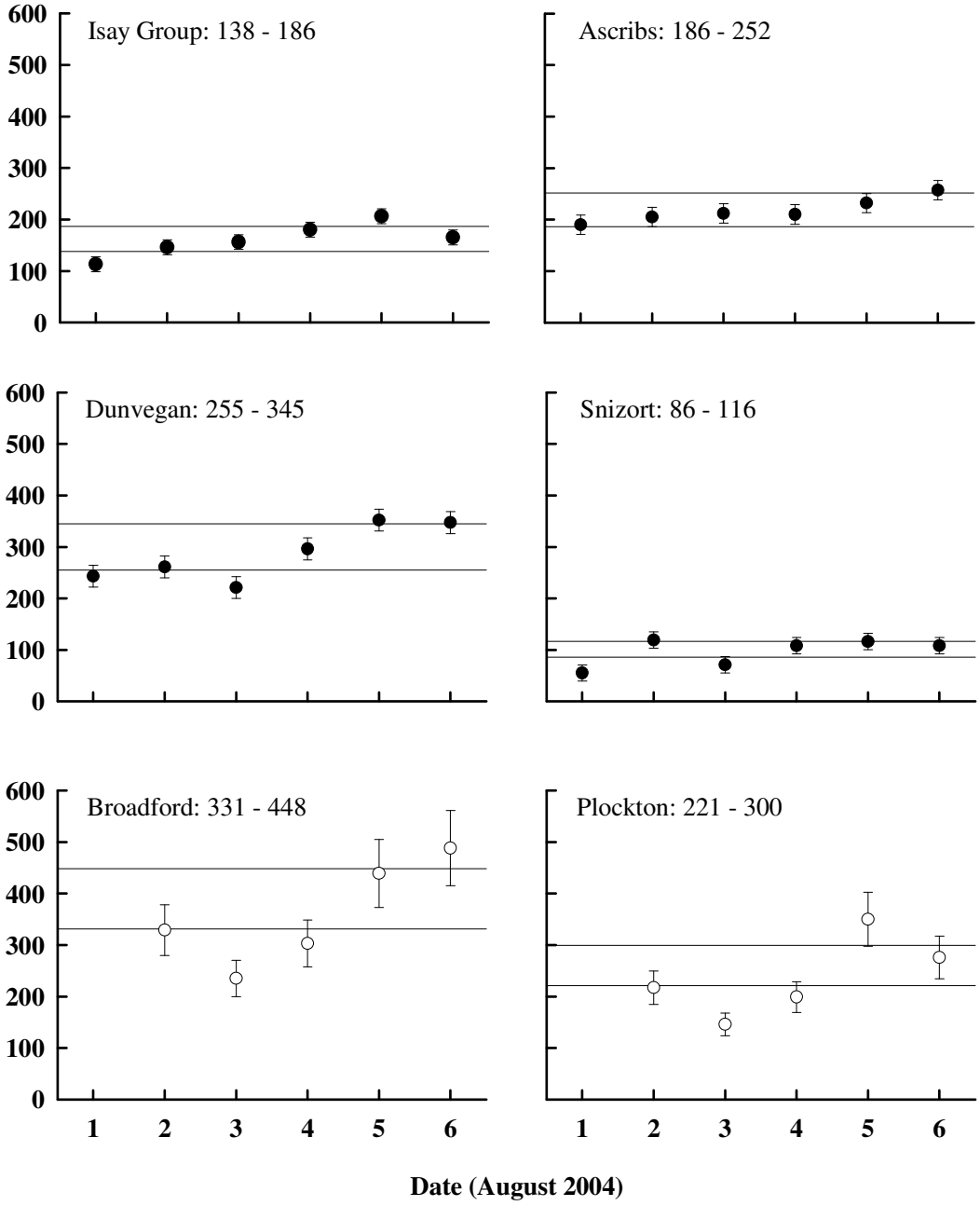

Figure 4.9: Daily aerial counts of harbour seals, ± 95% confidence intervals, for each sub-area around the Isle of Skye, where ● = northern sub-areas, ○ = southern sub-areas. Baseline abundance estimates are given for each sub-area and drawn as horizontal lines.

DISCUSSION

Variability in the number of seals hauled out

Harbour seal abundance surveys are designed to reduce variation in the numbers of seals hauled out by, for example, only surveying at certain times of the year and under certain weather conditions. However some factors, such as prey availability, habitat type and disturbance (e.g. Thompson *et al*., 1997) that may affect haul-out behaviour cannot be controlled for. In addition some studies have shown that there are site-specific variations in harbour seal behaviour patterns depending on factors such as habitat type. Although there were some similarities between the variation observed in this study and previous studies, there were also a number of disparities (e.g. the effect of the weather) that are probably the result of local conditions. In this study, on rocky habitat in north-west Scotland, two covariates, 'time since low tide' and 'date of survey', comprised the best-fitting GAM, the predictions of which were robust to changing the number of knots. Interestingly, 'time of day' was not important in the final model, thus the current practice of restricting surveys to the afternoon does not appear to be important in this region.

Tidal effects

Peaks in numbers of harbour seals hauled out around low tide have been observed both in areas where haul-out sites are only available at low tide (e.g. Thompson *et al.*, 2005), and elsewhere (e.g. Schneider & Payne, 1983; Allen *et al.*, 1984; Frost *et al.*, 1999; Boveng *et al.*, 2003). The GAM in this study predicted highest numbers of harbour seals hauled out one hour before low tide, with a gradual build up in seal numbers during the ebbing tide and a more rapid decline during the flooding tide. Thus this study indicates that surveys of seals hauled out in Kyle Rhea conducted 1½ hours earlier than the normal survey time will result in higher and less variable counts. The narrow channel at Kyle Rhea causes rapid tidal flooding, and this may have had some effect on the time when the maximum number of harbour seals was ashore. To determine whether these patterns are locally specific to Kyle Rhea or representative of

all rocky haul-out sites on the west coast of Scotland it is suggested that future studies are designed to examine the influence of temporal, tidal and environmental covariates on haul-out behaviour simultaneously at several harbour seal haul-out sites on the west coast of Scotland. In the meantime it is suggested that counts of harbour seals on the west coast of Scotland are, whenever possible, made earlier with respect to the tide, or that the survey window is limited to one hour either side of low tide.

Seasonal effect

Harbour seals should be surveyed when numbers of seals hauled out are highest and most consistent. This can occur either during the pupping (e.g. Brown & Mate, 1983; Huber *et al.*, 2001; Thompson *et al.*, 1997) or moulting (e.g. Thompson *et al.*, 1989; Boveng *et al.*, 2003; Harris *et al.*, 2003) period. Consequently there remains some debate over the most appropriate survey time. The highest number of adult harbour seals observed hauled out in this study occurred during the pupping season (late May to early July) although numbers of seals declined rapidly after this peak. In contrast, although fewer animals were counted during the moult period, the numbers were less variable. Interestingly, numbers of harbour seals in this study were therefore highest during the pupping season but most consistent during the moult. This may be a reflection of the age and sex composition of the haul-out site.

The raised temperature of moulting seals increases their visibility, and therefore detectability, on the thermal imager (Sharples, 2005), which is currently the favoured device for counting seals on the rocky shores of the west of Scotland. Not only are counts made during the moulting period more consistent than those made during the pupping period, but the error associated with these moult counts may also be less than during the pupping season. Further, a higher proportion of breeding seals may be ashore compared to non-breeders and consequently haul-out behaviour would not be recorded from a random sample of seals as it should (Southwell, 2005). This could bias population estimates unless correction factors, used to convert minimum abundance counts into population estimates, were equally biased. However counts during the pupping season are more sensitive to short-term changes in reproductive success than those obtained during the moult, and there is little information on the

amount of time individuals spend ashore during the moult because telemetric devices are usually lost at this time (Chapter 2). Surveys conducted during the pupping season, rather than during the moult, may therefore be more appropriate for assessing the conservation status of harbour seals and initiating timely response to any changes in population size.

Some authors (e.g. Thompson *et al.*, 1997; Reijnders *et al.*, 2003) suggest harbour seal monitoring should take place at two different points in the annual cycle. The results of the analyses in this study provide further evidence of the benefits of surveying during both these periods. However the costs of surveying twice a year are likely to be prohibitive, particularly on a nationwide scale and on a regular basis. However, occasional counts during the pupping period would provide valuable additional information (e.g. pup production, timing of birth and absolute abundance) and allow the relationship between the pupping and moulting counts to be established. This would allow predictions, on the number of harbour seals during the moult, to be made from the numbers of seals counted during pupping surveys, and thus, potentially, provide an early detection system for changes in abundance without having to increase the number of surveys during the moult period.

Moult plateau

One of the main assumptions in using counts of harbour seals made during the moult as an estimate of minimum population size is that the three-week survey window covers a period when variation is low and there is no significant trend in numbers hauled out. Thus counts at the start, middle and the end of the survey period should be comparable. However the predicted number of harbour seals in this study did not plateau during the survey window. Instead a peak was observed with the zenith of the predicted number of harbour seals hauled out occurring during the final quarter of the normal survey window. Consequently the number of harbour seals was predicted to rise during the first half of the survey window. A significant increase in counts was indeed observed over the five consecutive aerial surveys that were conducted near the beginning of the normal survey window in the northern area, but this was not the case in the southern area. These two areas are separated by approximately 100 km, and so

the difference could be a result of error in the counts, or due to spatial differences in the timing of the moult.

Harbour seals moult at different times according to their location, sex- and age-class (e.g. Thompson & Rothery, 1987; Härkönen *et al.*, 1999; Daniel *et al.*, 2003). Animals are therefore likely to moult in pulses, with males spending more time ashore at the end of the moult period (Thompson *et al.*, 1989) and yearlings being the first to moult (Thompson & Rothery, 1987). This may explain why a plateau in seal numbers was not observed, although it may also have been influenced by the nature of the GAM. Alternatively a plateau may have occurred subsequent to the repeat surveys in this study, perhaps delayed as a result of a shift in the timing of pupping and the moult as observed in harbour seals elsewhere (e.g. Jemison & Kelly, 2001; Daniel *et al.*, 2003). Once moulting is completed harbour seals haul out less frequently and for shorter periods of time (Chapter 2). Mathews and Kelly (1996) showed that the number of harbour seals in Alaska declined by 85% during the last three weeks of the moult. It is likely that a similar decline occurs in seals in north-western Scotland and, although the decline observed in this study in September was imprecise (due to the nature of the GAM), it is important that surveys are completed prior to this period of rapid decline.

Unexplained variability

There has been some debate over the effect of precipitation on the number of harbour seals seen hauled out. Godsell (1988) found a significant correlation, Grellier *et al.* (1996) a weak correlation, and Kovacs *et al.* (1990) no relationship at all. However rain decreases the ability to detect seals with the thermal imager (B. Mackey, *pers.comm.*). Including data from the wet day decreased the mean harbour seal aerial count in this study by 6.3%. However there was considerable spatial variation in the effect of precipitation, which could be due to differences in the strength, duration and direction of inclement weather as well as the availability of alternative, more sheltered, haul-out sites. Due to these observed spatial differences it is not advisable to use a correction factor to adjust wet-weather aerial surveys to estimate the number of animals hauled out under 'ideal conditions' (e.g. Boveng *et al.*, 2003; Simpkins *et al.*, 2003) for such a large survey area. The covariate precipitation was not deemed

sufficiently important to remain in the predictive model, which further suggested that the effect of weather conditions is locally specific and so varies spatially.

Coefficient of variation

The mean CV for the combined aerial survey counts in this study was 15%. Although the average variation among sub-areas may have provided a lower CV, it assumes independence between sub-areas, i.e. no movement of animals between the sub-areas, which is known not to be the case in at least part of the study area between September and July (Chapter 2).

There was spatial variation in the CV that may have been due to local environmental influences or as a result of disturbance affecting haul-out behaviour on a relatively small spatial scale. However the timing and height of the tide at the time of the repeat aerial surveys were similar in each area, and there were no notable weather differences during the four-hour survey periods. Weather conditions and disturbance before the survey were not monitored and could have influenced the number of animals hauling out subsequently because of lag effects that could last for several weeks. Unfortunately these factors are hard to account for when planning aerial surveys and so although using a mean may over- or under-estimate the true variation, at present this is the most appropriate CV for aerial surveys of harbour seals in Scotland.

Despite the spatial differences in count variation there was a degree of spatial coherence in the proportion of seals counted in each sub-area compared to the whole study site. These proportions were relatively stable over time regardless of the weather conditions. Thus in addition to monitoring the conservation status of harbour seals, future monitoring programmes could also investigate the general status (i.e. the relative use) of individual sites by comparing any unsynchronised change in the proportion of seals present in adjacent sub-areas. However minimum abundance estimates should also be compared with the baseline values calculated for each sub-

area (e.g. SAC = 579 - 783 harbour seals) to ensure that harbour seal abundance is not declining at multiple haul-out sites.

Repeat counts at haul-out sites provide a measure of uncertainty that is associated with a single count; information that is essential to determine the statistical significance of any observed changes in the number of seals using that site. However, as shown in Chapter 5, the high levels of variation observed in this study mean that only large changes in abundance can be detected using aerial surveys. Some of this variability, which is the result of variations in haul-out behaviour among individuals (Chapter 2; Brown & Mate, 1983; Thompson *et al.*, 1989) and among age and sex classes (Härkönen *et al.*, 1999), cannot be reduced by improvements in survey design. However, variability in haul-out behaviour that is the result of responses to different environmental conditions (cf. Chapter 1) can be addressed if a statistically significant relationship between haul-out behaviour and these covariates can be established.

Conclusions

Reliable abundance estimates of protected species are needed both for developing sound conservation management plans (Boveng *et al.*, 2003) and in order to comply with legislation; harbour seals are protected under the Habitats Directive, which requires that the population be maintained in 'favourable conservation status.' Thus the baseline minimum abundance of harbour seals was estimated for different sub-areas, which showed relatively high synchronicity over a short temporal scale, and these estimates together with the calculated CV (15%) will aid in determining long-term trends in abundance. This study illustrates the importance of both the time relative to low tide, and the date of aerial surveys, which aim to coincide with consistently high numbers of harbour seals hauled out. For the study area in north-west Scotland highest numbers of seals were predicted to haul out during the pupping period, whilst the most consistent counts were predicted to occur during the moult. Harbour seals in the UK are usually surveyed during the moult (SCOS, 2005). These data already span 18 years and provide a valuable resource for examining long-term

trends in abundance and consequently favour continuing surveys during the moult to obtain baseline minimum estimates of abundance. Occasional surveys during the pupping period would provide additional valuable information on the conservation status of harbour seals (e.g. life history of the population) and should be incorporated into monitoring programmes where possible. However in order to improve the aerial survey CV of 15%, and consequently allow more subtle changes in population size to be detected (Chapter 5), the current three-week survey window may need to be redefined or the consequences of not doing so re-examined.

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CHAPTER FIVE

DETECTING TRENDS IN HARBOUR SEAL POPULATIONS: IMPLICATIONS FOR MANAGEMENT

ABSTRACT

Detecting trends in abundance is a central requirement for the conservation and management of a species. Quantifying the uncertainty around observed trends in abundance is an essential component of a precautionary approach to management and this uncertainty must be reduced to the lowest value that is consistent with financial and operational constraints. In the present study power analysis was used to assess the time taken to detect specific changes in harbour seal abundance. This analysis indicated that an increase in population size would take longer to detect than a decrease, and that a population change of 5% would take around 14 years to detect with annual surveys with a coefficient of variation = 0.15. Surveying harbour seal abundance once every four years, as currently occurs for most haul-out sites in Scotland, was predicted to approximately double detection time compared with annual surveys. The precision of the estimates of population size had a considerable effect on the likelihood of detecting a trend. However as the rate of population change increased, the importance of precision in population estimates (CV = 0.04, 0.15 or 0.23) decreased. Practical limitations on the number and frequency of surveys mean that it is important to determine whether counts made at specific sites can be used for assessing trends in abundance of the wider harbour seal population. This study showed that trends at pairs of haul-out sites were not significantly correlated and exhibited asynchrony in population trends. Moreover, trends in harbour seal abundance in selected land-based protected areas deviated by up to 100% from the general trend observed in the population at large over four-year intervals. Consequently monitoring harbour seals within these areas is unlikely to reflect trends in the population as a whole, and so larger areas should be surveyed.

INTRODUCTION

Monitoring strategies increasingly exist not only for threatened or endangered species but also for currently unthreatened species as part of a precautionary approach to conservation (Gray & Bewers, 1996). This approach attempts to identify and prevent undesirable outcomes prior to their realisation (Jennings *et al.*, 2001). It is therefore particularly important for large mammal populations, where severe population crashes are relatively common (Young, 1994) and the causes not always known (e.g. Pitcher, 1990; Thompson *et al.*, 2001).

Historically, European harbour seal populations have been affected by hunting (Bonner *et al.,* 1973), pollution (Reijnders, 1986) and disease (e.g. phocine distemper virus: Dietz *et al.*, 1989; Härkönen & Heide-Jørgensen, 1990; Harwood & Grenfell, 1990; Reijnders *et al.*, 1997; Heide-Jørgensen *et al.*, 1992; Jensen *et al.*, 2002; Harding *et al.*, 2002; Thompson *et al.*, 2005). Elsewhere substantial declines in the number of harbour seals has been attributed to predation by sharks (Lucas & Stobo, 2000), disturbance effects and competition with grey seals (Bowen *et al.*, 2003).

Abundance estimates of harbour seals tend to have a high variance due to a combination of both natural variation in population growth/decline and measurement error (Chapter 4). Long inter-survey periods may also limit the power to detect trends (Gerrodette, 1987). This means that in some situations a biologically devastating decline, or a rapid population increase, could occur before there is a reasonable chance to detect the change in population size (Staples *et al*., 2005). More subtle fluctuations in abundance, though harder to detect, may also be important from both ecological and conservation points of view. Understanding these changes in population size is one of the primary aims of population ecology (Krebs, 1972; May, 1976).

Correctly evaluating the status of protected populations is critical both to detecting changes in abundance and to verifying the effectiveness of conservation management. Ideally population monitoring should reliably detect a small but biologically relevant change in conservation status in a short amount of time (Staples *et al.*, 2005). For

example, in Europe the Habitats Directive[1] requires the conservation status of the harbour seal population to be reported on a six-yearly cycle. Traditional statistical analyses of a time-series of abundance estimates can be used to infer whether the status of a population is changing (Thompson, 2000). Usually the probability value for accepting a Type I error (i.e. accepting a trend that did not occur) is 5% ($p = 0.05$). However it is also possible that a real trend in abundance exists but is not detected (Type II error). Monitoring programmes should therefore be designed to reduce the probability of making either Type I or Type II errors. A number of monitoring methods are used to survey harbour seals including aerial surveys, boat counts and capture-recapture techniques (Chapter 1). Although careful consideration should be given to the precision of these methods, other factors, such as financial constraints, must also be taken into account when selecting a survey method (Chapter 6). Power analysis (Gerrodette, 1987) provides an assessment of the time it takes to detect a trend given the degree of uncertainty in estimates of abundance provided by different monitoring methods.

Population regulation can operate at different scales. For example, in grey seals the potential number of breeding sites available at a specific colony and the availability of food, illustrate local and global density dependence respectively (Matthiopoulos *et al.*, 2005). In harbour seals, which do not disperse widely from colonies to feed, food availability may be important at a local scale, whereas the total number of breeding sites available to the species is a more likely to be a global factor. Hence, in addition to designing monitoring protocols that are sensitive to biologically significant change it is important to define the spatial scale at which population trends are being monitored. Indeed, the extent to which the scale of observation influences the description of temporal and spatial patterns in abundance, and consequently may affect the conclusions drawn about the conservation status of the species, remains one of the most fundamental questions in ecology (Levin, 1992).

The extent to which the dynamics of neighbouring populations are synchronised can provide important information on the processes that determine overall population

[1] The 1992 Council Directive on the Conservation of Habitats and of Wild Fauna and Flora (Appendix I)

dynamics. For example, climatic perturbations and dispersal within and between populations may affect the degree of synchrony of population trends (Hanski & Woiwod, 1993; Ranta *et al.*, 1995), as may the magnitude of predation rate (Ims & Steen, 1990; De Roos *et al.*, 1991). Climatic effects usually affect large areas simultaneously whereas migration is more spatially restricted (Ranta *et al.*, 1995). The Moran theorem (Moran, 1953) predicts that if dispersal among subpopulations (which could equate to movement between haul-out sites) is responsible for their synchrony, there would be a decay in synchrony with increasing distance between populations. Spatial correlation in trends in harbour seal abundance may be apparent between neighbouring haul-out sites. The distance at which the dynamics of neighbouring haul-out sites become independent is therefore critical in determining the appropriate scale for assessing harbour seal abundance. Grouping spatially correlated sites into clusters could provide biologically and statistically valid monitoring units (Guldager, 2001) whose trends are independent of those trends at surrounding clusters. Alternatively, trends in harbour seal abundance may show spatial variation between haul-out sites, for example if changes in harbour seal abundance are affected by local conditions or within-population processes (cf. aggressiveness in red grouse reducing population density - Mougeot *et al.*, 2003).

The effectiveness of site-based conservation for harbour seals is questionable due to their comparatively high mobility and the large proportion of time they spend in the water (Chapter 2). Yet harbour seals haul out on land, justifying legislation protecting haul-out sites that are important for moulting and pupping. For example, Special Areas of Conservation (SACs, designated under the Habitats Directive) include different types of harbour seal habitat, such as rocky skerries and estuarine sand bars, whilst also providing good spatial coverage over the species' distribution (Chapter 1). Current protection is limited to restricting new activities (e.g. construction work or scientific research) from taking place within the SAC if they are likely to have a significant effect on the seals. Furthermore, government has the legislative power to impose restrictions on current activities, including fishing, in the case of harbour seal population decline within SACs.

Due to financial and logistical constraints on the frequency of monitoring it is important to consider whether observed trends in harbour seal numbers within these protected areas, which could be considered as being representative of all harbour seal haul-out sites in Scotland, reflect the general pattern of the harbour seal population at large, and consequently whether trends in counts from these haul-out sites can be used to assess the conservation status of the Scottish harbour seal population as a whole. This study aims to determine whether monitoring small regions is sufficient to establish the conservation status of the Scottish harbour seal population as a whole, and assesses the predicted length of time required to detect a change in harbour seal abundance at (a) different levels of precision and (b) different sampling frequencies with a view to assisting and advising existing monitoring programmes.

METHODS

Field procedures

Aerial surveys

Aerial photographs of seals hauled out on sandy beaches were taken from a fixed-wing aircraft using colour reversal film in a vertically mounted 5 x 4 inch format image motion-compensated camera (Hiby *et al.*, 1987). A thermal imaging camera, mounted in a helicopter, was used to distinguish seals from the background at sites where seals were hauled out on rocky skerries. This method is described in detail in Chapter 4.

Harbour seals were counted during the aerial survey window (31st July to 23rd August, which coincides with the annual moult when high numbers of harbour seals haul ashore - Thompson & Harwood, 1990; Boveng *et al.*, 2003; Harris *et al.*, 2003) in Scotland in 1988, 1989, 1990, 1991, 1992, 1993, 1994, 1996, 1997, 1998, 2000, 2001, 2002, 2003, 2004, 2005 and 2006 (Figure 5.1). In addition, harbour seals on the south-east and north-west coasts of the Isle of Skye (Figure 5.2) were counted on five consecutive days (2nd – 6th August 2004) during the summer moult using a thermal imaging camera mounted in a helicopter (Chapter 4). The overall mean coefficient of variation (CV) was calculated based on the variability of the counts from these consecutive intra-annual aerial surveys.

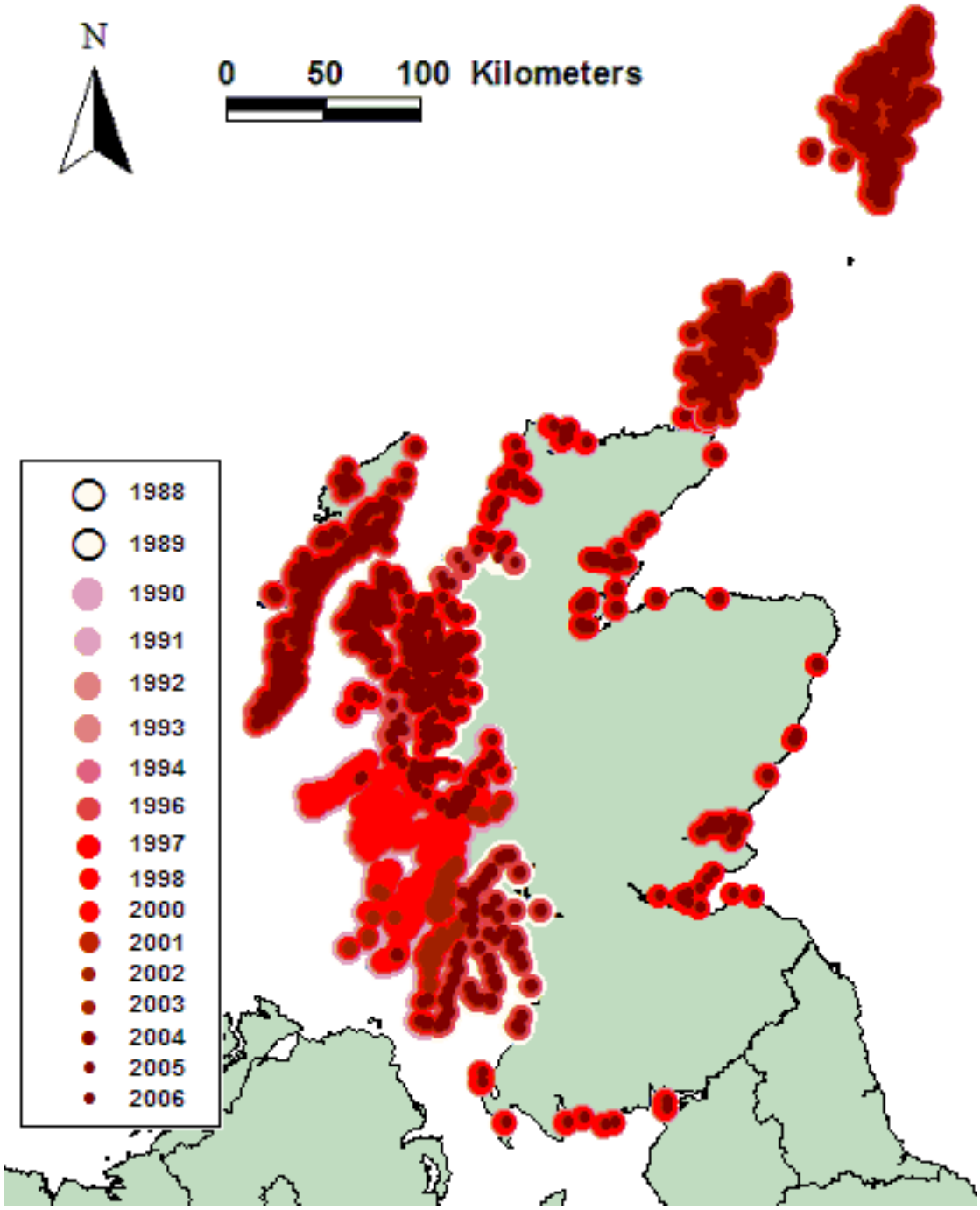

Figure 5.1: Location map of haul-out sites where harbour seals were observed during aerial surveys conducted between 1988 and 2006, colour coded according to survey year from light to dark red.

Boat counts

Three repeat boat surveys were conducted every month between April and October 2005 in Loch Dunvegan, Isle of Skye (59°27' N, 6°36' W, Figure 5.2). The survey route was dictated by weather conditions and the presence of other boats but an attempt was made to equalise coverage of the study area. The animals were approached in three-metre boats and the location and size of each group of seals hauled out was recorded. Only counts obtained in August were used to calculate the CVs used in this study, to coincide with the timing of the aerial surveys.

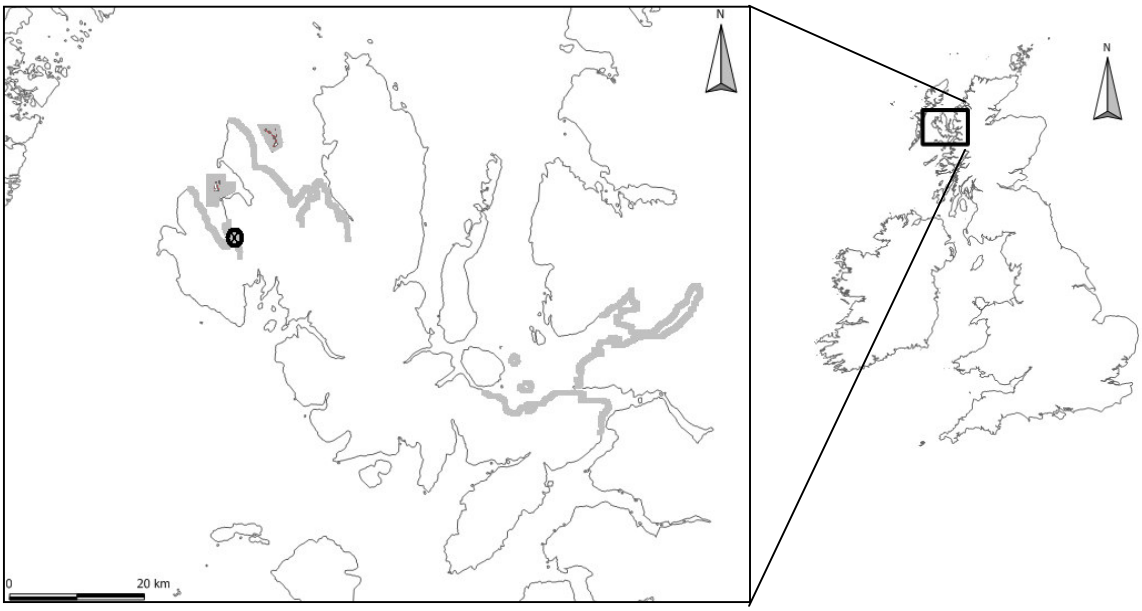

Figure 5.2: Location of data collection around the Isle of Skye, north-west Scotland. ⊗ = Boat-counts and photo-identification surveys; = repeat helicopter thermal imaging surveys.

Photo-identification & capture-recapture techniques

Harbour seals were photographed each month between April and October 2005 on the Isle of Skye (59°27' N, 6°36' W, Figure 5.2). Each seal was photographed several times from both sides and at different angles using a Canon EOS 20D digital camera with an image-stabilised lens (70 - 300mm f4.5 - 5.6). The size of the local population of adults harbour seals, and its associated CV, was estimated, for each month between April and October, using computer-assisted matching and a closed population model allowing for heterogeneity of capture probabilities (see Chapter 3 for details).

Satellite telemetry

Satellite relay data loggers (SRDLs) were deployed on 14 harbour seals caught on the Isle of Skye (59°27' N, 6°37' W, Figure 5.3a) and 10 on the Isles of Islay and Jura (55°39' N, 6°3' W, Figure 5.3b) between September 2003 and March 2005. Two deployments were made at each study site to improve data coverage over the year. The SRDLs were attached to the head using fast-setting epoxy resin as described in Fedak *et al*. (1983). Details of the capture procedure, SRDLs and seals tagged are given in Chapter 2.

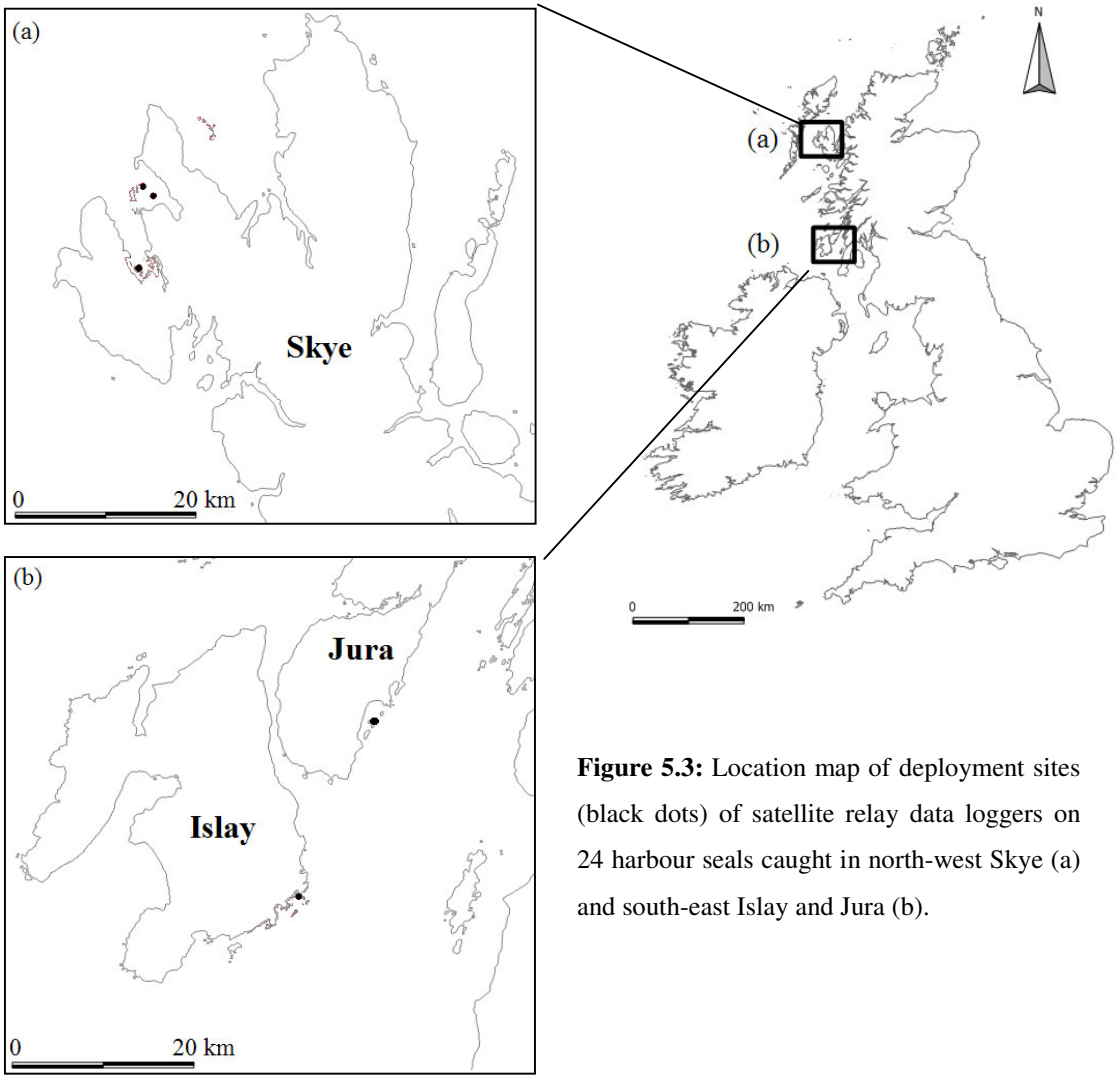

Figure 5.3: Location map of deployment sites (black dots) of satellite relay data loggers on 24 harbour seals caught in north-west Skye (a) and south-east Islay and Jura (b).

Power analysis

The statistical power of a time series of counts to detect linear trends in population size was investigated using the program TRENDS, version 3.0, according to Gerrodette (1987). Three CV values were used to represent the different precision of harbour seal abundance estimates calculated from boat-counts (0.23), thermal imaging aerial surveys (0.15) and photo-identification and capture-recapture methods (0.04) as detailed above.

Spatial scale analysis

Every location where harbour seals were observed hauled out during aerial surveys, conducted during the moult, was designated as a haul-out site. If a stretch of the coast was surveyed more than once in a single year, the mean number of seals counted was calculated to determine a yearly index of harbour seals for that haul-out site. The at-sea distance between each pair of haul-out sites was calculated using a simple diffusion model on a one-kilometre grid (M. Burrows, *pers.comm.*), implemented in Visual Basic 6.

The Mantel test (Mantel, 1967) estimates the association between two independent dissimilarity matrices and tests whether the association is stronger than expected by chance. The procedure involves using a randomisation test, such that one matrix is shuffled and the resulting regression coefficient is compared with the observed (un-shuffled) regression (Koenig, 1999). Using SACs to represent potential terrestrial monitoring units for harbour seals, Mantel tests were used to determine the spatial structure of harbour seal haul-out sites by examining the degree of congruence in the year-to-year minimum population estimates between haul-out sites within individual SACs.

The Mantel correlogram (Oden & Sokal, 1986; Legendre & Fortin, 1989) divides correlation coefficients into distance categories and tests the values for each distance

category against the overall average degree of correlation among sites present in the complete data set. Using distance categories of five kilometres, a Mantel correlogram was constructed to determine how far spatial correlation, if present, extended. As this involved many tests of significance a Bonferroni correction was applied.

Mantel tests were constructed in software package R, version 2.1, using function mantel(vegan), and the Mantel correlogram was constructed using function mgram(ecodist). For both the Mantel tests and the Mantel correlogram one matrix comprised the at-sea distances (in kilometres) between all pairs of haul-out sites, whilst the second matrix consisted of the correlation in harbour seal counts between all pairs of haul-out sites.

The correlation between population trends observed at SACs compared to the population at large was examined over four year intervals (roughly equivalent to current monitoring frequency). The deviation between the overall surveyed population and the number of harbour seals observed within 'adjacent areas', which include SACs and the surrounding haul-out sites as determined from gaps in the distribution (Figure 5.4), was also examined to determine the appropriateness of monitoring units.

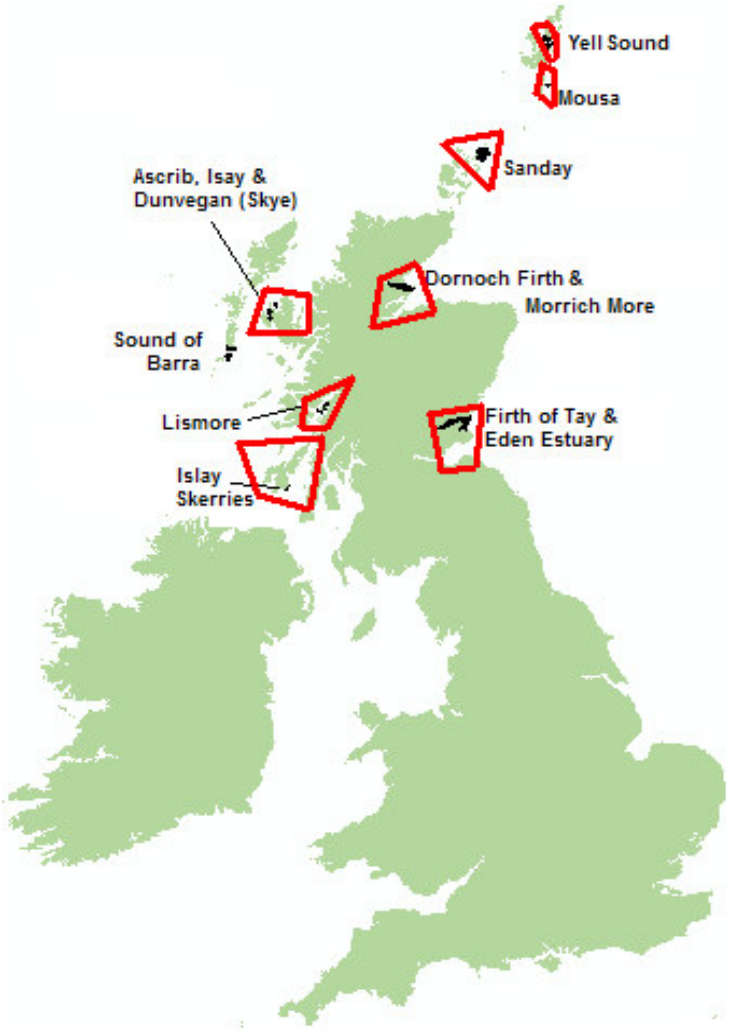

Figure 5.4: Location of Scottish Special Areas of Conservation (SAC) for harbour seals and 'adjacent areas' (haul-out sites within the red boundaries – details in Appendix IV, Table IV.i), which could be used for monitoring harbour seals in Scotland.

For each seal tagged with a SRDL the haul-out site where most haul-out events were recorded was designated as 'home.' Using at-sea distances, calculated as described above, a negative exponential decay curve was selected as the most appropriate trend line in CurveExpert, version 1.3, for the frequency with which haul-out clusters (as defined in Chapter 2) were visited with increasing distance from 'home.' Individual curves were combined to form separate curves for north-west and south-west Scotland in order to investigate general usage of space by harbour seals.

RESULTS

The predicted length of time to detect a trend in population size decreased with increasing rate of change (Figure 5.5). The precision of the annual estimates of population size had a considerable effect on trend detection, with lower CVs reducing the number of years required to detect a change in the population (Figure 5.5). As the rate of change increased, the importance of precision in population estimates decreased. However even with CV = 0.04, it would take about six years to detect an increase or decrease in population size of greater than 5% with annual surveys; detecting slower rates of change would take longer.

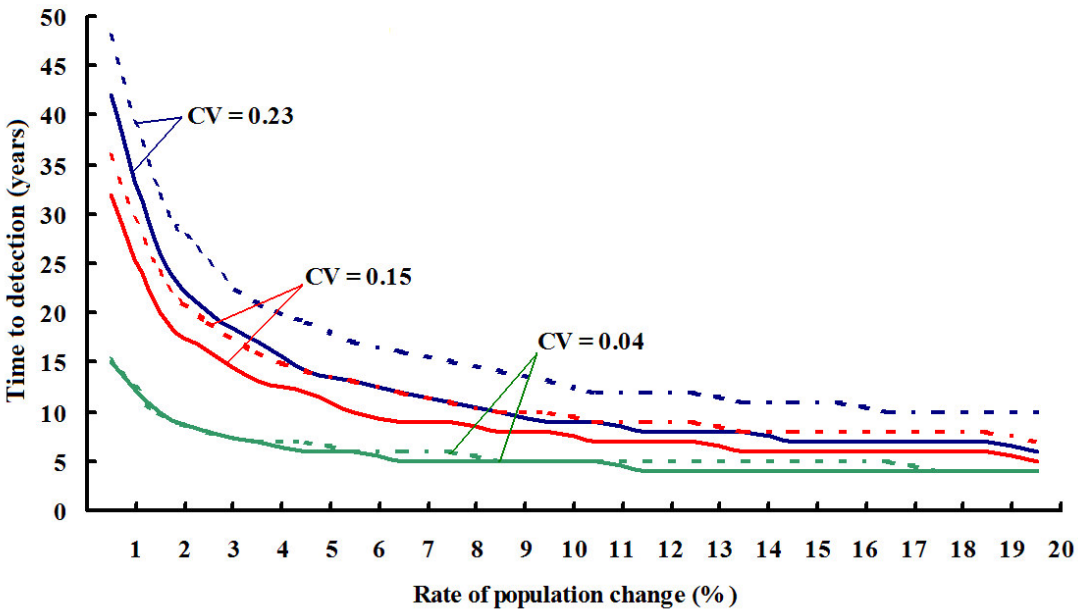

Figure 5.5: The relationship between the rate of population change (decrease illustrated with solid lines, increase with dotted lines) and time, in years, to trend detection at three levels of population estimate precision, assuming abundance is estimated annually. The CV values used were calculated from boat (0.23), aerial (0.15) and capture-recapture (0.04) abundance estimates. The probabilities of a Type I and Type II error were set at 0.05.

Although the overall shape of the detection curves were similar for decreasing and increasing trends in abundance, an increase in population size was predicted to take longer to detect than a decrease of the same amount, particularly for lower precision in population estimates (Figure 5.5). Thus with CV = 0.23 (as for the estimates of abundance determined from boat surveys) it would take nine years of annual surveys

to detect a 10% decrease in abundance and 13 years to detect a 10% increase. With improved precision of abundance estimates (CV = 0.04 as for the capture-recapture abundance estimate) both a 10% increase and decrease would take five years to detect.

Predicted detection time of changes in population size increased if the interval between surveys was increased. For example, a 10% decrease in population size that would take eight years to detect when conducting annual thermal imaging surveys (CV = 0.15) would take 17 years to detect if surveys were conducted every four years (Figure 5.6).

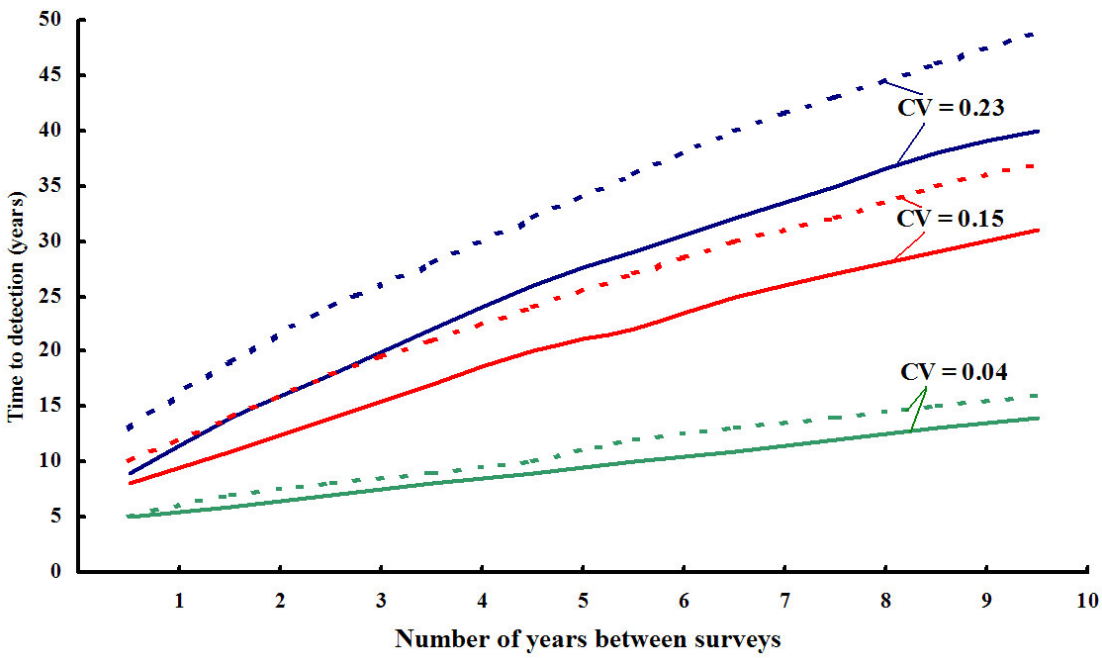

Figure 5.6: The relationship between the interval between abundance estimates and the time, in years, required to detect a 10% increase (dashed lines) or decrease (solid lines) in population size at three levels of population estimate precision. The CV values used were calculated from boat (0.23), aerial (0.15) and capture-recapture (0.04) abundance estimates. The probabilities of a Type I and Type II error were set at 0.05.

Spatial scale

No correlation pattern was observed between harbour seals counts and the distances between the haul-out sites (Figure 5.7); the step-change observed at 200 km was a result of the fractal structure of the Scottish coastline. Non-significant Mantel tests for spatial correlation showed that counts at haul-out sites within SACs (Dornoch, Sound of Barra, NW Skye, Lismore and Islay – selected according to data availability) were spatially random (p = 0.481, 0.842, 0.182, 0.395 and 0.949 respectively) and showed no synchrony years.

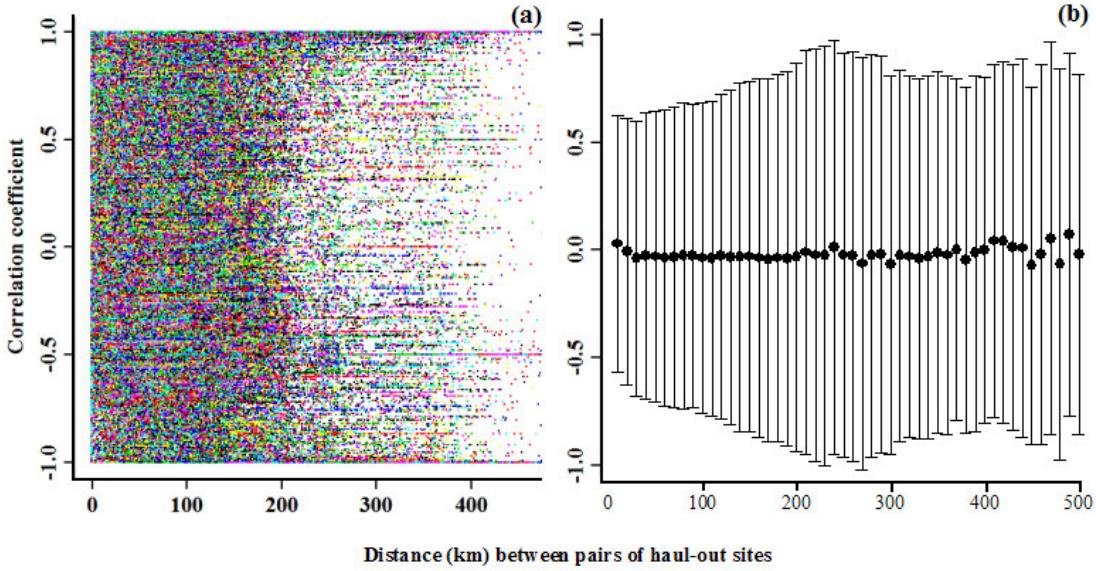

Figure 5.7: Scatterplot (a) and mean (with standard errors) (b) of the correlation coefficient of numbers of harbour seals observed hauled out between 1194 colour-coded pairs of haul-out sites in Scotland measured between 1988 and 2006 and plotted against the distance between the haul-out sites.

Numbers of harbour seals counted in some SACs (e.g. the Sound of Barra) showed dramatic changes over time (Figure 5.8). In others (e.g. Lismore), numbers were relatively constant (Figure 5.8).

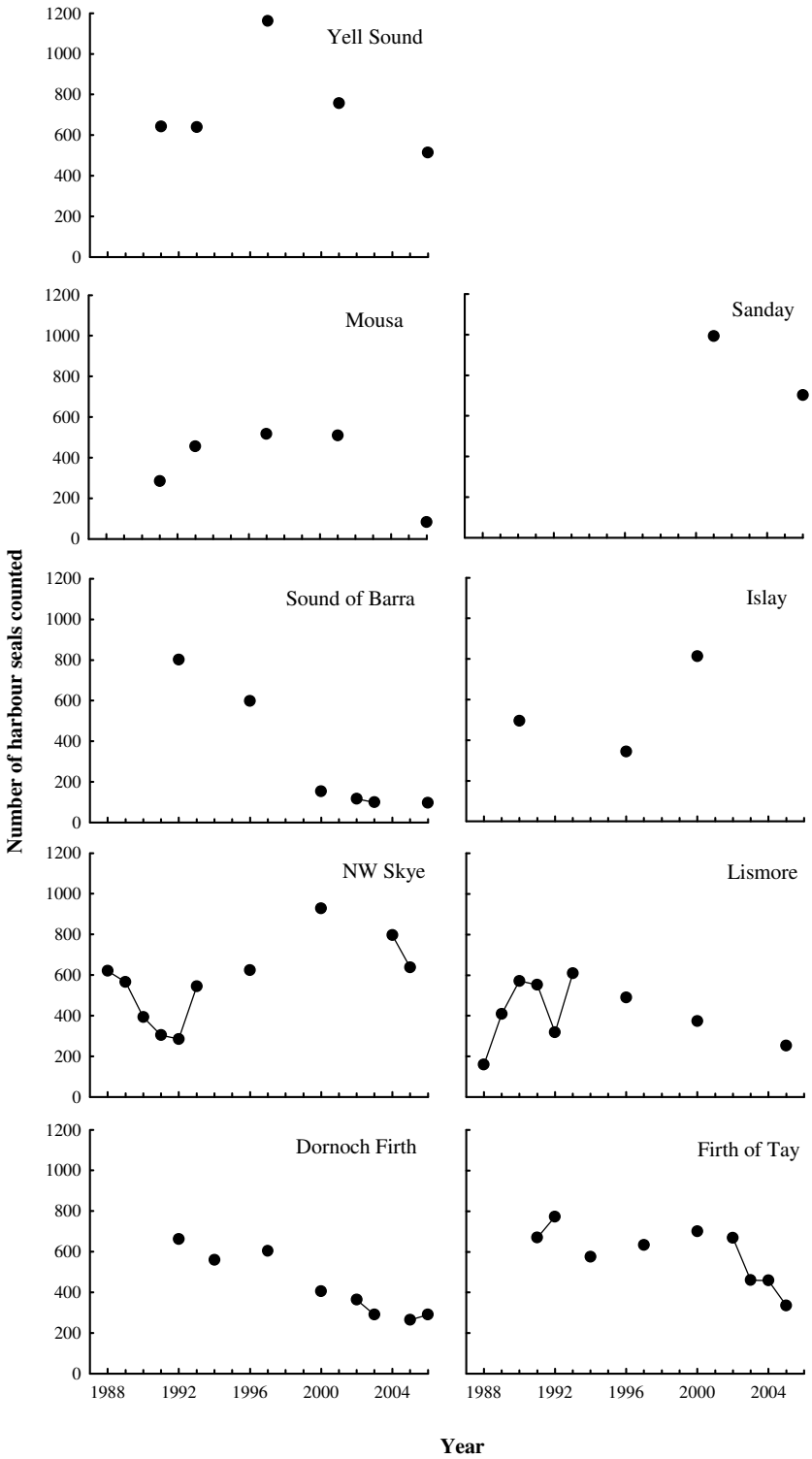

Figure 5.8: Observed abundance of harbour seals in potential harbour seal monitoring units (SACs), counted during the August annual moult over the 18-year study period (1988 - 2006). In August 2003 low cloud prevented the use of vertical photography in the Firth of Tay; counts were from photographs taken obliquely and from direct counts of small groups of seals.

The Mantel correlogram, based on correlated minimum population estimates between pairs of haul-out sites, also showed no correlation pattern regardless of the distance between the pairs of haul-out sites (all $p > 0.4$ – distance categories in five kilometre increments). Within SACs, selected to represent potential monitoring units, the observed change in harbour seal abundance during four-year periods (equivalent to the current survey frequency in Scotland) deviated by up to 100% from the total change of the population surveyed at both the start and end of this period (Figure 5.9). There was no apparent coherence in the extent or direction (positive or negative) of the deviation. Trends in harbour seal abundance observed at haul-out sites within adjacent areas, which include SACs, generally showed less deviation from the overall surveyed population than when these additional areas were excluded (Figure 5.9).

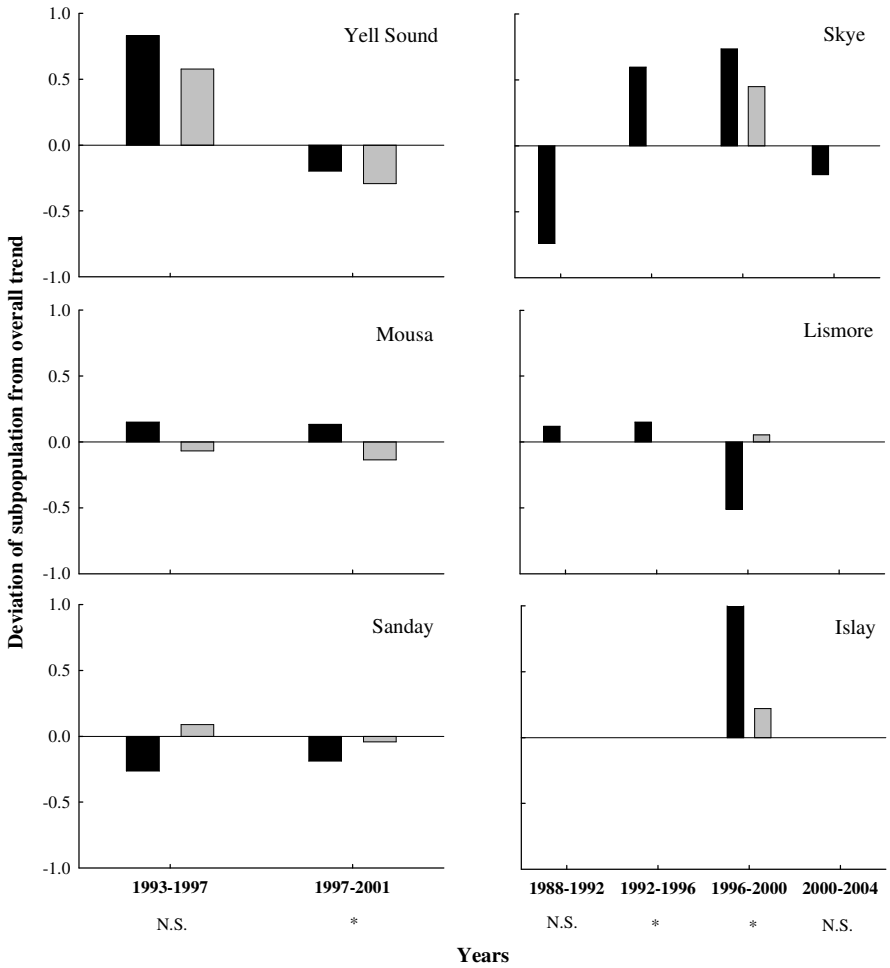

Figure 5.9: Deviations in estimated trends in harbour seal abundance within SACs (■) and adjacent areas (□) from the standardised trend across all surveyed haul-out sites at four-year intervals. * = Significant change in minimum population estimate (Wilcoxon signed ranks $Z = -3.713$, $p < 0.001$ for 1992-1996; $Z = -2.288$, $p = 0.022$ for 1996-2000 and $Z = -2.263$, $p = 0.024$ for 1997-2001), N.S. = Non-significant at $p = 0.05$ level.

The frequency with which individual haul-out sites were used decreased with increasing distance from the home haul-out site (Figure 5.10). The mean probability of a seal hauling out at the home haul-out site varied considerably between north-west and south-west Scotland (0.26 and 0.6 respectively).

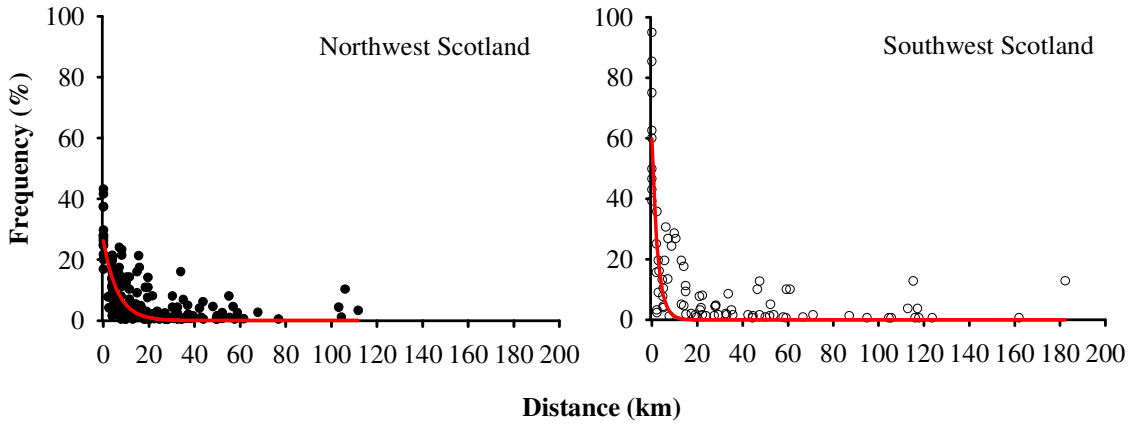

Figure 5.10: Frequency of haul-out usage at increasing distances from the home haul-out site. Data are from 24 seals tagged with SRDLs in north-west (Isle of Skye) and south-west (Isles of Islay and Jura) Scotland between 2003 and 2005.

DISCUSSION

Natural changes in the total size of the harbour seal population are likely to be gradual; long-term abundance studies report annual rates of change of 15% (e.g. Heide-Jørgensen & Härkönen, 1988; Olesiuk *et al.*, 1990). However anthropogenic influences or increased mortality, for example as a result of a phocine distemper epidemic, can cause sudden and rapid declines (e.g. Pitcher, 1990; Thompson *et al.*, 2005). It is thought that such catastrophic events may limit the viability of animal populations (Lande, 1988). In order to determine the status of a harbour seal population it is therefore important to know the detectability of trends in abundance, so that an appropriate monitoring method and scale of observation can be determined for each management unit. The general findings of this analysis are identical to those of Gerodette (1987): the time taken to detect a trend increases with the CV of the counts; decreasing trends can be detected more quickly than increasing ones; and CV has a reduced effect on the time taken to detect large trends.

With the precision of current thermal imaging aerial surveys it would take eight years to detect a 10% decrease and 10 years to detect a 10% increase in harbour seal abundance at the 0.05 significance level with annual surveys. These intervals increase to 17 and 21 years respectively if surveys conducted every four years, as is currently the case for most haul-out sites in Scotland (SCOS, 2005). Increasing the acceptance rates for Type I errors (e.g. to 10% as in Wilson *et al.*, 1999) also decreased the detection time. However it is suggested that, in order to monitor harbour seal population trends, the traditional value of $p = 0.05$ is maintained or that Bayesian methods are used to incorporate uncertainty (Wade, 2000).

At annual rates of change of between 10 - 15%, the precision of the estimated population size has a large effect on the length of time needed to detect a change with confidence (Wilson *et al.*, 1999). Hence it would take five years to detect a 10% decrease or increase in harbour seal abundance with annual surveys using capture-recapture methods (Chapter 3), and at least eight to ten years for surveys conducted

every four years. Although this is approximately half the time taken to detect the same trend using aerial surveys, it is still clear that frequent monitoring is required.

Ecological studies are often conducted over large regions and where many ecological processes may act at different temporal and spatial scales (Dungan *et al.*, 2002). Fortin and Dale (2005) therefore recommend dividing regions into smaller, spatially homogeneous patches both to facilitate resource monitoring and management, and because these patches are more likely to be controlled by the same ecological processes (cf. SCOS, 2006). Fine-scale studies may reveal detail about the biology underlying population patterns, whilst generalisations are more likely to emerge at broader scales (Wiens, 1989). If we adopt this philosophy, harbour seal haul-out clusters (see Chapter 2) could be considered as discrete subpopulations that form part of a much larger, spatially-structured population (Härkönen & Harding, 2001; cf. Chapter 5).

Harbour seal haul-out sites in this study did not show spatial correlation. Consequently sites could not be grouped into monitoring units according to similarities in trends. Furthermore, the extent (i.e. the overall area encompassed by the study) and resolution (i.e. the size of the individual units of observation) of the present study suggest that there is considerable asynchrony in harbour seal population trends between haul-out sites at both small- and large-scales (from < 5 km to > 1000 km). Important factors that are likely to influence harbour seal abundance, such as prey availability/distribution, predation and weather conditions, are usually correlated at some scale. The rather surprising result of the present study could either result from a failure to detect the presence of a correlation or from unexplained variation in local population dynamics.

There are a number of potential explanations for why spatial synchrony, if present, may not have been detected. For example, the frequency of aerial surveys may have been insufficient to describe complex population trends, or the study may have been conducted over too short a time frame. Furthermore, the measure of precision used in this study was based on thermal imaging surveys, yet it is likely that the fixed-wing

surveys used are less precise (Thompson & Harwood, 1990; Hiby *et al.*, 1996). CVs are also likely to vary on both temporal and spatial scales (Chapter 4). In addition, analyses performed in Chapter 4 indicate that there are systematic trends in the numbers of seals hauled out over the course of the three-week survey period that would add to the overall variance. Finally, the one kilometre grid used to calculate at-sea distances between haul-out sites may have been too coarse to detect fine-scale correlation. Further work should therefore be conducted to attempt to rule out the above factors as reasons for why synchrony in population trends was not detected in the present study, for example by investigating temporal, spatial and methodological (thermal imaging versus fixed-wing) variation in CVs. Failing to account for synchrony may lead to misinterpretation of the management implications of local changes in population size because if one subpopulation in a synchronous metapopulation decreases in abundance it is very likely that others will too (Ranta *et al.*, 1995; cf. harbour seal decline in Shetland, Orkney, north-east Scotland and south-east England: Lonergan *et al.*, 2007).

If changes in harbour seal numbers at neighbouring haul-outs are actually asynchronous, the observed decoupling of population trends between haul-out sites may result from intra- or inter-species competition between seal subpopulations at nearby haul-out sites (e.g. for food or mates) or represent a spatially-structured population process (e.g. low dispersal and predation rates: cf. Chapters 1 & 2). The apparent site-fidelity of harbour seals (Yochem *et al.*, 1987; Thompson, 1989; Härkönen & Harding, 2001), and the rapid drop in the probability of harbour seals using neighbouring haul-out sites, could help explain the observed spatial heterogeneities in harbour seal abundance, due to increasing isolation (i.e. reduced connectivity) with distance. Moreover, in spatially structured populations haul-out sites may exhibit different trends (e.g. Härkönen & Harding, 2001). Thus harbour seal studies based on a single haul-out site may not be representative of sites in the surrounding area, because of the effects of local weather conditions, disturbance factors and proximity to prime foraging areas.

The probability of encountering a seal whose home haul-out site is within a SAC at an alternative haul-out site decreased rapidly with increasing distance from the SAC. This relative isolation of individual haul-out sites could potentially lead to a network of effectively closed harbour seal subpopulations that could be used as management units. However the analysis in this chapter suggests that this is only likely to occur at a very fine resolution. The difference between site fidelity in north-west and south-west Scotland is probably related to the availability of haul-out clusters at different distances from 'home' (cf. Figure 2.3 in Chapter 2). There are more alternative harbour seal haul-out sites around the deployment site in north-west Scotland, than in south-west Scotland and so it is unsurprising that these seals were less likely to be found at the site where they were captured. Although the extent to which SACs are representative of the surrounding haul-out sites could not be determined, this study confirms the need to survey areas adjacent to SACs and for a network of protected areas for harbour seals in Scotland.

No spatial correlation was observed at a fine-scale between haul-out sites within SACs that were considered as potential sites for monitoring trends in the present study. The observed trends in harbour seal abundance, over four-year periods, varied with the scale and location of the observations. Thus patterns in harbour seal abundance differed at haul-out sites both within and between SACs. Moreover, harbour seal population trends observed within these potential trend sites were not representative of changes in the population at large. However including haul-out sites within areas adjacent to SACs improved the extent to which they were representative of the overall harbour seal population. Thus, although current land-based protected areas for harbour seals show limited potential as trend sites for monitoring the population (due to heterogeneity both within and between these areas, and when compared with the rest of the population), extending monitoring programmes to include haul-out sites in adjacent areas would provide better knowledge of trends in harbour seal abundance than restricting surveys to SACs. Despite the potential advantages of using monitoring units (such as adjacent areas) to detect trends in the harbour seal population at large, animals may move when confronted with localised change. Consequently, it is important to acknowledge that although monitoring units would greatly reduce the

time and cost of harbour seal surveys and permit an increase in survey frequency, harbour seal movement, for example as a result of disturbance (Adkinson *et al.*, 2003) or a change in prey distribution, reduces the potential of these sites to fully represent trends in abundance of the population at large.

Conclusions

The habits of harbour seals make them inherently difficult and expensive to study; the variances on estimates of abundance are usually high (Chapter 4) and the large interval between current surveys makes timely detection of a population trend unlikely. This study predicts that even with a low CV (0.04) a change in population size greater than 5% will take six years to detect. Surveying once every four years approximately doubles detection time compared with annual surveys. Thus it is strongly advised that the overall population be monitored frequently, and preferably annually, to ensure the earliest possible detection of any change in abundance. The implications of Gerrodette's (1987) power analysis depend on a correctly built model, which assumes normal error distribution, equal variances and independence of estimates. Furthermore, the CVs used in this study were obtained from surveys conducted in a small area in north-west Scotland. Nevertheless, the approximate values obtained in this study provide a useful guide for monitoring SACs and highlight the importance of frequent abundance surveys.

Despite evidence that seals move between haul-out sites (Chapter 2) there was no apparent synchrony between population trends at haul-out sites, even when they are less than five kilometres apart. Thus the conclusions appropriate to one scale of environmental or population patterning may be inappropriate if transferred to another scale (Addicott *et al.*, 1987) and it is likely that behavioural differences between demographic components of populations of harbour seals have created a complex pattern of connectivity between haul-out sites (Härkönen & Harding, 2001). The use of surveys within SACs to monitor trends in overall abundance and conservation status may therefore be limited. It is unlikely that SACs constitute biologically and

statistically appropriate trend sites and the consequences of focusing monitoring programmes on individual haul-out sites should be considered carefully. However, counts from larger clusters of haul-out sites, which include areas adjacent to SACs, are more likely to reflect trends in the overall harbour seal population.

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CHAPTER SIX

GENERAL DISCUSSION

The primary aim of this thesis was to investigate harbour seal ecology and describe the robustness of current and alternative monitoring methods for harbour seal populations in Scotland. This study focused on harbour seals on the west coast of Scotland to (i) provide detailed information on behavioural patterns to complement the aerial surveys in the area, and (ii) provide knowledge of harbour seals in this area comparable with studies conducted on the east coast of Britain. Using a combination of different methods to provide information from a number of approaches, each chapter in this thesis has considered how to incorporate new information on harbour seal ecology into monitoring strategies. The general results of this holistic approach to harbour seal conservation are reviewed below and placed within the context of the Habitats Directive[1], which provides the legal framework for harbour seal protection in the European Union (EU). Each Member State of the EU is legally required to designate land-based protected areas, known as Special Areas of Conservation (SACs), and to monitor the populations of species listed on Annex II of the Directive, which includes the harbour seal. Thus the current study focused on harbour seals using these SACs and has provided important ecological information for use in monitoring programmes and management plans. This chapter discusses the conservation implications, monitoring recommendations and suggested avenues of further research.

Many aspects of the behavioural ecology of harbour seals are poorly understood. This is probably due to the challenges associated with studying harbour seals; for example, in addition to financial, temporal and logistical constraints, seals spend a large proportion of their time at sea such that only a fraction of the population is visible. Furthermore, due to a high degree of individual variability, this fraction changes over

[1] The 1992 Council Directive on the Conservation of Habitats and of Wild Fauna and Flora (Appendix I)

time resulting in considerable uncertainty in harbour seal ecology (e.g. Chapter 2), and especially in abundance estimates (e.g. Chapters 3 & 4). An increasingly popular response to managing populations with high levels of uncertainty, such as harbour seals, is to adopt a precautionary approach to management (Turner, 1991; Myers & Mertz, 1998; Thompson, *et al.* 2000). This approach, as defined by Jennings *et al.* (2001), "is based on the idea that management actions in the present should consider the needs of future generations, avoid changes that are not reversible, identify undesirable outcomes of management action in advance, and identify measures to correct them." Implementation of a precautionary approach therefore relies on regular research and monitoring (Chapter 5) and is the principle behind the drive to protect currently unthreatened species.

The high number of harbour seal haul-out sites scattered along the west coast of Scotland, and the absence of visible barriers between groups of seals, could indicate that the population has little or no spatial structure, as has been suggested elsewhere (e.g. Heide-Jorgensen *et al.*, 1992). However, the haul-out behaviour of individuals utilising the same area is likely to be affected by similar weather/disturbance factors. Moreover, the occurrence of site-fidelity (Anderson, 1981; Yochem *et al.*, 1987; Thompson, 1989; Härkönen & Harding, 2001; Chapter 2) and asynchrony in trends in abundance (Chapter 5) suggests that groups of animals using a cluster of haul-out sites are likely to form a 'local population.'

In order to comply with the Habitats Directive the harbour seal population must remain in "favourable conservation status". In practical terms this emphasizes the need for long-term monitoring and for determining a baseline population estimate (e.g. local estimates calculated in Chapter 4).

Estimating abundance

Although methods have been developed for estimating grey seal population size from pup production data (SCOS, 2005), direct counts of harbour seal pups are difficult

because pups enter the water soon after birth (Thompson *et al.*, 1994b). Consequently there are two important factors when estimating harbour seal abundance. Firstly the complexity and high variability of harbour seal behaviour means that it is important to choose an appropriate method, or combination of methods, to address specific questions. This should include evaluating all sources of uncertainty in the estimation procedure to allow the variance associated with population estimates to be calculated (Chapter 4). Secondly, because current monitoring techniques only count the number of seals hauled out and, even under 'ideal' conditions, there is no way to estimate how many seals remain in the water (Boveng *et al.*, 2003), a method is needed to estimate absolute population size. Although minimum abundance estimates can be used as an index of population size, knowledge of the absolute number of seals present in a population is required to calculate their consumption of, and impacts on, populations of prey species (e.g. Harwood & Croxall, 1988).

Monitoring methods

It is essential that the best available data are used to designate appropriate protected areas for harbour seals, and are available to justify any subsequent management measures (Baxter, 2001). Thus one aspect to consider when choosing a monitoring method is that an animal's behaviour may appear very different if viewed over a scale of minutes compared to a scale of years, or over a few metres compared to thousands of kilometres (Hooker & Baird, 2001). This means that observations should take place at a similar scale to the behaviour being studied in order to gain insight into the underlying behaviour (Levin, 1992); ideally, management should also be linked to these scales. For example, satellite telemetry provides a long-term and large-scale picture of animal movements, whereas photo-identification and capture-recapture methods are more appropriate for determining and interpreting fine-scale movements (Table 6.1). Other aspects to consider when choosing an appropriate survey method include the habitat type of the study area and temporal and financial constraints. The various methods to estimate harbour seal abundance are explained in more detail in Chapter 1, with the advantages and disadvantages of current survey methods given below in Table 6.2. **Recommendation: An appropriate monitoring method should be**

selected for each study. There should be consistency in data collection methods, and the precision of abundance estimates should be maintained (or improved).

Table 6.1: An example of the manner in which the scale of observation of harbour seal movement depends on the monitoring method adopted. Here photo-identification and capture-recapture techniques are compared with satellite telemetry (adapted from Hooker & Baird, 2001).

	Method	
	Capture-recapture	**Satellite telemetry**
Temporal scale	From months to decades.	Up to several months.
Spatial scale	Fine (metres) to large (1000s of kms).	Coarse (several kilometres).
Sampling rate	Highly variable (hours – years).	Approximately 1-3 times/day.
Disadvantages	Biased by distribution of effort in time and space; often spatially limited to near shore areas.	High cost; small sample sizes; no information during moult; animals must be physically captured.
Advantages	Inexpensive for inshore areas; large sample sizes; no physical interaction.	Does not require field effort post-deployment; global coverage.

Table 6.2*:* Current survey methods for estimating harbour seal abundance (adapted from Duck, 2003).

Survey method	Technique	Advantages	Disadvantages	Sources
Land-based	Seals counted from suitable vantage points using binoculars or a telescope.	Detailed counts for specific sites with good opportunity for prolonged series of counts from same site. Relatively cheap.	Potential for missing seals hidden by others if not sufficiently high up. Restricted opportunity for same effort at different sites and potential access problems to some sites.	Thompson *et al.* 1997 Thompson *et al.* 2001 Chapter 4
Boat	Counts made with the aid of binoculars from small inflatable boats.	Precise location and good information on age and size class of seals. Access to SACs and adjacent coasts.	Very weather dependent and time consuming with reduced possibility of surveying several areas. Two boats needed for safety but may scare seals. Boat movement makes counting difficult.	Thompson & Harwood, 1990 Thompson *et al.* 2001 Sharples, 2005 Chapter 5
Fixed-wing	Large vertical camera mounted in the floor of the aircraft. Seals are located visually and counted or photographed.	Quick coverage of sites, repeatable and less expensive than helicopter. Excellent for seals hauled out on sandbanks and estuaries.	Species recognition difficult and reasonable chance of missing groups. Significant amount of post-processing necessary.	Olesiuk *et al.* 1990 Ries *et al.* 1998 Frost *et al.* 1999 Huber *et al.* 2001 Small *et al.* 2001 Chapter 5

Continued overleaf

Table 6.2 continued

Survey method	Technique	Advantages	Disadvantages	Sources
Helicopter	Seals are located visually and large groups photographed using handheld camera with zoom. Counts are obtained from projected image.	Rapid access, small groups need not be photographed.	Expensive and timely due to searching for seals prior to counting. Some groups can be missed and post-processing necessary.	Thompson & Harwood, 1990
Thermal imaging	Thermal imaging camera with telescope is mounted in helicopter and the thermal image of seals is determined in real time from VHS tapes.	Repeatable, consistent and complete cover providing accurate counts of all groups of seals in a short time period without disturbing seals.	Expensive and costly transit time between surveyed areas. Ineffective in poor/wet weather.	SCOS, 2005 Chapters 4 and 5
Remote cameras	Mast mounted cameras close to haul-out sites transmitting images via the internet.	Continuous data acquisition throughout the year and low operational costs.	Initial financial outlay. Not suitable for all locations. Sturdy masts and on-site maintenance required. Limited field of view or many cameras needed per haul-out site.	Allen *et al.*, 1984 Thompson & Harwood, 1990
Capture-recapture	Individuals are identified, e.g. using photo-identification methods, to produce a sighting history over a period of several surveys.	Includes animals not hauled out at time of survey. Gives information on health status and survival. See also Table 6.1.	Time-consuming, site-specific and not suitable for all habitats. See also Table 6.1.	Middlemas, 2003 Mackey, 2004 Chapter 3

Although expensive, aerial surveys are currently the favoured method for estimating harbour seal abundance in Scotland (SCOS, 2005) because they are deemed to be the most precise method for large-scale surveys and, unlike land-based or boat counts, the photographs/film can be reanalysed in the laboratory to reduce the risk of misidentification. However, different demographic components of the population vary in the timing of the moult period (Thompson & Rothery, 1987; Härkönen *et al.*, 1999; Daniel *et al.*, 2003). Thus the extent to which this period varies spatially and temporally should be investigated (e.g. using land-based counts) to determine if the timing of aerial surveys ought to be reconsidered (cf. Chapter 4). The factors that influence haul-out behaviour are also likely to show spatial variation (Chapter 4). Quantifying the potential effect of these factors on aerial counts is therefore vital for minimising any potential bias and thus optimising monitoring strategies (Boveng *et al.*, 2003). Repeat surveys should also be conducted in different locations to estimate the extent of inter-annual and spatial variation in the timing of the moult period, to determine coefficients of variation for different areas and to help determine the duration of the moult plateau. **Recommendation: The extent to which the moult period varies spatially and temporally should be investigated further and coefficients of variation in the correction factor for different areas should be determined. The duration of the plateau in the proportion of seals hauled out during the moult should be determined.**

Surveying harbour seal abundance during both the pupping period, when counts are highest (Chapters 3 & 4), and the moulting period, when counts are most consistent (Chapter 4), would aid our understanding of the relationship between these periods. Furthermore, counts of harbour seals during the pupping period can be corrected using telemetry data, they may also assist in determining the reproductive health of the population. Thus, whilst moult surveys should be continued to add to historical records, occasional surveys during the pupping period would provide additional information on the conservation status of harbour seals. **Recommendation: Harbour seal abundance should be surveyed during both the pupping and the moulting periods to aid our understanding of the relationship between these periods and provide additional information on the conservation status of harbour seals.**

Estimating absolute abundance

A number of methods can be used to account for animals in the water at the time of survey and thus estimate absolute abundance from counts of harbour seals hauled out. For example, correction factors have been calculated using time-lapse photography (Thompson & Harwood, 1990), freeze-branding (Härkönen & Harding, 2001) and, most frequently, the reciprocal of the proportion of seals hauled out determined using telemetry (e.g. Pitcher & McAllister, 1981; Yochem *et al.*, 1987; Thompson *et al.*, 1997; Ries *et al.*, 1998; Huber *et al.*, 2001). These correction factors range from 1.5 to over five (Table 6.3), depending upon the time of year and location of the study. Most of the studies are not comparable to the timing and location of harbour seal surveys in Scotland, and some had a small or skewed (by sex and/or age) sample.

Table 6.3: Summary of some of the correction factors used to estimate the total harbour seal population size from minimum abundance estimates obtained from observing the number of animals hauled out.

Study area	Seals tagged	Correction factor	Time of year	Source
Washington & Oregon	124	1.52	Pupping	Huber *et al.*, 2001
Dutch Wadden Sea	15	68% ashore (~ 1.47)	Breeding	Ries *et al.*, 1998
Moray Firth	26	1.64	Pupping	Thompson *et al.*, 1997
Orkney	5	1.69	Moult	Thompson & Harwood, 1990
Alaska	35	2.0	Pupping	Pitcher & McAllister, 1981
St Andrews Bay	25	36% ashore (~ 2.78)	Moult	Sharples, 2005
California	18	5.26	Post Moult	Yochem *et al.*, 1987

However, determining a correction factor by any of these methods assumes that the behaviour of the tagged or marked animals is representative of the population being surveyed. This requires the whole area to be surveyed under similar environmental conditions (e.g. within two hours of low tide on one day). Animals that are caught for marking or tagging may not be representative of the population as a whole (e.g. due to capture heterogeneity, age- or sex-biases). Moreover, sex biases in the haul-out composition (Kovacs *et al.*, 1990; Härkönen *et al.*, 1999) during the time of an aerial survey will affect the appropriate correction factor used to account for seals not hauled

out. There is also individual, spatial, temporal and sex-related variation in the proportion of time harbour seals spend hauled out, and the probability of a seal being hauled out is affected by seasonal, tidal state (Chapter 4) and time of day (Chapter 2). Telemetric devices usually do not provide information during the moulting period as they are generally attached to the fur and consequently are lost during the primary survey period for harbour seals, making correction factors impossible to determine. Consequently, with so much variation in haul-out patterns, the use of a generic correction factor must be questioned as it is highly probable that variation also occurs during the moult when harbour seal abundance is currently surveyed.

Due to the numerous difficulties in estimating absolute abundance, an alternative could be to obtain information on the number of seals using a specific area. For example, photo-identification and capture-recapture methods can be used to provide a measure of the number of seals using a particular haul-out site (Chapter 3), but this method does not provide an estimate of the absolute population size because seals use multiple clusters of haul-out sites (Chapter 2). Nevertheless capture-recapture may be the only way of obtaining information on the number of seals using a specific area. Long-term photo-identification surveys will allow fine-scale movements to be studied (e.g. Karlsson *et al.*, 2005), and, using Arnason-Schwarz multistate models (Arnason, 1973; Schwarz *et al.*, 1993), dispersal (e.g. Hestbeck *et al.*, 1991) and site-fidelity (e.g. Spendelow *et al.*, 1995) could be examined. Photo-identification and capture-recapture methods therefore show good potential as a monitoring technique for harbour seals. Consequently it is recommended that large-scale photo-identification surveys are conducted to determine their appropriateness in different areas, and to ascertain if the probability of recapture shows regional variation (which may indicate different levels of site-fidelity). **Recommendation: Capture-recapture techniques should be used to estimate the number of animals using a specific area. Movement probabilities between haul-out sites should be incorporated into capture-recapture models that allow for individual heterogeneity.**

The extent of emigration and immigration probably differs among haul-out sites, such that some sites are only ever used by seals in transit from one place to another, whilst other sites have high return rates. Results from satellite telemetry could be used to

identify haul-out sites with high return rates that would be particularly suitable for photo-identification and capture-recapture studies. **Recommendation: Satellite telemetry should be used to select haul-out sites to which seals exhibit high fidelity, these can then be used for photo-identification and capture-recapture studies.**

Conservation implications & future work

Conservation efforts have traditionally focused on threatened or rare species (Soulé & Orians, 2001) but recent moves to protect unthreatened species, in order to maintain biodiversity following a precautionary approach, are on the increase. This approach requires regular surveys to detect any notable changes in abundance (Chapter 5) and for suitable thresholds of changes in abundance to be selected to ensure that a timely response is initiated, thus preventing any further decline in seal numbers (Mapstone, 1995). However, although estimating absolute or relative abundance is of crucial conservation importance, simply detecting a decline in harbour seal numbers is in itself insufficient for preventing further change in numbers (Drechsler & Burgman, 2004). Thus it is also critical to understand the nature and potential causes of observed changes in abundance. There are a number of reasons for an observed decline in harbour seal numbers, these include:

(a) Increased mortality rate, potentially as a result of disease (including biotoxins and parasites), shooting, bycatch, predation or decreased prey availability. It is therefore recommended that an integrated strandings programme should be implemented to investigate causes (and distribution) of harbour seal deaths, and blood and other tissue samples should be taken to examine toxin levels in the population;

(b) Changes in the reproductive rate and consequent changes in the age structure of the population (also affected by mortality). Harbour seal pups lose the lanugo *in utero*, and hence are hard to distinguish from adults during aerial surveys. Moreover they can swim immediately from birth and so it is difficult to monitor reproductive rates of harbour seal populations. Nevertheless, it is recommended that detailed land-based counts or photo-identification studies

should be conducted during the pupping season to assist in determining reproductive rates. Tooth extractions from captured and stranded animals could help determine the age structure of the population;

(c) Behavioural changes altering the time spent hauled out. For example, a reduction in prey availability could result in seals foraging further afield and/or for longer. It is recommended that both land-based counts and satellite telemetry be used to compare present and historical patterns;

(d) Haul-out site switching or emigration. Tagging studies show that harbour seals remain within approximately 50 km of capture sites, but there is some movement between haul-out sites (Brown & Mate, 1983; Thompson & Miller, 1990; Tollit *et al.*, 1998; Lowry *et al.*, 2001; Chapter 2). Hoover-Miller *et al.* (2001) suggest that the rapid decline in harbour seal numbers following an oil spill in Prince William Sound (Frost *et al.*, 1999) was a result of a re-distribution of the animals. If emigration caused a local population decline, numbers of seals should increase at nearby haul-out sites. It is therefore recommended that nearby haul-out sites be surveyed. Integrated large-scale photo-identification and capture-recapture projects may also assist in determining emigration rates, provided animals remain within the study region;

(e) Natural fluctuation in population size, or large observational error. Most natural populations experience some fluctuation in population size over time (Pascual & Adkinson, 1994). Additionally, if observational error is large, even completely stable populations may generate sequences of counts that have an apparent trend (Mönkkönen & Aspi, 1997). In these situations an observed decline may not be reason for concern if the long-term dynamics of the population remain stable.

Recommendation: The underlying reason for any change in abundance should be determined. In addition, potential threats to the seals or to their habitat should be identified and, where possible, monitored.

Harbour seal population trends differ over small spatial scales (Chapter 5). As a result, counts made at individual haul-out sites, or small clusters of haul-out sites (e.g. SACs), are not representative of the population as a whole, and generalisations about

population status based on these counts are likely to be invalid (Adkinson *et al.*, 2003). As the Habitats Directive requires information on the overall population, the consequences of focusing monitoring programmes on individual haul-out sites should be considered carefully, as it is unlikely that SACs constitute biologically and statistically appropriate trend sites (Chapter 5). Monitoring should therefore take place on the widest possible scale, at the very least encompassing haul-out sites in areas adjacent to SACs, in order to detect local population dynamics. Careful consideration should be given to defining the boundaries of these adjacent areas. **Recommendation: Monitoring should take place on the widest possible scale to detect regional as well as local changes in population dynamics.**

Timely detection of a change in abundance is unlikely when there is a large interval between surveys (Adkinson *et al.*, 2003; Chapter 5). Population monitoring should therefore be conducted frequently (and where possible annually) to ensure the earliest possible detection of changes in population size. Moreover, acceptable thresholds of change in abundance should be agreed (e.g. a 20% increase or decrease) so that timely responses can be initiated (Chapter 5). **Recommendation: Population monitoring should be conducted frequently (and where possible annually). Minimum detectable changes in abundance should be determined so that timely responses can be initiated.**

The design of protected areas has led to a debate over whether a single large reserve (with a big population in a stable environment) is preferable to several smaller reserves, which are less susceptible to localised catastrophic events. This is commonly known as the SLOSS debate (Simberloff & Abele, 1982). Whilst the overall size of SACs was constrained by the Scottish Executive, the question of whether to have composite or homogeneous protected areas was not considered and may influence the effectiveness of these areas. A similar trade-off debate arises from limited financial resources restricting either the frequency (e.g. annual or quadrennial) or the extent (e.g. individual haul-out sites or synoptic coverage) of surveys. Ideally synoptic surveys should be carried out annually. However, biennial surveys of large clusters of haul-out sites (e.g. SACs and adjacent areas: Chapter 5 & Appendix IV) would provide information on the conservation status of the harbour seal. Future work should focus on investigating this relationship between the frequency and extent of surveys.

Appropriateness of protected areas

As with all protected species it is crucial to understand the relationship between harbour seal population dynamics and environmental characteristics. In particular, the relationship between where seals are counted (i.e. on land) and where they spend most of their time (i.e. at-sea) is vital for determining the appropriateness of land-based protected areas for harbour seals. The fact that harbour seals forage coastally (no more that 75 km offshore) in both the Pacific USA (e.g. Brown & Mate, 1983; Suryan & Harvey, 1998; Lowry *et al.*, 2001) and Europe (e.g. Thompson *et al.*, 1996; Chapter 2) suggests that they generally stay within the same area all year round. Moreover, both short-term (several months) and long-term (up to one year) studies have suggested that harbour seals show site-fidelity (Anderson, 1981; Yochem *et al.*, 1987; Thompson, 1989; Härkönen & Harding, 2001; Chapter 2). This supports the designation of protected areas for harbour seals at clusters of key haul-out sites, as is the case for SACs.

Historically most conservation work has focused on terrestrial systems, but the increased awareness of the vulnerability of many marine species (Roberts & Hawkins, 1999) has highlighted the need for conservation efforts in the oceans (e.g. Myers *et al.*, 1997; Casey & Myers, 1998). For example, whilst the availability of haul-out sites is undoubtedly important to harbour seals, especially for pupping and moulting, the availability of feeding grounds is likely to be equally important. In moving towards a precautionary approach to marine conservation, legislation is increasingly facilitating the establishment of protected areas in the marine realm, both in and beyond territorial seas (e.g. the Convention on Biological Diversity, 1992; the United Nations Convention on the Law of the Sea, 1994).

Although SACs are currently exclusively terrestrial, they are likely to be a first step towards creating protected areas for mammals using the marine environment. Therefore diving profiles and habitat preferences (cf. Matthiopoulos, 2003), as determined from satellite telemetry, may assist in locating foraging areas in future studies. Meanwhile, because most at-sea activity is likely to occur within 25 km of haul-out sites (Chapter 2), extending the boundaries of current land-based harbour seal SACs seaward by 25 km is likely to protect most of the foraging areas used by seals,

and could facilitate a move towards designating a marine component to SACs. The establishment of an integrated network of marine protected sites between existing terrestrial protected areas may increase the effectiveness of protection for harbour seals, particularly because of their high association with coastal areas and repeated trips to local foraging areas. Extending current SAC boundaries would also ensure that protected areas were selected for each distinct biogeographic region used by harbour seals, as advocated by Roberts *et al.* (2003). **Recommendation: The SAC boundaries should be extended seaward by 25 km as a first step towards designating a marine component to protected areas for harbour seals.**

A major criticism of protected areas, particularly those designated for marine mammals, is that they represent 'paper parks' with little regulation and consequently provide a false sense of conservation achievement (Hooker & Gerber, 2004). There are also some threats to harbour seals for which reserves offer no direct protection (e.g. disease, pollution: Chapter 1; climate change: Forcada *et al.*, 2005; interactions with fishing gear: Bjørge *et al.*, 2002a; Bjørge *et al.*, 2002b; Moore, 2003; direct killing by fishermen: Harwood, 1983; Reijnders *et al.*, 1993). Thus in addition to the legal requirement to monitor harbour seal abundance, a measure of the effectiveness of SACs should be determined, both in terms of their ecological appropriateness (Roberts *et al.*, 2001) and their political and social acceptability (Allison *et al.*, 1998). Indeed, the conservation of harbour seals is highly political due to conflicts of interest between conservationists and fishermen (e.g. Scott & Parsons, 2005) and, because one of science's roles is to inform the management process and to monitor the effectiveness of management (Jennings *et al.*, 2001), an integrated approach encompassing socio-economic, political and environmental factors should be adopted to ensure successful conservation and management of harbour seals. **Recommendation: Measures of the ecological and socio-political effectiveness of SACs should be developed, and an integrated management approach adopted.**

Site-based protection should protect the whole species distribution range, and so animals that respond best to site-based protection are often relatively sedentary (Gell & Roberts, 2003). Harbour seals exceed the limits of SACs by spending a large proportion of their time in the water (mean = 0.7 - 0.9: Chapter 2) and by using haul-

out sites that may be over 100 km apart (Lowry *et al.*, 2001; Thompson *et al.*, 1996; Chapter 2). In north-west Scotland it is likely that only 20% of the total time spent hauled out between September and July occurs at the same cluster of haul-out sites (Chapter 2), indicating the presence of mixing between groups of animals. From a conservation perspective this movement is important in maintaining genetic variation (Lacy, 1997) and suggests that many more animals use land-based protected areas than are seen during a single survey (Chapter 3). It also implies that local harbour seal populations (i.e. those using clusters of haul-out sites) do not comprise a completely closed population and so the extent to which specific haul-out sites are used by particular individuals is limited (Chapter 2). Consequently, although even the partial use of protected areas may substantially reduce the frequency with which each individual seal is exposed to certain impacts (e.g. tidal turbines), the conservation value of land-based protection for harbour seals may be limited at the population level.

Management units

Traditionally the harbour seal population has been divided up into monitoring and management units using practical and logistical considerations. Despite a degree of site-fidelity (Chapter 2), many more seals use a cluster of haul-out sites than are observed during a single survey (Chapter 3) and, in this study, individual seals showed only limited use of protected areas (Chapter 2). The timing (seasonal and diurnal) of surveys is likely to affect the number of animals counted at a particular haul-out site (Chapter 4). In addition, this study has indicated that SACs cannot be used as trend sites to monitor the status of the Scottish harbour seal population because trends in abundance both between pairs of individual haul-out sites and within SACs appear to be asynchronous (Chapter 5). Trends in abundance in larger clusters of haul-out sites (e.g. adjacent areas: Chapter 5) are more representative of trends in the overall population. However, until estimates of the connectivity between haul-out sites are available, for example by estimating movement probabilities and clustering methods, the designation of biologically appropriate management units for harbour seals remains a major challenge.

Limitations

The proportion of the harbour seal population ashore during aerial surveys is unlikely to be consistent over space and time, as currently assumed, because there is spatial, temporal and sex-related variation in the proportion of time harbour seals spend hauled out. Furthermore, the high degree of individual variability has important consequences for the practice of applying telemetry data to conservation problems, including biasing population estimates when using correction factors. Thus future theoretical and controlled experimental studies could potentially examine these tag-associated costs to adjust correction factors accordingly. A larger data set is required to capture the full extent of variation among individuals of different age- and sex-classes and to investigate spatial differences. Until then, caution should be applied when extrapolating information from different areas or times of year.

It is important when drawing conclusions from models, such as those in Chapters 2 and 4, to bear in mind that no model can reproduce observational data perfectly (Burnham & Anderson, 2002). As Box (1978) commented "all models are wrong, but some are useful". Akaike's Information Criterion (Akaike, 1973), for example, is useful for selecting the best model out of a proposed set; even if all the candidate models are very poor AIC will still select the best, even if it is poor in an absolute sense (Burnham & Anderson, 2002). Thus, although modelling can be a powerful analytical tool, and is essential to help interpret data, the results need careful evaluation before conclusions are drawn or generalisations made. An under-fitted model will often provide biassed parameter estimates, underestimate the sampling variance and result in poor confidence interval coverage due to missing effects in the model (Burnham & Anderson, 2002). In contrast, over-fitted models have excessively large sampling variances causing estimator precision to be worse than would have resulted from the use of a more parsimonious model (Burnham & Anderson, 2002).

One major limitation to using telemetry data for location information (e.g. Chapter 2) is the associated error, which itself is variable, of locations both at-sea and of haul-out events. Fortunately, a new generation of satellite telemetry devices are being tested

that provide locations via GPS allowing spatial information to be obtained at a very high resolution (B. McConnell, *pers. comm.*). These tags will allow a detailed picture of harbour seal movements and will improve estimates of the probability of hauling out within a given distance of a haul-out site, thus complementing the findings of the present study.

Recommendations

The costs of establishing protected areas and post-designation monitoring can be considerable (Balmford *et al.*, 2004) and yet the appropriateness of focusing monitoring efforts on trend sites appears limited for assessing changes in harbour seal abundance (Chapter 5). Monitoring harbour seal population size, range, recruitment success and health is crucial for detecting ecologically important changes and so it is of paramount importance that monitoring strategies are carefully planned to optimise the quality, quantity and relevance of data collected. Information on population trends cannot be produced within the space of a few years because ecological research limited to such a time-scale would fail to encompass the life span of seals (Jackson *et al.*, 2001). Provision should therefore be made to ensure the continuation of a consistent research effort as part of an overall management plan (Wilson *et al.*, 1999). Moreover, by adopting a precautionary approach, a step in the right direction is being taken to ensure the effective management of harbour seals and preserve the terrestrial habitat in which they pup, breed, rest and moult.

Summary

The broad achievements of this thesis are summarised below:

- Correction factors that relate absolute population size to minimum abundance estimates, obtained during the moult, should be used with caution because at other times of year there is substantial spatial, temporal (seasonal & diurnal) and sex-related variation in the proportion of time harbour seals hauled out.
- Some seals travelled over 100 km, yet 50% of trips were within 25 km of the haul-out site. Consequently, although seals do not comprise closed populations, their high usage of coastal areas should assist in designating a marine component to protected areas.
- Photo-identification and capture-recapture techniques can be used to determine the number of seals using a haul-out site, or cluster of sites, over a period of several months. This may be the only way to estimate the absolute number of seals using a protected area.
- Individual haul-out sites did not show synchrony in population trends and so it is unlikely that SACs can be used as biologically and statistically appropriate trend sites for the overall population.
- Highest numbers of seals hauled out were observed during the pupping period, whilst the most consistent numbers were during the moult. Consideration should be given to conducting occasional surveys during the pupping period to provide additional information on the conservation status of harbour seals. Minimum abundance was estimated for parts of north-west Scotland to be used as a baseline for future monitoring during the moult.
- The coefficient of variation for aerial surveys in north-west Scotland was calculated as 15%. Surveying 1½ hours earlier in the tide and delaying the survey window by a week was predicted to reduce the count variation in this area.
- A 5% change in harbour seal population size was predicted to take around six years to detect using annual surveys and a CV = 0.04. This detection period increases when monitoring methods with lower precision are used, or as a result of fewer surveys. For example detection time is predicted to double when surveys are conducted quadrennially, as is currently the case for most areas in Scotland.

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APPENDICES

APPENDIX I

COUNCIL DIRECTIVE ON THE CONSERVATION OF HABITATS AND OF WILD FAUNA AND FLORA (EU HABITATS DIRECTIVE, 1992).

COUNCIL DIRECTIVE 92/43/EEC
of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora

THE COUNCIL OF THE EUROPEAN COMMUNITIES,

Having regard to the Treaty establishing the European Economic Community, and in particular Article 130s thereof,

Having regard to the proposal from the Commission,

Having regard to the opinion of the European Parliament,

Having regard to the opinion of the Economic and Social Committee,

Whereas the preservation, protection and improvement of the quality of the environment, including the conservation of natural habitats and of wild fauna and flora, are an essential objective of general interest pursued by the Community, as stated in Article 130r of the Treaty;

Whereas the European Community policy and action programme on the environment (1987 to 1992) makes provision for measures regarding the conservation of nature and natural resources;

Whereas, the main aim of this Directive being to promote the maintenance of biodiversity, taking account of economic, social, cultural and regional requirements, this Directive makes a contribution to the general objective of sustainable development;

Whereas the maintenance of such biodiversity may in certain cases require the maintenance, or indeed the encouragement, of human activities;

Whereas, in the European territory of the Member States, natural habitats are continuing to deteriorate and an increasing number of wild species are seriously threatened; whereas given that the threatened habitats and species form part of the Community's natural heritage and the threats to them are often of a transboundary nature, it is necessary to take measures at Community level in order to conserve them;

Whereas, in view of the threats to certain types of natural habitat and certain species, it is necessary to define them as having priority in order to favour the early implementation of measures to conserve them;

Whereas, in order to ensure the restoration or maintenance of natural habitats and species of Community interest at a favourable conservation status, it is necessary to designate special areas of conservation in order to create a coherent European ecological network according to a specified timetable;

Whereas all the areas designated, including those classified now or in the future as special protection areas pursuant to Council Directive 79/409/EEC of 2 April 1979 on the conservation of wild birds, will have to be incorporated into the coherent European ecological network;

Whereas it is appropriate, in each area designated, to implement the necessary measures having regard to the conservation objectives pursued;

Whereas sites eligible for designation as special areas of conservation are proposed by the Member States but whereas a procedure must nevertheless be laid down to allow the designation in exceptional cases of a site which has not been proposed by a Member State but which the Community considers essential for either the maintenance or the survival of a priority natural habitat type or a priority species;

Whereas an appropriate assessment must be made of any plan or programme likely to have a significant effect on the conservation objectives of a site which has been designated or is designated in future;

Whereas it is recognised that the adoption of measures intended to promote the conservation of priority natural habitats and priority species of Community interest is a common responsibility of all Member States; whereas this may, however, impose an excessive financial burden on certain Member States given, on the one hand, the uneven distribution of such habitats and species throughout the Community and, on the other hand, the fact that the 'polluter pays' principle can have only limited application in the special case of nature conservation;

Whereas it is therefore agreed that, in this exceptional case, a contribution by means of Community co-financing should be provided for within the limits of the resources made available under the Community's decisions;

Whereas land-use planning and development policies should encourage the management of features of the landscape which are of major importance for wild fauna and flora;

Whereas a system should be set up for surveillance of the conservation status of the natural habitats and species covered by this Directive;

Whereas a general system of protection is required for certain species of flora and fauna to complement Directive 79/409/EEC;

Whereas provision should be made for management measures for certain species, if their conservation status so warrants, including the prohibition of certain means of capture or killing, whilst providing for the possibility of derogation's on certain conditions;

Whereas, with the aim of ensuring that the implementation of this Directive is monitored, the Commission will periodically prepare a composite report based, inter alia, on the information sent to it by the Member States regarding the application of national provisions adopted under this Directive;

Whereas the improvement of scientific and technical knowledge is essential for the implementation of this Directive;

Whereas it is consequently appropriate to encourage the necessary research and scientific work;

Whereas technical and scientific progress mean that it must be possible to adapt the Annexes; whereas a procedure should be established whereby the Council can amend the Annexes;

Whereas a regulatory committee should be set up to assist the Commission in the implementation of this Directive and in particular when decisions on Community co-financing are taken;

Whereas provision should be made for supplementary measures governing the reintroduction of certain native species of fauna and flora and the possible introduction of non-native species;

Whereas education and general information relating to the objectives of this Directive are essential for ensuring its effective implementation,

HAS ADOPTED THIS DIRECTIVE:

Definitions

Article 1

For the purpose of this Directive:

(a) *conservation* means a series of measures required to maintain or restore the natural habitats and the populations of species of wild fauna and flora at a favourable status as defined in (e) and (i);

(b) *natural habitats* means terrestrial or aquatic areas distinguished by geographic, abiotic and biotic features, whether entirely natural or semi-natural;

(c) *natural habitat types of Community interest* means those which, within the territory referred to in Article 2:

(i) are in danger of disappearance in their natural range; or

(ii) have a small natural range following their regression or by reason of their intrinsically restricted area; or

(iii) present outstanding examples of typical characteristics of one or more of the six following biogeographical regions: Alpine, Atlantic, Boreal, Continental, Macaronesian and Mediterranean. Such habitat types are listed or may be listed in Annex I;

(d) *priority natural habitat types* means natural habitat types in danger of disappearance, which are present on the territory referred to in Article 2 and for the conservation of which the Community has particular responsibility in view of the proportion of their natural range which falls within the territory referred to in Article 2; these priority natural habitat types are indicated by an asterisk (*) in Annex I;

(e) *conservation status of a natural habitat* means the sum of the influences acting on a natural habitat and its typical species that may affect its long-term natural distribution, structure and functions as well as the long-term survival of its typical species within the territory referred to in Article 2. The conservation status of a natural habitat will be taken as 'favourable' when: its natural range and areas it covers within that range are stable or increasing, and the specific structure and functions which are necessary for its long-term maintenance exist and are likely to continue to exist for the foreseeable future, and the conservation status of its typical species is favourable as defined in (i);

(f) *habitat of a species* means an environment defined by specific abiotic and biotic factors, in which the species lives at any stage of its biological cycle;

(g) *species of Community interest* means species which, within the territory referred to in Article 2, are:

(i) endangered, except those species whose natural range is marginal in that territory and which are not endangered or vulnerable in the western palearctic region; or

(ii) vulnerable, i.e. believed likely to move into the endangered category in the near future if the causal factors continue operating; or

(iii) rare, i.e. with small populations that are not at present endangered or vulnerable, but are at risk. The species are located within restricted geographical areas or are thinly scattered over a more extensive range; or

(iv) endemic and requiring particular attention by reason of the specific nature of their habitat and/or the potential impact of their exploitation on their habitat and/or the potential impact of their exploitation on their conservation status.

Such species are listed or may be listed in Annex II and/or Annex IV or V;

(h) *priority species* means species referred to in (g) (i) for the conservation of which the Community has particular responsibility in view of the proportion of their natural range which falls within the territory referred to in Article 2; these priority species are indicated by an asterisk (*) in Annex II;

(i) *conservation status of a species* means the sum of the influences acting on the species concerned that may affect the long-term distribution and abundance of its populations within the territory referred to in Article 2; The *conservation status* will be taken as 'favourable' when: population dynamics data on the species concerned indicate that it is maintaining itself on a long-term basis as a viable component of its natural habitats, and the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future, and there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis;

(j) *site* means a geographically defined area whose extent is clearly delineated;

(k) *site of Community importance* means a site which, in the biogeographical region or regions to which is belongs, contributes significantly to the maintenance or restoration at a favourable conservation status of a natural habitat type in Annex I or of a species in Annex II and may also contribute significantly to the coherence of Natura 2000 referred to in Article 3, and/or contributes significantly to the maintenance of biological diversity within the biogeographic region or regions concerned. For animal species ranging over wide areas, sites of Community importance shall correspond to the places within the natural range of such species which present the physical or biological factors essential to their life and reproduction;

(l) *special area of conservation* means a site of Community importance designated by the Member States through a statutory, administrative and/or contractual act where the necessary conservation measures are applied for the maintenance or restoration, at a favourable conservation status, of the natural habitats and/or the populations of the species for which the site is designated;

(m) *specimen* means any animal or plant, whether alive or dead, of the species listed in Annex IV and Annex V, any part or derivative thereof, as well as any other goods which appear, from an accompanying document, the packaging or a mark or label, or from any other circumstances, to be parts or derivatives of animals or plants of those species;

(n) *the committee* means the committee set up pursuant to Article 20.

Article 2

The aim of this Directive shall be to contribute towards ensuring bio-diversity through the conservation of natural habitats and of wild fauna and flora in the European territory of the Member States to which the Treaty applies.

Measures taken pursuant to this Directive shall be designed to maintain or restore, at favourable conservation status, natural habitats and species of wild fauna and flora of Community interest. Measures taken pursuant to this Directive shall take account of economic, social and cultural requirements and regional and local characteristics.

Conservation of natural habitats and habitats of species

Article 3

A coherent European ecological network of special areas of conservation shall be set up under the title Natura 2000. This network, composed of sites hosting the natural habitat types listed in Annex I and habitats of the species listed in Annex II, shall enable the natural habitat types and the species' habitats concerned to be maintained or, where appropriate, restored at a favourable conservation status in their natural range.

The Natura 2000 network shall include the special protection areas classified by the Member States pursuant to Directive 79/409/EEC.

Each Member State shall contribute to the creation of Natura 2000 in proportion to the representation within its territory of the natural habitat types and the habitats of species referred to in paragraph 1. To that effect each Member State shall designate, in accordance with Article 4, sites as special areas of conservation taking account of the objectives set out in paragraph 1.

Where they consider it necessary, Member States shall endeavour to improve the ecological coherence of Natura 2000 by maintaining, and where appropriate developing, features of the landscape which are of major importance for wild fauna and flora, as referred to in Article 10.

Article 4

On the basis of the criteria set out in Annex III (Stage 1) and relevant scientific information, each Member State shall propose a list of sites indicating which natural habitat types in Annex I and which species in Annex II that are native to its territory the sites host. For animal species ranging over wide areas these sites shall correspond to the places within the natural range of such species which present the physical or biological factors essential to their life and reproduction. For aquatic species which range over wide areas, such sites will be proposed only where there is a clearly identifiable area

representing the physical and biological factors essential to their life and reproduction. Where appropriate, Member States shall propose adaptation of the list in the light of the results of the surveillance referred to in Article 11.

The list shall be transmitted to the Commission, within three years of the notification of this Directive, together with information on each site. That information shall include a map of the site, its name, location, extent and the data resulting from application of the criteria specified in Annex III (Stage 1) provided in a format established by the Commission in accordance with the procedure laid down in Article 21.

On the basis of the criteria set out in Annex III (Stage 2) and in the framework both of each of the five biogeographical regions referred to in Article 1 (c) (iii) and of the whole of the territory referred to in Article 2 (1), the Commission shall establish, in agreement with each Member State, a draft list of sites of Community importance drawn from the Member States' lists identifying those which lost one or more priority natural habitat types or priority species.

Member States whose sites hosting one or more priority natural habitat types and priority species represent more than 5 % of their national territory may, in agreement with the Commission, request that the criteria listed in Annex III (Stage 2) be applied more flexibly in selecting all the sites of Community importance in their territory.

The list of sites selected as sites of Community importance, identifying those which host one or more priority natural habitat types or priority species, shall be adopted by the Commission in accordance with the procedure laid down in Article 21. The list referred to in paragraph 2 shall be established within six years of the notification of this Directive.

Once a site of Community importance has been adopted in accordance with the procedure laid down in paragraph 2, the Member State concerned shall designate that site as a special area of conservation as soon as possible and within six years at most, establishing priorities in the light of the importance of the sites for the maintenance or restoration, at a favourable conservation status, of a natural habitat type in Annex I or a species in Annex II and for the coherence of Natura 2000, and in the light of the threats of degradation or destruction to which those sites are exposed.

As soon as a site is placed on the list referred to in the third subparagraph of paragraph 2 it shall be subject to Article 6 (2), (3) and (4).

Article 5

In exceptional cases where the Commission finds that a national list as referred to in Article 4 (1) fails to mention a site hosting a priority natural habitat type or priority species which, on the basis of

relevant and reliable scientific information, it considers to be essential for the maintenance of that priority natural habitat type or for the survival of that priority species, a bilateral consultation procedure shall be initiated between that Member State and the Commission for the purpose of comparing the scientific data used by each.

If, on expiry of a consultation period not exceeding six months, the dispute remains unresolved, the Commission shall forward to the Council a proposal relating to the selection of the site as a site of Community importance.

The Council, acting unanimously, shall take a decision within three months of the date of referral. During the consultation period and pending a Council decision, the site concerned shall be subject to Article 6 (2).

Article 6

For special areas of conservation, Member States shall establish the necessary conservation measures involving, if need be, appropriate management plans specifically designed for the sites or integrated into other development plans, and appropriate statutory, administrative or contractual measures which correspond to the ecological requirements of the natural habitat types in Annex I and the species in Annex II present on the sites.

Member States shall take appropriate steps to avoid, in the special areas of conservation, the deterioration of natural habitats and the habitats of species as well as disturbance of the species for which the areas have been designated, in so far as such disturbance could be significant in relation to the objectives of this Directive.

Any plan or project not directly connected with or necessary to the management of the site but likely to have a significant effect thereon, either individually or in combination with other plans or projects, shall be subject to appropriate assessment of its implications for the site in view of the site's conservation objectives. In the light of the conclusions of the assessment of the implications for the site and subject to the provisions of paragraph 4, the competent national authorities shall agree to the plan or project only after having ascertained that it will not adversely affect the integrity of the site concerned and, if appropriate, after having obtained the opinion of the general public.

If, in spite of a negative assessment of the implications for the site and in the absence of alternative solutions, a plan or project must nevertheless be carried out for imperative reasons of overriding public interest, including those of a social or economic nature, the Member State shall take all compensatory measures necessary to ensure that the overall coherence of Natura 2000 is protected. It shall inform the Commission of the compensatory measures adopted.

Where the site concerned hosts a priority natural habitat type and/or a priority species, the only considerations which may be raised are those relating to human health or public safety, to beneficial consequences of primary importance for the environment or, further to an opinion from the Commission, to other imperative reasons of overriding public interest.

Article 7

Obligations arising under Article 6 (2), (3) and (4) of this Directive shall replace any obligations arising under the first sentence of Article 4 (4) of Directive 79/409/EEC in respect of areas classified pursuant to Article 4 (1) or similarly recognised under Article 4 (2) thereof, as from the date of implementation of this Directive or the date of classification or recognition by a Member State under Directive 79/409/EEC, where the latter date is later.

Article 8

In parallel with their proposals for sites eligible for designation as special areas of conservation, hosting priority natural habitat types and/or priority species, the Member States shall send, as appropriate, to the Commission their estimates relating to the Community co-financing which they consider necessary to allow them to meet their obligations pursuant to Article 6 (1).

In agreement with each of the Member States concerned, the Commission shall identify, for sites of Community importance for which co-financing is sought, those measures essential for the maintenance or re-establishment at a favourable conservation status of the priority natural habitat types and priority species on the sites concerned, as well as the total costs arising from those measures.
The Commission, in agreement with the Member States concerned, shall assess the financing, including co-financing, required for the operation of the measures referred to in paragraph 2, taking into account, amongst other things, the concentration on the Member State's territory of priority natural habitat types and/or priority species and the relative burdens which the required measures entail.

According to the assessment referred to in paragraphs 2 and 3, the Commission shall adopt, having regard to the available sources of funding under the relevant Community instruments and according to the procedure set out in Article 21, a prioritised action framework of measures involving co-financing to be taken when the site has been designated under Article 4 (4).

The measures which have not been retained in the action framework for lack of sufficient resources, as well as those included in the above mentioned action framework which have not received the necessary co-financing or have only been partially co-financed, shall be reconsidered in accordance with the procedure set out in Article 21, in the context of the two-yearly review of the action framework and may, in the maintime, be postponed by the Member States pending such review. This review shall take into account, as appropriate, the new situation of the site concerned. In areas where the measures

dependent on co-financing are postponed, Member States shall refrain from any new measures likely to result in deterioration of those areas.

Article 9

The Commission, acting in accordance with the procedure laid down in Article 21, shall periodically review the contribution of Natura 2000 towards achievement of the objectives set out in Article 2 and 3. In this context, a special area of conservation may be considered for declassification where this is warranted by natural developments noted as a result of the surveillance provided for in Article 11.

Article 10

Member States shall endeavour, where they consider it necessary, in their land-use planning and development policies and, in particular, with a view to improving the ecological coherence of the Natura 2000 network, to encourage the management of features of the landscape which are of major importance for wild fauna and flora.

Such features are those which, by virtue of their linear and continuous structure (such as rivers with their banks or the traditional systems for marking field boundaries) or their function as stepping stones (such as ponds or small woods), are essential for the migration, dispersal and genetic exchange of wild species.

Article 11

Member States shall undertake surveillance of the conservation status of the natural habitats and species referred to in Article 2 with particular regard to priority natural habitat types and priority species.

Protection of species

Article 12

Member States shall take the requisite measures to establish a system of strict protection for the animal species listed in Annex IV (a) in their natural range, prohibiting:

(a) all forms of deliberate capture or killing of specimens of these species in the wild;
(b) deliberate disturbance of these species, particularly during the period of breeding, rearing, hibernation and migration;
(c) deliberate destruction or taking of eggs from the wild;
(d) deterioration or destruction of breeding sites or resting places.

For these species, Member States shall prohibit the keeping, transport and sale or exchange, and offering for sale or exchange, of specimens taken from the wild, except for those taken legally before this Directive is implemented.

The prohibition referred to in paragraph 1 (a) and (b) and paragraph 2 shall apply to all stages of life of the animals to which this Article applies. Member States shall establish a system to monitor the

incidental capture and killing of the animal species listed in Annex IV (a). In the light of the information gathered, Member States shall take further research or conservation measures as required to ensure that incidental capture and killing does not have a significant negative impact on the species concerned.

Article 13

Member States shall take the requisite measures to establish a system of strict protection for the plant species listed in Annex IV (b), prohibiting:

(a) the deliberate picking, collecting, cutting, uprooting or destruction of such plants in their natural range in the wild;

(b) the keeping, transport and sale or exchange and offering for sale or exchange of specimens of such species taken in the wild, except for those taken legally before this Directive is implemented.

The prohibitions referred to in paragraph 1 (a) and (b) shall apply to all stages of the biological cycle of the plants to which this Article applies.

Article 14

If, in the light of the surveillance provided for in Article 11, Member States deem it necessary, they shall take measures to ensure that the taking in the wild of specimens of species of wild fauna and flora listed in Annex V as well as their exploitation is compatible with their being maintained at a favourable conservation status.

Where such measures are deemed necessary, they shall include continuation of the surveillance provided for in Article 11. Such measures may also include in particular:

- regulations regarding access to certain property,
- temporary or local prohibition of the taking of specimens in the wild and exploitation of certain populations,
- regulation of the periods and/or methods of taking specimens,
- application, when specimens are taken, of hunting and fishing rules which take account of the conservation of such populations,
- establishment of a system of licences for taking specimens or of quotas,
- regulation of the purchase, sale, offering for sale, keeping for sale or transport for sale of specimens,
- breeding in captivity of animal species as well as artificial propagation of plant species, under strictly controlled conditions, with a view to reducing the taking of specimens of the wild,
- assessment of the effect of the measures adopted.

Article 15

In respect of the capture or killing of species of wild fauna listed in Annex V (a) and in cases where, in accordance with Article 16, derogation's are applied to the taking, capture or killing of species listed in Annex IV (a), Member States shall prohibit the use of all indiscriminate means capable of causing local disappearance of, or serious disturbance to, populations of such species, and in particular:

(a) use of the means of capture and killing listed in Annex VI (a);

(b) any form of capture and killing from the modes of transport referred to in Annex VI (b).

Article 16

Provided that there is no satisfactory alternative and the derogation is not detrimental to the maintenance of the populations of the species concerned at a favourable conservation status in their natural range, Member States may derogate from the provisions of Articles 12, 13, 14 & 15 (a) and (b):

(a) in the interest of protecting wild fauna and flora and conserving natural habitats;

(b) to prevent serious damage, in particular to crops, livestock, forests, fisheries and water and other types of property;

(c) in the interests of public health and public safety, or for other imperative reasons of overriding public interest, including those of a social or economic nature and beneficial consequences of primary importance for the environment;

(d) for the purpose of research and education, of repopulating and re-introducing these species and for the breeding operations necessary for these purposes, including the artificial propagation of plants;

(e) to allow, under strictly supervised conditions, on a selective basis and to a limited extent, the taking or keeping of certain specimens of the species listed in Annex IV in limited numbers specified by the competent national authorities.

Member States shall forward to the Commission every two years a report in accordance with the format established by the Committee on the derogation's applied under paragraph 1. The Commission shall give its opinion on these derogation's within a maximum time limit of 12 months following receipt of the report and shall give an account to the Committee. The reports shall specify:

(a) the species which are subject to the derogation's and the reason for the derogation, including the nature of the risk, with, if appropriate, a reference to alternatives rejected and scientific data used;

(b) the means, devices or methods authorised for the capture or killing of animal species and the reasons for their use;

(c) the circumstances of when and where such derogation's are granted;

(d) the authority empowered to declare and check that the required conditions obtain and to decide what means, devices or methods may be used, within what limits and by what agencies, and which persons are to carry but the task;

(e) the supervisory measures used and the results obtained.

Information

Article 17

Every six years from the date of expiry of the period laid down in Article 23, Member States shall draw up a report on the implementation of the measures taken under this Directive. This report shall include in particular information concerning the conservation measures referred to in Article 6 (1) as well as evaluation of the impact of those measures on the conservation status of the natural habitat types of Annex I and the species in Annex II and the main results of the surveillance referred to in Article 11. The report, in accordance with the format established by the committee, shall be forwarded to the Commission and made accessible to the public.

The Commission shall prepare a composite report based on the reports referred to in paragraph 1. This report shall include an appropriate evaluation of the progress achieved and, in particular, of the contribution of Natura 2000 to the achievement of the objectives set out in Article 3. A draft of the part of the report covering the information supplied by a Member State shall be forwarded to the Member State in question for verification. After submission to the committee, the final version of the report shall be published by the Commission, not later than two years after receipt of the reports referred to in paragraph 1, and shall be forwarded to the Member States, the European Parliament, the Council and the Economic and Social Committee. Member States may mark areas designated under this Directive by means of Community notices designed for that purpose by the committee.

Research

Article 18

Member States and the Commission shall encourage the necessary research and scientific work having regard to the objectives set out in Article 2 and the obligation referred to in Article 11. They shall exchange information for the purposes of proper co-ordination of research carried out at Member State and at Community level.

Particular attention shall be paid to scientific work necessary for the implementation of Articles 4 and 10, and transboundary co-operative research between Member States shall be encouraged.

Procedure for amending the Annexes

Article 19

Such amendments as are necessary for adapting Annexes I, II, III, V and VI to technical and scientific progress shall be adopted by the Council acting by qualified majority on a proposal from the Commission.

Such amendments as are necessary for adapting Annex IV to technical and scientific progress shall be adopted by the Council acting unanimously on a proposal from the Commission.

Committee

Article 20

The Commission shall be assisted by a committee consisting of representatives of the Member States and chaired by a representative of the Commission.

Article 21

The representative of the Commission shall submit to the committee a draft of the measures to be taken. The committee shall deliver its opinion on the draft within a time limit which the Chairman may lay down according to the urgency of the matter. The opinion shall be delivered by the majority laid down in Article 148 (2) of the Treaty in the case of decisions which the Council is required to adopt on a proposal from the Commission. The votes of the representatives of the Member States within the committee shall be weighted in the manner set out in that Article. The Chairman shall not vote. The Commission shall adopt the measures envisaged if they are in accordance with the opinion of the committee.

If the measures envisaged are not in accordance with the opinion of the committee, or if no opinion is delivered, the Commission shall, without delay, submit to the Council a proposal relating to the measures to be taken. The Council shall act by a qualified majority. If, on the expiry of three months from the date of referral to the Council, the Council has not acted, the proposed measures shall be adopted by the Commission.

Supplementary provisions

Article 22

In implementing the provisions of this Directive, Member States shall:

(a) study the desirability of re-introducing species in Annex IV that are native to their territory where this might contribute to their conservation, provided that an investigation, also taking into account experience in other Member States or elsewhere, has established that such re-introduction contributes effectively to re-establishing these species at a favourable conservation status and that it takes place only after proper consultation of the public concerned;

(b) ensure that the deliberate introduction into the wild of any species which is not native to their territory is regulated so as not to prejudice natural habitats within their natural range or the wild native fauna and flora and, if they consider it necessary, prohibit such introduction. The results of the assessment undertaken shall be forwarded to the committee for information;

(c) promote education and general information on the need to protect species of wild fauna and flora and to conserve their habitats and natural habitats.

Final provisions

Article 23

Member States shall bring into force the laws, regulations and administrative provisions necessary to comply with this Directive within two years of its notification. They shall forthwith inform the Commission thereof.

When Member States adopt such measures, they shall contain a reference to this Directive or be accompanied by such reference on the occasion of their official publication. The methods of making such a reference shall be laid down by the Member States.

Member States shall communicate to the Commission the main provisions of national law which they adopt in the field covered by this Directive.

Article 24

This Directive is addressed to the Member States. Done at Brussels, 21 May 1992.

For the Council

The President

Arlindon Marques Cunha

Annex I: Natural habitat types of community interest whose conservation requires the designation of special areas of conservation.

Annex II: Animal and plant species of community interest whose conservation requires the designation of special areas of conservation.

Annex III: Criteria for selecting sites eligible for identification as sites of community importance and designation as special areas of conservation.

Annex IV: Animal and plant species of community interest in need of strict protection.

Annex V: Animal and plant species of community interest whose taking in the wild and exploitation may be subject to management measures.

Annex VI: Prohibited methods and means of capture and killing and modes of transport.

APPENDIX II

MONTHLY PROPORTION OF TIME HARBOUR SEALS HAULED OUT PER MONTH AND DURATION OF MARINE TELEMETRY STUDIES.

Table II.i: Mean and associated standard errors of the proportion of time harbour seals were hauled out per month for both sexes in south-west (2003/2004) and north-west (2004/2005) Scotland.

Month	South-west Scotland				North-west Scotland			
	Female		Male		Female		Male	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Sept.	26.4	3.9	13.5	3.0	43.1		21.7	12.2
Oct.	17.5	1.9	17.1	1.5	8.5	8.5	8.2	1.6
Nov.	17.5	1.0	15.9	0.3	9.0	2.4	10.8	2.1
Dec.	18.1	1.1	15.6	1.5	3.9	3.0	19.7	4.7
Jan.	13.5	3.5	12.4		7.1	2.8	11.3	1.6
Feb.	15.0	2.3	27.0		6.1	1.5	32.3	13.5
Mar.	15.5				21.8	5.2	29.7	10.2
Apr.	21.9		20.7	2.5	16.9	6.9	25.1	5.7
May	11.3		24.9	9.0	23.2	5.5	33.8	4.6
Jun.					35.8	20.3	23.0	3.8
Jul.							21.0	7.9
Overall	*18.1*	*1.2*	*20.1*	*3.1*	*16.4*	*2.0*	*21.3*	*1.6*

Table II.ii: Mean duration of harbour seal telemetry studies using different devices on free-ranging animals. Mean durations of some telemetry studies in other species of marine animals are included for comparison.

Species	**Deployment site**	**Mean tagging duration (days)**	***n***	**Type of tag** *	**Source(s)**
Harbour seal, *Phoca vitulina*	Orkney, Scotland, UK	62	14	VHF	Thompson *et al.*, 1989
	Rømø, Danish Wadden Sea	74	10	SLTDR	Tougaard *et al.*, 2003
	Rødsand, Western Baltic	89	4	PTT	Dietz *et al.*, 2003
	Prince William Sound, Alaska, USA	126.9	49	SRDL	Lowry *et al.*, 2001
	St Andrews Bay, Scotland, UK	131.3	25	SRDL	Sharples, 2005
Grey seal, *Halichoerus grypus*	Rødsand, Western Baltic	108.3	6	PTT	Dietz *et al.*, 2003
	Farnes, N. England, UK	121.75	12	SRDL	McConnell *et al.*, 1999
S. Elephant seal, *Mirounga leonina*	Peninsula Valdes, Argentina	74.29	7	SRDL	Campagna *et al.*, 1999
Crabeater seal, Lobodon carcinophaga	East Antarctica	57.21	24	SLTDR	Southwell, 2005
Bottlenose dolphin, *Tursiops truncatus*	Gulf of Mexico & Virgin Islands, USA	45	2	PTT	Wells *et al.*, 1999
Harbour porpoise, *Phocoena phocoena*	Bay of Fundy, Canada & Gulf of Maine, USA	49.6	9	PTT	Read & Westgate, 1997
Narwhal, *Monodon monoceros*	Baffin Island, Canada	106	13	SLTDR	Laidre *et al.*, 2003
Whale shark, *Rhincodon typus*	Sea of Cortez & N. Pacific Ocean, Mexico	140.9	15	PTT	Eckert & Stewart, 2001
Green turtle, *Chelonia mydas*	Ascension Island, South Atlantic	38	5	PTT	Hays *et al.*, 2001

* VHF = time-depth records that transmit by VHF to a nearby receiver; SLTDR = satellite linked time-depth recorders; PTT = platform terminal transmitter, also known as satellite-linked radio transmitters; SRDL = satellite relay data logger (i.e. PTT coupled with sensors)

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APPENDIX III

ENCOUNTER HISTORIES FOR HARBOUR SEALS PHOTOGRAPHED IN LOCH DUNVEGAN

Table III.i: Encounter histories of harbour seals in inner Loch Dunvegan in 2005.

Sex	Side		Seal	April	May	June	July	Aug.	Sep.	Oct.
Male	L	R	Fuday	1	1	1	1	1	0	1
Unknown	L	R	Tanera	1	0	0	0	0	0	0
Male	L	R	Uist	1	1	0	0	0	0	0
Unknown	L		158	1	0	0	0	0	0	0
Unknown	L	R	142	1	0	0	0	0	0	0
Unknown		R	143	1	0	0	0	0	0	0
Unknown	L	R	148	1	0	0	0	0	0	0
Unknown		R	152	1	0	0	0	0	0	0
Unknown	L	R	162	1	0	0	0	0	0	0
Unknown		R	167	1	0	0	0	0	0	0
Unknown	L	R	169	1	0	0	0	0	0	0
Unknown	L	R	173	1	0	0	0	0	0	0
Unknown	L	R	197	1	0	0	0	0	0	0
Male	L	R	198	1	0	0	0	0	0	0
Unknown	L	R	205	1	0	0	0	0	0	0
Unknown	L	R	Ailsa	1	0	1	1	1	0	0
Unknown		R	Arran	1	1	0	0	0	0	0
Female	L	R	Balta	1	0	0	3	0	1	0
Unknown	L	R	Barra	3	0	1	0	0	1	1
Male	L	R	Bute	1	0	1	2	2	1	0
Unknown	L	R	Canna	2	0	0	0	0	0	1
Male	L	R	Coll	1	0	1	0	0	0	1
Unknown	L	R	Flotta	2	2	1	0	0	0	0
Unknown		R	Gunna	1	1	1	0	0	0	0
Unknown	L	R	Jura	1	0	2	1	0	1	0
Male	L	R	Lamba	1	0	1	1	0	1	0
Unknown	L	R	Lewis	1	1	0	0	0	0	0
Unknown	L	R	Luing	1	1	0	1	1	1	0
Unknown	L	R	Kerrera	1	0	0	0	0	0	1
Unknown	L	R	Nista	1	0	0	0	0	1	0
Unknown	L	R	Oxna	1	1	1	2	3	0	0
Unknown	L	R	Rumble	1	2	0	0	0	0	1

Table III.i continued

Sex	Side		Seal	April	May	June	July	Aug.	Sep.	Oct.
Unknown	L	R	Scarba	1	1	0	0	2	1	0
Unknown	L	R	Shuna	1	1	0	0	0	0	0
Unknown	L	R	Stuley	1	0	1	3	0	1	0
Unknown	L	R	Ulva	1	1	2	0	0	0	0
Male	L	R	Unst	1	1	0	0	1	0	0
Unknown	L	R	Vaila	1	0	0	1	0	0	0
Female	L	R	Wyre	2	0	0	2	0	1	0
Unknown	L	R	Yell	1	2	0	1	0	0	0
Unknown	L	R	Flodday	0	1	0	0	0	0	0
Male	L	R	Groay	0	1	0	0	0	0	0
Unknown	L	R	Keava	0	1	0	0	0	0	0
Unknown	L	R	Shillay	0	1	0	0	0	0	0
Unknown	L	R	217	0	1	0	0	0	0	0
Female	L	R	218	0	1	0	0	0	0	0
Male	L	R	223	0	1	0	0	0	0	0
Unknown	L		238	0	1	0	0	0	0	0
Unknown		R	249	0	1	0	0	0	0	0
Male	L	R	251	0	1	0	0	0	0	0
Unknown	L	R	252	0	1	0	0	0	0	0
Unknown	L	R	256	0	1	0	0	0	0	0
Unknown	L	R	281	0	1	0	0	0	0	0
Unknown		R	285	0	1	0	0	0	0	0
Unknown	L		295	0	1	0	0	0	0	0
Unknown	L		297	0	1	0	0	0	0	0
Unknown	L		299	0	1	0	0	0	0	0
Unknown		R	308	0	1	0	0	0	0	0
Unknown		R	318	0	1	0	0	0	0	0
Unknown		R	320	0	1	0	0	0	0	0
Unknown		R	324	0	1	0	0	0	0	0
Unknown	L		330	0	1	0	0	0	0	0
Unknown	L		336	0	1	0	0	0	0	0
Unknown	L		344	0	1	0	0	0	0	0
Unknown		R	615	0	1	0	0	0	0	0
Female	L	R	Bressay	0	1	0	0	0	1	0
Male	L	R	Cava	0	2	1	1	2	0	0
Unknown	L	R	Coppay	0	2	0	0	0	1	0
Unknown		R	Crowlin	0	1	0	0	0	1	0
Male	L	R	Danna	0	1	0	0	0	0	1
Male	L	R	Eigg	0	2	0	0	1	1	0
Male	L	R	Eorsa	0	2	0	1	1	0	0
Unknown		R	Eriskay	0	1	1	0	0	0	0
Unknown		R	Fara	0	2	0	0	0	0	0
Male	L	R	Fetlar	0	1	0	0	1	1	0
Female	L	R	Gigha	0	1	1	1	0	1	0

Table III.i continued

Sex	Side		Seal	April	May	June	July	Aug.	Sep.	Oct.
Male	L	R	Handa	0	1	0	2	0	0	0
Unknown	L	R	Harris	0	1	1	0	0	0	0
Unknown	L		Hinba	0	1	0	0	0	0	1
Unknown		R	Hoy	0	2	0	0	0	0	0
Unknown		R	Lismore	0	1	0	0	1	0	0
Unknown	L	R	Longa	0	2	0	0	0	0	0
Unknown	L	R	Lunga	0	1	2	1	0	0	0
Unknown	L	R	Insh	0	1	0	0	1	1	0
Male	L	R	Iona	0	2	2	0	0	0	0
Unknown	L	R	Islay	0	1	1	0	0	0	0
Unknown		R	Mousa	0	2	0	0	0	0	0
Unknown	L	R	Muck	0	1	0	0	1	1	0
Male	L	R	Noss	0	2	1	0	0	0	2
Male	L	R	Raasay	0	2	1	1	0	0	2
Unknown	L	R	Rockall	0	1	0	0	0	0	1
Unknown	L	R	Rona	0	1	1	1	0	0	0
Unknown	L		Ronay	0	1	1	0	0	0	0
Unknown	L	R	Sanday	0	1	1	2	1	0	0
Unknown	L	R	Soa	0	1	0	0	0	1	0
Unknown	L	R	Soay	0	1	3	1	2	1	0
Unknown	L	R	Staffa	0	1	0	0	0	1	1
Unknown	L	R	Swona	0	1	2	1	2	0	0
Unknown	L	R	Tahay	0	1	0	2	0	1	1
Unknown	L	R	Texa	0	2	1	1	0	0	0
Male	L	R	Tiree	0	2	0	0	0	0	0
Unknown	L	R	Vacsay	0	1	1	1	0	0	0
Unknown	L	R	Whalsay	0	1	0	0	0	1	0
Unknown	L	R	Wiay	0	2	0	1	1	0	0
Unknown	L	R	Westray	0	0	1	0	0	0	0
Unknown		R	376	0	0	1	0	0	0	0
Unknown		R	378	0	0	1	0	0	0	0
Unknown		R	379	0	0	1	0	0	0	0
Unknown	L		382	0	0	1	0	0	0	0
Unknown		R	398	0	0	1	0	0	0	0
Unknown	L	R	403	0	0	1	0	0	0	0
Unknown		R	406	0	0	1	0	0	0	0
Unknown	L		414	0	0	1	0	0	0	0
Unknown	L		421	0	0	1	0	0	0	0
Unknown	L		423	0	0	1	0	0	0	0
Unknown		R	433	0	0	1	0	0	0	0
Unknown		R	442	0	0	1	0	0	0	0
Unknown		R	448	0	0	1	0	0	0	0
Unknown		R	461	0	0	1	0	0	0	0
Unknown	L		464	0	0	1	0	0	0	0

Table III.i continued

Sex	Side		Seal	April	May	June	July	Aug.	Sep.	Oct.
Unknown	L		470	0	0	1	0	0	0	0
Unknown		R	471	0	0	1	0	0	0	0
Unknown	L		473	0	0	1	0	0	0	0
Unknown	L	R	474	0	0	1	0	0	0	0
Unknown		R	477	0	0	1	0	0	0	0
Unknown		R	478	0	0	1	0	0	0	0
Unknown		R	482	0	0	1	0	0	0	0
Unknown	L	R	485	0	0	1	0	0	0	0
Unknown		R	488	0	0	1	0	0	0	0
Unknown		R	490	0	0	1	0	0	0	0
Unknown	L		616	0	0	1	0	0	0	0
Unknown	L	R	Bigga	0	0	2	0	0	0	0
Female	L	R	Carna	0	0	1	2	1	0	0
Female	L	R	Fiaray	0	0	1	2	2	1	0
Unknown	L	R	Fuiay	0	0	1	2	1	1	0
Unknown	L	R	Gasay	0	0	1	0	0	1	0
Unknown	L		Gighay	0	0	1	0	3	0	0
Unknown	L	R	Havra	0	0	1	0	1	0	0
Unknown	L	R	Humla	0	0	1	0	0	0	1
Unknown	L	R	Isay	0	0	1	0	1	0	0
Unknown	L	R	May	0	0	1	1	0	1	0
Male	L	R	Nave	0	0	1	0	0	0	1
Female	L		Pabay	0	0	1	1	0	0	0
Unknown	L	R	Monach	0	0	1	0	0	1	0
Unknown	L	R	Rousay	0	0	1	0	1	0	0
Female	L	R	Rum	0	0	1	1	1	0	0
Unknown	L	R	Scarp	0	0	1	1	1	0	0
Unknown	L		Seil	0	0	1	0	0	1	0
Female	L	R	Switha	0	0	1	1	1	1	1
Unknown	L	R	Uyea	0	0	1	2	0	0	0
Unknown	L	R	Direy	0	0	0	1	0	0	0
Unknown	L	R	578	0	0	0	1	0	0	0
Unknown	L		518	0	0	0	1	0	0	0
Unknown		R	519	0	0	0	1	0	0	0
Unknown		R	525	0	0	0	1	0	0	0
Female		R	527	0	0	0	1	0	0	0
Unknown	L		528	0	0	0	1	0	0	0
Female		R	537	0	0	0	1	0	0	0
Female	L	R	540	0	0	0	1	0	0	0
Unknown	L	R	548	0	0	0	1	0	0	0
Unknown	L	R	572	0	0	0	1	0	0	0
Unknown	L		577	0	0	0	1	0	0	0
Female		R	596	0	0	0	1	0	0	0
Unknown	L		600	0	0	0	1	0	0	0

Table III.i continued

Sex	Side		Seal	April	May	June	July	Aug.	Sep.	Oct.
Unknown	L	R	602	0	0	0	1	0	0	0
Unknown		R	610	0	0	0	1	0	0	0
Unknown		R	697	0	0	0	1	0	0	0
Male	L	R	Cara	0	0	0	1	1	0	0
Unknown	L	R	Ensay	0	0	0	2	0	0	0
Unknown	L	R	Faray	0	0	0	2	0	1	0
Female	L	R	Fair	0	0	0	2	0	0	0
Unknown	L	R	Foula	0	0	0	1	1	0	0
Unknown	L	R	Gairsay	0	0	0	1	1	0	1
Unknown		R	Hirta	0	0	0	2	0	0	0
Male	L	R	Holy	0	0	0	2	0	0	0
Female	L	R	Housay	0	0	0	2	0	0	0
Male	L	R	Linga	0	0	0	3	0	0	0
Male	L	R	Mooa	0	0	0	2	1	1	0
Unknown	L	R	Orsay	0	0	0	1	0	1	0
Female	L	R	Sanda	0	0	0	1	1	0	0
Unknown	L		Shiant	0	0	0	1	0	1	0
Female	L	R	Stroma	0	0	0	2	1	0	0
Unknown	L	R	622	0	0	0	0	1	0	0
Unknown	L	R	623	0	0	0	0	1	0	0
Unknown		R	627	0	0	0	0	1	0	0
Unknown	L	R	650	0	0	0	0	1	0	0
Unknown	L	R	659	0	0	0	0	1	0	0
Unknown	L	R	671	0	0	0	0	1	0	0
Unknown	L		672	0	0	0	0	1	0	0
Unknown	L	R	694	0	0	0	0	1	0	0
Unknown	L		Egilsay	0	0	0	0	2	0	0
Female	L	R	Hellisay	0	0	0	0	2	0	0
Male		R	Colonsay	0	0	0	0	0	1	0
Unknown		R	921	0	0	0	0	0	1	0
Unknown	L		922	0	0	0	0	0	1	0
Unknown		R	926	0	0	0	0	0	1	0
Unknown	L	R	930	0	0	0	0	0	1	0
Unknown		R	932	0	0	0	0	0	1	0
Unknown		R	943	0	0	0	0	0	1	0
Unknown	L		945	0	0	0	0	0	1	0
Unknown		R	948	0	0	0	0	0	1	0
Unknown		R	952	0	0	0	0	0	1	0
Unknown	L	R	971	0	0	0	0	0	1	0
Unknown	L		972	0	0	0	0	0	1	0
Unknown	L	R	983	0	0	0	0	0	1	0
Unknown	L	R	985	0	0	0	0	0	1	0
Male	L	R	Pladda	0	0	0	0	0	1	2
Unknown	L		988	0	0	0	0	0	0	1

Table III.i continued

Sex	Side		Seal	April	May	June	July	Aug.	Sep.	Oct.
Unknown	L	R	990	0	0	0	0	0	0	1
Unknown	L		993	0	0	0	0	0	0	1
Unknown	L	R	994	0	0	0	0	0	0	1
Unknown	L		996	0	0	0	0	0	0	1
Unknown	L		997	0	0	0	0	0	0	1
Unknown	L	R	998	0	0	0	0	0	0	1
Unknown	L		999	0	0	0	0	0	0	1
Unknown	L	R	1000	0	0	0	0	0	0	1
Unknown		R	1001	0	0	0	0	0	0	1
Unknown		R	1003	0	0	0	0	0	0	1
Unknown		R	1004	0	0	0	0	0	0	1
Unknown	L		1005	0	0	0	0	0	0	1
Unknown		R	1010	0	0	0	0	0	0	1
Unknown	L		1011	0	0	0	0	0	0	1
Unknown	L		1013	0	0	0	0	0	0	1
Unknown	L	R	1017	0	0	0	0	0	0	1
Unknown	L	R	1025	0	0	0	0	0	0	1
Unknown	L		1029	0	0	0	0	0	0	1
Unknown	L		1031	0	0	0	0	0	0	1
Unknown	L		1040	0	0	0	0	0	0	1

Table III.ii: Encounter histories of harbour seals in inner Loch Dunvegan in 2005, which were also sighted in the Ascribs in September 2005.

Seal	April	May	June	July	Aug.	Sept.	Oct.
Ailsa	1	0	1	1	1	0	0
Flodday	0	1	0	0	0	0	0
Keava	0	1	0	0	0	0	0
Kerrera	1	0	0	0	0	0	1
Tanera	1	0	0	0	0	0	0

Table III.iii: Encounter histories of harbour seals in inner Loch Dunvegan in 2005, which were also sighted in western Loch Dunvegan in September 2005.

Seal	April	May	June	July	Aug.	Sept.	Oct.
Faray	0	0	0	2	0	1	0
Gasay	0	0	1	0	0	1	0
Housay	0	0	0	2	0	0	0
Iona	0	2	2	0	0	0	0
Shillay	0	1	0	0	0	0	0
Westray	0	0	1	0	0	0	0

Health status

Two adult harbour seals had eye lesions, one of which was seen in May and re-sighted in September (Figure 1). A blood sample provided no evidence that these seals were infected with conjunctival papillomavirus (A. Hall, *pers.comm.*). The cause of the eye lesions therefore remains unknown.

Figure 1: Photographs of one adult harbour seal with an eye lesion in May (a) and September (b) 2005, sighted in Loch Dunvegan, north-west Skye.

Most of the current knowledge on marine mammal diseases comes from investigations of stranded animals (Gulland, 1999), despite these animals representing an inherently skewed sample of the free-living population. Ocular disease is a common secondary factor for Pacific harbour seal strandings, with reports of keratitis, corneal ulcers, conjunctivitis, lens luxation, cataracts, hyphema and prolapse of the third eyelid (Colegrove *et al.*, 2005). Although the cause of the eye lesions observed in this study was not determined, photo-identification techniques and mark-recapture methods provided information on the local prevalence of the disorder, and could provide important information on recovery rates as part of a longer-term study.

APPENDIX IV

DESCRIPTION OF ADJACENT AREAS TO HARBOUR SEAL HAUL-OUT SITES

Table IV.i: Descriptions of the areas adjacent to Special Areas of Conservation (SAC), which could be used for monitoring harbour seals in Scotland. The boundaries were selected based on gaps in the seal distribution.

Name of harbour seal SAC	Adjacent area
Ascrib, Isay and Dunvegan	From Loch Brachadale clockwise round Skye up to and including Loch Sligachan, plus Rona and Raasay.
Dornoch Firth and Morrich More	Includes all coastline between Helmsdale and Findhorn.
Firth of Tay and Eden Estuary	South to North Berwick, including the Firth of Forth as far west as Dalgety Bay, including the Black Rocks off Burntisland and the islands to the south of Aberdour.
Eileanan agus Sgierean Lios mor (Lismore)	Includes Lochs Linnhe, Leven, Creran, Etive, Feochan and joining coastline south to a line between Beinn Mhor and Rubh' Aoineadh Mheinis on Mull north to Ardtornish Point including Loch Spelve.
Mousa	From Sumburgh Head to Lerwick.
Sanday	All islands to the north of Westray Firth N.B. Muckle and Little Green Holm are not included.
South East Islay Skerries	Includes the coast of Islay outside the SAC, Jura, Gigha, Colonsay, Orasay and the mainland coast from Ardnoe Point to Macrihanish.
Yell Sound Coast	From Lunna Ness up through Yell Sound, including Sullom Voe. The northern boundary is between Whale Firth, Yell across to Fethaland, Mainland.