Habitat Use, Haul-Out Behaviour & Site Fidelity of Grey Seals (*Halichoerus grypus*) along the Ceredigion Marine Heritage Coast, Wales

Kate Michelle Lewis

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School of Biological Sciences, University of Wales, Bangor
Deiniol Road, Bangor, Gwynedd
LL57 2UW

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Cyngor Cefn Gwlad Cymru
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My dearest little sister Pippa

You are a brave & beautiful rose…stay strong.

Abstract

Grey seals were sighted from visitor passenger boat (VPB) trips within all ten zones of the Ceredigion Marine Heritage Coast between New Quay and Ynys Lochtyn in 2004 and 2005, demonstrating their presence along the coastline within Cardigan Bay Special Area of Conservation (SAC). Environmental variables, collected via VPB trips and direct observation from Bird's Rock, a designated Site of Special Scientific Interest, were analysed using univariate and multivariate methods to investigate whether a particular factor influenced grey seal haul-out behaviour. Although tide, time of day, adjusted air temperature and disturbance primarily influenced haul-out behaviour at Bird's Rock, it is evident a complex dynamic of intrinsic and extrinsic factors interact to determine haul-out behaviour. Potential human-induced disturbance was investigated via logging grey seal-vessel interactions observed during direct observation surveys at Bird's Rock. Vessel traffic appeared not to induce short-term behavioural responses in the majority of seals present, suggesting vessels abiding the Ceredigion Marine Conservation Code of Conduct did not disturb seals in the short-term. Although infrequent, research vessels abiding and canoes violating the Code of Conduct resulted in seals permanently modifying their behaviour and/or escaping Bird's Rock. Given long-term effects of vessel disturbance are unknown, this study supports requirements of further study. Photo-identification of grey seals encountered along the Ceredigion coastline exhibited a degree of intra-seasonal and inter-annual site fidelity, particularly to Bird's Rock and Cwmtydu, a pupping beach. 52% of individuals were resighted at least twice within the initial season photographed. One bull (ID: 015) was encountered in three successive years (2003-2005) whereas a female (ID: 007) known to have pupped at Cwmtydu in 2003 was resighted there in August 2005. Furthermore, grey seals at Bird's Rock exhibited preference for specific haul-out rocks at Bird's Rock. Finally, direct observation revealed that education of tourists remains paramount in maintaining the protection of Grey Seals along the Ceredigion Marine Heritage Coast. The continuation of a precautionary approach to management within this area is required.

Table of Contents

List of Figures

List of Tables

List of Appendices

List of Accompanying Material

CD-Rom containing:

* Direct observational data from Bird's Rock during 8th June – 1st September 2005
* Grey seal sightings data from one-/two-hour trips during 10th April – 10th September 2004 and 1st May – 7th October 2005.
* Catalogue of 27 grey seals identified and accompanying information.
* Copy of thesis in PDF format (*requires Adobe Acrobat Reader*).

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Declaration

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed ………………………………………………… (candidate)

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STATEMENT 1

This dissertation is being submitted in partial fulfilment of the requirements for the degree of

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This dissertation is the result of my own independent work/investigation, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

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Glossary

Bottling	behaviour in which a seal is positioned vertically in the water column, with either head* or just its nose protruding the surface. *Head is held backwards with nose pointing towards the sky. Seals often submerge in this position.
CMHC	Ceredigion Marine Heritage Coast
Disturbance	'any activity that changes the contemporaneous behaviour or physiology of one or more' seals; disturbance always elicits a short-term response in the seal(s) (Nisbet, 2000)
Encounter	synonymous with *Interaction*
Habituation	typically refers to the loss of avoidance and escape responses resulting from repeated stimuli which provides the individual with no reward or harmful consequences (Constantine, 2001; Smith *et al.*, 2005)
Logging	when seals float at the surface of the water, with little/no movement of flippers; behaviour appears effortless.
Matriline	maternally related females in association with one another
Seal-vessel interaction (*Interaction*)	when person(s) onboard a vessel and seal(s) are mutually aware of one another (Smith *et al.*, 2005)
Site Fidelity	an individual's inclination to return to a location previously occupied (Switzer, 1997b). Site fidelity can be studied on a broad-scale, relating to a general coastal area or fine-scale, relating to a particular position within a breeding colony.
SRDL	Satellite Relay Data Logger, e.g. ARGOS (White & Sjöberg, 2002)
Tolerance	the intensity of disturbance that an individual tolerates without responding in a defined way (Nisbet, 2000)
Vigilance	a motor act which corresponds to a head-lift interrupting ongoing activity, followed by a visual scan of the environment' (Quenette, 1990)

1.0 Introduction

1.1 Cardigan Bay

Situated on the western coast of Wales and forming the North-eastern end of North Celtic Sea Trough (Dobson & Whittington, 1987), bound by St. George's Channel of the Irish Sea directly to the west and the Celtic Sea in the south, Cardigan Bay is the largest bay in the British Isles, measuring approximately 60miles across its westernmost extent from Llyn Peninsula to St. David's Head, covering ca. 5500km^2 (Gregory & Rowden, 2001; Lamb, 2004). The bay lays within the boreal biogeographic region hence its temporal climate, demonstrating strong seasonality for various environmental parameters, such as temperature, rainfall, water turbidity and wind velocity (Anon., unknown date).

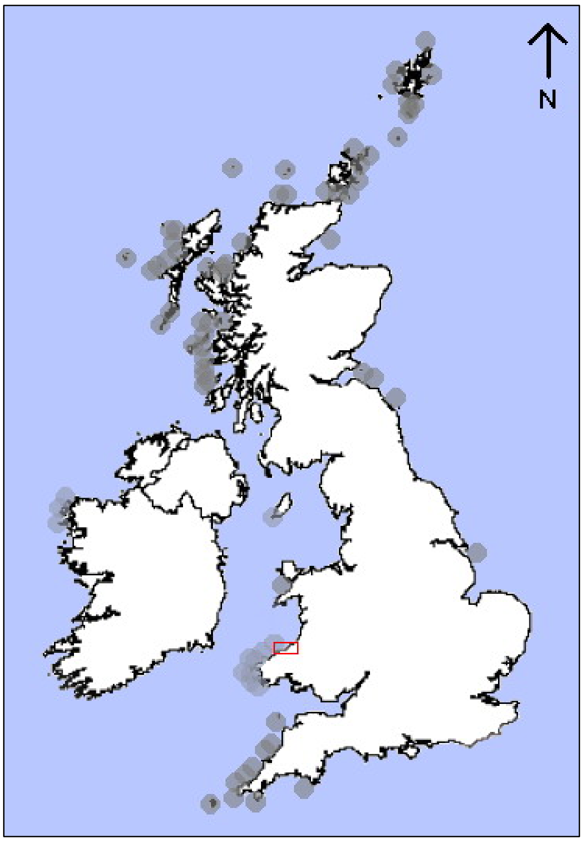


Figure 1: Map of United Kingdom and Ireland illustrating the grey seal (*H. grypus*) distribution. Red box indicates the study area within the Cardigan Bay Special Area of Conservation (SAC), Wales. Image adapted from Lamb (2004).

1.1.1 Bathymetry

Cardigan Bay is a 'shallow smooth-floored embayment' (Evans, 1995) gently sloping into the Irish Sea. Although St. George's Channel reaches depths in excess of 100m (Evans, 1995), within the Special Area of Conservation (SAC) depths generally reach no greater than 30m (Anon., unknown date).

1.1.2 Sedimentology

The Ceredigion coastline consists of steep cliffs interjected by small bays, (i.e. Cwmtydu, Llangrannog and Tresaith), examples of littoral sediment areas as well as New Quay shores and the mouth of the Teifi Estuary (Brazier *et al.*, 1999). The underlying shores predominantly range from rock, boulders and shingle in the south to sandy beaches in the north (Brazier *et al.*, 1999). Overall seabed ranges from sandy gravel, gravely sand, various grades of sand, broken shell and muddy sand (Evans, 1995; Brazier *et al.*, 1999; Lamb, 2004). Offshore from Bird's Rock, seabed consists of muddy sand. *Refer to Dobson & Whittington, 1987; Evans, 1995; Brazier et al., 1999 for further details on geology/sedimentology.*

1.1.3 Sea-Surface Temperature & Salinity

Sea-surface temperature of Cardigan Bay varies with season, proximity to land and water depth (Evans, 1995; Anon., unknown date); coldest during February/March (approx. 6.0-8.5˚C), in contrast to warmer August/September (14-16˚C offshore/20˚C inshore) (Evans, 1995; Anon., unknown date). Salinity also varies seasonally (highest during summer) and proximity to freshwater inflows (e.g. Teifi Estuary). Summer salinity ranges from 33-35‰ between Anglesey and St. George's Channel (Evans, 1995).

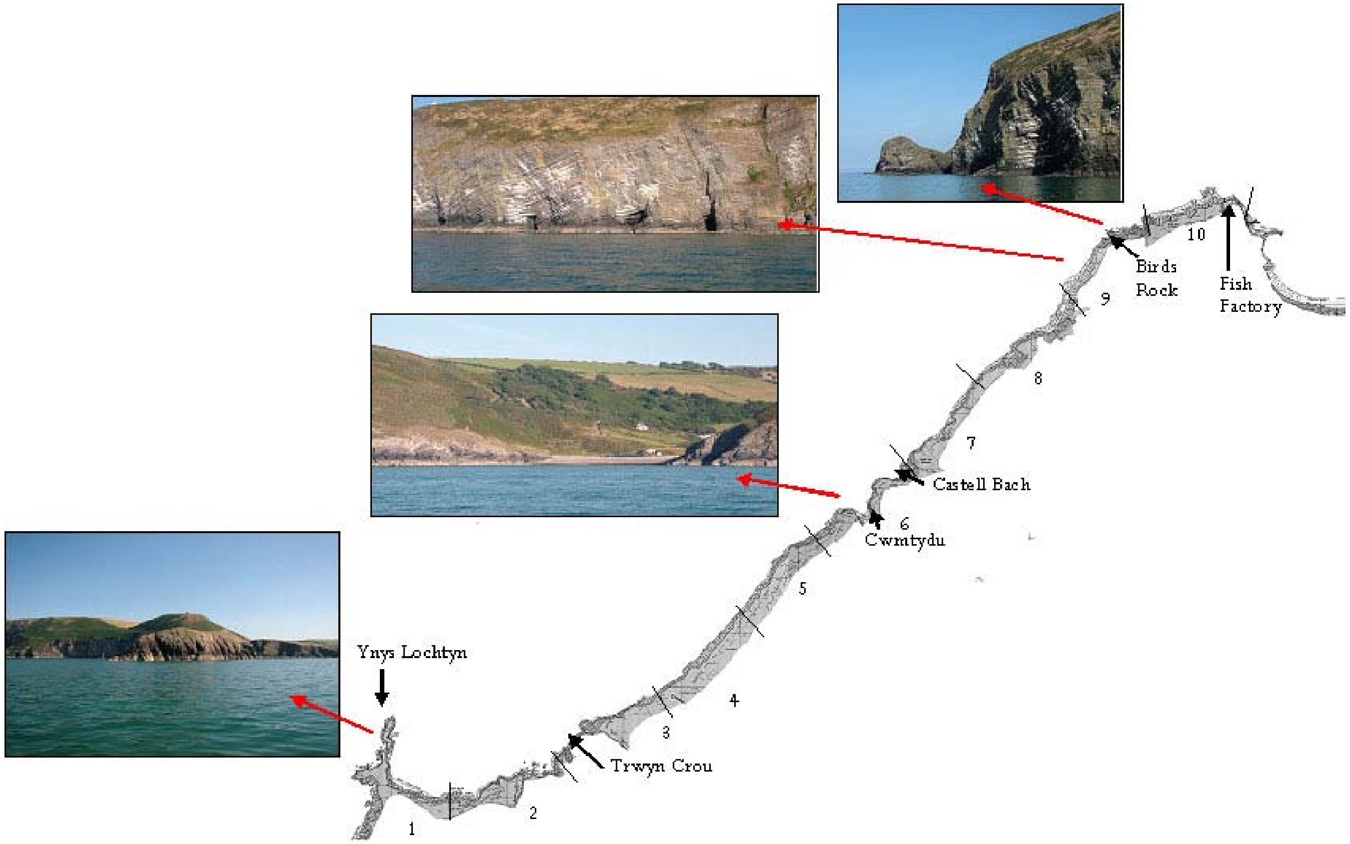
1.1.4 Water Masses & Circulation

The warm Gulf Stream, branching from the oceanic North Atlantic Current moves in a weak anti-cyclonic direction, up through the Celtic Sea, along St. George's Channel northwards through the Irish Sea towards the Arctic (Pugh & Thompson, 1986; Evans, 1995; OSPAR Commission, 2000; Brown *et al.*, 2003). *Further oceanography of area can be found in Bowden, 1950; Evans, 1995 and Horsburgh et al., 1998.*

Given its shallow bathymetry and exposure to strong prevailing south-westerly and westerly winds as a consequence of its predominantly open north-west facing coastline (Evans, 1995; Brazier *et al.*, 1999; Anon., unknown date), the majority of waves in the bay are locally generated (Anon., unknown date) giving rise to a well-mixed, turbid body of water particularly during winter due to increased winds. Contrastingly, water exchange between southern Irish and the Celtic Seas is significantly reduced during summer because of surface and bottom fronts which develop in St. George's Channel as a result of stratification (Evans, 1995; Horsburgh *et al.*, 1998; Brown *et al.*, 2003). During calm summer periods, a front approximately 5-10km wide can occur, separating the stratified from the well-mixed regions of the Irish Sea (Evans, 1995). Hence wind plays an influential role in the oceanographic dynamics of the area (Pugh & Thomson, 1986; Pingree & Le Cann, 1989; Evans, 1995; Horsburgh *et al.*, 1998). Moreover, the coastal circulation of Cardigan Bay, like any coastal region, is highly influenced by shoreline geometry and offshore topography (Knauss, 1997).

Figure 2 illustrates the specific study area along the Ceredigion Marine Heritage Coastline and highlights important zones, described:

Figure 2: Map of study area. One-/two-hour visitor passenger boat trips travelled between New Quay and Cwmtydu/Ynys Lochtyn via which grey seal sightings data was collected. Map courtesy of Sea Watch Foundation; *images copyright Kate Lewis, 2005*.



1.2 Bird's Rock

Named after its magnificent array of coastal birds, Bird's Rock (Craig Yr Adar) is also a significant site for grey seals (*Halichoerus grypus*) and bottlenose dolphins (*Tursiops truncates*). Both species frequent the area, foraging within 30m of the rocks. Therefore, Bird's Rock is a designated Site of Special Scientific Interest (S.S.S.I.). It is one of the most distinctive landmarks of the coastline, comprising a focal outcrop giving rise to two alcoves either side in which grey seals haul-out on several rocky ledges situated either side of the outcrop, owing to their gentle gradient into the sea (*Figure 6*). Most of the coastline including Bird's Rock (excluding Cwmtydu, Llangrannog and Tresaith), is inaccessible by land. A coastal path exists between New Quay and Cwmtydu, on which a point is reached overlooking the outcrop and its immediate vicinity, thereby lending itself as the vantage point for direct observational aspect of this study. Numerous sea caves penetrate the cliffs, particularly between Cwmtydu and Cardigan Island. Their importance to local ecology and utilisation by grey seals during pupping/moulting seasons (Brazier *et al.*, 1999), these caves are a feature of the SAC.

1.3 Cwmtydu

Located approximately 4miles southwest of New Quay, Cwmtydu is a secluded bay breaking the rugged coastline (Ceredigion County Council, 2005). The predominantly shingle beach has been used for countless years by female grey seals as a pupping site; low tides expose an area of sand. Volunteer-based *Cwmtydu Bay Wildlife Organisation* has been monitoring seals visiting Cwmtydu annually since 2001, via which information and photographs have been collected of the individuals.

1.4 Ynys Lochtyn

Ynys Lochtyn, a peninsula projecting into Cardigan Bay, is one of the most wave-exposed locations along the Ceredigion coast; it is cut off from the mainland at high tide (Brazier *et al.*, 1999). It is the furthest point the two-hour visitor passenger boat trips reach.

2.0 Local Conservation & Management

2.1 Ceredigion Marine Heritage Coast (CMHC)

Four sections, together extending 21miles of the 50mile-long Ceredigion coastline were designated 'Heritage Coast' in December 1982 (Williams & Morgan, 1995; Ceredigion Council Council, 2005). Continued local concern for the area, led to establishment of Ceredigion Marine Heritage Coast in 1992 by Ceredigion County Council, the first of its kind in Great Britain (Ceredigion County Council, 2005). 1995 saw the introduction of a voluntary speedboat zone, which led to implementation of a voluntary Ceredigion Marine Conservation code of conduct (*Appendix 1*), firmly established by commercial passenger boat operators in 1997 (Anon., unknown date).

2.2 Special Area of Conservation (SAC)

Primarily for its bottlenose dolphin population, southern Cardigan Bay was one of two sites proposed by UK Government to the European Commission (EC) as a candidate Special Area of Conservation (cSAC) in 1996, identified under the European Habitats and Species Directive[1]; Moray Firth (Scotland) being the second site (Anon., unknown date). Between 1996 and 2001, grey seals and ecologically important sea caves were added as features of cSAC (Anon., unknown date), emphasising diversity of marine species and habitat. By December 2004 EC designated the area as SAC; it is situated between north Pembrokeshire and south Ceredigion, with the landward boundary running along the coast at the mean high water mark, from Aberarth to south of Teifi Estuary and extends approximately 12 miles offshore (Anon., unknown date).

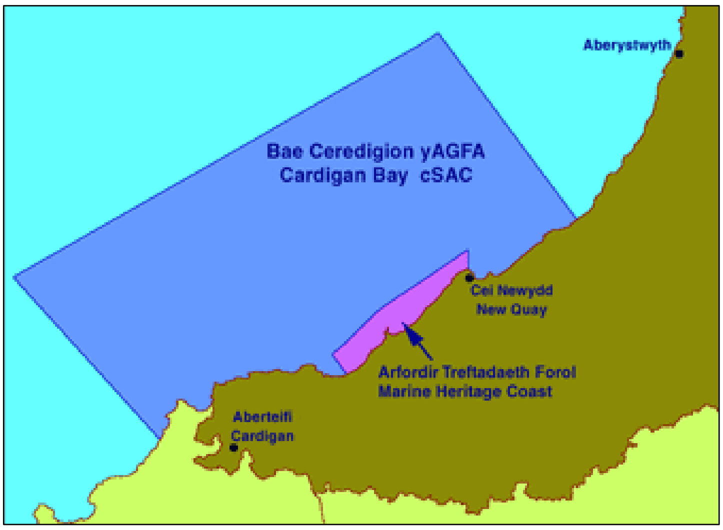


Figure 3: Map illustrating the Ceredigion Marine Heritage Coast (CMHC) within the Cardigan Bay Special Area of Conservation (SAC), the latter extends from Aberarth to just south of the Teifi Estuary covering an area 12 miles offshore. *Image courtesy of website http://www.cardiganbaysac.org.uk.*

[1] Council Directive 92/43/EEC. The conservation of natural habitats and of wild flora and fauna.

3.0 Protection of Grey Seals

As a consequence of over-exploitation grey seals were once highly endangered worldwide. Although no longer considered endangered, UK seal populations remain protected since almost 40% of world population inhabits the UK (Moore, 2003). Seals were initially granted government protection in 1914 in Scotland with the Grey Seals Act (Summers, 1978; Anon., 1984; Kiely *et al.*, 2000). The updated Act in 1932 extended the closed season in Scotland and England to 1st September until 31st December, coinciding with breeding season of most UK seal populations, enabling annual Suspension of Close Season Orders to be made separately in Scotland & England (Summers, 1978; Anon., 1984). 1970 saw the development of the Conservation of Seals Act for England, Wales and Northern Ireland denoting it an offence 'to kill or take seals at specific periods of the year or by prohibited means' (Anon., 1984; Kiely *et al.*, 2000). Despite this law, it remains legal to shoot a seal under license if it is observed taking fish from fixed engine salmon nets (Kiely *et al.*, 2000). Seals along CMHC are subject to the Ceredigion Marine Conservation Code of Conduct (A*ppendix 1*) hence it is an offense to cause 'reckless or intentional disturbance' under the Wildlife and Countryside Act 1981 and Countryside and Rights of Way Act 2000. Furthermore, the species is a conservation priority under UK Biodiversity Action Plan, listed under Annex II and V of the EC Habitats Directive and under Appendix III of the Bern Convention (Anon., unknown date; Moore, 2003; Parsons, 2003; Westcott & Stringell, 2003). Despite such regulations, culls are sought after in areas of the UK where it is claimed seals compete with commercial fisheries for prey (Parsons, 2003).

4.0 Grey Seal Distribution, Population Status & Life History

4.1 Worldwide

Endemic to North Atlantic (Smith, 1966; Bonner, 1972, 1989; Coulson, 1991; Murie & Lavigne, 1992; Baker *et al.*, 1995; Martin & Reeves, 2002; Moore, 2003), grey seals (*Halichoerus grypus*, Fabricius, 1791) are the largest carnivores of the British Isles (Moore, 2003). Three principal populations exist in the northern hemisphere, namely northeast Atlantic, northwest Atlantic and Baltic Sea populations, separated geographically (Smith, 1966; Bonner, 1972; Summers, 1978; Boness & James, 1979; Haug *et al.*, 1994; Moore, 2003); recent genetic developments reveal they are genetically distinct (Boskovic *et al.*, 1996; Hammill *et al.*, 1998; Hall, 2002; Reeves *et al.*, 2002). Northwest Atlantic population comprises Gulf of St. Lawrence breeding group and the largest single colony on Sable Island, Canada (Bowen *et al.*, 1993; Hammill *et al.*, 1998; Hall, 2002; Beck *et al.*, 2003; Bowen *et al.*, 2003); a well-studied population which is estimated at 85,000 individuals, increasing approx. 12% per annum (Hammill *et al.*, 1998; Hall, 2002). With such numbers, it is difficult to comprehend northwest Atlantic population had declined to merely 5,000 individuals in 1960's (Hammill *et al.*, 1995). Northeast Atlantic populations inhabit coasts of Iceland, Faeroe Islands, Norway, UK and Baltic Sea (Lockley, 1966; Smith, 1966; Bonner, 1972; Anon., 1984; Hall, 2002). The latter population declined from approx. 100,000 individuals in early 20th century to 1,500 individuals by 1980 (Sjöberg et al, 1995); the population is in resurgence, estimated at 5,000 animals (Sjöberg et al, 1995; Hall, 2002). Such catastrophic declines resulted from over-exploitation for blubber, meat and pelt; inevitably worldwide population diminished to approx. 50,000 individuals, of which almost 75% inhabited UK (Lockley, 1966; 65% Bonner, 1972).

4.2 United Kingdom

Approximately 120,000 grey seals inhabit UK waters (*Figure 1*), 90% of which are in Scotland (Parsons, 2003). Colonies inhabit the Farne Islands; smaller breeding groups exist off the Cornwall coast, Scilly Isles, Ireland and along western and south-western coast of Wales (Bonner, 1972; Anon., 1984). Census data suggests an average 6% annual increase in Great Britain (Pomeroy *et al.*, 2000). Grey seals have been studied in southwest Wales since the late 1940's/early 1950's, with most pupping beaches occurring in Pembrokeshire, e.g. Ramsey and Skomer Islands. From the Teifi Estuary northwards, grey seals numbers are much reduced (Anon., unknown date; Baines *et al.*, 1995). In early 1990's, detailed investigations of west Wales coast utilized by the species were undertaken (Baines *et al.*, 1995) and estimated the all-age population along the western coast to be approximately 5000 individuals. Pup censuses to estimate annual pup production have been undertaken across Wales (Baines *et al.*, 1995; Westcott, 2002). Pupping sites in west Wales are mainly situated under cliffs, among boulders or in caves (Baines *et al.*, 1995), e.g. Bird's Rock and Cwmtydu.

4.3 Morphology

Grey seals are within Order Pinnipedia, Latin for "wing-footed" referring to their webbed feet; they have a streamlined, spindle-shaped body (Bonner, 1989) essential for fast, agile swimming. A thick subcutaneous blubber layer covers the underlying frame providing protection of internal organs, insulation and hydrodynamic locomotion (Bonner, 1989; Boily & Lavigne, 1996). Although well-adapted for aquatic locomotion, seals' mobility is hindered on land resulting from an inability to rotate hind-limbs forward beneath their bodies

(Bonner, 1989; Hammill, 2002; Martin & Reeves, 2002; Reeves *et al.*, 2002) as otariids and odobenids do. Being phocids, grey seals lack external pinnae (Lockley, 1966; Bonner, 1972, 1989; Hammill, 2002; Martin & Reeves, 2002; Reeves *et al.*, 2002; Beck *et al.*, 2003); additional physical characteristics include inguinal testes in males whereas females possess two teats which are retracted at rest (Bonner, 1989). Exhibiting sexual dimorphism, males grow larger than females (Boness & James, 1979; Anderson & Fedak, 1987; Murie & Lavigne, 1992; Amos *et al.*, 1995, 2001; Bowen *et al.*, 2002a; Hall, 2002; Martin & Reeves, 2002; Beck *et al.*, 2003; Bowen *et al.*, 2003). Adult males of northeastern Atlantic population weigh approx. 170-350kg (Anon., 1984; Boness *et al.*, 2002; Hall, 2002; Reeves *et al.*, 2002) whereas adult females reach between 100-207kg in weight (Anon., 1984; Boness *et al.*, 2002; Boyd, 2002; Hall, 2002; Reeves *et al.*, 2002). Adult males reach between 2.1-2.6m in length whereas females reach 1.84 -2.01m (Anon., 1984; Boness *et al.*, 2002; Reeves *et al.*, 2002; Beck *et al.*, 2003). The sexes also differ in colouration and markings (Hickling, 1962; Martin & Reeves, 2002) which is useful for identification of the sexes in the field since genital organs are generally concealed within the overall body contour (Bonner, 1989). Males generally exhibit a more uniformly dark brown/grey/black fur, sometimes with lighter coloured blotches (Hewer & Backhouse, 1959; Hickling, 1962; Anon., 1984; Hall, 2002; Reeves *et al.*, 2002). Illustrated in *Figure 4*, mature males are distinguished by their robust neck, often heavily wrinkled and scarred from conflict with conspecifics (Reeves *et al.*, 2002). In contrast, females are paler creamy white/pale grey with dark brown/black irregular mottling over the body (Hewer & Backhouse, 1959; Hickling, 1962; Anon., 1984; Martin & Reeves, 2002; Reeves *et al.*, 2002), the dorsal half darker than the ventral underside. Immature individuals appear light brown in colour, making it difficult to determine age/sex (Hickling, 1962) from a distance. Furthermore, sub-adult males are easily confused for adult females in the field since they can have similar cream coloured patches, particularly on the neck and side of head (Hewer & Backhouse, 1959; Hickling, 1962; Hall, 2002). Sex can also be determined by the profile view since adult males have a longer face, with a broad, convex "Roman" nose and nostrils wide apart (Lockley, 1966; Hewer & Backhouse, 1959; Westcott & Stringell, unpubl.) in contrast to the straighter nose of the female.

Figure 4: a) Mature bull grey seal (ID: 015) hauled out near Mwnt, Cardigan Bay. Image courtesy of Hanna Nuuttila (2005) b) Adult female grey seal (ID: 007) following birth at Cwmtydu (Mother of pup 1), 2003; Image courtesy of John Newell, Cwmtydu Bay Wildlife Org.

4.4 Diet

Grey seals are opportunistic foragers (Thompson *et al.*, 1991; Murie & Lavigne, 1992); foraging trips away from main haul-out site last between 1-5 days (Sjöberg *et al.*, 1995; McConnell *et al.*, 1999; Hall, 2002; Stevick *et al.*, 2002). Although considered generalists, feeding on a multitude of benthic and demersal fish/invertebrate species (Benoit & Bowen, 1990; Thompson *et al.*, 1991a; Murie & Lavigne, 1992; Hammond *et al.*, 1994a,b; Hauksson & Ólafsdóttir, 1995; Tollit & Thompson, 1996; Berta & Sumich, 1999; Browne *et al.*, 2002; Hoelzel, 2002; Walton & Pomeroy, 2003), with seasonal and geographic variation of diets (Bowen *et al.*, 1993; Tollit & Thompson, 1996; McConnell *et al.*, 1999), they tend to primarily consume less than five species in any one season or geographic location (Murie & Lavigne, 1992; Bowen *et al.*, 1993; Bowen & Harrison, 1994). Grey seal diet has been documented by numerous authors using stomach/faecal analyses (Pierce *et al.*, 1991; Murie & Lavigne, 1992; Bowen *et al.*, 1993; Bowen & Harrison, 1994; Hammond *et al.*, 1994ab; Mikkelson *et al.*, 2002), in addition to molecular genetic analyses (Walton & Pomeroy, 2003). Otolith/cephalod beak analyses of scat revealed a diet composed of sandlance, gadoids, flatfish and cephalopods (Hammond *et al.*, 1994a,b; Thompson *et al.*, 1996; McConnell *et al.*, 1999). Diet of grey seals inhabiting the CMHC is currently unknown.

4.5. Life History

4.5.1. Annual & Temporary Haul-Out

Their amphibious existence means it is obligatory grey seals return to land annually specifically to moult, give birth and breed, in addition to their temporary periods of rest when they haul-out between periods at sea (Pomeroy *et al.*, 2000; Boness *et al.*, 2002; Martin & Reeves, 2002). The annual moult commences in spring in British Isles (Beck *et al.*, 2003), during which seals tend to haul-out more to reduce risk of extreme heat loss since new hair growth requires increased blood supplies to the skin (Martin & Reeves, 2002). For seals whose moulting sites are near to foraging areas, movements may not appear different from usual haul-out behaviour during the remaining year (Stevick *et al.*, 2002). Exact causes of annual moult are not fully known but endocrines, thermal and nutritional requirements have been suggested (Yochem & Stewart, 2002). There are several reasons regarding haul-out behaviour outside moulting and breeding seasons, such as thermoregulation, predator avoidance, rest and sociality *(refer to discussion for detail).*

4.5.2 Breeding

Their longevity (max. lifespan: males 25years, females ~40years, Bonner, 1972; Boness *et al.*, 2002; Reeves *et al.*, 2002) means the species exhibits delayed sexual maturation (Boyd, 2002; Hammill, 2002; Hall, 2002). Females reach sexual maturity approx. 3-5years of age whereas males mature at approx. 6years, although not socially mature until 8 years (Lockley, 1966; Anderson & Fedak, 1987; Boness *et al.*, 2002; Hall, 2002). Females produce a single pup (Reilly, *et al.*, 1996; Boyd, 2000; Lydersen & Kovacs, 2000; Amos *et al.*, 2001; Boness *et al.*, 2002; Bowen *et al.*, 2003; Hall, 2002). Parturition can occur on a diversity of habitats e.g. isolated beaches, islands or ice (Anderson & Harwood, 1985; Baker *et al.*, 1995). In UK pupping typically commences in autumn, beginning in southwest England/Ireland in September but typically occurs later (October–November) the more north the population is situated (Coulson, 1981; Hall, 2002). Pupping commences even later Canadian and Baltic populations (Coulson, 1981; Hall, 2002). Overall, sex ratios are 1:1 (Lockley, 1966); although Andersen & Fedak (1987) reported early on in the breeding season the sex ratio is skewed in favour of male pups. If a female expends more on her offspring one year she is likely to have reduced fitness in the following year (Pomeroy *et al.*, 1999; Boyd, 2002). Neonates are precocious, born with eyes open and able to move short distances to its mother to begin suckling (Bowen *et al.*, 2002a). Akin to other phocids, grey seal pups have a white-coloured lanugo *in utero* (*Figure 5*) which is shed at weaning several weeks after birth (Hickling, 1962; Lockley, 1966; Lydersen & Kovacs, 2000; Hall, 2002; Hammill, 2002; Yochem & Stewart, 2002).

Figure 5: Second pup born in a cave at Cwmtydu. Image taken on 26th August 2005; the white lanugo has not yet been shed. Image copyright of Kate Lewis, 2005.

The lanugo is not waterproof thus it is essential parturition occurs in an area above the mean high water mark; lanugo provides insulation until pup has gained thicker blubber (Würsig, 2002; Yochem & Stewart, 2002) during lactation. Pups weigh 11-20kg at birth but rapidly increase to 40kg once weaned (Hall, 2002; 50–55 kg, Lydersen & Kovacs, 2000). Because lactation is short, lasting 14 -18 days (Bonner, 1972), the mother provides fat-rich milk containing 50-65% lipids by mid-lactation enabling mother to mobilise blubber stores (Anderson & Fedak, 1987; Lydersen *et al.*, 1994; Boness & Bowen 1996; Boness *et al.*, 2002; Bowen *et al.*, 2002a; Hall, 2002; Hammill, 2002). Although some mothers undertake a "fasting strategy" during lactation (Bonner, 1972; Twiss *et al.*, 1994; Thompson *et al.*, 1996; Reilly *et al.*, 1996; Schweigert *et al.*, 2002), other females return to sea (Boyd *et al.*, 1962) undertaking a "facultative feeding strategy"; it is believed these females are unable to accumulate sufficient energy stores to satisfy their own requirements and those of the pup, therefore pup is hidden in a cave or taken foraging with mother (Hammill, 2002). Pups vocalise minutes after birth (Bowen *et al.*, 2002a) and research suggests each pup bleat has ample acoustic variation required for use in individual vocal recognition (Fogden, 1971; Bonner, 1972; Caudron *et al.,* 1998), enabling a returning mother to find her pup amongst a dense colony. However, direct observations illustrated grey seals do not call in mother-pup reunion sequences (Caudron *et al.*, 1998). On returning to beach to feed pup, mother initially nuzzles and smells the pup to aide recognition at close range (Lockley, 1966; Fogden, 1971; Caudron *et al.*, 1998; *pers. obs.*); combined with auditory and olfactory cues, visual recognition also occurs (McCulloch *et al.*, 1999). On weaning, lanugo is shed and pup undertakes a post-weaning fast for 10-28days on land (Reilly *et al.,* 1996; Hall, 2002), possibly attributed to development of diving ability (Hall, 2002). Literature denotes females exclusively provide parental care (Boness & Bowen, 1996; Boness *et al.*, 2002; Bowen *et al.*, 2002a), nonetheless personal observations by *Cwmtydu Bay Wildlife Organisation* suggests males do participate to a degree. Upon weaning, maternal care fades rapidly (Fogden, 1971; Amos *et al.*, 2001; Stevick *et al.*, 2002); pups reportedly travel hundreds of kilometres in their first months at sea, presumably exploring/learning how to survive (Hickling, 1962; Stevick *et al.*, 2002), however they generally return to their natal site (Baker *et al.*, 1995; Miller, 2002).

Grey seals exhibit polygynous mating systems; females becoming receptive post-weaning. Following breeding, seals return to sea but typically return to the same breeding site the following year, i.e. display site fidelity. Further information on parturition/breeding cycle refer to Hewer, 1957; Boyd *et al.*, 1959; Boyd *et al.*, 1962; Hewer, 1964; Boyd & Laws, 1962; Hewer & Backhouse, 1968; Boyd & Campbell, 1971; Fogden, 1971; Bonner, 1972; Boness & James, 1979; Coulson, 1981; Anderson & Harwood, 1985; Boyd, 1985; Anderson & Fedak, 1987; Wiig, 1987; Bowen *et al.*, 1992; Pomeroy *et al.*, 1994; Twiss *et al.*, 1994; Amos *et al.*, 1995; Baker *et al.*, 1995; Reilly *et al.*, 1996; Hammill *et al.*, 1998; Ambs *et al.*, 1999; Pomeroy *et al.*, 2000a,b; Amos *et al.*, 2001; Boness *et al.*, 2002; Bowen *et al.*, 2002a; Hall, 2002.

5.0 Introduction to Photo-identification

A form of capture-recapture, photo-identification is ideal for species difficult to capture or disturbance of study population is a concern (Stevick *et al.*, 2001), and was developed to exploit individual natural markings (Stevick et al, 2002; Wells, 2002). It has been successfully used in numerous mammals (Slooten & Dawson, 1992; Samuels & Tyack, 2000; Whitehead *et al.*, 2000; Stevick et al, 2002; Hillman *et al.*, 2003) since it provides a non-invasive technique of acquiring information on population dynamics compared to historic invasive methods (Slooten & Dawson, 1992; Bejder *et al.*, 1998; Samuels & Tyack, 2000). Pinniped capture-recapture studies have involved branding, temporary dye marking or gluing tags to the pelage which is shed during the following moult (Baker *et al.* 1995; McConkey *et al.*, 1999; Hastings *et al.*, 2001; Stevick *et al.*, 2002) therefore require physical capture/handling of individuals (Wells & Scott, 1990; McConkey, 1999; Stevick *et al.*, 2002) causing stress. High rates of tag loss, illegibility of tag numbers and non-reporting of recoveries compromises their utility subsequently reduces likelihood of recapture at a later date (Gunnlaugsson & Sigurjónsson, 1990; Øien & Øritsland, 1995; McConkey, 1999; Hastings *et al.*, 2001). Mammalian coat patterns are genetically determined (Yochem *et al.*, 1990); preliminary short-term studies of captive seals indicate pelage patterns are stable through juvenile and adult stages (Yochem *et al.*, 1990; Hastings *et al.*, 2001), hence variations in natural markings an ideal tool. Successful species-specific photo-identification methods have been devised for numerous pinnipeds (*grey seals*, Hiby & Lovell, 1999, Westcott, 2002; *New Zealand sea lion,* McConkey, 1999; *Mediterranean monk seals*; Forcada & Aguilar, 2000; *harbour seals*, Yochem *et al.*, 1990, Crowley *et al.*, 2001, Hastings *et al.*, 2001).

Photo-identification methodology incorporates several assumptions, i.e. no animals lose their marks during the study, all marked animals are reported when sighted and the population is closed (Stevick *et al.*, 2001). Biases may be introduced into population and/or social structure analyses using photo-identification data by inclusion/exclusion of poor/high quality photographs of well-/subtly-marked individuals, respectively (Whitehead *et al.*, 2000). A 'false positive' error may occur by incorrectly identifying two individuals as the same individual, leading to underestimations in population estimates, particularly in large samples (Stevick *et al.*, 2001). A 'false negative' error results from misidentifying the same individual as to different individuals, i.e. erroneously assign multiple permanent animal numbers to a single seal, leading to overestimations of populations (Hastings *et al.*, 2001; Stevick *et al.*, 2001; Garrigue *et al.*, 2004). Prevention of false positives inevitably increases the number of false negatives (Stevick *et al.*, 2001). Errors and mismatches made are inversely proportional with time taken to match images. Also, a more experienced 'matcher' is less likely to make mismatches (Wells, 2002). The more individuals identified the more labour-intensive and probability of errors increases (Stevick *et al.*, 2001). Therefore, computer technology has been developed for comparison of pinniped images, similar to that constructed for cetaceans (e.g. Hiby & Lovell, 1990; Kiely *et al.*, 2000; Hastings *et al.*, 2001; Stevick *et al.*, 2001; Hillman *et al.*, 2003; Gope *et al.*, 2005). The three-dimensional computer model developed by Hiby & Lovell (1990) has been used to recognise, match and catalogue over 6,000 individual greys seals to date (Hastings *et al.*, 2001). Further information regarding assumptions/errors with photo-identification method refer to: Slooten & Dawson, 1992; Mills *et al.*, 1997; Stevick *et al.*, 2001; Stevick *et al.*, 2002; Abt *et al.*, 2002; Perrin, 2002; Wells, 2002; Westcott, 2002 Patenaude, 2003; Garrigue *et al.*, 2004).

6.0 Aims and Objectives

Given limited information regarding grey seals along the Ceredigion Marine Heritage Coast within the SAC, the principal aim was to gather necessary data, via two platforms (visitor passenger boats and direct observation at Bird's Rock/Cwmtydu), to investigate habitat use, haul-out behaviour, extent of site fidelity and potential human-induced disturbance. Five objectives of this study were as follows:

1. Identify which areas of the Ceredigion Marine Heritage Coast/SAC are important for grey seals;

2. Describe haul-out behaviour and identify the factors which determine grey seals to haul-out at Bird's Rock;

3. Identify whether grey seals have a preference to haul-out on particular rocks at Bird's Rock;

4. Investigate how grey seals behave towards vessel traffic passing Bird's Rock;

5. Using photo-identification, investigate whether grey seals display a degree of site fidelity to Bird's Rock and Cwmtydu.

7.0 Methodology

7.1. One-/Two-Hour Visitor Passenger Boat (VPB) Trips

Daily VPB trips were the platform from which sightings data was collected between 1st May and 7th October 2005. *Sea Watch Foundation* forms were completed by author and volunteers (*Appendix 2*). Time, longitude and latitude of the vessel on initial sighting of seal(s) were obtained using *Garmin* hand-held GPS. Seal(s)-vessel distance (m) was estimated by eye; angle of seal(s) to vessel was estimated using an angle board whereby 0° was equivalent to the bow of vessel. Data recorded included seal count; sex/age-group of individual(s); behaviour exhibited (hauled-out/water); effort data was also collected every 30-minutes. Several limitations of utilising VPBs from which to collect data, for instance VPB surveys were dependent on weather conditions; number of trips per day depended upon customer demand and time of low tide, in terms of feasibility of collecting passengers from pier. Acquired data was entered into *Microsoft Excel* database held by *Sea Watch Foundation*. Tide times were obtained from 'Tablau Llan Ceredigion Tide Tables 2005'; estimated tide times for New Quay were 7-minutes prior to those predicted for Aberystwyth. Data acquired during 10th April-10th September 2004 was also analysed.

7.2 Direct Observation at Bird's Rock

Data were collected via direct observation surveys at Bird's Rock (52°12'.900N, 004°22'.573W), providing an excellent vantage point overlooking haul-out area (*Figure 2/6*); all seals could be observed when hauled-out. Three-hour surveys were undertaken between 06:00-21:00 hours, thereby acquiring behavioural information in absence/presence of vessel activity. Initially one survey/day was carried out on rolling basis (first survey period chosen at random); however effort soon increased to achieve multiple surveys/day for a sufficient dataset. Surveys were not undertaken during extreme weather conditions owing to risk of injury when walking along the precarious coastal path. Appropriate wind-/water-proof clothing/footwear were worn at all times. A *Garmin* handheld GPS was used to obtain position and altitude of Bird's Rock. *Nikon Sporter I* (10x36) binoculars were used to observe behaviour and aide sex determination.

Figure 6: Direct observation study area at Bird's Rock. Major rocks on which grey seals were observed hauled-out were labelled from A to K, as illustrated (K is not shown; refer to Appendix 3 for map to see its location). Images copyright Kate Lewis, 2005.

7.2.1 Environmental & Behavioural Observations

Abiotic variables, measured at 15-minute intervals, were as follows: weather conditions; wind direction; sea state (Beaufort scale); wind speed (mph) and ambient air temperature (˚C). Two latter variables were measured using '*Skywatch Xplorer 2*' handheld device *(JD Instruments)*. To account for wind-chill factor, ambient air temperature and wind speed were used to calculate adjusted temperature (˚C) using the equation:

$$[1] \qquad T_c = 32.6 - [(0.126\sqrt{W} + 0.25 - 0.0067W)(59.4 - 1.87\,T_o)]$$

Where, T_c = adjusted temperature (˚C), T_o = observed temperature (˚C), W = wind velocity (kmh^{-1}) (Boulva & McLaren, 1979; Grellier *et al.*, 1996).

Tide times were obtained from 'Tablau Llan Ceredigion Tide Tables 2005'; tidal heights were ±1.0m depending on wind/swell conditions. Biotic variables comprised number and sex of individual(s) hauled-out or in adjacent water. Sex of individuals was determined by profile of head and nose (following Hewer & Backhouse, 1959; Westcott, 2002), in addition to overall body size, contrast in pelage and presence of scars. A labelled map of principal rocks (*Appendix 3*) recorded specific rock preferences by seals within overall site. Additional notes were recorded by hand or dictaphone (*Olympus VN-120*) and transcribed that day. A tally of walkers/vessel types were logged throughout each three-hour survey to gain insight of activity within area. Author took photographs (*Fuji Finepix S7000)* to record individual seals and rocks on which they hauled.

7.2.2. Grey Seal-Vessel Interactions

Time was noted representing the start of a potential seal-vessel interaction, when seal(s) within area and approaching vessel observed at headland either side of Bird's Rock (ca. 300m distant). Seals at Bird's Rock were counted before and after interaction; notes were made regarding behaviour of seal(s) before, during, at closest seal-vessel distance, and after vessel had passed through the area. Vessel type and its approach (i.e. abiding the conduct of conduct) were recorded. Each seal-vessel interaction was assigned an interaction number (e.g. BR007) to aide cross-referencing. Interaction data was easier to record with two observers present but this was not always feasible.

Refer to *Appendix 3* for forms 1-3 and key to codes utilised. Data were entered into a *Microsoft Excel* database every surveyed day and checked by author to minimise input errors. From the onset inherent limitations of this survey existed:

1. Complete diurnal haul-out behaviour was not surveyed given restriction to daylight hours;

2. Haul-out behaviour during extreme weather conditions was not investigated;

3. Number of seals counted in water at any given time is always an underestimate; times of turbid water, high tide (increased water depth) and/or low light intensity reduced ease of counting seals in water, unlike days of clear water and adequate light intensity.

4. Ambient air temperature at cliff-top is presumed to be markedly different to that at sea/rock level where seals haul-out particularly on hot, sunny days at times when the sun is situated in the south, behind the observer on the cliff since the cliff casts a shadow over rocks utilised by seals. Consequently air temperature is expected to be cooler near the rocks than on the cliff. Air temperatures at cliff- and sea-level (aboard Ermol VI) were obtained simultaneously on 14 trips over three days, using two '*Skywatch Xplorer 2*' devices to investigate approximate temperature discrepancies.

5. In absence of suitable equipment, distance (m) was estimated by eye. A yellow marker buoy calculated to be ca. 300m (using GPS) from the cliff and knowledge that VPBs were approximately 10m in length were used as a guide. Distances were potentially underestimated.

6. Sex determination was not always possible since it depended on an adequate profile view of the seal's head. Seals often appeared at water's surface for a few seconds before diving immediately, providing insufficient time to accurately determine sex.

All data were statistically analysed with SPSS (*Version 11.5.0*, 2002). Univariate tests used: Pearson's/Spearman's Rank correlation; one-/two-way ANOVA, Kruskal-Wallis, Mann-Whitney U, Chi-square and regression analysis. All tests significant at P = 0.05. Multivariate tests: Principal components analysis and multiple stepwise regression (significance levels for entry/removal: P =0.05/P =0.10) were undertaken to identify main factors influencing haul-out behaviour (*Table 1*). Log-linear analysis used to identify significant associations of seal-vessel interaction variables (*Table 2*).

Table 1: Variables and coded variables utilised in principal components analysis and multiple stepwise regression.

Number	Variable	Coding
1	Date of observation	Converted into observation number, first day = 1
2	Time of day	15-minute intervals
3	Human-induced disturbance	0 = Absence; 1 = Presence
4	Ambient air temperature	Continuous variable (°C)
5	Adjusted air temperature	Continuous variable (°C) following Boulva & McLaren (1979)
6	Weather conditions	Ordinal variable: 1 = sunny; 2 = fair; 3 = overcast; 4 = rain; 5 = mist; sun & showers were not experienced during study. Also coded into dichotomous 'dummy' variables when necessary, all but one dummy variable entered into regression analysis to minimise multicollinearity.
7	Wind speed	Continuous variable (mph)
8	Sea state	Ordinal variable: 0 - 5 Beaufort Scale
9	Time of each count from low tide	Continuous variable; calculated from the local tidal almanac.
10	Time of each count from sunrise	Continuous variable; calculated from the local tidal almanac.
11	Tidal amplitude	Continuous variable (m); calculated from the local tidal almanac.
12	Wind direction (N, S, E, W, etc.)	Not used in regression due to limited sample; often direction was difficult to identify

Table 2: Variables and coded variables used in log-linear analysis of grey seal-vessel interactions.

Number	Variable	Coding
1	Seal Response	0 = no change/increase in count; 1 = reduced count after interaction
2	Day	0 = weekday; 1 = weekend/bank holiday
3	Interaction Duration	1 = 0 - 10 mins; 2 = 11 - 20 mins; 3 = 21 - 30 mins; 4 = 31 - 40 mins
4	Closest seal-vessel interaction	1 = 0 - 100 m; 2 = 101 - 200 m; 3 = 201 - 300 m
5	Vessel type	1 = Canoe (C); 2 = Commercial fishing boat (CF); 3 = Motorboats (MB); 4 = Research vessels (R); 5 = Sail boats (SAIL); 6 = Ribs/Speedboats (SB/SS); 7 = Visitor passenger boats (VPB)
6	Vessel conduct	1 = Y1; 2 = Y2; 3 = N1; 4 = N2

7.3. Opportunistic Photo-Identification

To determine whether seals exhibit a degree of site fidelity to areas within CMHC/SAC, opportunistic photographs were taken during VPB trips and from Bird's Rock during direct observation surveys; with use of binoculars, certain individuals identified by dorsal-side pelage markings appeared to return to haul-out at Bird's Rock for several days. Historic photographs and information regarding females, pups and associated bulls observed at Cwmtydu during 2003-2005 breeding seasons were provided by *Cwmtydu Bay Wildlife Organisation*. All age-groups/sexes were photographed, but pups were excluded from analysis given presence of lanugo hiding any distinctive markings. Left, right and head-on profiles per encountered seal were ideally photographed since pelage pattern on head/neck of grey seals is distinct, especially in females (Hiby & Lovell, 1990; Westcott, 2002). Given less distinct natural neck markings of bulls, scars produced by conflict with conspecifics were used to identify individuals, although require caution in long-term studies. A *Minolta Dynax 404si* 35mm camera with 300mm fixed lens was used with 200 ASA colour slide film. Once processed and mounted, slides were digitised using *Nikon Super Coolscan 4000ED* and *Nikon Scan 4* (© 1998-2003, Nikon Inc. & Nikon Corporation) software was used to crop images where appropriate. A *Fuji Finepix S7000* digital camera with polarising lens was also used enabling efficient viewing since images were downloaded onto computer daily. Additional information, camera and photograph number were recorded on one-/two-hour forms alongside corresponding sighting to minimise error of matching sightings and images. Wet/dry wipes were on hand to clean cameras, in addition to spare batteries. Initially, digitised images were separated by date and time to aide in matching images with sightings data. Images were graded by quality (excellent/good/bad) in terms of focus and seal profile, following Hiby & Lovell (1990). Images of suitable quality were systematically matched, checked and given a specific filename (following Westcott & Stringell (unpubl.); *Appendix 4*).

8.0 Results

8.1 One-/Two-Hour Visitor Passenger Boat (VPB) Trips Sightings Data

A total of 290 hours and 313 hours effort were achieved from VPB trips operating between New Quay and Cwmtydu/Ynys Lochtyn during 2004 and 2005 seasons, respectively.

8.1.1. Habitat Use along the Ceredigion Marine Heritage Coast (CMHC)

Overall, 345 grey seal sightings were recorded in 2004 compared to 266* sightings in 2005, this was significantly different (χ^2 =10.21, *d.f.* =1, *P*<0.05). During 2004, all ten zones between New Quay and Ynys Lochtyn were utilised by seals, however sightings were not equally distributed across all zones (χ^2 =212.13, *d.f.* =9, *P*<0.05). As illustrated (*Figure 7a*), maximum proportion of seals were observed within zone five (24%, *n* =83; hauled: 13%; water: 11%), followed by zone 9 (21%, *n* =72; hauled: 15%; water: 6%). Minority of sightings occurred within zone eight (1%, *n* =4). Seals were not observed hauled-out in zones one and eight, whereas within remaining zones seals exhibited both behaviours. Two-way ANOVA performed on 2004 data, indicated although mean score of seals hauled (1.19 ±0.06S.E.) exceeded that in water (1.09 ±0.03S.E.), the difference was not significant ($F_{(1, 230)}$ =1.65, *P* =0.201). Similarly, no significant difference between mean scores of seals per zone was found ($F_{(9, 230)}$ =1.64, *P* =0.104). The 'Zone x Seal Behaviour' interaction was non-significant ($F_{(7, 230)}$ =1.71, *P* =0.107) despite a trend whereby mean score of seals in water was greater than hauled in zones one-three and seven whereas zones four-six and eight-ten score of seals hauled exceeded that in water.

Similar to 2004, sightings in 2005 were not equally distributed across all zones (χ^2 =1102.84, *d.f.* =8, *P*<0.05). Furthermore, sightings were not recorded within zone four. *Figure 7b* demonstrates most sightings were occurred within zone nine (75%, *n* =194; hauled: 51%; water: 24%), followed by zone six (12%, *n* =31; hauled: 3%; water: 9%). Excluding zone four, minority of sightings occurred within zone seven (0.4%, *n* =1, water). Significantly more seals were observed hauled-out than in water (χ^2 =4.14, *d.f.* =1, *P*<0.05). Two-way ANOVA indicated mean scores of hauled seals, 1.29 ±0.09S.E., were significantly higher than those in water, 1.03 ±0.07S.E., ($F_{(1, 159)}$ =4.93, *P*<0.05). In contrast, mean scores of seals per zone were non-significant ($F_{(8, 159)}$ =0.37, *P* =0.937). Although *figure 7b* illustrates zones two, six, eight & nine had higher proportions of seals hauled than in water, zone five had

* 266 total grey seal sightings; 9 sightings excluded from analysis due to ambiguity of zone/behaviour.

equal proportions of seals displaying both behaviours and hauled seals were not observed in the remaining zones, on comparing means no significant interaction exists between seal behaviour and zone ($F_{(4, 159)}$ =0.31, P =0.873).

Considering both years, hauled seals were not observed within zone one whereas both behaviours were exhibited within the remaining zones. Two-way ANOVA indicated no significant difference between mean scores of seals observed per year ($F_{(1, 402)}$ =0.90, P =0.343) since mean scores were similar (1.12 ±0.03S.E., *2004*; 1.07 ±0.06S.E., *2005*). Contrastingly, mean scores of seals per zone differed significantly ($F_{(9, 402)}$ =2.92, P<0.05); a posteriori Tukey-HSD tests performed suggested mean seals counted in zones four and six were significantly lower from zone nine (P<0.05). No other pairwise differences were statistically significant. Although mean scores of seals observed in zone one, two and eight in 2004 was lower than that 2005 and the opposite occurred in the remaining zones, no significant interaction existed between zone and year ($F_{(8, 402)}$ =0.57, P =0.802).

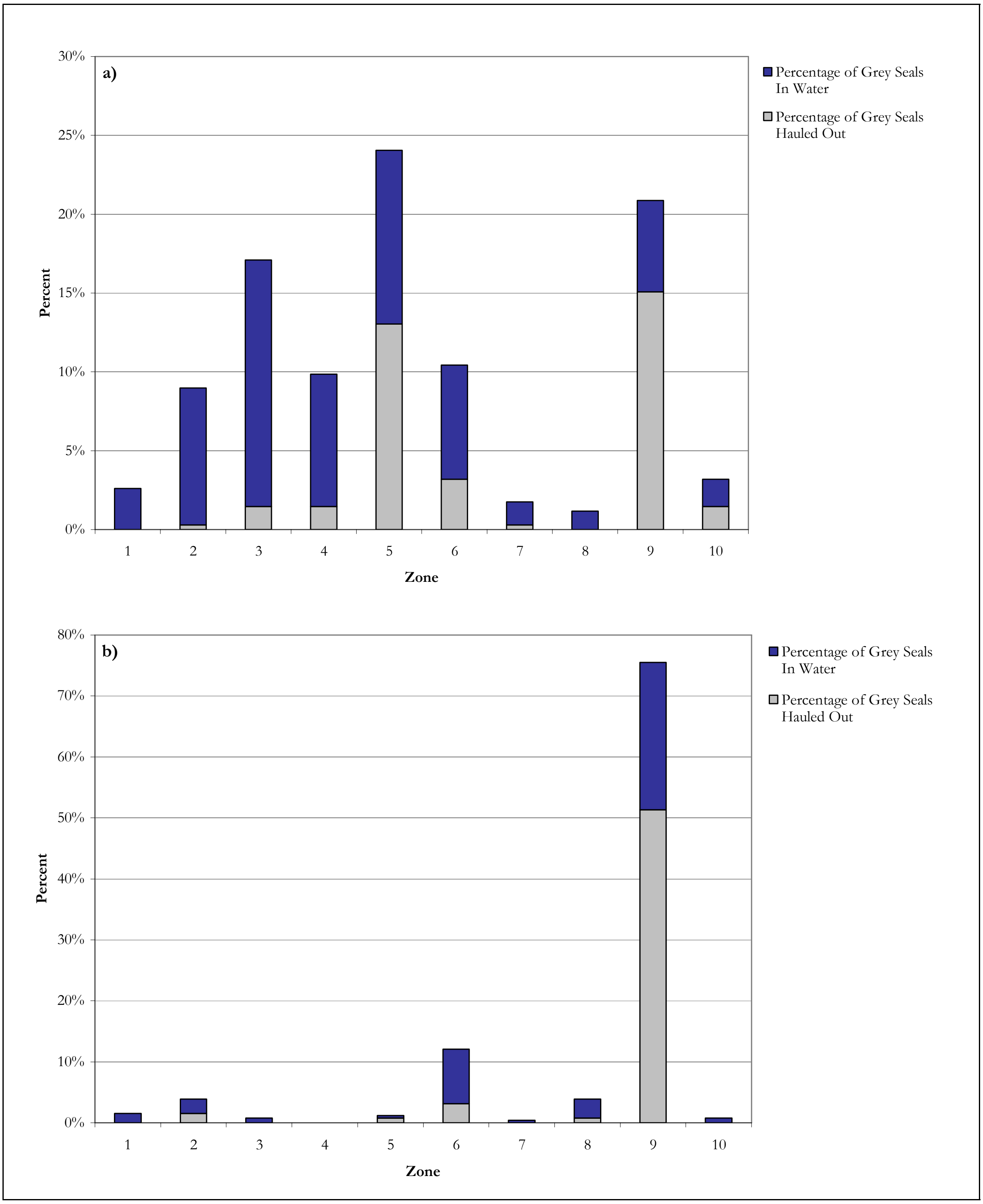


Figure 7: Percentage of grey seals sighted within each of the ten zones along the Ceredigion Marine Heritage Coast between New Quay and Ynys Lochtyn, during the a) 2004 and b) 2005 sampling seasons. The proportions of grey seals seen as hauled out and/or in the water are illustrated by the grey and blue sections, respectively.

8.1.2. Monthly Variation

Sightings per hour effort from VPB trips decreased slightly with date, given the significant but weakly negative correlation existing between total number of grey seals observed and date during both sampling seasons (r =- 0.143, n =238, P<0.05, *2004*; r =- 0.324, n =177, P<0.05, *2005*). Given mean number of seals sighted/hour effort in 2004 fluctuated slightly around one seal/hour effort each month (*Figure 8)* no significant difference was found in mean seals sighted per month (*Kruskal-Wallis*, H =10.40, *d.f.* =5, P =0.065). Similarly, in 2005 no significant difference in mean seals sighted/hour effort per month was found (H =10.23, *d.f.* =5, P =0.069), despite mean seals/hour effort peaking in June (1.29, ±0.17S.E.). Overall, mean number of seals sighted/hour effort per month in 2005 was significantly lower than that observed in the previous year (H =34.63, *d.f.* =1, P<0.05). Post-hoc pairwise comparisons (Mann-Whitney U; *Table 3*) tested for significant differences in mean seals sighted/hour effort between May and September of each year; June 2004 had significant difference of mean seals sighted/hour effort with July/September 2005; both July/August 2004 had significant differences with May, July, August and September 2005; September 2004 had significant differences with May, July and September 2005. No other pairwise comparisons were significant.

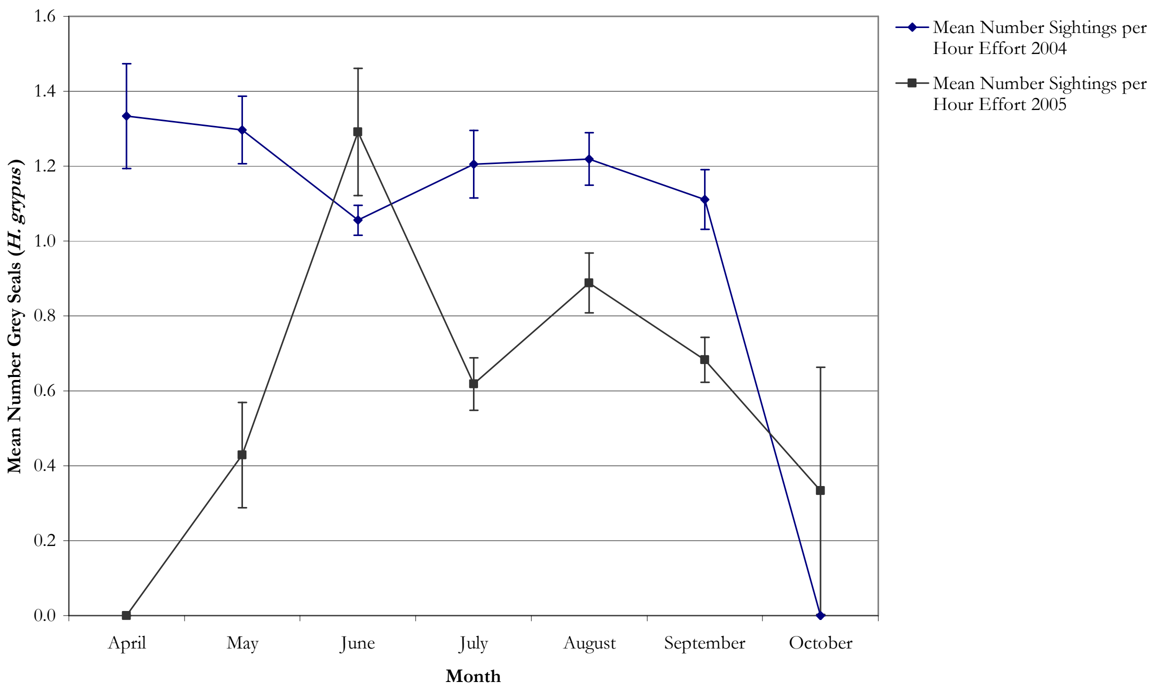


Figure 8: Mean (± S.E.) number of grey seals sighted per hour of effort from visitor passenger boat trips (VPBs) during the 2004 and 2005 sampling seasons. Data were not collected during October 2004 nor April 2005, hence values of zero.

Month 2004	Month 2005	*U*	*P*
June	July	624.5	0.019
	September	786.5	0.001
July	May	141.5	0.003
	July	797.5	0.001
	August	2340.0	0.003
	September	1000.0	0.001
August	May	208.0	0.003
	July	1174.0	0.002
	August	3400.0	0.013
	September	1475.5	0.001
September	May	34.5	0.048
	July	194.5	0.043
	September	244.0	0.004

Table 3: Post-hoc pairwise multiple comparisons using non-parametric Mann-Whitney U tests. Only significant differences between means of total grey seals per month in 2004 and 2005 are shown; significant at P = 0.05 level.

8.1.3. Daily Variation

Seals were observed at numerous times throughout the day. *Figure 9* illustrates in both years overall maximum count occurred within the typically warmest period of day (2004, n =8 at 13:07, hauled; 2005, n =7 at 12:51, hauled and 15:01, six hauled). However for both years, no significant correlation existed between number of seals hauled and time of day (r =0.019, n =70, P =0.875, *2004*; r =0.002, n =74, P =0.990, *2005*).

8.1.4. Hours from Low Tide

In 2004 no significant linear correlation existed between number of seals hauled-out and hours from low tide (r =0.141, n =68, P =0.253), however seals often hauled-out between one hour before and three hours after low tide, with overall maximum haul-out count at approximately 2½ hours after low tide (n =8, *Figure 10a*). Similarly, during 2005 the overall maximum haul-out count (n = 7, *Figure 10b*) was observed between one and two hours post low tide. In 2005, a significant, yet weakly positive correlation existed between number of seals hauled and hours from low tide (r =0.243, n =68, P<0.05).

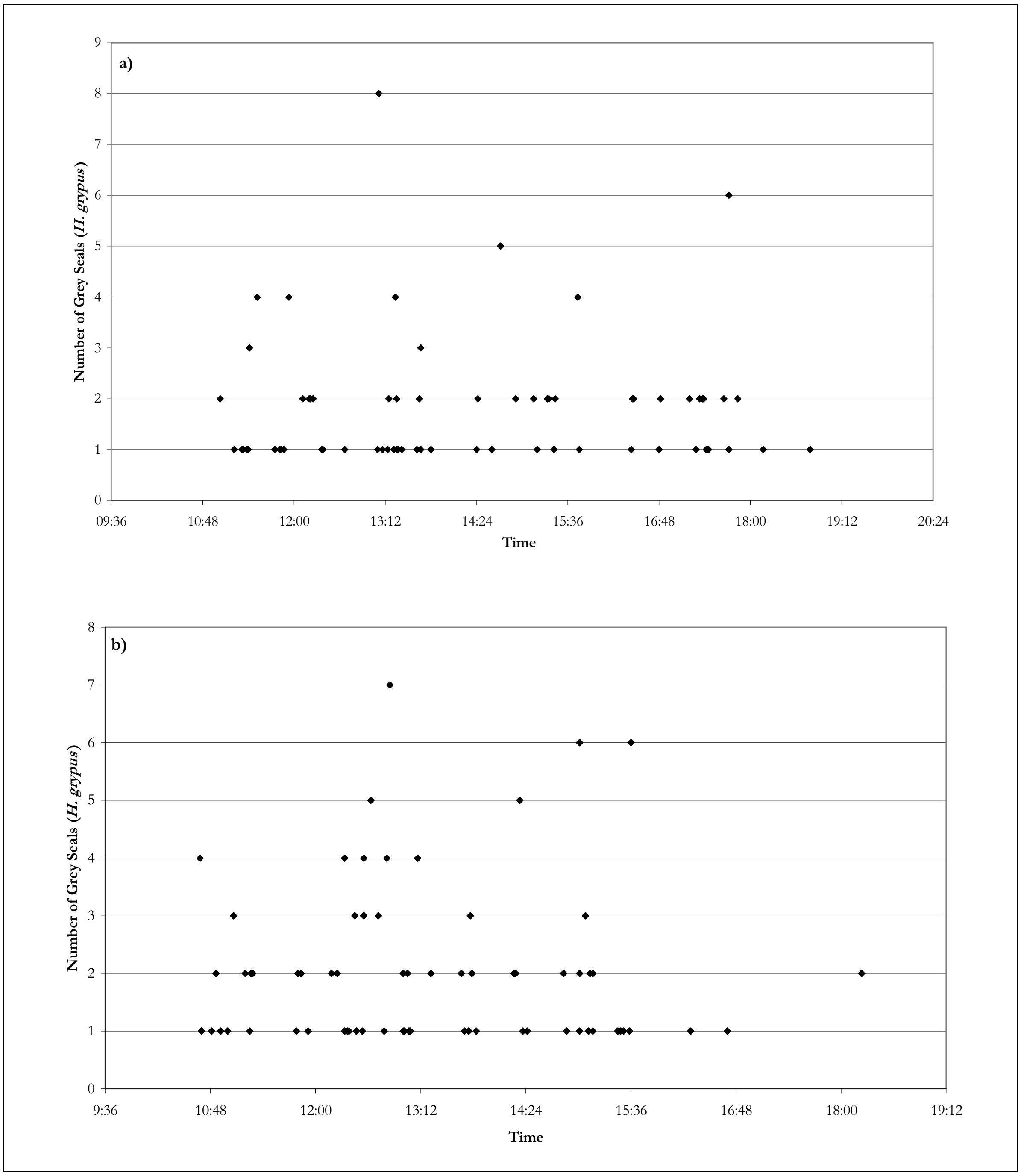


Figure 9: Number of grey seals seen hauled out from the visitor passenger boat trips (VPBs) over time during the a) 2004 and b) 2005 sampling season.

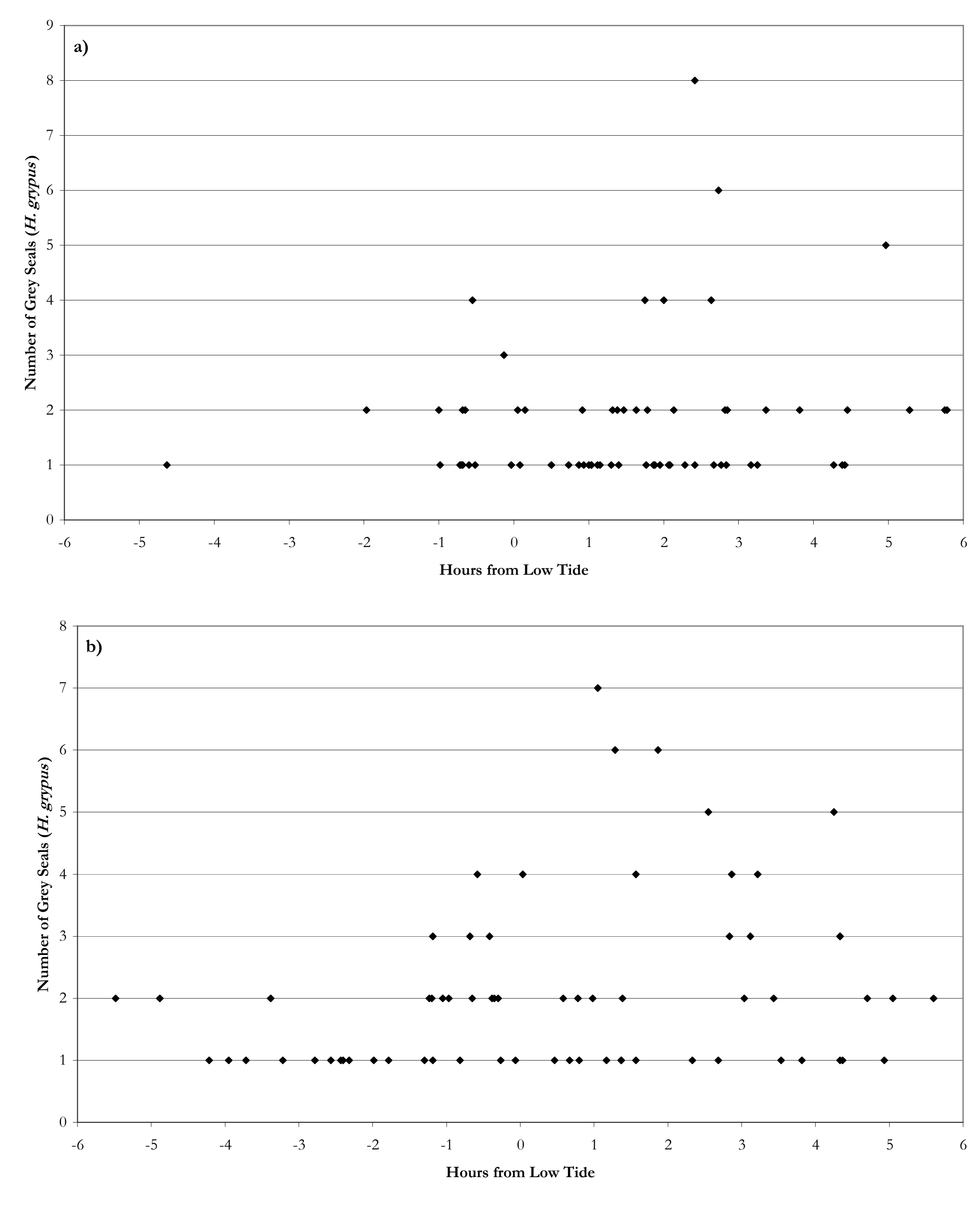


Figure 10: Number of grey seals sighted hauled out per hour from low water from visitor passenger boat trips (VPBs) during a) 2004 and b) 2005 sampling season.

8.1.5. Tidal Phase

Figure 11 shows a significantly greater proportion of seals were observed during ebbing tides than flood tides in both years (χ^2 = 149.36, *d.f.* = 1, P<0.05, *2004*; χ^2 = 22.87, *d.f.* = 1, P<0.05, *2005*). Two-way ANOVA results (*Table 4*) indicated a significant effect of tidal phase on mean score of seals observed per VPB trip in 2004, such that more seals on average were sighted on a flood tide (1.32 ±0.05S.E.) than ebb tide (1.16 ±0.02S.E.). Behaviour also significantly affected mean score of seals sighted, with greater scores attributed to hauled seals (1.36 ±0.04S.E.) than those in water (1.13 ±0.03S.E.). Tidal phase and behaviour did not significantly interact; mean scores of both behaviours exhibited increased with flood tide and more hauled-out seals were observed, hence tidal phase did not determine which behaviour prevailed. In 2005, similar mean scores of seals were observed during ebb (1.23 ±0.03S.E.) and flood tides (1.15 ±0.04S.E.) hence tidal phase did not significantly affect mean count of seals sighted per VPB trip. In contrast, behaviour displayed by seals significantly affected mean score of seals observed per VPB trip, with greater mean score of seals sighted hauled-out (1.33 ±0.03S.E.) than in water (1.04 ±0.03S.E.). Unlike 2004, significant interaction existed between tidal phase and behaviour in 2005, such that during a VPB trip one was more likely to observe seals in water during flood tides and more likely to see hauled seals on ebb tides.

Overall in 2004 a significantly greater proportion of seals were observed from VPBs in water than hauled-out (χ^2 =26.16, *d.f.* =1, P<0.05) whereas in 2005 significantly more seals were observed hauled-out (χ^2 =4.14, *d.f.* =1, P<0.05). Furthermore, two-way ANOVA indicated behaviour of seals significantly affected mean scores of seals observed from VPBs in both years however sampling year did not. Significant interaction existed between sampling year and behaviour of seals with greater scores of seals observed in water in 2004 in contrast to greater scores of seals observed hauled-out in 2005. A significant interaction occurred between tidal phase and year, such that greater score of seals were observed on a flood tide in 2004 as opposed to greater score of seals sighted during ebb tide in 2005.

Table 4: Two-way ANOVA results (SPSS, Version 11.5.0), showing the main effects of tidal phase, behaviour and year on the mean scores of grey seals observed from visitor passenger boats (VPB) in 2004 & 2005. Also shows significance of interactions of main effects (effect X effect) on mean scores of seals sighted per VPB trip in both years.

Year	Effects/Interactions	F-value	Degrees of Freedom: Regression	Degrees of Freedom: Residual	*P*
2004	Tidal Phase	9.67	1	244	<0.05
	Behaviour	17.96	1	244	<0.05
	Tidal Phase X Behaviour	1.73	1	244	0.189
2005	Tidal Phase	3.09	1	175	0.081
	Behaviour	42.93	1	175	<0.05
	Tidal Phase X Behaviour	4.87	1	175	<0.05
2004 + 2005	Tidal Phase	2.35	1	423	0.126
	Behaviour	69.62	1	417	<0.05
	Year	0.14	1	417	0.709
	Year X Behaviour	4.01	1	417	<0.05
	Year X Tidal Phase	9.02	1	423	<0.05

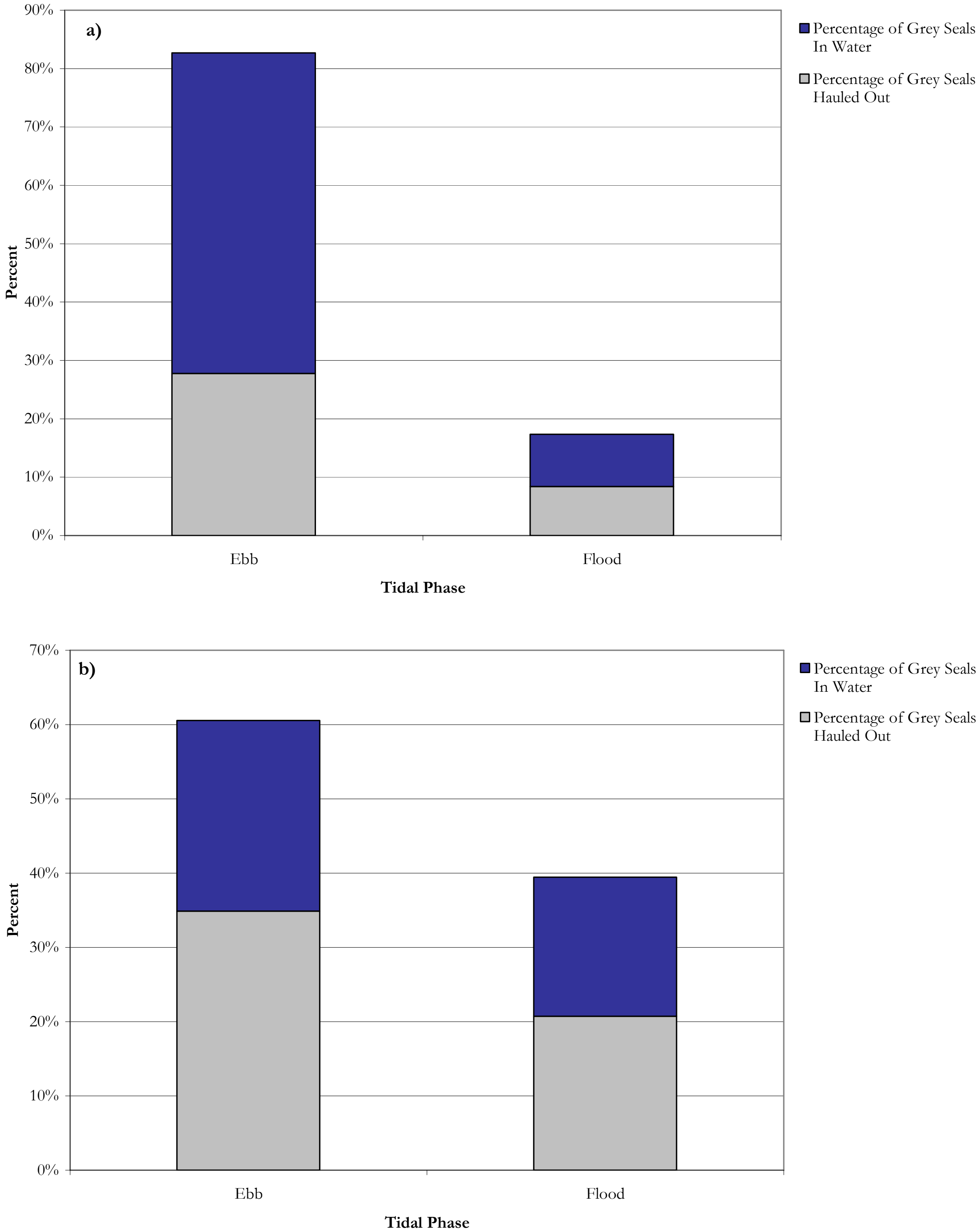


Figure 11: Percent of grey seals sighted from the Visitor Passenger Boat (VPBs) trips during ebb and flood tides in a) 2004 and b) 2005 sampling season. The proportion of grey seals observed hauled out on land or in the water, demonstrated by the grey and blue sections, respectively. Total numbers & percentages per behaviour, tidal phase and year may be referred to in Appendix 6.

8.2. Direct Observation at Bird's Rock

Grey seals were observed from Bird's Rock across various temporal, tidal and environmental states. 54 dates were sampled between 8th June and 1st September 2005, comprising 86 surveys, 1093 15-minute intervals, 258 hours of effort and involving a total count of 1510 seals. Univariate and multivariate analyses were performed to identify which environmental variables influenced haul-out behaviour.

8.2.1. Monthly Variation

Overall, mean number of seals observed per hour effort decreased from June to September, however differences were not significant (H =0.339, *d.f.* =3, P =0.953). It is evident from *Table 5* that one is likely to see greater mean number of seals/hour effort during direct observation at Bird's Rock than during a one-/two-hour VPB trip.

Table 5: Mean number of grey seals observed per hour effort during direct observation surveys at Bird's Rock in 2005 and visitor passenger boat trips along the Ceredigion Marine Heritage Coast in 2004 & 2005.

	Mean Number Grey Seals Observed Per Hour Effort		
Month	Direct Observation	VPB 2004	VPB 2005
June	6.32	1.06	1.29
July	5.64	1.20	0.62
August	6.01	1.22	0.89
September	4.00	1.11	0.68

8.2.2. Daily Variation

Figure 12 demonstrates how mean number of seals observed per hour effort during each survey period declined between 06:00 and 21:00 hours. Significant negative correlations occurred between time of day and mean number of seals observed in total, in water and hauled-out (r =-0.354, n =642; r =-0.195, n =474; r =-0.337, n =299; P< 0.05, respectively).

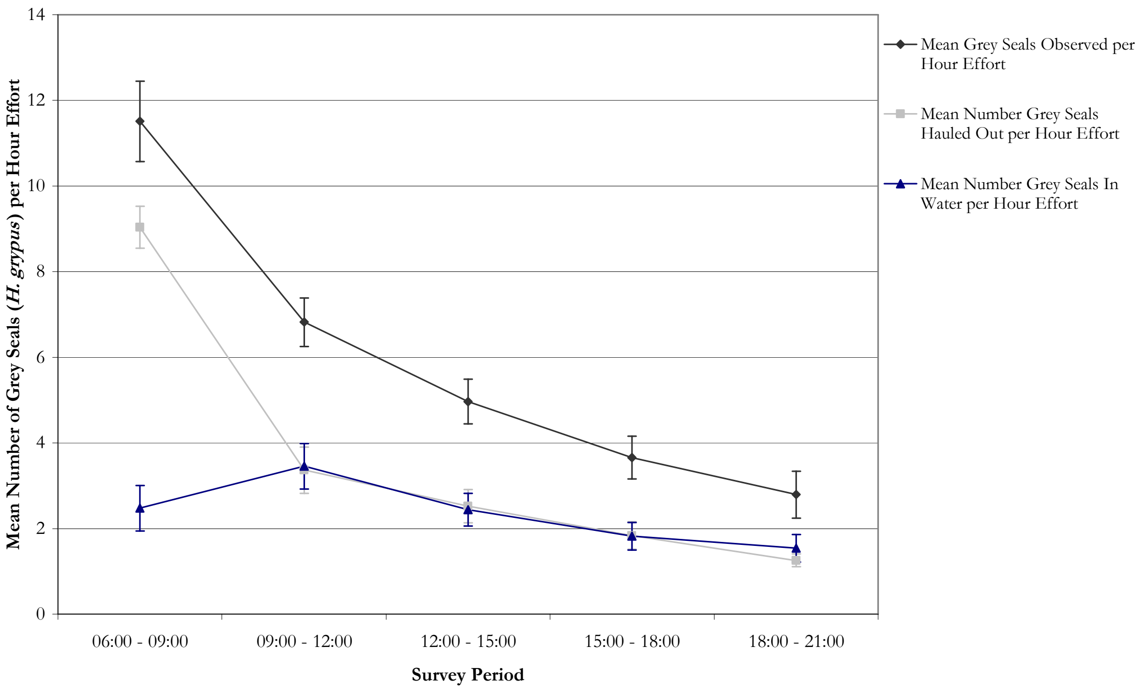


Figure 12: Mean (±S.E.) total number, hauled-out and in water of grey seals per hour of effort for each of the five survey periods, illustrating an overall decline in numbers of grey seals seen per hour of effort.

8.2.3. Time since Sunrise

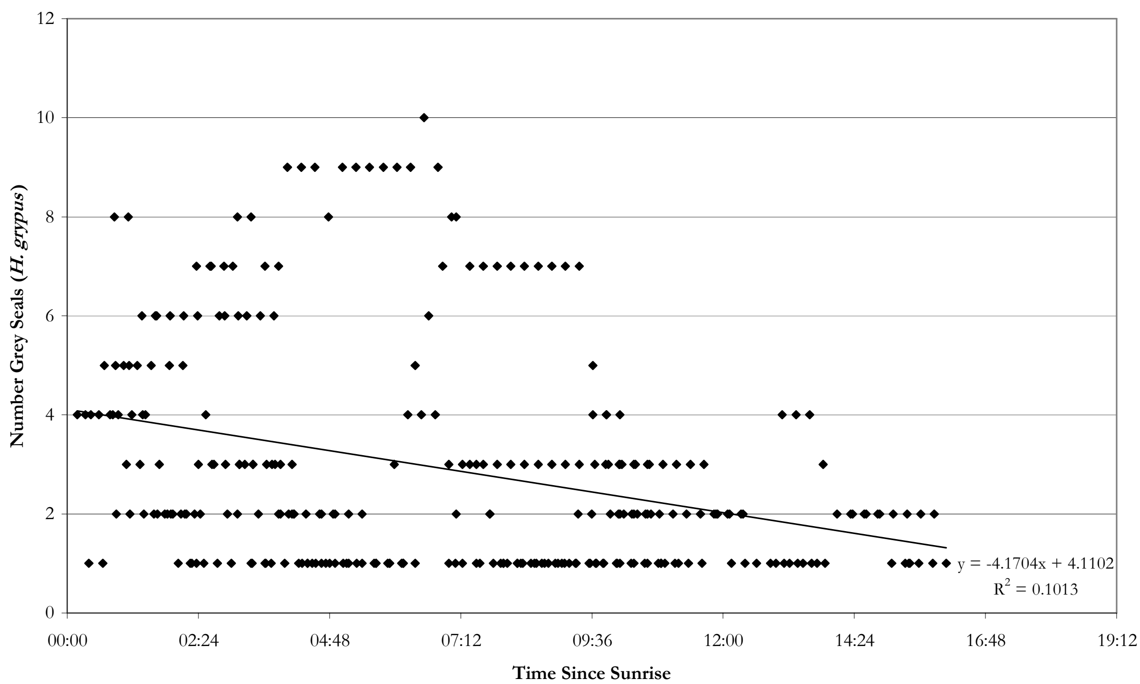


Figure 13: Number of grey seals hauled-out at Bird's Rock at different times since sunrise (BST). Times of sunrise taken from the local tidal almanac (Tablau Llanw Ceredigion Tide Tables, 2005).

A significant negative correlation existed between time since sunrise and number of seals hauled-out at Bird's Rock (r = -0.301, n =642, P<0.05), such that greater haul-out counts were observed in the early morning than evening. Maximum daily haul-out counts were also significantly negatively correlated with time since sunrise (r = -0.496, *d.f.* =92, P<0.05).

8.2.4. Time from Low Tide

Grey seals were observed at Bird's Rock numerous times during the tidal cycle, with highest counts observed between approximately two hours before/after low tide (*Figure 14*). Similarly, *Figure 15* illustrating mean proportion of maximum daily haul-out counts shows times of greatest haul-out occurred approximately three hours prior to and up to four hours post low tide. No linear correlation existed between number of hauled seals and time from low tide (r = -0.048, n =304, P =0.402). However, *Figure 16* focusing on maximum daily haul out numbers indicates that when low tide was earlier in the day, grey seals delayed hauling out typically until after low tide, whereas when low tide occurred in late afternoon, seals tended to haul-out earlier in the tidal cycle. Regression analysis revealed a significant relationship between these data ($F_{(1, 90)}$ =26.05, n =92, R^2 =0.22, P<0.05), thus time of day influenced the seals' haul-out behaviour, such that time of peak haul-out in the tidal cycle changed with time of low tide, similar to that displayed by harbour seals at Saint Croix Island (Pauli & Terhune, 1987).

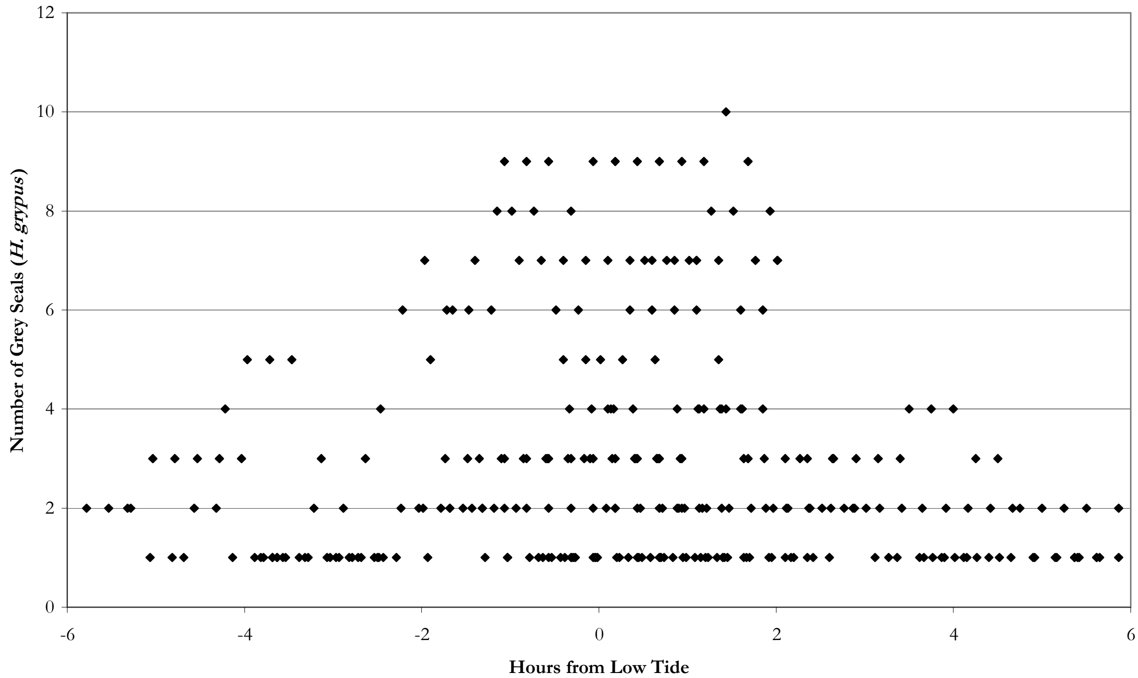


Figure 14: Number of grey seals hauled out at Bird's Rock at different times from low tide between 8th June and 1st September 2005.

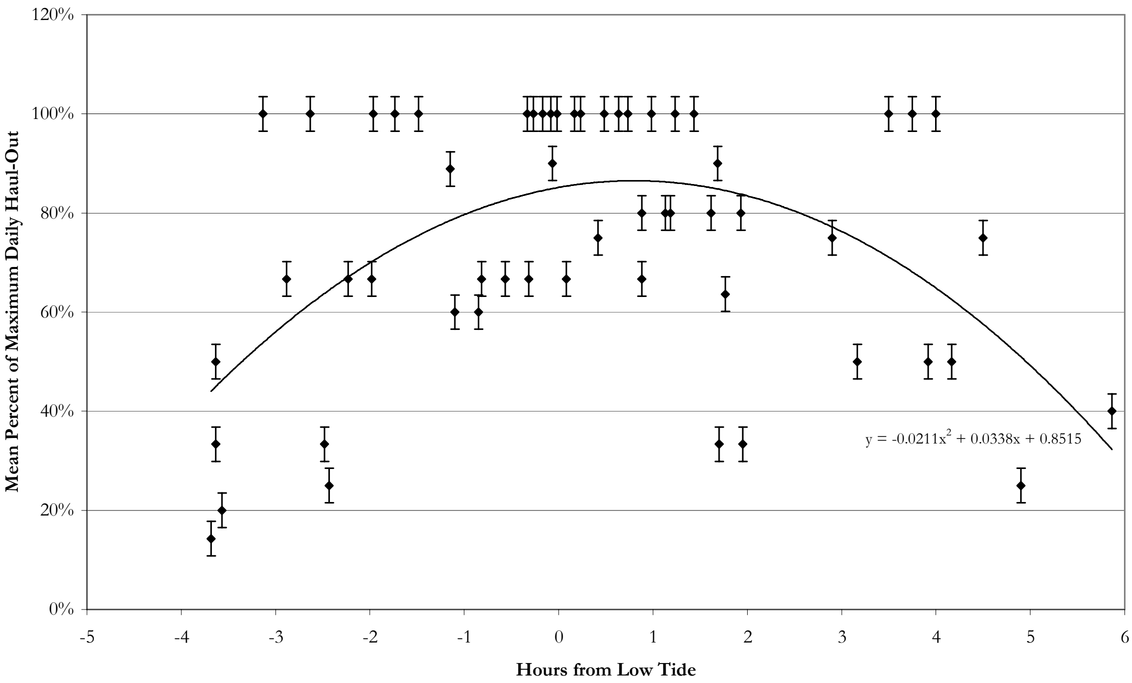


Figure 15: Mean percent (± SE) of the maximum number grey seals hauled out relative to time from low tide at Bird's Rock; 8th June to 1st September 2005.

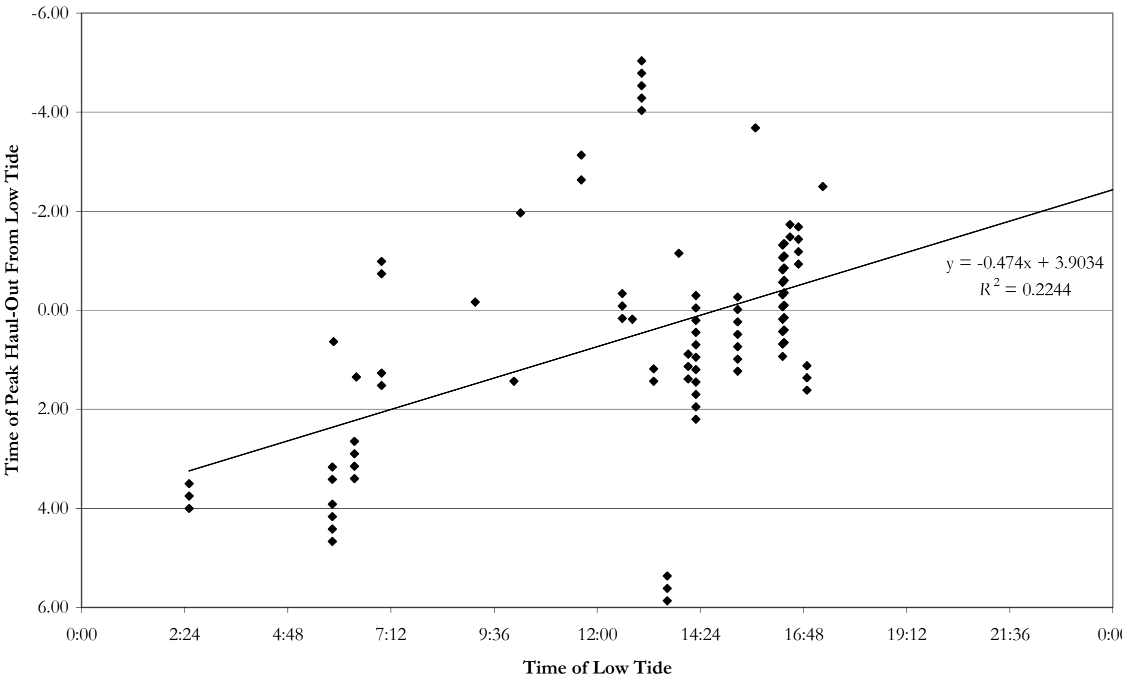


Figure 16: Time of maximum grey seal haul-out from low tide by time of day (BST) at Bird's Rock, 8th June to 1st September 2005.

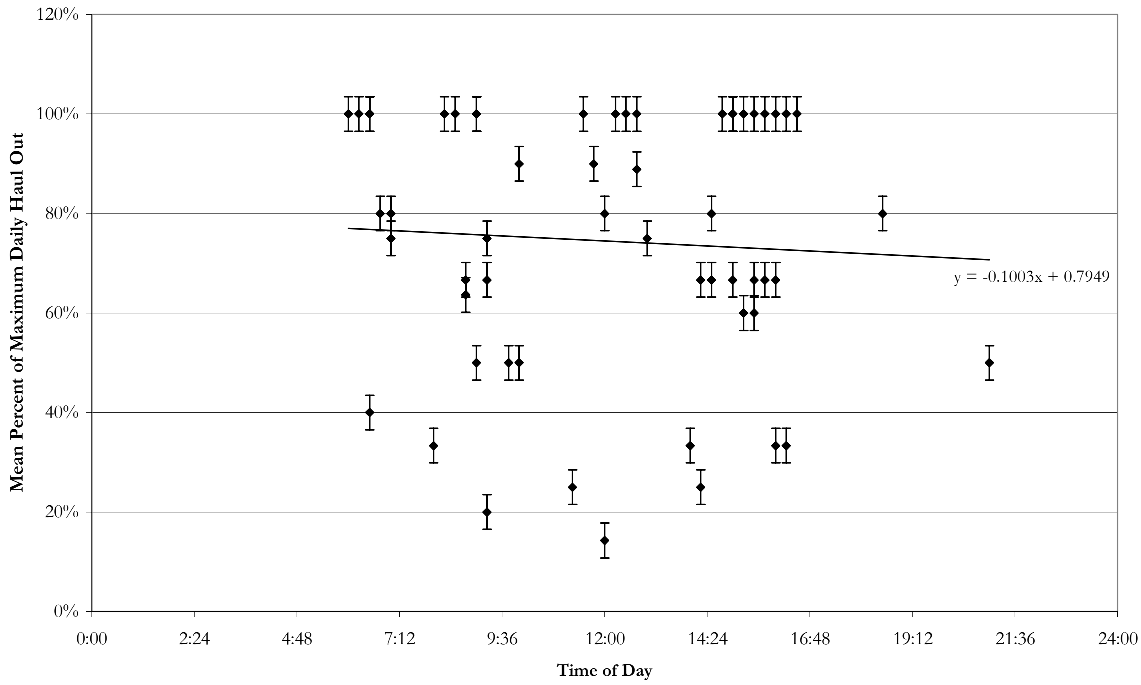


Figure 17: Mean percent (± SE) of the maximum number grey seals hauled out at Bird's Rock at 15-minute intervals; 8th June to 1st September 2005.

On examining mean percent of daily maximum number of seals hauled at 15-minute intervals, regression analysis was non-significant ($F_{(1, 54)}$ =0.20, *n* =55, R^2 =0.004, *P* =0.656), thus seals' haul-out pattern may have followed the tidal cycle more closely than a diurnal pattern.

8.2.5. Tidal Phase

Overall *Figure 18* demonstrates a significantly greater proportion of seals were observed during flood tides than ebb tides (χ^2 =5.61, *d.f.* =1, *P*<0.05). Moreover, significantly higher proportion of seals were observed hauled-out than in water (χ^2 =31.47, *d.f.* =1, *P*<0.05). Two-way ANOVA revealed mean scores of seals observed per 15-minute interval on flood tides (1.38 ±0.02S.E.) was marginally higher than during ebb tides (1.35 ±0.02S.E.), thus no significant difference existed ($F_{(1, 769)}$ =0.72, *P* =0.396) suggesting tidal phase did not affect number of seals observed from Bird's Rock. Contrastingly, the effect of behaviour on mean number of seals observed per 15-minute interval was significant ($F_{(1, 769)}$ =199.0, *P*<0.05) with mean score of seals hauled-out exceeding that in water (1.59 ±0.03S.E.; 1.14 ±0.02S.E., respectively). It can be concluded that no significant interaction occurred between tidal phase and behaviour exhibited by grey seals ($F_{(1, 769)}$ =2.29, *P* =0.130).

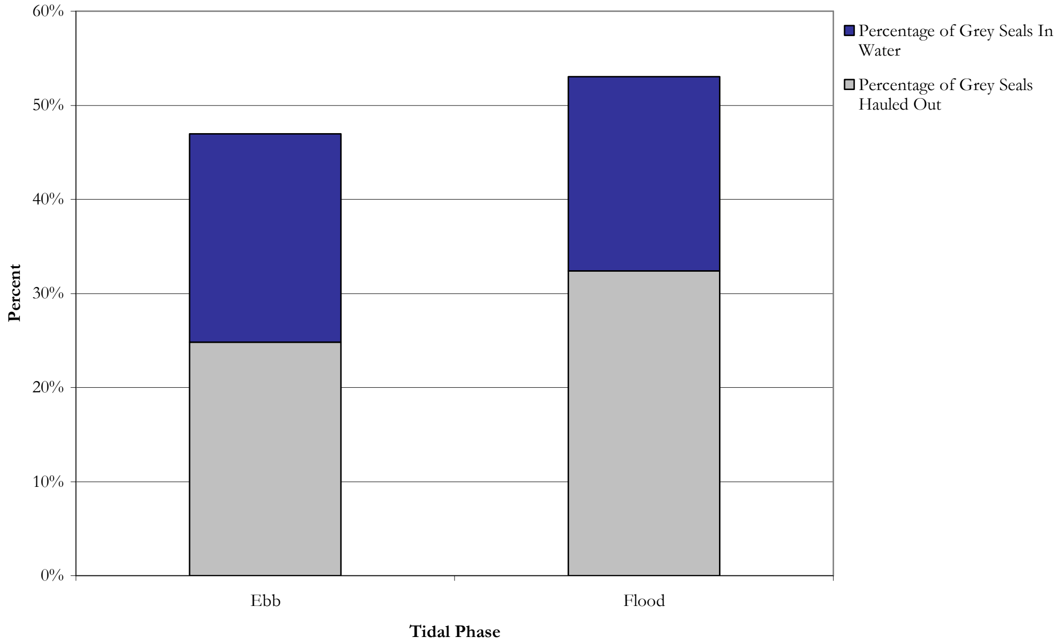


Figure 18: Percentage of grey seals observed from Bird's Rock. Behaviour in terms of being hauled out or in the water is demonstrated by the grey and blue columns, respectively. Total numbers & percentages can be referred to in Appendix 6.

8.2.6. Tidal Height

As expected the majority of seals hauled out at lower tidal heights; a weak negative correlation existed between tidal height and number of hauled seals (r = -0.364, n =180, P<0.05). Similarly proportion of seals hauled per 15-interval and maximum daily haul-out count are significantly negatively correlated with tidal height (r = -0.286, n =641, P<0.05; r = -0.127, n =92, P<0.05, respectively).

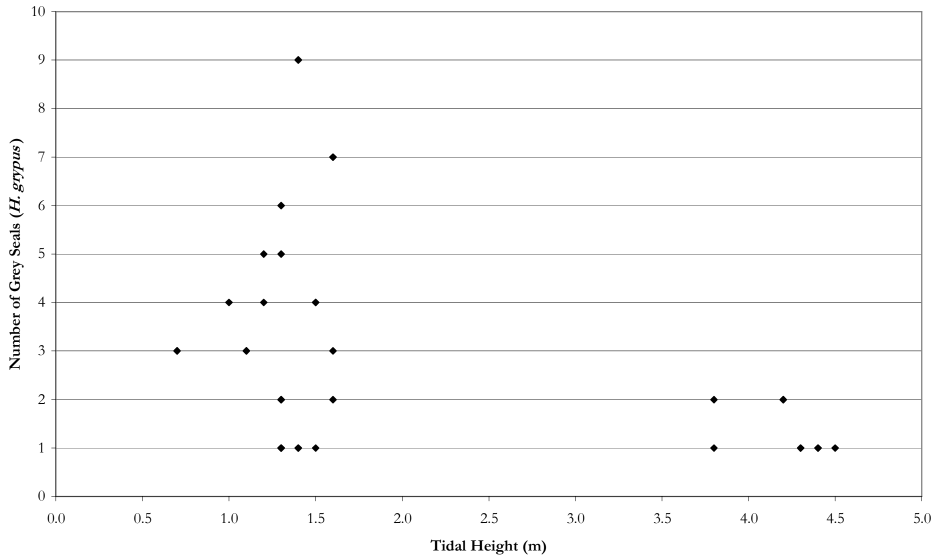


Figure 19: Number of grey seals hauled out within 15-minutes of low or high tide at Bird's Rock. Estimated maximum tidal height ranged from 0.5m – 5.6m during study; tidal heights are approximate values as given in the local tidal almanac (Tablau Llanw Ceredigion Tide Tables, 2005) and are accurate to within ± 1.0m depending on sea state.

8.2.7. Tidal Amplitude: Spring & Neap Tides

Throughout the study, mean daily tidal amplitude ranged between 1.8–5.1m. *Figure 20* illustrates the relationship between mean total seals per 15-interval, mean daily tidal amplitude and date throughout the study period. Three major peaks in mean total seals per 15-interval were observed on 30th June, 16th July and 2nd August, occurring seven, ten and twelve days post spring tide[2] respectively. Two smaller peaks in mean total seal count occurred on 11th July and 9th August, occurring five and four days after spring tides respectively. Thus on average, grey seal counts peaked eight days following spring tide. Data partitioned into six fortnightly periods were analysed using Pearson correlation; five fortnightly periods displayed significant correlations between mean tidal amplitude and mean total seals observed per 15-minute interval (*Table 6).* During the first fortnight mean number seals observed from Bird's Rock increased with increasing mean daily tidal height leading up towards the spring tide on 22nd June. In the successive five fortnights, the mean number of seals observed decreased with increasing tidal height over time.

Fortnight	Date	*r*	*n*	*P*
1	08.06.05 - 15.06.05	0.465	43	<0.05
2	16.06.05 - 30.06.05	-0.314	98	<0.05
3	02.07.05 - 13.07.05	-0.135	175	0.074
4	15.07.05 - 31.07.05	-0.260	140	<0.05
5	01.08.05 - 16.08.05	-0.168	140	<0.05
6	17.08.05 - 01.09.05	-0.312	46	<0.05

Table 6: Pearson correlation coefficients and significance values for six fortnightly periods between 8th June and 1st September 2005.

[2] Maximum tidal amplitude (m) occurring every new and full moon.

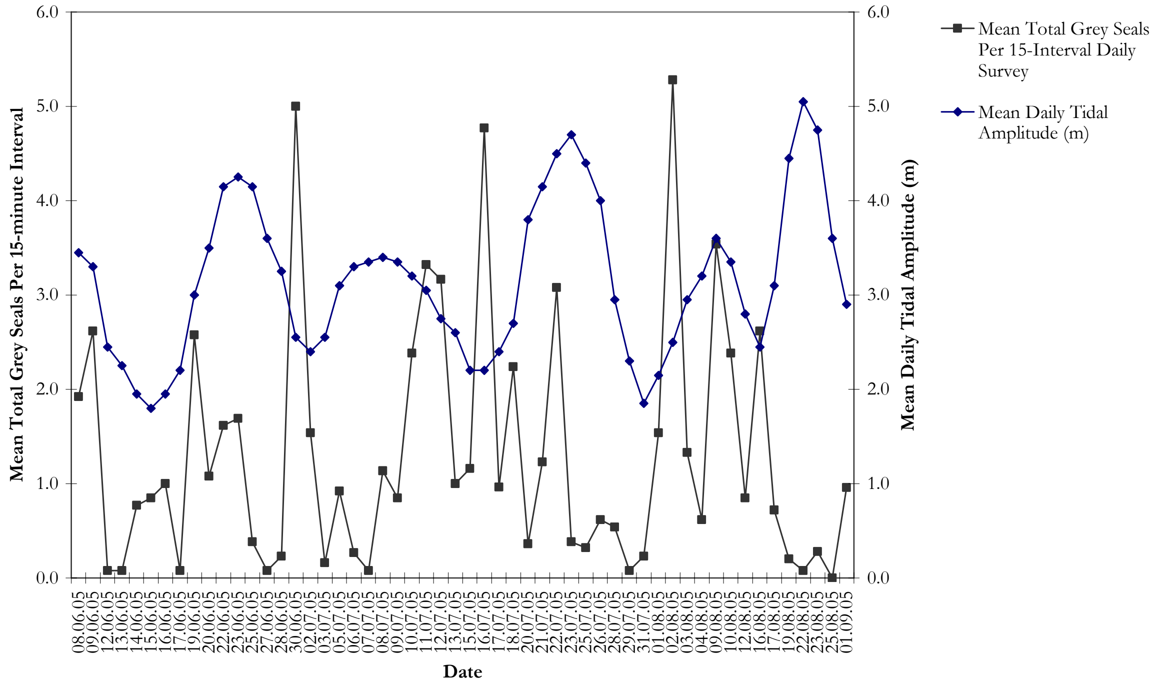


Figure 20: Mean total of grey seals observed per 15-minute interval during daily surveys at Bird's Rock and mean daily tidal amplitude (m) throughout the complete sampling season (8th June to 1st September 2005). Spring tides occurred on 22nd June, 6th July, 21st July and 5th August 2005.

8.2.8. Air Temperature (°C)

Mean ambient air temperature differed significantly with time of day (one-way ANOVA, $F_{(1,\ 1093)} = 2.90$, $P<0.05$). Maximum mean temperatures occurred between noon and 15:45 hours. On the whole, mean maximum proportion of seals hauled out over the course of the day did not strictly follow this pattern; *Figure 21* illustrates greatest mean relative number of seals hauled out during early morning, declined to a minimum at 11:45 hours as mean air temperatures increased. The next peak in mean relative number of seals coincided with the warmest period of day. A third peak in mean relative number of hauled seals occurred in the evening, when air temperatures were decreased. Results suggest ambient air temperature is not the focal factor determining haul-out behaviour in seals at Bird's Rock.

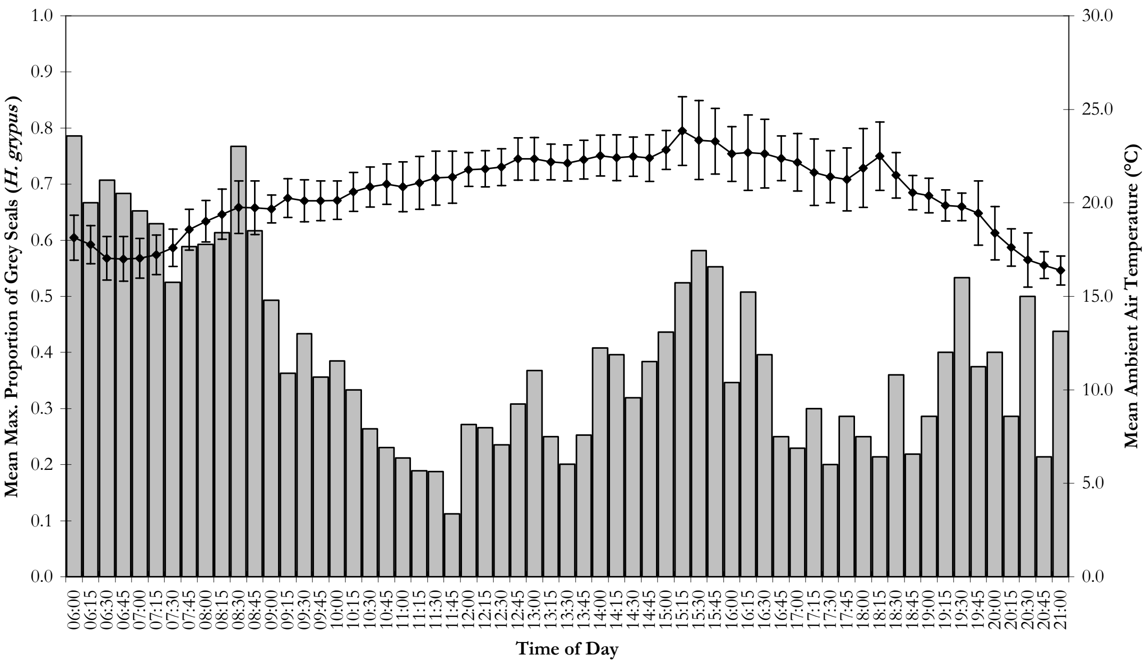


Figure 21: The relative number, i.e. mean per interval effort (±S.E.) of grey seals out during the survey (grey columns) shown in relation to mean ambient air temperature (°C) per 15-minute interval.

Grey seals were observed to haul-out between ambient air temperatures of 13.6˚C and 33.9 °C *(Figure 22a)* corresponding to adjusted temperatures of 10.1˚C and 33.2˚C *(Figure 22b)*. During the study the mean ambient air temperature experienced was 21.9 °C (±4.26 SD) corresponding to 24.1°C (±4.1 SD) adjusted temperature. The maximum haul-out count of ten seals occurred at 21°C (24.5˚C adjusted temperature). A weak yet significant correlation existed between ambient air temperature and number of hauled seals (r =-0.122, n =301, P<0.05); regression analysis revealed a significant relationship suggesting extremely warm times coincided with a slight decline in number of seals hauled out, however only 1.5% of variation in the data was explained ($F_{(1, 299)}$ =4.66, n =300, R^2 =0.015, P<0.05). Contrastingly, a weak negative correlation existed between adjusted temperature and number of seals hauled, yet it was non-significant (r =-0.087, n =301, P =0.131); regression analysis also showed no significant relationship between variables ($F_{(1, 299)}$ =2.45, n =300, R^2 =0.008, P =0.119). Three ambiguous temperatures were excluded from analysis (38.4, 39.5, 41.5 °C) and regarded as erroneous. Although initially concerned about temperature difference between cliff and sea-/rock-level, simultaneous measurements indicated a discrepancy of 1.3°C.

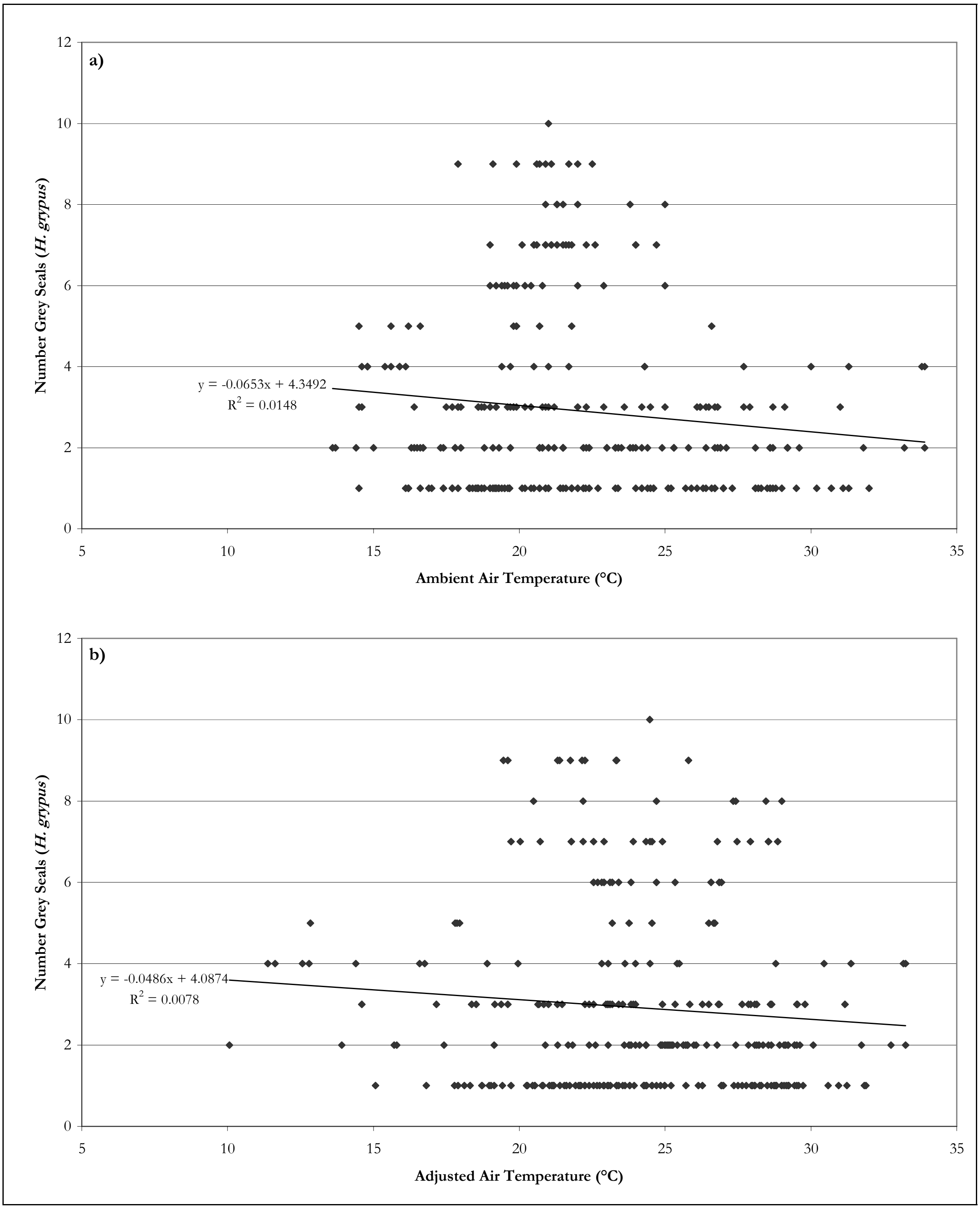


Figure 22: Number of grey seals hauled out during various a) ambient air temperatures (°C) and b) adjusted air temperatures at Bird's Rock between 8th June and 1st September 2005.

8.2.9. Wind Speed (mph), Sea State (Beaufort scale) & Weather

As expected, wind speed was positively correlated with sea state (r_s =0.701, n =1093, P<0.05), such that higher wind velocities resulted in higher sea states. Throughout the study, a mean wind speed of 3.78 mph (±3.9 SD) and mean sea state of Beaufort scale 2 (±1.1 SD) were recorded.

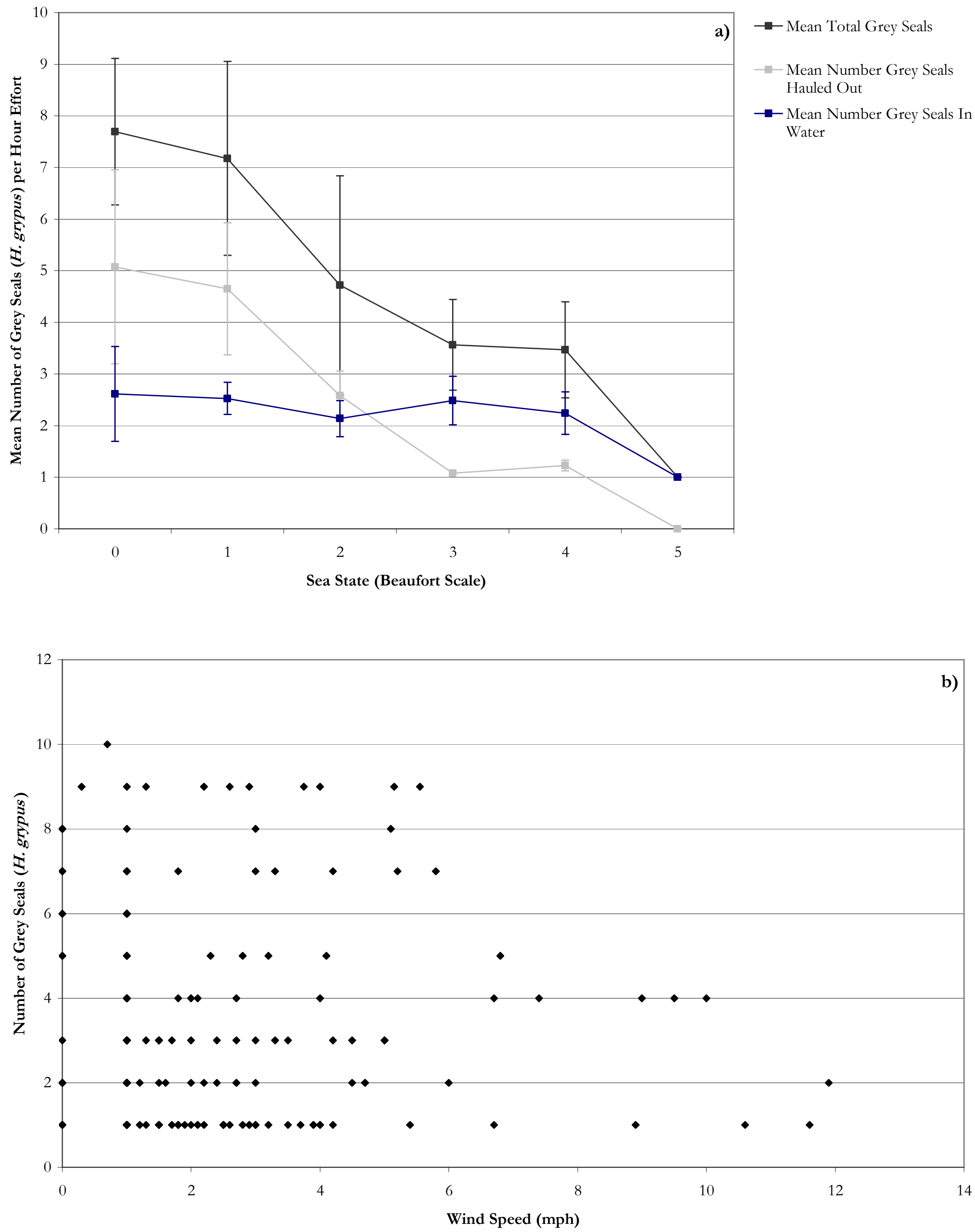


Figure 23: a) Mean (±S.E.) total, number hauled out and in water of grey seals observed per hour of effort during six different sea states during study period; b) Number of grey seals (H. grypus) hauled out at various wind speeds (mph) at Bird's Rock during study period. Study period: 8th June to 1st September 2005.

Figure 23a demonstrates how total number of seals observed decreased with increasing sea state thus seal count was significantly different per sea state (χ^2 =2275.52, *d.f.* =5, *P*<0.05) as expected (Barraclough, 2000). Mean number of hauled seals followed a similar trend whereas number of seals in water fluctuated between two and three seal sightings per hour effort at sea states zero to four, yet decreased to one seal sighting per hour effort at sea state five. A statistically significant relationship was found between sea state and behaviour exhibited by the seals (χ^2 = 98.13, *d.f.* = 5, P<0.05) such that between sea states zero and two the majority of seals were hauled-out, conversely at sea states three to five a greater proportion of seals were observed in water. Interestingly, no significant correlation was found between number of seals hauled-out and sea state (r_s =0.012, n =299, P =0.838) nor wind speed (r =0.046, n =299, P =0.425). A maximum of ten seals hauled-out at 0.7 mph and no seals hauled at wind speeds in excess of 11.9 mph (*Figure 23b*).

Weather is significantly weakly positively correlated with sea state (r_s = 0.061, n = 1093, P<0.05), such that as weather worsened, as did sea state. *Figure 24* illustrates mean number of seals observed from Bird's Rock per hour effort during various weather categories. A significant difference was found between observed and expected numbers of seals observed during each weather category (χ^2 = 1002.67, *d.f.* = 4, P<0.05) indicating one was not likely to see an equal proportion of grey seals during all weathers; overall more seals were observed during sunny, fair and overcast conditions than times of rain or mist. Furthermore, a significant interaction was found between behaviour expressed by the seals and weather category (χ^2 = 30.01, *d.f.* = 4, P<0.05) such that when the weather was fair or sunny, a greater proportion of seals were hauled as opposed to in the water. In contrast, during rainy/misty conditions a greater proportion of seals were observed in water than hauled on ledges. Grey seals were equally observed hauled out and in water at overcast times. Sun & shower conditions were not encountered during the survey.

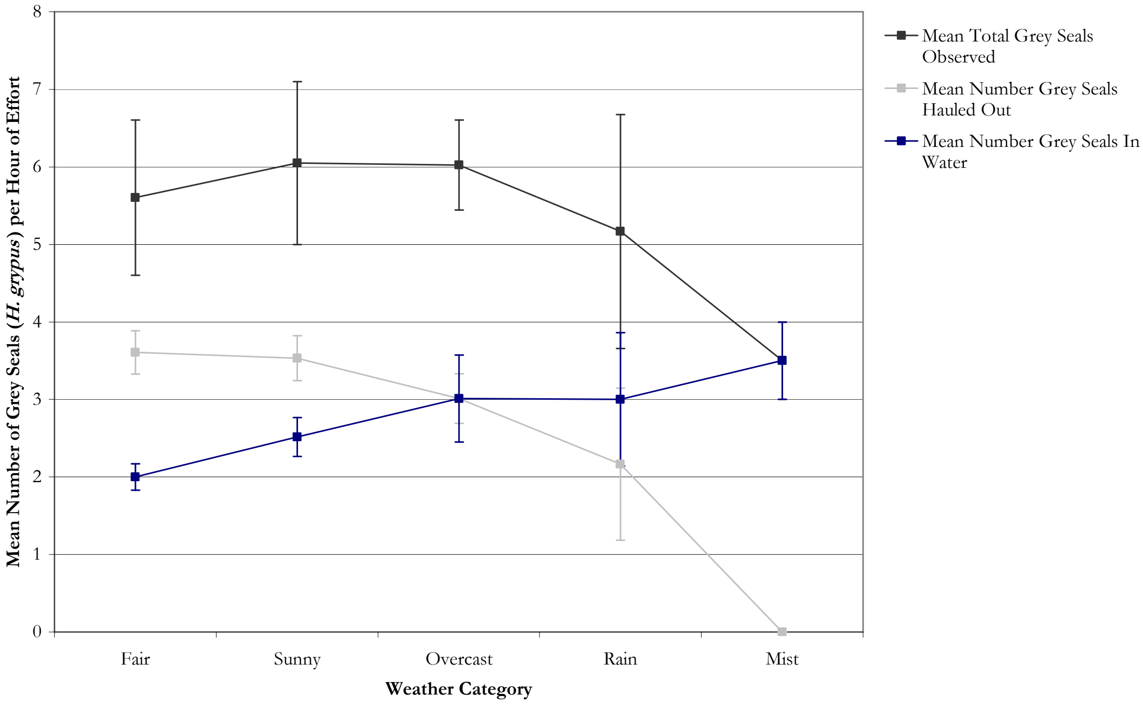


Figure 24: Mean (±S.E.) of total, hauled out and in water numbers of grey seals observed per hour of effort in six different weather categories at Bird's Rock between 8th June and 1st September 2005. Note that 'Sun & Showers category was not encountered during the sampling season, thus not included.

8.3.0. Multivariate Analysis: Principal Components Analysis (PCA) & Stepwise Multiple Regression

Following univariate analysis, correlation matrices were produced using *SPSS (Version 11.5.0)* for all recorded variables to examine their independence/multicollinearity. Data were analysed separately in terms of number of seals hauled at a given time, proportion of seals hauled at any one time, i.e. number of seals hauled-out divided by total number of seals observed (hauled/swimming/bottling) and finally maximum daily haul-out count. Prior to PCA, the dependent variable regarding proportions was arcsine transformed and the dependent count variable was square-root transformed in order to minimise heterogeneity of variances and to normalise data. Ambient air temperature and wind speed were $\log_{10}$ transformed, and tidal amplitude was inverse transformed to improve distributional symmetry and achieve normalisation. Transformed independent/dependent variables appear *italic*. It is apparent that not one variable or combination of variables had significant predictive power to explain all the variation in the data, as supported by the PCA extraction and varimax rotation performed, yet sufficient components in each case were extracted to explain approximately 70-75% of the variance in the original data. Stepwise multiple regressions followed maximum R^2 procedure; multicollinearity was minimised by omitting redundant variables from the stepwise regressions, thereby increasing stability of the regression coefficients.

8.3.1. Number of Grey Seals Hauled Out

PCA performed on number of seals hauled-out at any given time indicated that from twelve variables analysed, four components were extracted explaining 69.96% of variance in data *(Table 7)*. The variables adjusted temperature, sea state and *ambient air temperature* had high component loadings on component one; variables time since sunrise and time of day were highly correlated with component two; time since low tide and tidal phase variables had high component loadings on component three and disturbance was highly correlated with the fourth component.

Table 7: PCA results regarding number of grey seals hauled-out at any given time. *Time since sunrise excluded from stepwise multiple regressions to reduce multicollinearity, assessed by condition indices.

Component	Percentage Variation Explained	Independent Variable (Predictor)	Component Loading
1	28.46%	Adjusted air temperature Sea state Ambient air temperature	0.86 0.73 0.70
2	20.19%	Time since sunrise* Time of day	0.94 0.92
3	12.46%	Time since low tide Tidal phase	0.88 0.87
4	8.85%	Disturbance	0.86

Subsequently, these components (excluding time since sunrise) were entered into a stepwise multiple regression. The final model *(Equation 2)* incorporated time of day and disturbance, accounting for 13.8% of variance in the original variables. Although the regression was a poor fit (R^2_{adj} =13.2%) the association between the two predictor variables and *number of seals hauled-out* was significant ($F_{(2, 297)}$ =23.77, P<0.05). Both predictors had significant, negative effects on predicted *number of grey seals hauled-out* at any given time when the other variable was held constant. Despite data transformation, residuals were not normalised thus validity of the statistical tests are ambiguous. On removal of outliers, the final model *(Equation 3)* had an improved fit, although it remained relatively poor (R^2_{adj} =20.9%). The model incorporated time of day, disturbance, adjusted air temperature and tidal phase and explained 22% of variance in the original data. The association between these four predictors together and *number of seals hauled-out* at a time was significant ($F_{(4, 274)}$ =19.36, P<0.05). All four predictors significantly affected *number of grey seals hauled-out (Table 8)*. In absence of outliers, residuals became more normalised. However, the outliers were not erroneous values but occasions when the highest numbers of seals hauled-out. Therefore it would be wrong to discount them. Clearly, more data collection is required.

Table 8: Results for stepwise multiple regressions of the number of grey seals hauled out at any one time. *Italics* refer to regression in absence of outliers. Eqn 2: Predicted (*No. Hauled Grey Seals*) = 2.233 – 0.33(time of day) – 0.12(disturbance); Eqn 3: Predicted (*No. Hauled Grey Seals*) = 1.508 – 0.38(time of day) – 0.23(disturbance) + 0.15(adjusted air temperature) + 0.13(tidal phase).

	Standardised Coefficients		Unstandardised Coefficients	t-test		
Variable	B	S.E.	β	t-value	*d.f.*	*P*
Time of Day	0.000	0.000	-0.325	-5.842	297	<0.05
Disturbance	-0.149	0.070	-0.118	-2.119	297	<0.05
Time of Day	0.000	0.000	-0.375	-6.705	274	<0.05
Disturbance	-0.241	0.061	-0.225	-3.972	274	<0.05
Adjusted Air Temperature	0.017	0.007	0.146	2.557	274	<0.05
Tidal Phase	0.134	0.056	0.130	2.401	274	<0.05

8.3.2. Proportion of Grey Seals Hauled-Out

PCA was performed on *proportion of seals hauled-out*; proportions based on less than four individuals were considered unreliable thus excluded from analysis (following Schneider & Payne, 1983). Four components *(Table 9)* with eigenvalues exceeding one were extracted from twelve variables entered in analysis and cumulatively explained 75.64% of variance in the data. The remaining components were not retained as they did not provide sufficient additional information, yet seven components were required to explain 93.40% of the variance in the original data. The variables time since sunrise and time of day had extremely high positive component loadings on component one. The variable adjusted air temperature was highly correlated with component two whereas time from low tide and tidal phase were correlated with factor three. Finally, date had an extremely high component loading on component four.

Table 9: PCA results regarding proportion of grey seals hauled-out at any given time. *Time since sunrise excluded from stepwise multiple regressions to reduce multicollinearity, assessed by condition indices.

Factor	Percentage Variation Explained	Independent Variable (Predictor)	Component Loading
1	27.56%	Time since sunrise* Time of day	0.94 0.93
2	21.21%	Adjusted air temperature	0.88
3	15.91%	Time from low tide Tidal phase	0.89 0.89
4	10.96%	Date (observation no.)	0.90

These components, explaining the greatest proportion of variance in the original data (except time since sunrise), were entered into stepwise multiple regression however it failed to work. On entering the same variables into an 'enter' only multiple regression, three outliers were highlighted; their removal enabled stepwise multiple regression to run. The model *(Equation 4)* produced incorporated predictor variables time since low tide, adjusted air temperature and date, and explained 40% of variance in the original data. The regression had a relatively adequate fit of the data (R^2_{adj} =37.4%) and predictors together were significantly associated with predicted *proportion of seals hauled-out* ($F_{(3, 68)}$ =15.12, P<0.05). All predictors had significant negative effects on predicted *proportion of seals hauled-out* at any one time (*Table 10*). The unstandardised residuals were normalised according to Q-Q plot and Kolmogorov-Smirnov test (*K-S statistic* =0.053, *d.f.* =72, *P* =0.200), thus validity of ANOVA/t-tests were fairly stable. However, three outliers were removed to enable stepwise regression therefore interpretation of results should be in light of this. Furthermore, the outliers were not erroneous values but infrequent occasions when number of seals in water exceeded that hauled. Although removing outliers enhanced/enabled the fit of the regression, it would be invalid to disregard them. In conclusion, further data is required to more accurately interpret the regression and identify predominant environmental influences on proportion of seals hauled-out at a given time.

Table 10: Results for stepwise multiple regressions of the proportion of grey seals hauled out at any one time. Italics refer to regression in absence of outliers; regression did not occur in their presence. Eqn 4: Predicted (Proportion Grey Seals Hauled) = 132.863 – 0.56(time since low tide) – 0.28(adjusted air temperature) – 0.24(date).

	Standardised Coefficients		Unstandardised Coefficients	t-test		
Variable	B	S.E.	β	t-value	*d.f.*	*P*
Time Since Low Tide	-0.002	0.000	-0.557	-5.909	68	<0.05
Adjusted Air Temperature	-0.889	0.641	-0.278	-2.945	68	<0.05
Date (Observation Number)	-0.368	0.146	-0.238	-2.524	68	<0.05

8.3.3. Maximum Daily Haul-Out Count (MDHO)

To explain 91.62% of variance in original data, seven components were required to be extracted. However, four components *(Table 11)* were extracted from twelve variables entered into analysis and explained 75.70% variance in the original data. Adjusted air temperature and *ambient air temperature* had high negative component loadings on component one, time since sunrise and time of day correlated highly with component two; tidal phase and time since low tide correlated with component three whereas disturbance had high component loadings on component four.

Table 11: PCA results regarding proportion of grey seals hauled-out at any given time. *variable excluded from stepwise multiple regressions to reduce multicollinearity, assessed by condition indices.

Factor	Percentage Variation Explained	Independent Variable (Predictor)	Component Loading
1	32.20%	Adjusted air temperature*	0.93
		Ambient air temperature	0.87
2	21.08%	Time since sunrise*	0.94
		Time of day	0.94
3	13.67%	Tidal phase	0.86
		Time since low tide	0.83
4	8.75%	Disturbance	0.86

Five variables corresponding to these four components were entered into stepwise multiple regression. Following Pauli & Terhune (1987a), maximum daily haul-out (*MDHO*) counts were used to eliminate autocorrelation among counts on a minute-by-minute basis, thereby diminishing the strong tidal influence. The final model incorporated time of day and disturbance (*Equation 5*), explaining 36.7% of variance in the data. Although the regression was a fairly inadequate fit of the data (R^2_{adj} = 35.3%), association between the predictors and *MDHO* was significant ($F_{(2, 89)}$ =25.85, P<0.05). With either variable held constant, the other variable had a negative effect on predicted *MDHO*, such that with disturbance held constant, for every 15-minute increase in time of day predicted *MDHO* count decreased by 0.53 seals; with time of day constant, presence of disturbance at Bird's Rock caused predicted *MDHO* count to be 0.18 seals less than times without disturbance. Both predictors had significant negative effects on *MDHO* (Table 12). To assess validity of statistical tests residuals were checked; Q-Q plot/Kolmogorov-Smirnov test indicated residuals were normal at P =0.01 level (*K-S statistic* =0.106, *df* =92, P =0.012). Following subsequent removal of three outliers revealed in initial regression, regression was re-run to asses their effect. In their absence, the model produced incorporated identical predictors entered, having similar significant directional relationships. Therefore removing outliers did not greatly affect outcome, however in their absence the resultant model explained a greater proportion of variance in the data (R^2 =41.5%) with an improved fit to the data (R^2_{adj} = 40.2%) and a significant linear relation between predictors and *MDHO* ($F_{(2, 87)}$ =30.90 P<0.05). The outliers were not erroneous values but correct data whereby the *MDHO* count was high (e.g. 8-10 seals) compared to the majority of maximum daily haul-out counts.

Table 12: Results for stepwise multiple regressions of the maximum daily haul out count (square-root transformed) data. Regular font refers to initial regression; italics refer to regression output in absence of outliers. Eqn 5: Predicted(MDHO) = 2.749 – 0.53(time of day) – 0.18(disturbance); Eqn 6: Predicted MDHO = 2.681 – 0.547(time of day) – 0.216(disturbance).

	Standardised Coefficients		Unstandardised Coefficients	t-test		
Variable	B	S.E.	β	t-value	*d.f.*	*P*
Time of Day	0.000	0.000	-0.527	-5.977	89	<0.05
Disturbance	-0.191	0.092	-0.183	-2.079	89	<0.05
Time of Day	*0.000*	*0.000*	*-0.547*	*-6.381*	*87*	*<0.05*
Disturbance	*-0.209*	*0.083*	*-0.216*	*-2.520*	*87*	*<0.05*

Finally, consistency in the regression outcomes regarding number of hauled seals and maximum daily haul-out count reveal that time of day and disturbance are the main influential variables on grey seal haul-out numbers. The tidal cycle, temperature & date have greater influence on the proportion of grey seals hauled-out at Bird's Rock.

8.4. Potential Human-Induced Disturbance

Significant variation in frequency of each type of human activity passing Bird's Rock was found (χ^2 =4288.35, *d.f.* =7; P<0.05), such that coastal path walkers (W) were by far most numerous (67%), followed by VPBs (11%). Walkers did not appear to evoke a response in seals hence were not further analysed as it was assumed they did cause 'disturbance'. Seal responses to vessel activity were investigated.

8.4.1. Vessel Traffic

Between zero and 34 vessels per 3-hour survey passed Bird's Rock. On average 6.0 (±0.8 S.E.) vessels were counted per 3-hour survey, and 2.0 (±0.11 S.E.) vessels counted per hour effort travelling past the focal haul-out site each month. Therefore, vessel traffic did not significantly increase as study progressed (r =0.032, n =86, P =0.771). Significant variation existed in frequency of vessel type passing through the area (χ^2 =279.91, *d.f.* =6; P <0.05), whereby VPBs were most frequently observed (33%), followed by motorboats (MB, 26%), sailing boats (SAIL, 13%), RIBS/speedboats (SB/SS, 11%), commercial fishing vessels (CF, 10%), research vessels (R, 4%) and canoes (C, 3%). Jet skis (J) were not encountered.

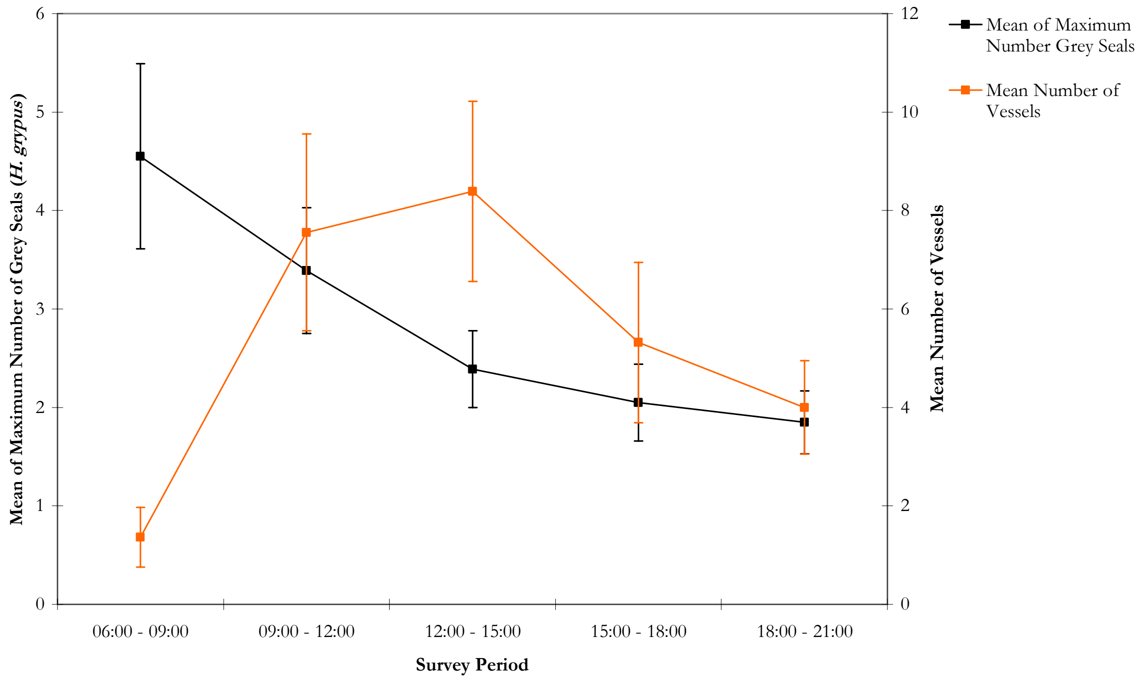


Figure 25: Mean (±S.E.) of maximum number of grey seals and mean (±S.E.) of total vessels observed from Bird's Rock per three-hour survey period during the complete sampling season.

Figure 25 illustrates how early morning surveys were least busy in terms of vessel traffic whereby hauled seals encountered 1.0 (±0.61 S.E.) vessel on average. A significant variation (χ^2 =192.29, *d.f.* =4, *P*<0.05, *vessels*; χ^2 =17.45, *d.f.* =4, *P*<0.05, *seals*) in vessel and grey seal counts per survey period existed throughout the day. Vessel traffic increased dramatically to an average 8.0 (±1.83 S.E.) vessels during 12:00-15:00 survey period, after which it progressively decreased to an average four vessels during evening surveys. However, one-way ANOVA revealed no significant difference in mean vessels counted per survey period ($F_{(4,\ 81)}$ =2.36, *P* =0.06), although Tukey-HSD tests revealed early morning surveys significantly differed in mean rank of vessels to mid-day period (12:00-15:00, *P*<0.05). Conversely, average maximum seal count per 3-hour survey steadily declined throughout the day from 5.0 (±0.94 S.E.) seals on average during 06:00-09:00 to 2.0 (±0.32 S.E.) seals on average during 18:00-21:00 survey period. A significant difference in mean seal counts per survey period ($F_{(4,\ 1088)}$ =31.23, *P*<0.05) were revealed; Table 13 shows such differences. Notably, initial decline in seals corresponds with the increase in vessels passing Bird's Rock.

Table 13: Pairwise comparison results of post-hoc Tukey-HSD tests (SPSS, Version 11.5.0) demonstrating which survey periods were significantly different in terms of mean counts of grey seals. Significant at P = 0.05 level.

Survey Period	Post-hoc Tukey-HSD outcome
06:00 - 09:00	All other survey periods
09:00 - 12:00	All survey periods except 12:00-15:00
12:00 - 15:00	06:00-09:00 and 18:00-21:00
15:00 - 18:00	06:00-09:00 and 09:00-12:00
18:00 - 21:00	All survey periods except 15:00-18:00

8.4.2. Grey Seal Behavioural Reactions in Response to Human Proximity

199 grey seal-vessel interactions were logged from Bird's Rock vantage point during direct observation surveys. Mean interaction time was five minutes in duration (range: 1–34 min), whereas interactions of three minutes were most frequently observed (n =41). The majority of vessels abided the code of conduct (n =190). A contingency table analysis performed between vessel type and vessel conduct (CF/MB and SAIL/R/VPB data were pooled respectively to fulfil analysis assumptions) indicated a significant relationship (*Fisher's Exact Test* χ^2 =37.21, P<0.05), such that most vessels primarily slowed down when passing seals. However of those observed, canoes approached seals more often than not (n = 4; *Figure 26*).

Figure 27 illustrates overall majority of interactions resulted in no change in numbers of seals observed after vessels passed them at Bird's Rock. Furthermore, a high frequency of interactions observed involved seals which permanently changed their behaviour after vessel had passed. A statistically significant relationship existed between seal behavioural response to interaction and seal response, in terms of seals counted, post interaction (χ^2 =116.70, *d.f.* =4, P<0.05), such that when seals did not change/temporarily changed their behaviour as vessels passed, the majority of pre-interaction counts did not differ from post-interaction counts. However, when seals changed behaviour completely, it more frequently resulted in a reduced seal count after the vessel departed the area.

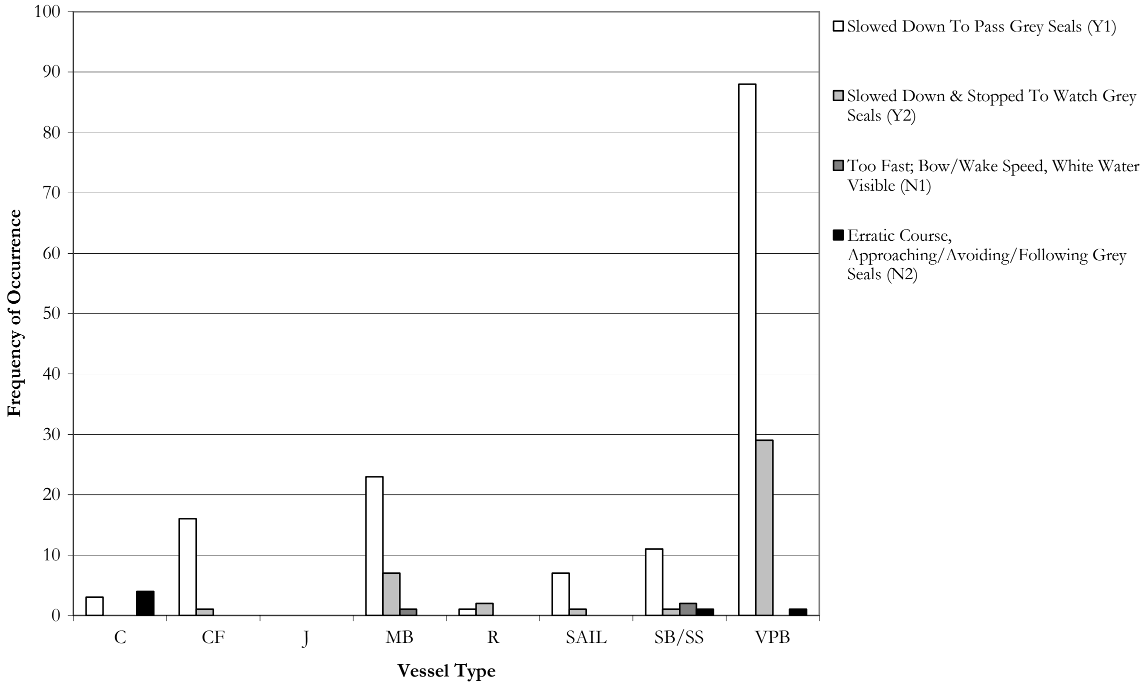


Figure 26: Total frequencies of vessel conduct per vessel type in response to grey seals, where C = canoe/kayak; CF = commercial fishing vessels; J = jet skis; MB = personal motorboats; R = research vessels; SAIL = sailing boats; SB/SS = RIBs and speedboats; VPB = visitor passenger boats (vessel categories following Lamb, 2004).

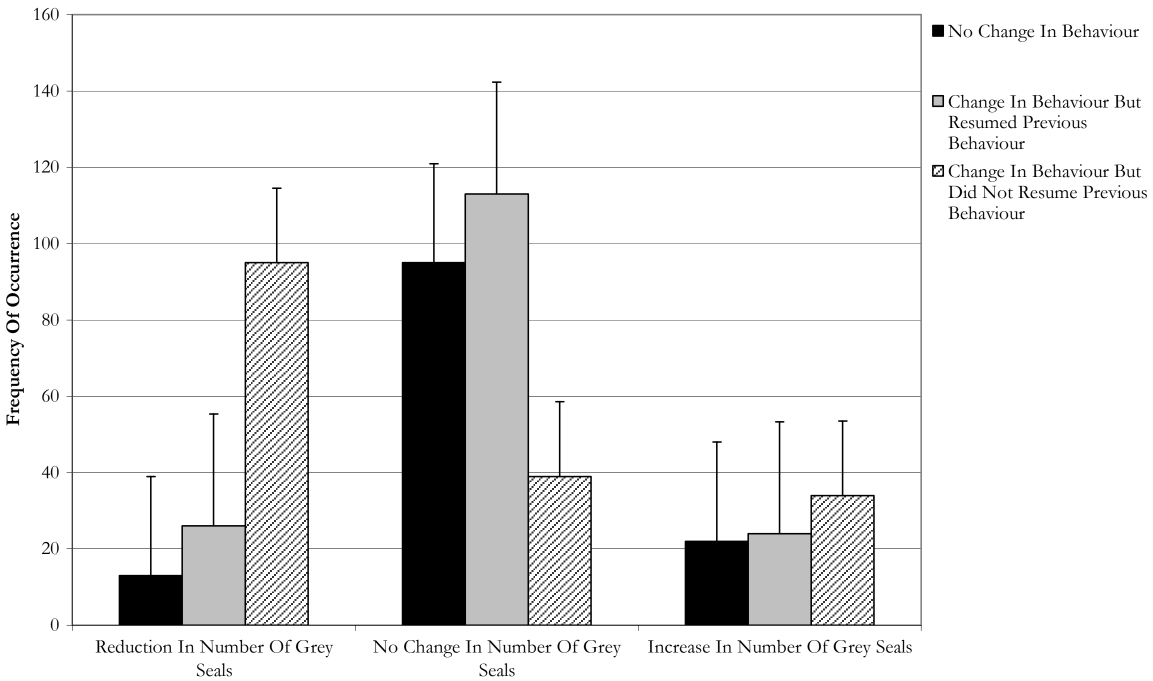


Figure 27: Total frequency (+S.E.) of behavioural responses of grey seals in terms of a reduction, no change or an increase in numbers observed per "interaction" depending on whether individual grey seals change their behaviour or not as vessels pass them at Bird's Rock.

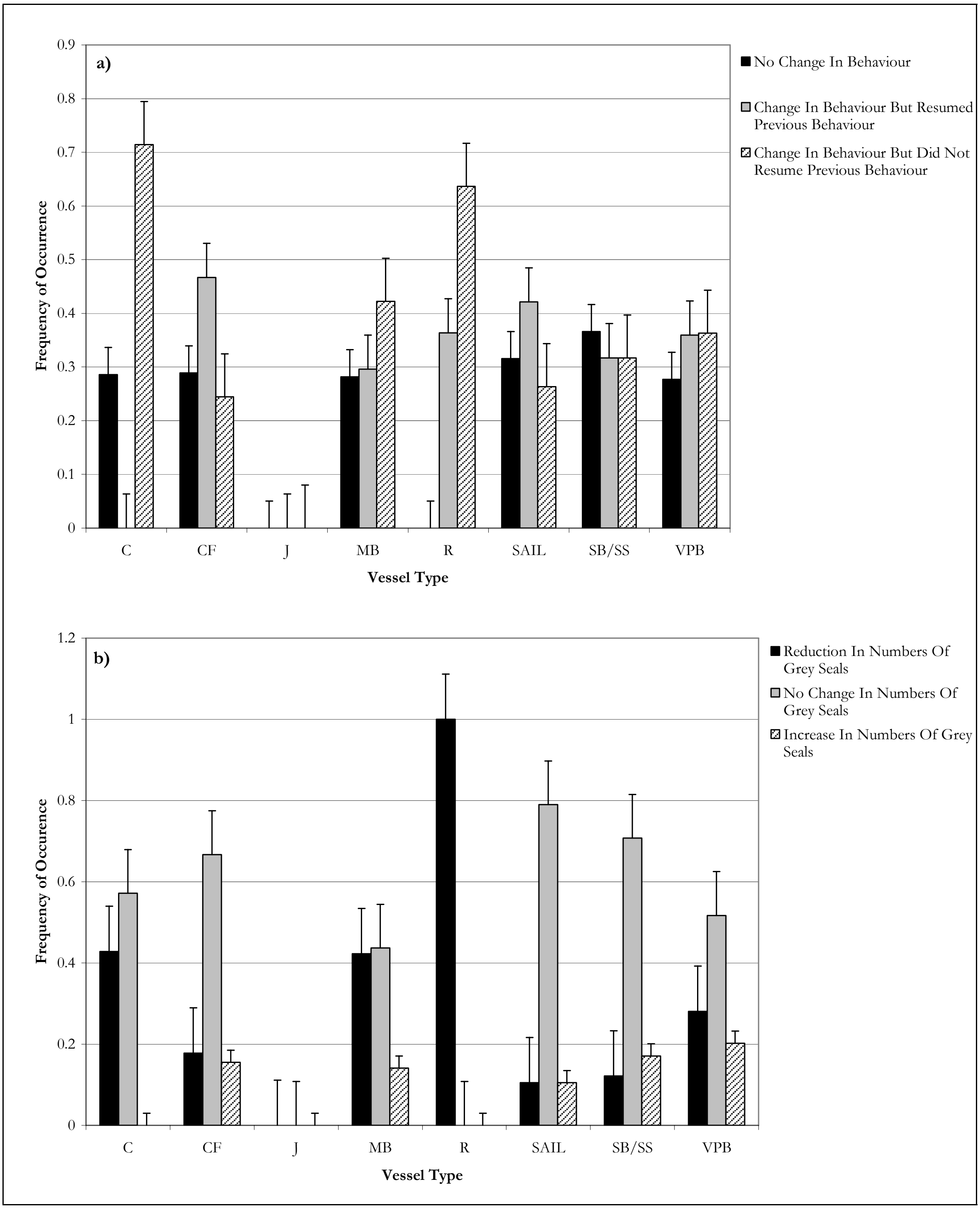


Figure 28: Mean frequency (+S.E.) of grey seal behaviour (a) in terms in terms of no change, change in behaviour but resuming previous behaviour (temporary) or changing behaviour completely (permanent) in response to vessel type. (b) Mean frequency (+S.E.) of grey seal response in terms of no change, increase or reduction in count between before/after interaction; C = canoe; CF = commercial fishing vessels; J = jet skis; MB = personal motorboats; R = research vessels; SAIL = sailing boats; SB/SS = RIBs and speedboats; VPB = visitor passenger boats (vessel categories following Lamb, 2004).

Fairly similar frequencies of grey seals displayed either no change, a temporary or permanent change in behaviour with each vessel type encountered during interaction (*Figure 28a*). No statistically significant relationship was found between behavioural response of seals and vessel type (χ^2 =6.76, *d.f.* =8, *P* =0.562) hence there appeared to be no particular type of vessel which principally induced a permanent negative behavioural reaction in the seals at Bird's Rock. Furthermore, most interactions involved vessels which slowed down on passing seals at Bird's Rock (*n* =340); in such interactions similar mean frequencies of seals did not change, temporarily or permanently changed their behaviour (*Figure 29*). When vessels slowed to a halt, the majority of seals modified their behaviour temporarily yet continued the pre-interaction behaviour after the interaction. A higher mean frequency of seals temporarily or permanently changed behaviour in response to fast moving vessels than not; only interactions resulting in seals completely changing behaviour in response to erratically moving vessels were recorded, such interactions predominantly involved canoes (*n* =7). However, no statistically significant relationship was found between vessel conduct and behavioural reaction of seals towards the passing vessel (*Fisher's Exact Test,* χ^2 =12.45, *P*<0.05).

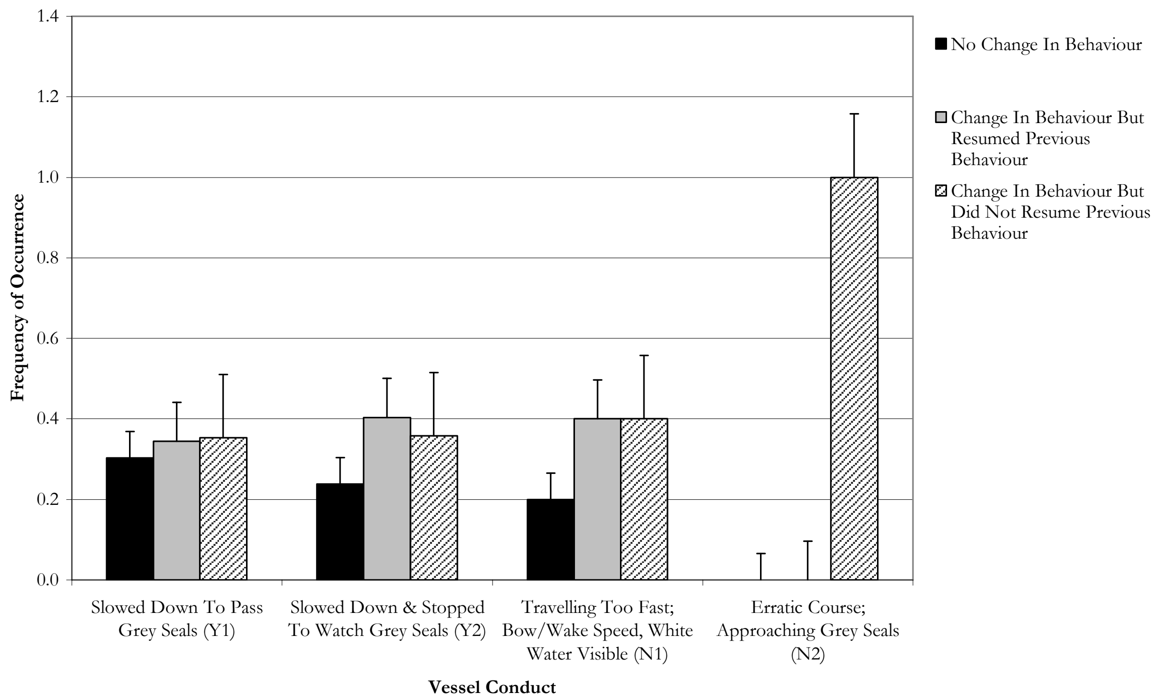


Figure 29: Mean frequency (+S.E.) of grey seal behaviour in response to vessel conduct, where Y1 = vessel slowed down to pass the grey seals; Y2 = vessel slowed down & stopped to watch grey seals; N1 = vessel moved too fast, bow/wake speed, white water visible; N2 = vessel moved erratically, approaching/avoiding/following grey seal(s), (vessel categories following Lamb, 2004).

The closest grey seal-vessel distance was recorded for every interaction (*Figure 30*). Overall, a higher frequency of interactions occurred within 21–30m category (*n* =100); few interactions occurred within 81–90 m category (*n* =1). A statistically significant relationship occurred between closest seal-vessel distance and seal behavioural reaction (χ^2 =23.02, *d.f.* =12, *P*<0.05), such that when vessels were closer to the seals (0–30m) the majority of seals temporarily changed behaviour whereas when the distance exceeded 31m most seals permanently changed their behaviour following interaction.

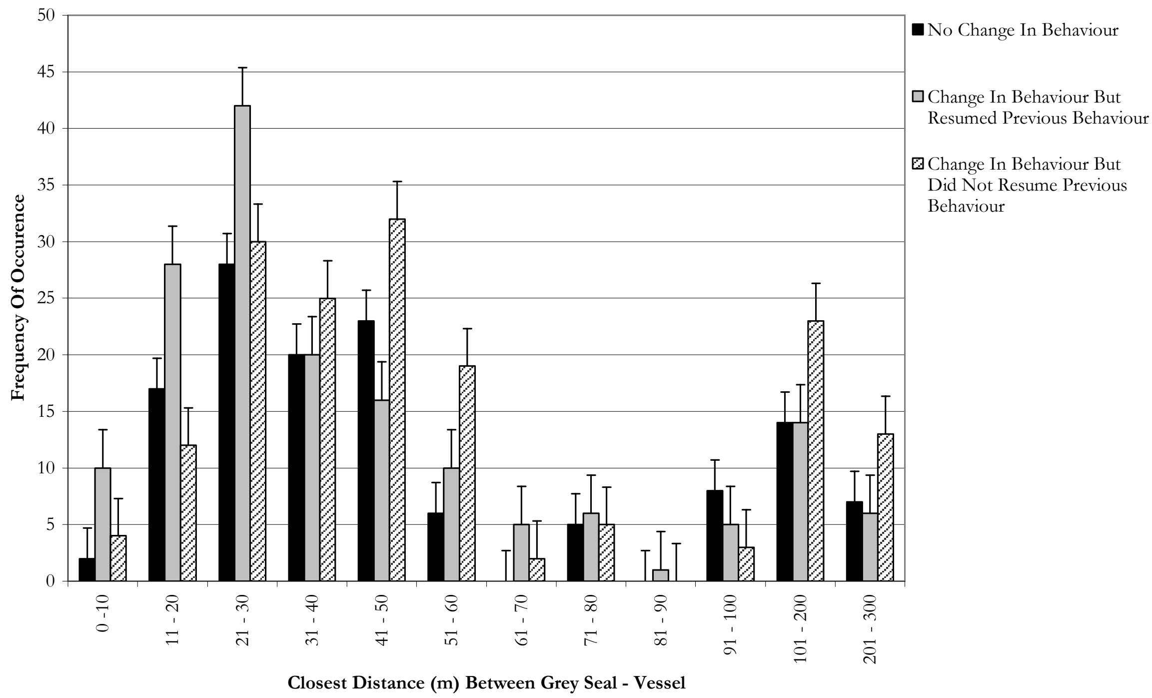


Figure 30: Mean frequency (+S.E.) of grey seal behaviour in terms of no change, change in behaviour but resuming previous behaviour (temporary) or changing behaviour completely (permanent) to closest proximity of vessel (m).

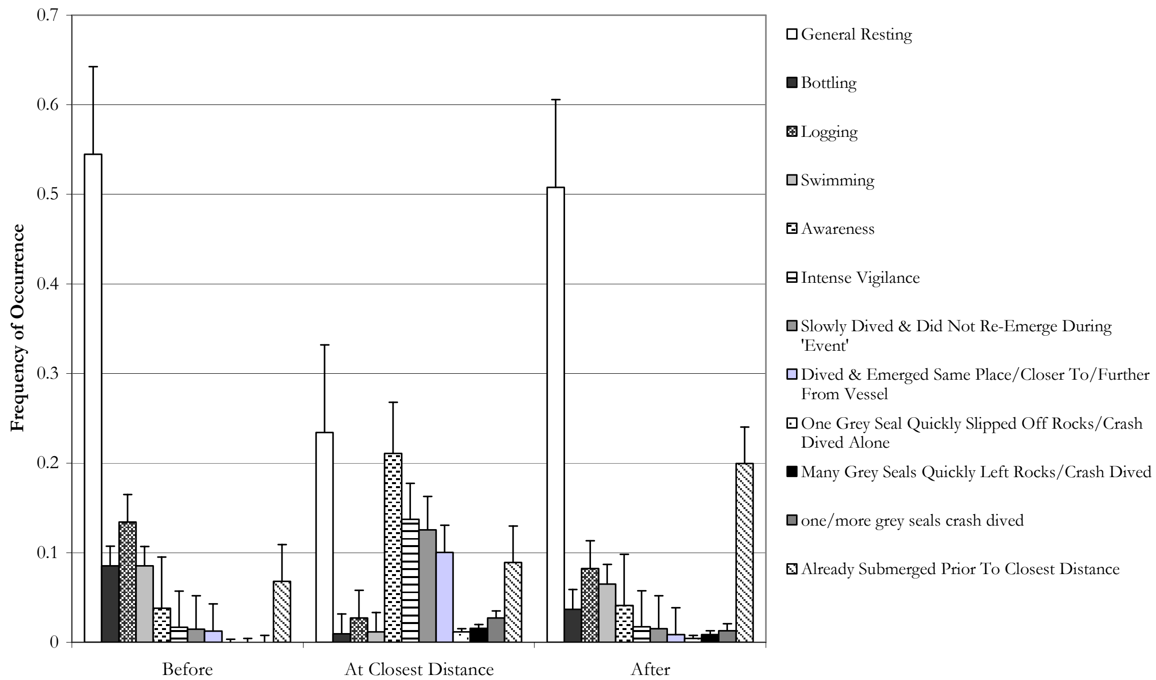


Figure 31: Mean frequency (+S.E.) of specific grey seal behaviour before, at closest distance to vessel and after vessel has passed them Bird's Rock.

Figure 31 illustrates how mean frequencies of grey seals resting, bottling, logging and swimming decreased when vessels were at their closest distance to the seals yet increased back to a similar pre-interaction levels once vessels had departed the area. Conversely, mean frequencies of seals displaying behaviour equating to an awareness of vessels (i.e.: intense vigilance, diving without re-emergence, or diving/leaving rocks quickly etc.) increased when vessels were at the closest distance yet declined to pre-interaction levels after the interaction. Therefore, a significant relationship existed between behaviour exhibited by the seals and the stage (before/closest distance/after) of interaction (χ^2 =544.24, *d.f.* =22, P<0.05).

Prior to log-linear analysis, cross-tabulation was undertaken between seal response and the variables: day, interaction duration, closest seal-vessel distance, vessel type, and vessel conduct. Significant associations were not found between seal response and interaction duration, closest distance or vessel conduct, however significant associations were revealed between seal response and day and vessel type (*Table 14*). The latter variables were used in a three-way interaction hierarchical log-linear analysis using backward elimination to determine which associations existed between day and vessel type with seal response (*Table 15*). One-way effects were found to be significant, Likelihood Ratio (LR) $\chi^2(8)$ =720.12, P<0.05; two-way effects were also significant, LR $\chi^2(13)$ =39.25, P<0.05. Three-way effects were not significant (LR $\chi^2(6)$ =5.64, P =0.464). Interactions mainly resulted in no change in seal counts before/after interaction; however of those observed, research vessels only resulted in a reduction of seals counted post-interaction (*Figure 28b*). Nonetheless, the 'Vessel Type x Seal Response' interaction was not significant hence the generating class of the final model comprised the interactions 'Day x Vessel Type' and 'Day x Seal Response'. Therefore, a higher proportion of all seven vessel types were involved in an interaction during weekdays than weekends and a greater proportion of interactions resulted in no change/increased seal count rather than a reduced seal count post-interaction. No bias was found between seal response and vessel type, hence seals did not appear to react more negatively towards a particular vessel type. However, since the sample size is small and LR χ^2 goodness of fit test indicated the model was a poor fit of data (LR $\chi^2(12)$ =15.93, P =0.195), further data collection would enable valid interpretation of the impact of potential disturbance variables on seal response.

Table 14: Results of cross-tabulation (Fisher's Exact Test) between grey seal response and five potential 'disturbance' variables. Bold typeface indicates significant association. *used chi-square test of association because all expected values exceeded 5.0; degrees of freedom in parentheses.

Variable	χ^2	*P*
Day*	**10.82 (1)**	**0.001**
Interaction Duration	0.94	0.920
Closest Distance	5.59	0.056
Vessel Type	**11.96**	**0.045**
Vessel conduct	6.32	0.075

Table 15: Backward selection of log-linear analysis. Variables are: 1 (seal response), 2 (vessel type), 3 (day of week).

Model	LR χ^2	d.f.	*P*	Term deleted
[123]	5.64	6	0.464	
[12] [13] [23]	15.93	12	0.195	[12]
Final model = [13] [23]				

8.5. Site Fidelity

Photographs were obtained opportunistically during VPB trips, direct observational surveys at Bird's Rock and provided by *Cwmtydu Bay Wildlife Organisation* (2003–2005). Overall 27 individuals, comprising 19 females, 5 males and 3 juveniles, were identified within three key areas along CMHC, namely Bird's Rock (BR), Cwmtydu (CT) and Cardigan Island Farm (CIF). At least 6[*] pups were born and photographed at Cwmtydu between 2003 and 2005 however were excluded from analysis due to their lack of distinguishing features imperative for individual recognition. During 2005 breeding season three pups were born at Cwmtydu, the first pup left the beach by August Bank Holiday hence it and its mother were not photographed; pup 2 was born in a cave on approximately 31st July yet it was weaned on discovery thus images of its mother were not obtained. Pup 3 (male) was associated with female 032, despite its mother's persistence pup 3 was reluctant to feed. Given its malnourished state (See Boyd *et al.*, 1962) it was rescued, rehabilitated and released by *Welsh Marine Life Rescue*. *Table 16* specifies sighting frequencies per identified grey seal; 13 individuals (48%) were identified for the first time for the season sampled, thus site fidelity for these individuals is yet to be established. Furthermore 14 individuals (52%) identified were resighted at least twice within one season (range:2–11 sightings/season), indicating grey seals display a degree of intraseasonal site fidelity within a 4-month period (June to

[*] Seven pups are known to have been born at Cwmtydu but only six were photographed.

September). Two individuals (7%) demonstrated a level of interannual fidelity specifically to Bird's Rock and Cwmtydu: individual 015 (male) was the most frequently sighted seal, first sighted at Cwmtydu in 2003 where it was resighted in 2004, then resighted at Cwmtydu and Bird's Rock in 2005. Individual 007 (female) was initially sighted at Cwmtydu in 2004 where she was known to have pupped; she was re-sighted once at Cwmtydu on 20th August 2005, however it is unknown whether she pupped. For an image of each identified grey seal refer to *Appendix 5.*; attached CD-Rom holds further images.

Table 16: Sighting frequencies of 27 identified grey seals between 2003 and 2005 along the Ceredigion Marine Heritage Coast. Bold type signifies individuals which demonstrated a degree of interannual site fidelity to Cwmtydu and/or Bird's Rock.

		Frequency of Sightings			
Number	Identification Number	2003	2004	2005	Total
1	001	7	0	0	7
2	002	8	0	0	8
3	**007**	**0**	**7**	**1**	**8**
4	008	0	10	0	10
5	009	0	11	0	11
6	**015**	**3**	**2**	**9**	**14**
7	016	0	0	1	1
8	018	0	0	2	2
9	019	0	0	7	7
10	020	0	0	1	1
11	021	0	0	1	1
12	022	0	0	1	1
13	023	0	0	3	3
14	024	0	0	2	2
15	025	0	0	2	2
16	026	0	0	2	2
17	027	0	0	1	1
18	028	0	0	6	6
19	029	0	0	1	1
20	030	0	0	1	1
21	031	0	0	1	1
22	032	0	0	4	4
23	033	0	0	1	1
24	034	0	0	1	1
25	035	0	0	1	1
26	036	0	0	1	1
27	037	0	0	1	1

8.5.1. Specific Rock Preferences

Specific rocks within the Bird's Rock haul-out site, on which seals hauled, were recorded for 882 observations. A significant variation in the rocks utilised for hauling-out was found (χ^2 =1704.97, *d.f.* =12, P<0.05), such that seals were not observed hauled upon rocks F and J;

rock A was most frequently hauled on (*n* =299), followed by rocks D, B and H (*n* =185, 169 & 135, respectively). The remaining rocks were hauled upon less frequently (*Figure 32).* In conclusion, grey seals appear to have a preference for the rocks they haul-out on at Bird's Rock.

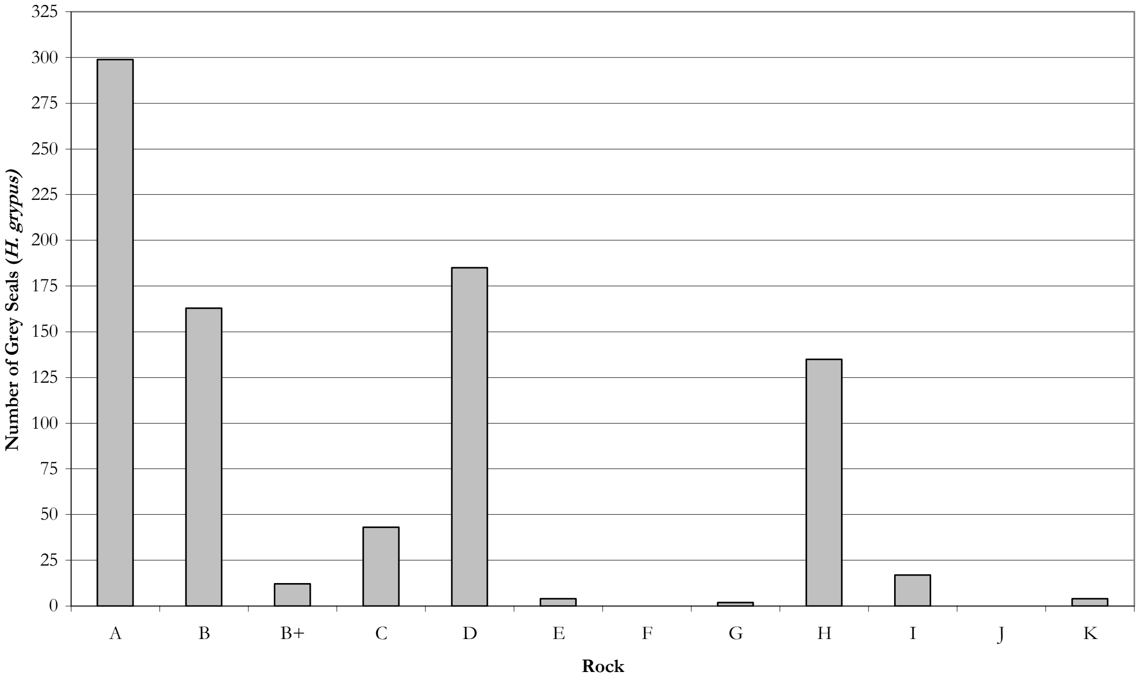


Figure 32: Total number of grey seals observed hauled-out on each major rock (labelled A to K) at Bird's Rock during 8th June and 1st September 2005.

9.0. Discussion

It has long been established that pinnipeds have an innate obligation to the land at particular stages within their annual cycle, to moult and produce offspring. While outside such seasons, grey seals (and other phocids) spend the majority of time at sea (Thompson *et al.*, 1991a; Sjöberg *et al.*, 1999), they exhibit a habitual behavioural trait entailing temporary haul-out bouts ashore. Exact benefits of hauling-out which outweigh costs of travel/foraging are uncertain (Stevick *et al.*, 2002) but numerous studies investigating the function of such behaviour besides the intrinsic breeding/moulting activities, attribute hauling-out to rest/sleep (Kreiber & Barrette, 1984; Brasseur *et al.*, 1996), thermoregulation (Watts, 1992), routine skin growth/maintenance (Watts, 1996), predator avoidance (Terhune, 1985; *DaSilva* & Terhune, 1988; Watts, 1992), sociality (Kreiber & Barrette, 1984; Godsell 1988; Pomeroy *et al.*, 2005) and vitamin-D synthesis (Watts, 1996). Several extrinsic factors are regarded to influence haul-out behaviour of seals at any given time, such as tide (Cameron, 1970; Schneider & Payne, 1983; Allen *et al.*, 1984; Pauli & Terhune, 1987a; Watts, 1992; Bjørge *et* *al.*, 1995; Roen & Bjørge, 1995; Watts, 1996; Bjørge *et al.*, 2002), seasonality (Grellier *et al.*, 1996; Watts, 1996), time of day (Finley, 1979; Allen *et al.*, 1984; Yochem *et al.*, 1987; Watts, 1992; Bjørge *et al.*, 1995; Roen & Bjørge, 1995; Watts, 1996; Sjöberg *et al.*, 1999), weather (Boulva & McLaren, 1979; Finley, 1979; Thomas & DeMaster, 1983; Pauli & Terhune, 1987b; Stewart, 1987; Godsell 1988; Kovacs 1990), availability of haul-out space, and disturbance (Calambokidis *et al.*, 1987; Henry & Hammill, 2001; Nordstrom, 2002). Analyses of data obtained via sightseeing (VPB) trips and direct observation shed light on haul-out behaviour, habitat use and site fidelity of grey seals populating the Ceredigion Marine Heritage Coast.

Overall, the mean number of grey seals observed per hour effort from VPB trips or direct observation each month did not significantly increase as the study progressed from April towards the breeding season in September. This is surprising since phocids are renowned to increase their numbers towards the breeding season (Calambokidis *et al.*, 1987). Perhaps lack of a marked increase in numbers in the area towards breeding season results from the dynamics of the apparently small population, compared to larger colonies inhabiting Ramsey & Skomer Islands, Pembrokeshire.

Results suggested one is more likely to observe a greater average of grey seals per hour effort watching from Bird's Rock than from VPB trips; this is logical since sightings from a moving vessel are reliant on chance. Furthermore, engine noise may indeed negatively affect grey seal sightings, perhaps causing seals to remain submerged or leave the area; sighting grey seals from a VPB at sea state three or above is difficult, whereas seals were clearly observed from the cliff up to sea state five.

9.1. Habitat Use

Although seals were not sighted within zone four in 2005, on the whole grey seals utilised all ten coastal zones between New Quay and Ynys Lochtyn. Overall, sighting frequencies were not equally distributed across all zones, such that in 2004 the greatest proportion of sightings occurred within zones five (n =83, 24%) and nine (n =72, 21%) as opposed to zones nine (n =194, 75%) and six (n =31, 12%) in 2005. Fewer seal sightings occurred in zones one to five, seven and ten during 2005 than the previous year, whereas more seal sightings were encountered in zones eight and nine in 2005 than 2004; similar sightings occurred within zone six in both years. The disproportionate sighting frequencies per year in zone nine, within which Bird's Rock haul-out site is situated (*Figure 2*), probably resulted from accidental sampling bias. Since the photo-identification aspect of this study primarily focused on Bird's Rock, increased effort was undertaken in zone nine to find seals suitable for photography. Furthermore, cumulative experience gained during direct observation from the cliff overlooking Bird's Rock inevitably enhanced the author's awareness of specific areas seals positioned themselves as VPB travelled by. It is believed the seals became more conspicuous to the author with increasing familiarity of the haul-out area and seal behaviour, e.g. when bottling, seals were typically well-camouflaged against the cliff within the coves of Bird's Rock thus difficult to spot unless this behaviour is anticipated, hence sightings at Bird's Rock inadvertently became easier to achieve.

The significant interaction found between seal behaviour and year, whereby a greater frequency of seals were observed in water in 2004 compared to the majority of sightings in 2005 involving hauled seals, may be a consequence of the individual observers' ability to sight seals in water/on land. This in turn is influenced by sea state (Barraclough, 2000); it is easier to observe seals on land from a VPB than in water, particularly when sea state exceeds Beaufort scale three.

Though no significant interaction was revealed, behaviour exhibited by seals appeared to differ within some coastal zones, presumably influenced by topographical/environmental factors specific to each zone, i.e. haul-out site availability, each of access to haul-out sites in terms of gradient and terrain, bathymetry of seabed and availability of 'patchy' prey. In both years seals were not observed hauled-out in zone one, this was likely due to chance since anecdotal evidence suggests seals do haul-out near Ynys Lochtyn. Alternatively, a strong tidal race exists in this area, which consequently increases productivity therefore prey abundance, potentially explaining why seals were always observed in water. Contrastingly, zones five and six had similar hauled/water sighting frequencies each year, suggesting these zones offer ample available haul-out habitat in addition to the adjacent sea; amongst other smaller ledges, rocks and coves, beaches such as Cwmtydu and Castell Bach are situated within zone six, the former being a prominent pupping site. It is unsurprising that a greater frequency of seals were observed hauled-out within zone nine since it comprises the renowned haul-out site, Bird's Rock. Furthermore, this haul-out site is inaccessible to humans by land thereby providing a relatively 'secure' area to rest (despite vessel traffic) when compared to the shingle-beaches further down the coast in zones five and six which are easily accessible to the public. Interestingly, seals select haul-out sites with distinctive features (Kreiber & Barrette, 1984); Bird's Rock is a pronounced landmark of the Ceredigion coastline. Seals were more frequently sighted in water within the remaining coastal zones, possibly due to limited haul-out sites, absence of prominent landmarks or simply chance. Numerous submerged/semi-submerged caves perforate the cliffs, providing potential secluded haul-out areas for seals; within zones where seals were only observed in water, on ebbing tides seals may potentially haul-out inside the caves, out of sight of observer. Grey seals have been observed in caves between New Quay and Bird's Rock; on two occasions during surveys, loud growling noises from a seal were heard and presumed to be coming from the cave at the front of Bird's Rock, as seals were not visible in the area.

9.2. Influence of Tide on Haul-Out Behaviour

Tides within Cardigan Bay are semi-diurnal with average tidal amplitude of 5.1m range. Consequently, quantity of seals hauled-out along the coast will be essentially influenced by tide as it directly affects availability of haul-out space. Seals were not observed hauled-out at Bird's Rock on tides above approximately 4.5m (*Figure 19*); such haul-out sites composed of several sloping rocky ledges which are almost all fully submerged at high tide, remove likelihood of hauling behaviour at such times. Although available at high tide, seals were not seen to haul-out on the main rock attached to the focal outcrop (*Figure 6*). However, haul-out space is available for six hours prior/post low water. Contrastingly, beaches along coast become partially submerged at high tide, providing alternative haul-out sites if necessary. This has been exploited by postparous seals at Cwmtydu, coming ashore near high tide to suckle their pup, (*pers. obs.*; Cameron *et al.*, 1970). Hence, when haul-out space is available at high tides, tidal height fails to influence time of peak haul-out (Yochem *et al.* 1987; Terhune & Brillant, 1996; Bjørge *et al.*, 2002).

Perhaps resulting from the time in the tidal cycle VPB trips typically commenced, a greater proportion of seals were observed during ebb tides in both years; hence higher mean score of seals hauled-out in both years. Tidal phase significantly influenced overall mean count of individuals sighted per trip in 2004 since it was revealed a higher mean score of seals were sighted during flood tides, subsequently corresponding to a significantly greater proportion of seals sighted in water. Conversely tidal phase did not significantly influence mean count of seals observed per trip in 2005, although a marginally higher proportion of seals were sighted during an ebbing tide also corresponding with more seals observed hauled-out. Similarly, although a significantly greater proportion of seals were observed on a flood tide during direct observation, tidal phase did not significantly influence mean scores of seals observed per survey at Bird's Rock.

In both years, significantly higher mean scores of seals were observed hauled-out than in water, suggesting seals ashore are easier to observe from VPBs/direct observation.

Furthermore the gregariousness of seals typically ensues that when one seal hauls-out, others follow.

Resembling Cameron *et al.* (1970), a significant interaction between tidal phase and seal behaviour existed in 2005, such that one typically observed seals in water during flood tides and hauled-out on ebb tides. Surprisingly, this association was not apparent in 2004 VPB data or from direct observation. In the latter instance, lack of interaction between tidal phase and seal behaviour may be understandable given personal observations where on numerous occasions during a rising tide, seals(s) already hauled-out (typically on rock A/C) at Bird's Rock would merely shift their position higher up the rock to a drier area until eventually the seal(s) was forced to enter the water; the seal(s) would either relocate to another rock with a higher gradient hence available haul-out space or remain logging/bottling in the vicinity. Therefore, seals could remain hauled on a flood tide up to the last instant on the highest of tides. This has also been witnessed in sea lions (*Zalophus californianus*) in Humboldt County, California (Sullivan, 1980). Another behaviour exhibited by seals particularly when hauled on rock B during a flooding tide was the 'banana' position, whereby the seal raises its head and hind-flippers into the air so as to reduce the body area getting wet by the incoming water; when the rock became fully submerged the seal would be forced into the sea. Conversely, on calm days when ample haul-out space was available, seals were observed to refrain from hauling-out, tending to effortlessly float next to the rocks instead; this has been reported in grey and harbour seals (Thompson *et al.*, 1991; Watts, 1996). Therefore, although haul-out space is available on an ebbing/low tide, the individual intrinsic requirements of the seal(s) influenced its hauling behaviour and not merely tidal phase alone. Future data collection is necessary to minimise discrepancies between sampled years to interpret extent of how tidal phase influences hauling behaviour, to improve use in local abundance estimates (*see* Grellier *et al.*, 1996).

VPB/direct observation data indicated no major linear correlations between number of hauled-out seals and hours from low tide, explicable since maximum haul-out numbers in numerous pinniped species reportedly peak at low tide (Schneider & Payne, 1983; Pauli & Terhune, 1987a; Roen & Bjørge, 1995; Bjørge *et al.*, 2002). Although maximum seal counts did not occur at exactly low tide in this study, VPB data revealed the maximum haul-out count occurred approximately 2.5 hours (n=8) and one hour (n=7) after low tide in 2004 and 2005, respectively. Overall in both years, highest haul-out numbers occurred one hour prior and between two and three hours after low tide; the majority of maximum haul-outs occurred after low tide. Direct observations indicated seals frequently hauled-out across the

12-hour tidal cycle, with the majority of seals hauled-out between two hours either side of low tide. Similarly, the maximum proportion of seals hauled of the maximum daily count occurred between three hours prior and up to four hours after low tide. During the study, an overall maximum of ten seals hauled-out at Bird's Rock approximately 1.5 hours post low tide (*Figures 14/33*). Furthermore, maximum daily haul-out counts demonstrated a significant linear relationship with time from low tide, such that when low tide occurred earlier in the morning the seals delayed hauling-out until after low tide, when the tide was rising. Whereas when low tide occurred later in the afternoon, the seals hauled-out on an ebbing tide prior to low water. This haul-out pattern, where time of peak haul-out in the tidal cycle changes with time of low tide, was also exhibited by harbour seals at St. Croix Island, Canada (Pauli & Terhune, 1987a). Analysis of the mean proportion of daily maximum number of seals hauled over time revealed no significant regression, suggesting that the seals followed the tidal cycle much more than a diurnal cycle.

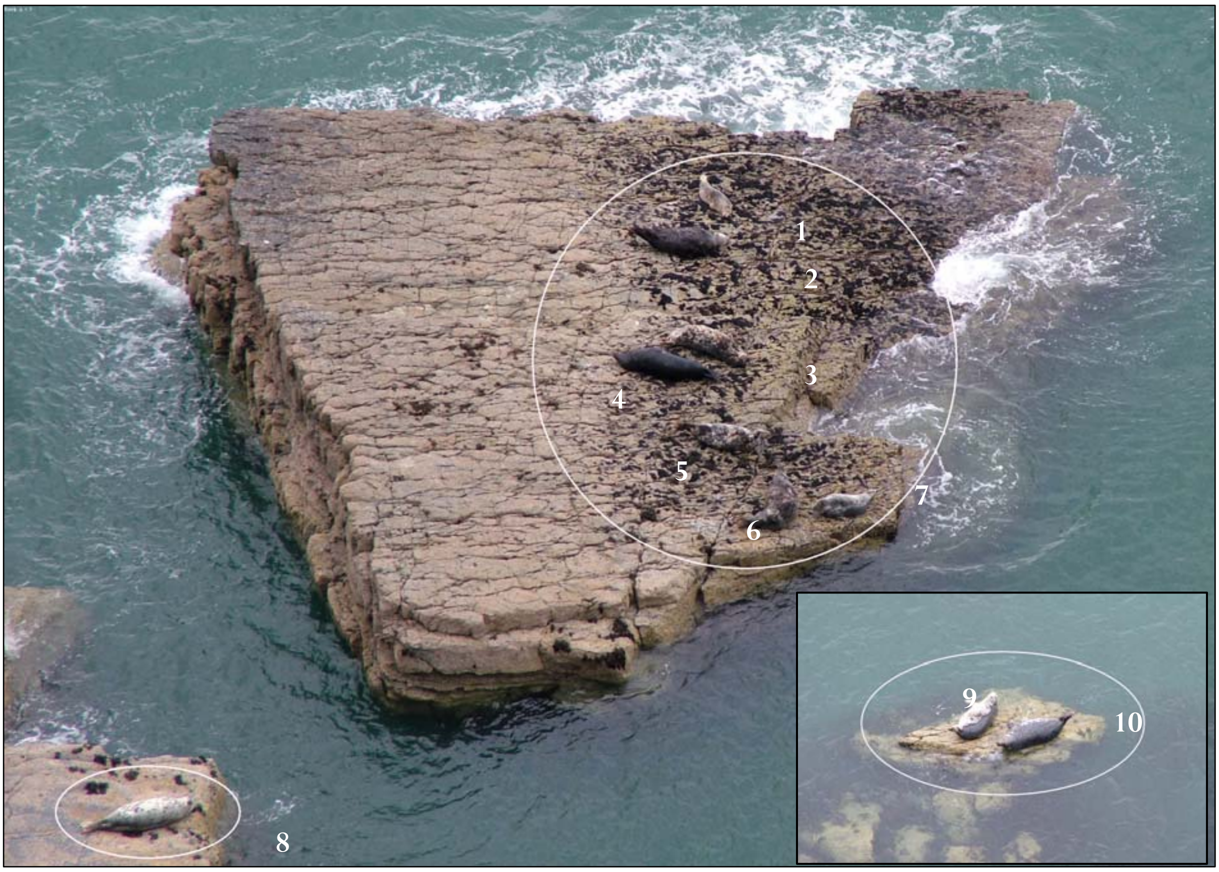


Figure 33: Distribution of the maximum number (n = 10) of grey seals hauled-out at Bird's Rock at 11:30 hours on 30th June 2005; a group of seven seals (juveniles & adults of both sexes) hauled on rock A, one pregnant female on rock D and two pregnant females hauled on rock B (inset). Low tide was at approximately 10:04 hours, thus maximum daily haul-out count occurred ca. 1.5 hours post low tide; ambient air temperature = 21.0°C; wind speed = 0.7mph; weather = overcast; sea state = 2. It can be seen that rock A is covered in lichen/seaweed on the lower half aiding the camouflage of the seals.

Although only basic analysis was undertaken, *figure 20* illustrates how the three major peaks in total grey seals observed at Bird's Rock on 30th June, 16th July and 2nd August, followed a spring tide (seven, ten and twelve days post spring tide, respectively). Spring tides are associated with strong tidal currents, therefore increased primary productivity upon which benthic and demersal fish feed. It is speculated the coincidental trend may have resulted from concentration of prey species by powerful spring tidal currents (Alldredge & Hamner, 1980; Irons, 1998) causing the influx in overall grey seals observed at Bird's Rock, a foraging area for grey seals and bottlenose dolphins (*pers. obs.*); a grey seal was observed foraging at Bird's Rock during two direct observation surveys. However, this necessitates further investigation of prey/fish abundance, grey seal diet and activities at Bird's Rock simultaneously.

9.3. Influence of Environmental Variables on Haul-Out Behaviour

9.3.1. Wind Speed & Sea State

Numerous studies demonstrate the effects of wind speed on haul-out behaviour of sub-/polar pinnipeds; however no consistent relationship exists for all populations or species. The discrepancies potentially a consequence of short-term research (see Grellier *et al.*, 1996). Several studies suggest increased wind speeds significantly result in a reduction of haul-out numbers (*ringed seals*, Finley, 1979; *harbour seals*, Watts, 1993; *Weddell seals*, Lake *et al.*, 1997; leopard *seals*, Rogers & Bryden, 1997), whereas other studies report haul-out behaviour to be independent of wind speed (*harbour seals in temperate regions*, Godsell, 1988; Grellier *et al.*, 1996). Similarly, no significant linear relationship was revealed between haul-out numbers of grey seals and wind speed at Bird's Rock despite the majority of high haul-out counts were observed at wind speeds less than 6.0mph, the overall maximum haul-out count occurred at 0.7mph and individuals did not haul-out at wind speeds exceeding 11.9mph. Stronger winds lead to increased sea states, thus despite no significant linear relationship between wind speed and haul-out numbers, both the mean total number of seals observed and mean number of seals hauled-out at Bird's Rock significantly declined from sea state zero (*total*: 8 seals/hour effort, *hauled*: 5.1 seals/hour effort) to five (*total*: 1 seal/hour effort, *hauled*: 0 seals/hour effort). Furthermore, a significant interaction existed between behaviour exhibited by seals and sea state; such that a greater proportion of seals were hauled-out between sea states zero and two whereas a higher proportion of seals were in water at sea states three to five. It follows that seals would be inclined to find hauling-out on land more challenging and energy-draining when contending with waves and swell of higher sea states, hence their tendency to remain in the water. Notably when seals were already hauled-out during calmer seas, with worsening sea states (>3) they would often be splashed by waves/sea spray and eventually move into the sea or relocate to a less wave-exposed rock. Similarly, Sullivan (1980) reported seals temporarily abandoned haul-out areas continually subjected to surf spray and wave action for less exposed areas. Pup and adult harbour seals' haul-out behaviour was also influenced by wave and wind intensity, preferring to haul-out during calm wind and remain in water during strong winds (Schneider & Payne, 1983; Lesage *et al.*, 1999; Bjørge *et al.*, 2002). In extreme conditions seals were washed off rocks A and C whereby individuals were committed to rolling down the rock in the backwash of a large wave into the sea; a form of energy-efficient locomotion observed by Bonner (1989) and serving as an alternative to expending energy on maintaining position on the rock during such conditions. It appears pointless for a seal to expend energy to remain on rocks which are continually swept by waves or hit by sea-spray during higher sea states/wind speeds, when rest/sleep can be achieved at the water's surface (bottling) and underwater (Ridgway *et al.*, 1975). Indeed, at sea states exceeding three seals present at Bird's Rock tended to adopt the bottling position; on several occasions one seal was seen bottling in the left alcove gradually drifting with the waves towards the cliffs, on almost reaching the cliff the seal would submerge briefly, re-emerging in the approximate place it had begun bottling and continue to rest. On two occasions a seal repeated this behaviour at least five times. Therefore, when resting on land becomes too energy demanding as a result of high wind speeds and subsequent rough sea states, it must be energy profitable to resort to resting at sea (Lydersen *et al.*, 1994).

9.3.2. Weather

Initial analysis suggested that as the weather category worsened (i.e. sunny, fair, overcast, rain, mist), total number of seals observed from the cliff declined from a mean of a six seals/hour effort during sunny weather to a mean of four seals/hour effort during misty weather. Further analysis revealed a significant interaction between weather and behaviour exhibited by the seals, such that during times of fair and sunny weather, a higher mean number of seals per hour effort were hauled-out on rocks than in water whereas when rain or mist occurred, a greater mean number of seals per hour effort were in the water. Interestingly, during overcast weather mean numbers of seals hauled-out and in water were equal. This may occur due to the interaction of weather and sea state because sunny and fair days tended to be calmer sea state days, rainy days tended to be rougher sea states whereas overcast days generally were either calm or rough sea states (note: unfortunately weather/sea state interaction could not be tested for significance in *SPSS*). Given the effect of sea state on grey seal haul-out numbers at Bird's Rock, one would expect a higher proportion of seals hauled-out on calm, sunny days than windy/rainy, rough days. Similarly, Pacific walruses, harbour seals and ringed seals have all been reported to haul-out more on sunny days (Fay & Ray, 1968; Boulva & McLaren, 1979; Moulton *et al.*, 2002); elephant seals are also affected by weather (Cruwys & Davis, 1995). Again the relation between haul-out behaviour and weather is inconsistent across species and populations, since Finley (1979) reported haul-out numbers of ringed seals declined in unusually warm, bright, calm weather conditions.

9.3.3. Air Temperature

Ambient air temperature and wind speed interact such that different combinations result in variations of the temperature experienced by seals on land, thus adjusted air temperature was calculated (Boulva & McLaren, 1979; Grellier *et al.*, 1996) to account for such wind chill factors. Grey seals hauled-out at Bird's Rock at temperatures between 13.6 to 33.9°C (adjusted air temperatures of 10.1 and 33.2°C), and a significant linear relationship was found whereby number of seals hauled-out decreased with increasing ambient air temperature. As reported by Lydersen *et al.* (1994), grey seal haul-out numbers decreased non-significantly with rising adjusted air temperatures. An overall maximum of ten seals hauled-out at 21.0°C (24.5°C, adjusted temperature). A negative relationship with temperature is to be expected such that seals enter the water when conditions become too hot, particularly when the thermoregulatory bases of the grey seal pelt are considered. Thermoregulation is required to maintain a specific core body temperature by way of balancing heat production with heat loss (Lavigne, 1982), however given their amphibious nature, pinnipeds, such as grey seals, must be capable of maintaining a stable body temperature within two media of different thermal properties, water and air. Water conducts air away from the body 25-times more efficiently than air (Castellini, 2002), thus potential high rates of heat loss when submerged are prevented by the seal either increasing metabolic rates (short-term physiological, energy expensive method) or increasing the insulative blubber layer (long-term morphological method, Williams & Worthy, 2002). Grey seals' blubber exhibits excellent insulative properties, permeated with blood vessels which constrict/dilate depending on whether a reduction/increase of blood flow to the skin is required to control for heat loss/gain (Bonner, 1989; Kvadsheim & Folkow, 1997; Williams & Worthy, 2002). Pinnipeds have arteriovenous anastomoses, specialised blood vessels in their skin which bypass the insulating blubber layer during extreme heat-stress, carrying excess heat to the skin's surface for dissipation (Kvadsheim & Folkow, 1997; Williams & Worthy, 2002). Seals' core temperature is near or slightly warmer than the external environment (Hart & Irving, 1959; Bonner, 1989).

Composed of stiff, dense hair the grey seal pelt traps a layer of stationary air within it to reduce heat loss (Williams & Worthy, 2002), this combined with the insulative properties and poor conductivity of blubber (Castellini, 2002) can have serious implications for seals on land during high temperatures, causing hyperthermia as observed in harbour seals (Watts, 1996). Other species have developed behavioural mechanisms to deal with extreme temperatures, i.e. repositioning into the shade when too hot (*Monk Seals, Castellini, 2002*), flipping cool sand onto themselves (*elephant seals,* Hindell & Burton, 1988), fanning flippers when hot/huddling when cold (*walrus*, Fay & Ray, 1968). On land, seals mainly lose heat via poorly insulated areas, e.g. flippers, anterior of head with its sense organs, nostrils and jaws (Williams & Worthy, 2002), however evaporation from the respiratory tract in grey seals accounts for merely 6–13% of the total heat production (Watts, 1992). To further complicate matters, phocids do not possess sweat glands hence cannot substantially cool down using the evaporative cooling technique (Watts, 1992; Kvadsheim & Folkow, 1997; Williams & Worthy, 2002), thus changing posture to increase area readily available to evaporative cooling (*walrus*, Fay & Ray, 1968) does not occur. Major evaporative cooling in phocids only occurs on initial emergence onto land, when the seawater evaporates from their pelt (Hind & Gurney, 1998). Continual conduction of heat via the pelt to the substrate on which it hauled provides another essential method of thermoregulation in phocids (Watts, 1992; Hind & Gurney, 1998). Often on hot, sunny days hauled-out seals would shift from one side to the next, perhaps as a method of cooling down one side of the body that had been absorbing heat. Behavioural thermoregulation by way of moving into the sea appears an adequate method of preventing hyperthermia. Weddell seals and walruses also retreat into water when temperatures become extreme (Fay & Ray, 1968; Castellini, 2002).

As expected ambient air temperature significantly varied during the day; highest average temperatures occurred between noon and 15:45 hours. However, on the whole maximum proportions of seals hauled per 15-minute interval did not synchronise with the average air temperature trend. Maximum proportions of hauled seals occurred in the early hours of the morning, when air temperatures were relatively low; a second smaller peak in proportion of maximum seals hauled occurred between 15:15 and 16:30 hours approximately near the warmest time of day; proportions of maximum seals hauled appeared to begin to rise from 19:30 hours onwards, as ambient air temperature began to decline into the night. Although restricted to daylight hours, the interesting diel cycle of behaviour revealed by surveys at Bird's Rock is unusual since several pinniped studies report a midday peak in haul-out numbers, synchronous with both diel light and temperature cycles (*crabeater seals*, Erickson *et al.*, 1989; *grey seals*, Lydersen *et al.*, 1994; *harbour seals*, Boulva & McLaren, 1979, Stewart, 1984, Calambokidis *et al.*, 1987, Watts, 1992, Roen & Bjørge, 1995, Watts, 1996; *leopard seals*, Rogers & Bryden, 1997; *ringed seals*, Finley, 1979, Moulton *et al.*, 2002; *Weddell seals*, Thomas & DeMaster, 1983, Lake *et al.*, 1997). Given their inability to sweat, during periods of high ambient air temperature and minimal wind (high adjusted temperatures), grey seals are threatened with hyperthermia unless they retreat into the sea. Therefore, the lack of midday peak in haul-out numbers of grey seals may result from a behavioural thermoregulatory mechanism, where seals remain in water during the warmest period of day to avoid excessive heat absorption (Watts, 1992; Williams & Worth, 2002). Furthermore, most literature investigates pinnipeds in polar climates, thus seals' insulative blubber/pelt may become more problematic on land during midday in warmer climates.

9.4. Influence of Time of Day on Haul-Out Behaviour

Further research suggests the decline in average seal count (total & hauled-out) per survey period from 06:00 to 21:00 hours at Bird's Rock may not be so atypical. Although based on SRDL information of one Baltic grey seal, Sjöberg *et al.* (1995) reported it chiefly hauled-out at dawn, dusk and over night; a later study of several tagged grey seals reported maximum proportions ashore occurred between 21:00-23:00 hours and 00:00-02:00 hours (Sjöberg *et al.*, 1999). Furthermore, Lydersen *et al.* (1994) report tagged female grey seals follow a diel haul-out pattern, hauling more at night (19:00-07:00 hours) than the remaining daylight hours. Harbour seals in Norway reportedly haul-out in the early morning (Roen & Bjørge, 1995). It would be of further interest to investigate those dark hours (21:00-06:00 hours) to find whether grey seals at Bird's Rock indeed haul-out overnight, tide permitting. Authors have attributed daily activity and subsequent rest from dusk to dawn with spatio-temporal behaviour of the seals' main prey species (Erickson *et al.*, 1989; Thompson *et al.*, 1991a,b; Lydersen *et al.*, 1994; Sjöberg *et al.*, 1995; Watts, 1996; Sjöberg *et al.*, 1999). Information regarding typical diet of grey seals along the CMHC is rare; it proved difficult to classify prey species eaten by a grey seal on two occasions of direct observation at Bird's Rock, however initial identification via binoculars on one occasion inferred sandlance (Ammodytidae spp.). Sandlance, consumed by grey seals in North Sea exhibit a diurnal activity pattern, feeding on zooplankton by day and burrowing into gravely/sand sediment by night (McConnell *et al.*, 1999; Freeman *et al.*, 2004). Thompson *et al.* (1991a,b) suggest harbour seals typically foraged during daylight because clupeoids formed dense schooling aggregations near the benthos during the day, making them easier to forage as opposed to the more dispersed distribution in the water column at night.

When the early morning haul-out peak is considered in light of vessel traffic, the decline in total seals observed at Bird's Rock evidently coincided with increased vessel traffic in the area. Seals encountered, on average, two vessels/hour effort during the early morning period (typically the local commercial fishing vessel or *Sea Watch Foundation* research vessel). During 09:00-12:00 survey, the balance shifted such that mean vessel count increased and mean seal count decreased. Vessel traffic peaked during 12:00-15:00 hours, coinciding with a smaller peak in haul-out count and the warmest period of day, but gradually decreased towards evening. Vessel traffic in Métis Bay (Quebec) followed a comparable trend, peaking at 14:00-15:00 hours; moreover the harbour seal daily haul-out pattern on disturbed days exhibited a parallel early morning maximum haul-out count which declined until approximately noon when a second smaller haul-out peak occurred, succeeded by a gradual decline towards evening (Henry & Hammill, 2001). Additionally, Calambokidis *et al.* (1987) reported the 12:00 harbour seal haul-out count in Muir Inlet (Alaska) was affected by the 11:30 arrival of the daily boat tour, causing varying numbers of seals to retreat into the sea. At Bird's Rock, during the morning period with infrequent vessel traffic a greater proportion of seals were hauled-out whereas during the remaining busier periods of day, similar proportions of seals were hauled-out/in water; suggesting seals seek refuge in water when vessel traffic is high. Furthermore, when five days without vessel traffic were analysed, Calambokidis *et al.* (1987) found a midday peak in haul-out numbers indicating vessel traffic impacted on harbour seal haul-out behaviour, displacing peak haul-out to 09:00 hours. Other authors report vessel disturbance alters pinniped haul-out behaviour (Sullivan, 1980; Watts, 1992, 1996).
Therefore, preliminary evidence from this study suggests a potential displacement of peak haul-out numbers of grey seals from midday to early morning, yet this necessitates further investigation. Daily VPB trips typically commenced at 10:30 hours, initially reaching Bird's Rock by 10:45 hours and could run up to 20:00 hours during peak summertime. Given the location of Bird's Rock and owing to fieldwork only undertaken during summer months, it was not possible to achieve sufficient days without vessel traffic to analyse data separately. Two 15-hour surveys and numerous intervals were undertaken within which seals did not encounter vessel activity, however the underlying reason no vessels ventured by Bird's Rock on such days was due to extreme weather conditions: on 20th July/3rd August 2005 seals were not observed hauled-out between 06:00-21:00 probably due to high wind speeds/sea states. Given the influence of weather on haul-out behaviour, this data alone would not be representative for comparison; investigation of calm days in absence of vessel traffic is

required to ascertain whether a midday haul-out peak occurs. However, such data would be difficult to obtain at Bird's Rock during the summer.

Although vessel activity may have induced the morning peak in haul-out count at Bird's Rock, the apparent disturbance by vessels may actually mask the true diurnal activity cycle of these grey seals.

9.5. Vessel Traffic as a Potential Source of Human-Induced Disturbance

Given popularity of the Ceredigion coastline for recreation and ecotourism, their obligatory use of coastal habitat inevitably exposes grey seals to high levels of human activities. As found, summer months are vibrant with tourists therefore vessel traffic increases in volume compared to winter months. Although it is assumed seals are vulnerable to human-induced disturbances particularly at times of heightened human activity, little information exists regarding the behaviour of grey seals at Bird's Rock to human proximity in terms of vessel traffic. A vast body of work has focused on human-disturbance of waterbirds (Burger, 1981; Pfister *et al.* 1992; Burger, 1994; Brown & Morris, 1995; Klein *et al.*, 1995; Gill *et al.*, 1996; Galicia & Baldassarre, 1997; Burger, 1998; Burger & Leonard, 2000; Leseberg *et al.*, 2000; Nisbet, 2000; Gill *et al.*, 2001a,b; Lafferty, 2001; Verhulst *et al.*, 2001; Ronconi & St. Clair., 2002). The parallels between waterbirds and pinnipeds (reliance on coastal habitat/colonialism) enable application of theory to both taxa. Nisbet (2000) defines *human disturbance* as 'any activity that changes the contemporaneous behaviour or physiology of one or more' seals; disturbance always elicits a short-term response in the seal(s). Pinniped studies document short-term responses to disturbance by unfamiliar humans (Taylor *et al.*, 1998), tourists (Kovacs & Innes, 1990; Cassini, 2001), air traffic (Born *et al.*, 1999) and vessels (Allen *et al.*, 1984; Calambokidis *et al.*, 1987; DaSilva & Terhune, 1988; Henry & Hammill, 2001; Engelhard *et al.*, 2002; Stevens & Boness, 2003). Further marine mammal research has shed light on behavioural responses towards human-induced disturbance (*bottlenose dolphins*, Acevedo, 1991; Constantine, 2001; Gregory & Rowden, 2001; Nowacek *et al.*, 2001; Constantine, 2004; *killer whales,* Williams *et al.*, 2002; *polar bears*, Dyck & Baydack, 2004; Lamb, 2004).

Short-term effects of vessels passing Bird's Rock were investigated by opportunistically logging *seal-vessel interactions*. Unequal sample sizes per vessel type/conduct/closest seal-vessel distance were obtained therefore definite conclusions cannot be drawn however preliminary evidence of short-term seal response to vessels is reported.

As expected, seal response (whether seals remained in or fled the area, deduced from counts before/after interaction) was significantly associated with seal behavioural response towards the passing vessel(s), such that when individuals did not change/temporarily changed behaviour the seals subsequently remained in the area whereas individuals that permanently modified their behaviour frequently resulted in reduced counts post-interaction, potentially fleeing the area. Given the majority of encounters resulted in seals displaying no apparent behavioural modification and no immediate flight from the area, by definition most seals did not appear to be disturbed in the short-term by such presence of vessels. Interactions leading to permanent behavioural modifications and reduced counts were secondarily prevalent, therefore suggesting a degree of disturbance by vessels occurred. Notably, significant association existed between actual behaviour displayed at three stages of interaction; mean frequencies of seals resting/bottling/logging/swimming decreased when vessels were at their closest distance yet increased to similar levels post-interaction as before interaction. Conversely, mean frequencies of seals exhibiting behaviour analogous to a degree of awareness of vessels increased when vessels were close and declined to similar levels post-interaction as observed pre-interaction (*see also* Galicia & Baldassarre, 1997; Engelhard *et al.*, 2002; Dyck & Baydack, 2004). Therefore seals which discontinued their archetypal behaviour engaged in *vigilance* when vessels were nearby, which is attributed to predator detection, foraging, observation of conspecifics, kleptoparasitism avoidance, and social cohesion maintenance (Lendrem, 1984; Hart & Lendrem, 1984; Quenette, 1990; Dyck & Baydack, 2004).

The risk-disturbance hypothesis stipulates animals perceive human-induced disturbance similarly to nonlethal predation stimuli thus behavioural responses exhibited during interactions are analogous to those elicited by natural predators[3] (Gill *et al.*, 1996; Gill & Sutherland, 2000; Gill *et al.*, 2001; Frid & Dill, 2002; Peters & Otis, 2005). Increased vigilance induced by predators/vessels prevents other fitness-enhancing activities (rest/parental-care/feeding/mating) therefore if unnecessary vigilance becomes costly to the individual (Gill *et al.*, 1996; Frid & Dill, 2002; Dyck & Baydack, 2004; Peters & Otis, 2005). Essentially, individuals must have a healthy balance between the benefits of increasing vigilance to reduce 'capture' and the energetic costs of locomotion/not foraging/not mating, i.e. optimise trade-offs in order to maximise individual and population fitness (Frid & Dill, 2002; Peters & Otis, 2005).

[3] Grey seals have no predators within Cardigan Bay; hunting is illegal.

Seal-vessel interactions predominantly involved VPBs undergoing either one or two hour trips to Cwmtydu or Ynys Lochtyn respectively. However, no significant association was revealed between vessel type and seal behavioural response since similar mean frequencies of seals exhibited no change/temporary/permanent changes in behaviour for most vessels encountered. Similarly seal response (pre-/post-interaction count) and vessel type were not associated. Overall, no particular vessel type significantly induced a negative short-term behavioural response in the seals. Although less frequently observed, interactions involving canoes/research vessels invoked the most interesting behavioural responses in seals. Similar frequencies seal-canoe of interactions resulted in no behavioural response/no change in count and permanent behavioural change/no change in count, occurring when canoes were between 25-55m distances and abiding the code of conduct. Interactions resulting in seals permanently modifying behaviour yet remaining in the area generally involved canoes abiding the code of conduct. However, the majority of seal-canoe interactions resulted in seal(s) permanently changing behaviour leading to a reduction of seals in the area; such negative interactions occurred when canoes violated the code of conduct by directly approaching seal(s), for example: Prior interaction, a female seal was observed logging between rocks B/C, apparently unaware of two approaching canoes. When canoes were approximately 20m distant the seal periscoped in their direction; one canoe remained at far-edge of rock-A and second canoe landed on rock-C, and the man got out of canoe to stand upon the rock, looking in direction of seal. The periscoping seal dived rapidly; on several occasion over ten minutes the seal submerged/resurfaced to resume vigilance, inquisitively periscoping at the man on rock-C. When canoes had departed the area, the seals resurfaced approximately 1m north of rock-A, scanned the area before diving out of sight. The delayed escape may have resulted since the water offered refuge and rapid escape if necessary; no seal-canoe interactions occurred with hauled-out seals. The next day, three canoeists[4] approached a seal in water. After initially periscoping, the seal swam further away, periscoped again then submerged, fleeing the area. Perhaps more canoes in proximity induced its hasty disappearance since increased humans/vessel numbers per interaction can induce escape-response (Constantine, 2001). Research vessel interactions primarily resulted in permanent behavioural modifications and reduction in seal counts, for example: six seals were resting at Bird's Rock (rock-A: 1 bull/2 juveniles, rock-D: 3 females), such group-hauling is documented as an anti-predation mechanism enabling individuals to increase sleep/rest time whilst raising their level of corporate vigilance (Hart & Lendrem, 1984; Kreiber & Barrette,

[4] The same two men were involved in negative seal-canoe interactions on successive days in June 2005.

1984; *DaSilva* & Terhune, 1988). At 08:20 hours, a research vessel approached Bird's Rock slowly/quietly, stopping briefly to undertake photo-identification of foraging bottlenose dolphins. When vessel was ~200m east, three females (rock-D) and one juvenile (rock-A) rushed with haste into adjacent water, the typical response of alarmed pinnipeds (Fay & Ray, 1968; Terhune & Brillant, 1996); the second juvenile (rock-A) scanned the area then slipped into the water ~two minutes later and the bull remained on rock A. Both juveniles and one female submerged, fleeing the area immediately; two females initially submerged then re-emerged closer, periscoping at vessel. At the closest seal-vessel distance, both females submerged whereas the bull increased vigilance, staring continuously at the passing vessel. Post-interaction, the bull continued resting; two females surfaced (scanning/logging) between rocks-B/C. All three interactions occurred during periods when vessel traffic is infrequent thus the startled response of unexpected activity. True behavioural responses of seals in water to vessels is difficult to assess, when it appears seals have fled the area, they may actually remain within the area, potentially interacting with vessel, submerged at depths invisible to observer.

Vessel approach/conduct is of interest; the significant relationship between vessel type and vessel conducted resulted since canoes approached seals more often than not, owing to their manoeuvrability and accessibility of shallower water. However, although research vessels abided the code of conduct yet short-term disturbance was clearly evident. Though large enough for visual detection the quiet, lingering, stop-start approach could be perceived as threatening. The observed response corroborates with other studies that suggest escape-responses result from unpredictable vessel approach. If seals do not detect slow-moving vessels until they are close there may not be sufficient time to modify behaviour in anticipation of vessel as they would for louder, constant approaching vessels (Terhune & Brillant, 1996; Henry & Hammill, 2001; Nowacek *et al.*, 2001). Given the infrequency of such interactions, the greater level of disturbance elicited is difficult to quantify in terms of long-term effects on seals; human disturbance can result in abandonment of haul-out sites (Sullivan, 1980).

Fortunately, most vessels abided the code of conduct, hence absence of association between seal behavioural response and vessel conduct; vessels slowly/constantly travelling past seals invoked similar frequencies of behavioural response whereas vessels stopping coincided with more seals temporary changing behaviour.

Within all distance categories, the majority of interactions did not result in seals fleeing the area. Regarding closest seal-vessel distance, converse results were revealed to that expected;

significant association existed such that vessels <30m to seal(s) mainly corresponded to seals temporarily modifying behaviour whereas when vessels were 31-300m distance, the majority of seals permanently changed behaviour. Such an outcome may be a consequence of vessels abiding the code of conduct, approaching/passing seals at Bird's Rock in a manner which mainly resulted in seals not changing or temporarily changing behaviour. Beyond the code of conduct boundary, vessels tended to move faster and engines produced greater in-air noise, potentially inducing permanent behavioural responses (Burger, 1981; Acevedo, 1991); however, acoustic cues were not measured.

It is suggested the term habituation has been widely misused within literature to describe behavioural responses that really denote variation in tolerance levels of individual(s) to a disturbance (Smith *et al.*, 2005) because evidence regarding repetitious measures of responses of individuals subject to true controlled repetition of the same stimulus is difficult to find. Since the majority of seal-vessel interactions resulted in no apparent behavioural response, the seals involved appear to have become highly tolerant to vessel presence/traffic. The remaining interactions involved seals exhibiting varying degrees of behavioural response/vigilance are indicative of various tolerance levels towards vessels, as demonstrated in other species (Acevedo, 1991; Constantine, 2001; Kelly *et al.*, 2004; Smith *et al.*, 2005). Such tolerance supports the risk-disturbance hypothesis because seals at Bird's Rock minimise energy expenditure by not increasing vigilance/fleeing area unnecessarily. With at least three decades of exposure to VPB trips operating from New Quay and escalation of coastal recreation, it is plausible cumulative experience has enabled grey seals to become tolerant of vessel activity. Having adequate in-air visual acuity, phocids can discriminate between objects of varying sizes, shapes and hues (Taylor *et al.*, 1998) and combined with their cognitive learning capacity (Nordstrom, 2002) and frequent exposure to vessels abiding the code of conduct, seals regularly visiting Bird's Rock have the potential capability to learn whether an approaching vessel (even at <30m) is a nonlethal stimulus hence safe to ignore or threatening and worthy of reducing rest/foraging to increase energetic costs via vigilance. It is evident a seal's tolerance towards vessels alters under certain circumstances (similar to Constantine, 2001; Frid & Dill, 2002), such that a fast, direct approach elicits permanent modifications of behaviour and even an escape-response, unsurprising when a direct approach by vessel/predator insinuates detection and intent to capture (Frid & Dill, 2002). Similarly, as indicated by this study quiet, slow/stop-start approaches may increase vigilance hence lower tolerance because approaching vessel is unpredictable and deserving of energy utilised in reducing likelihood of 'capture'.

The code of conduct appears successful in minimising permanent behavioural changes, seals' inclination to temporarily flee Bird's Rock hence unnecessary energy loss. Similar management plans elsewhere have notably reduced vessel-disturbance and increased fitness of wildlife (Burger & Leonard, 2000). However, in absence of data regarding seal-vessel interactions prior to implementation of the speed restriction imposed by the code of conduct, it is difficult to assess its overall effect on the seals.

It is speculated, many years without the code of conduct combined with ignorance regarding potential affects of vessels on wildlife, historic negative interactions between seals and fast-moving/inquisitive vessels could have resulted in the population becoming sensitised to such stimuli; sensitivity to exposure increases likelihood of an avoidance response (Constantine, 2001, 2004). Thereby modifying haul-out behaviour over time, resulting in the early morning haul-out trend observed today. One theory regarding the function of sleep suggests provision of time for recovery/maximally restoring depleted resources (physiological recuperation); the second (ecological) theory maintains sleeps 'is an appropriately timed period of non-responding, making the individual immobile and unresponsive when it is of adaptive advantage' (Meddis, 1975; Lendrem, 1984). Research on sleep deprivation indicates seals must sleep (Brasseur *et al.*, 1996; Sjöberg & Ball, 2000). Slow-wave sleep is achieved while submerged, yet grey seals only achieve rapid-eye-movement sleep when at water's surface or hauled-out thus hauling-out is essential for quality sleep (DaSilva & Terhune, 1988). Furthermore phocids are reportedly thermo-neutral when immersed, thus hauling-out may avoid elevated metabolic costs while sleeping (Watts, 1996) since phocids undergo voluntary apnea while sleeping on land, during which they experience physiological changes similar to those encountered when diving (Knopper & Boily, 2000). Early morning maximum haul-out is beneficial at individual and population level since it enables sleep/rest to occur within a period of minimal disturbance owing to low vessel traffic and provides protection required for potential vessel approach via corporate vigilance. Such haul-out behaviour exhibited at Bird's Rock may have resulted from a behavioural adjustment to vessel traffic to maximise sleep and retain energy for more worthwhile activities as opposed to hauling-out at midday which wastes energy on unnecessary vigilance towards vessels for those individuals with low tolerance.

Counting seals before/after a disturbance does not provide definite evidence the disturbance caused an overall reduction in numbers using the site (Gill & Sutherland, 2000; Gill *et al.*, 1996, 2001a,b; Henry & Hammill, 2001), because seals may only temporarily leave the site and return in hours/days. Juvenile 023 continued to haul-out at Bird's Rock throughout the study, despite involvement in numerous seal-vessel interactions, including one resulting in a hasty escape, suggesting abandoning this site may be too costly given limited availability of alternative hauling grounds inaccessible to humans along the coast. Seals often haul-out close to foraging grounds (Sjöberg & Ball, 2000), hence if Bird's Rock is regarded a high quality foraging site then seals will continue to haul-out despite continual disturbance (opting to increase tolerance) since it is less advantageous to abandon the site (Gill *et al.*, 2001b).

Finally, long-term affects of disturbance are difficult to establish; studies suggest long-term disturbance could result in subtle changes in body condition, growth rates, reproductive success, foraging success owing to relocating to less favourable sites (Gill & Sutherland, 2000; Gill *et al.*, 2001a,b Gregory & Rowden 2001; Engelhard *et al.*, 2002; Kelly *et al.*, 2004) and/or detrimental hormonal responses from stress (Fowler, 1999) therefore affecting individual and population fitness and survival. Assessment of long-term disturbance to the population should analyse behavioural responses in terms of individual fitness, focusing on parameters with known or expected links to reproductive success and subsequent survival (Gill *et al.*, 2001a,b; Engelhard *et al.*, 2002).

9.6. Site Fidelity

Site fidelity is prevalent in numerous territorial, colonially breeding insects, birds and mammals (*sparrowhawks*, Newton, 1993; *amberwing dragonfly*, Switzer, 1997b; *buffleheads*, Gauthier, 1990; *Ciconiiforms*, Cézilly *et al.*, 2000; Matthiopoulos *et al.*, 2005). For decades it has been recognised that seals reoccupy the same breeding grounds in successive years, i.e. *breeding* site fidelity (Boyd *et al.*, 1962; Lockley, 1966; Smith, 1966; Boness & James, 1979) as a result of their life history; pups evidently return to their birth site, i.e. *natal* site fidelity (Baker *et al.*, 1995; Miller, 2002). Breeding site fidelity is reportedly stronger than natal site fidelity (Pomeroy *et al.*, 2000b; Matthiopoulos *et al.*, 2005). Until focal studies emerged it was unknown whether the same individuals returned each year. Literature reports several pinnipeds, including grey seals, display site fidelity (*harbour seals*, Yochem *et al.*, 1987; Bjørge *et al.*, 1995; *southern elephant seal*, Hindell & Little, 1988; *northern fur seals*, Baker *et al.*, 1995; *grey seals*, Boness & James, 1979; Pomeroy *et al.*, 1994, 2000a, 2000b; Twiss *et al.*, 1994; Kiely *et al.*, 2000; Gaggiotti *et al.*, 2002; Miller, 2002; Stevick *et al.*, 2002; Vincent *et al.*, 2005).

Identification of 27 grey seals encountered during VPB trips along the CMHC demonstrated photo-identification as a successful method, giving rise to promising results; the majority of known individuals were resighted at least twice within the season first encountered, inferring intra-seasonal fidelity to Cwmtydu and Bird's Rock. Evaluation of inter-seasonal site fidelity was possible owing to images provided by *Cwmtydu Bay Wildlife Organisation*; images illustrated two individuals returned inter-annually.

9.6.1. Cwmtydu

Several advantages of site fidelity are documented; for species exhibiting sexual-segregation for most of their annual cycle, the mechanism of site fidelity ensures spatio-temporal aggregation of the sexes for procreation resulting in annual synchronous events (Pomeroy *et al.*, 1994; Stevens & Boness, 2003). Furthermore, site fidelity has been positively related to reproductive success (Newton, 1993; Baker *et al.*, 1995; Switzer, 1997a,b; Gauthier, 1990); an individual's existence is primary evidence its natal site was successful for rearing offspring to weaning age and finding a mate. Successful pupping seasons at the same site builds cumulative experience and reduces potential of relocation to an alternative site (Newton, 1993; Baker *et al.*, 1995). Given such potential effect of reproductive success, grey seals may have a capacity to combine intrinsic habitat cues with historic reproductive experience to assess the current/future quality of the site (Switzer, 1997b). Like colonially breeding insects, seals may also utilise reproductive success of conspecifics to assess site quality, thereby influencing future fidelity (Switzer, 1997b). Of 19 females identified, female 007 displayed intra-seasonal and inter-annual breeding site fidelity to Cwmtydu; initially observed in September 2004 with her pup, she was sighted seven successive days until her pup was weaned. During the same period female 009 and associated pup inhabited Cwmtydu beach. Presence of conspecifics potentially provided evidence the pupping site is successful. Female 007 was resighted at Cwmtydu in August 2005; it is unknown whether she pupped, however nulliparous females in Scotland return to the vicinity of locations occupied in a previous successful pupping year (Pomeroy *et al.*, 1994).

Correlation between onset of maturity/age and site fidelity is documented in numerous taxa, such that a propensity to switch breeding sites lessens with age (*sparrowhawks*, Newton, 1993; *northern fur seals*, Baker *et al.*, 1995; *amberwing dragonflies*, Switzer, 1997a,b). A female's faithfulness to an area is likely to cease following an unsuccessful breeding season, particularly if female is young (Newton, 1993; Switzer, 1997a,b) and inexperienced. Indeed, grey seals are known to relocate after a failed breeding season (Boness & James, 1979) and indirect evidence suggests this may have occurred in 2005; a female pup was born on Dolau beach (New Quay), popular with tourists and not typically regarded as a pupping site. This is possibly an example of a mother relocating to a new pupping site, either because the last site proved unsuccessful during pupping/breeding or a disturbance was encountered at the usual site. Disturbance of a female during the initial selection process of pupping sites, in which females come ashore and return to sea multiple times prior to site selection, may result in selection of an alternative pupping site (Anderson *et al.*, 1975; Pomeroy *et al.*, 1994). The pup was abandoned by its mother, attributed to known interaction with tourists despite the code of conduct prohibiting human approach/contact, illustrating alternating pupping/breeding sites is costly, since much energy is invested into reproduction (Bowen *et al.*, 1992; Twiss *et al.*, 2000a).

Figure 34: Female pup that was subsequently abandoned following human interaction on 4th September 2005, Dolau Beach, New Quay. The pup was rescued, rehabilitated & released by Welsh Marine Life Rescue, Milford Haven.

The mother was not photographed hence it remains unknown if she previously pupped at Cwmtydu and whether she returns to Dolau beach in future breeding seasons. Interestingly, female grey seals in Scotland return to previous pupping sites irrespective of interbirth interval and pupping history (Pomeroy *et al.*, 1994). Females must innately assess pros and cons of remaining at or changing pupping/breeding sites similarly to optimisation of trade-offs regarding vigilance and disturbance. Using photo-identification, it will be of interest whether the females identified return to CMHC in future seasons.

Male 015 initially photographed at Cwmtydu in September 2003 displayed the greatest degree of site fidelity than other identified seals, being resighted twice/once in 2004/2005 respectively (*Appendix 5*). Male grey seals witnessed at Cwmtydu behave synonymously with those in Scotland, not coming ashore prior to females giving birth (Twiss *et al.*, 1994). Similarly to bulls in Pembrokeshire, they remain almost exclusively in the adjacent sea to the breeding site, defending females rather than territories (Davies, 1949; Hewer, 1957).

9.6.2. Social Associations

As demonstrated by this and other studies, both grey seal sexes exhibit site fidelity (Pomeroy *et al.*, 1994; Twiss *et al.*, 1994; Amos *et al.*, 1995), yet further research is required to determine whether the sexes are equally faithful to Cwmtydu. Female spatial clustering at a breeding colony is determined by their gregariousness, pupping site selection, site fidelity (Boyd *et al.*, 1962; Anderson *et al.*, 1975; Fedak & Anderson, 1982; Anderson & Fedak, 1985, 1987a,b; Twiss 1991; Pomeroy *et al.*, 1994) and fine-scale topography of pupping/breeding site (Anderson & Harwood, 1985; Pomeroy *et al.*, 1994); all potentially enable development of non-random social associations and sociality (Twiss *et al.*, 1994; Pomeroy *et al.*, 2000b, 2005).

Literature reports female grey seals occupy a breeding site in the same orderly progression in successive years (Boness & James, 1979; Twiss *et al.*, 2000a), such that larger, older, dominant females arrive at pupping sites initially, followed by smaller, younger and less experienced females, thereby determining social structure within a colony. Furthermore, site faithful mothers inevitably become associated in consecutive years owing to their high annual return rates and tendency to give birth on approximately the same date annually (Boness & James, 1979; Coulson, 1981; Boyd, 1985; Jemison & Kelly, 2001). Annual proximity between specific individuals may promote advantageous associations that reinforce bonds, enabling cross-suckling among other altruistic behaviours (Pomeroy *et al.*, 2005) and reduced conflict (Pomeroy *et al.*, 2005) therefore increasing the mother's fitness. Female associations occurred at Cwmtydu: Females 001 and 002 were simultaneously present for at least ten days in 2003. On one occasion they were observed interacting/howling to one another at water's edge; interactions are likely when mothers are <3-4m apart (Pomeroy *et al.*, 2005). Similarly, in 2004 females 007 and 009 were ashore at overlapping periods when suckling young. Conversely in 2005, female 032 was not witnessed ashore with any other females.

Mothers at Cwmtydu ventured into the sea between suckling periods (similar to Orkney, Fogden, 1971; dissimilar to North Rona & Sable Island, Anderson & Harwood, 1985), and were often observed pacing back/forth along width of the beach seemingly looking for her pup ashore yet waiting for tide to be sufficiently high to reach pup with ease. Therefore females potentially associate with other individuals in adjacent sea to pupping site, as observed at Cwmtydu.

Where access to adjacent sea is difficult, grey seals in UK often breed close to pools in which mothers spend significant time resulting in temporary separation from their pups (Hewer & Backhouse 1960; Boyd *et al.* 1962; Anderson *et al.* 1975; Pomeroy *et al.* 1994; Twiss *et al.*, 2000a). Anecdotal evidence suggests the stream running to the upper shore at Cwmtydu is used more by moulting pups than mothers. Inter-annual associations reportedly exist between mothers that have switched to alternative pupping sites (Pomeroy *et al.*, 2005) thus further photo-identification of pupping females along CMHC would investigate this.

While mothers allegedly have no involvement with offspring post weaning, mother-daughter associations have been documented (Pomeroy *et al.*, 2000b). Strong site fidelity of mothers and philopatric daughters could produce matrilines to aide reproductive success by reducing agonistic encounters with conspecifics (Pomeroy *et al.*, 2000a,b). High pup mortality and low reproductive rates suggest matrilines are only feasible if related individuals aggregate via a mechanism (Pomeroy *et al.*, 2000b), for instance active coordinated movement was revealed when a mother-daughter grey seal pair were found on a different North Rona site to the daughter's natal site, inferring a level of individual recognition.

9.6.3. Mate Fidelity

As both sexes exhibit similar degrees of site fidelity and owing to their reproductive longevity (males: 10yrs, Twiss, 1991; females: ~30yrs, Twiss *et al.*, 1994), grey seals potentially form long-term mate associations, leading to specific repeated seasonal matings that give rise to full sibling offspring in successive years (Twiss *et al.*, 1994; Amos *et al.*, 1995; Pomeroy *et al.*, 2005). Indeed genetic analyses provide evidence supporting mate fidelity in grey seals; a high proportion of pups at North Rona were determined as full siblings, a proportion greater than that expected purely from site fidelity (Amos *et al.*, 1995; Worthington Wilmer *et al.*, 1999; Pomeroy *et al.*, 2000b; Worthington Wilmer *et al.*, 2000; Amos *et al.*, 2001).

Potential mate associations were observed at Cwmtydu. Although mating was not observed, females 001 and 002 were seen in close proximity to male 015 in 2003. Typical aggressive behaviour associated with polygyny (Amos *et al.*, 1995; Ambs *et al.*, 1999) was witnessed on 16th September 2004 between males 008 and 015, probably competing for access to one/both potentially receptive females 007 and 009. Aggression observed (17th September) between female 007 and male 008 was attributed to the female's nonchalance towards the male's advances. Further aggression observed (19th September) between the same pair was characteristic agonistic behaviour attributed to the primary stages of a sexual encounter (Anderson & Harwood, 1985; Bonner, 1989). Unsurprisingly, coitus was witnessed at the water's edge ~15-minutes later, demonstrating a polygynous mating system.

Although 007 was observed in the presence of 015 in 2004, it is unknown whether they mated. In 2005, female 007 and male 015 were sighted at Cwmtydu approximately a month apart thus mate association is possible. Additionally, female 032 was observed agonistically warning off male 015 in 2005, therefore this pair potentially mated.

With ongoing photo-identification effort along CMHC, particularly at Cwmtydu, future social/mate associations can be profiled and will potentially reveal maintenance of the highlighted associations as shown in Scotland; a par of grey seals known to have previously mated at one site were documented to have produced a pup at another site six years later, inferring long-term consortship with coordinated movement (Amos *et al.*, 1995; Worthington Wilmer *et al.*, 1999; Pomeroy *et al.*, 2000b; Worthington Wilmer *et al.*, 2000). Mammals that actively maintain inter-seasonal sociality are believed to uphold a level of social grouping outside the breeding season, potentially sustained via associations at temporary haul-out sites

during the year (Pomeroy *et al.*, 2005), e.g. Bird's Rock. Site fidelity outside the breeding season is less known, particularly along the CMHC, but continued photo-identification (and potential future use of SRDLs e.g. Vincent *et al.*, 2005) will broaden this knowledge.
Grey seal social/mate associations signify a degree of individual recognition, as observed in birds and primates (*rhesus monkeys*, Rendell *et al.*, 1996; *waterbirds*, Cézilly *et al.*, 2000; *California sea lions*, Pomeroy *et al.*, 2005). Vocal call recognition feasibly plays a role throughout a seals' life, since grey seal pup calls are sufficiently distinct for individual recognition by its mother (Fogden, 1971; Bonner, 1972; Caudron *et al.*, 1998; McCulloch *et al.*, 1999). Furthermore, northern fur seals (*Callorhinus ursinus*) retain memories of offspring's vocalisations for at least four years (Pomeroy *et al.*, 2005). Individual recognition would benefit site-faithful species since familiarity between related and non-related individuals should reduce aggression between associates and rival males (Twiss *et al.*, 1994, 2000a,b; Pomeroy *et al.*, 2005); knowledge of local terrain also potentially reduces inter-male aggression, increasing pup survival rates (Amos *et al.*, 1995). Reduced female aggression can result from familiarity with potential mates as new males arriving to a site disturb females greater than presence of dominant males (Pomeroy *et al.*, 2005).

Considering a traditional polygynous system of grey seals, strong philopatry (Pomeroy *et al.*, 2000b; Bowen *et al.*, 2003; Matthiopoulos *et al.*, 2005) could potentially result in detrimental inbreeding, particularly in small colonies where pups return and recruit into the adult breeding population (Pomeroy *et al.*, 2000b; Bean *et al.*, 2004). Grey seal daughters return close to their natal site thus remain spatially and temporally associated with their mothers and in potential range of their father or uncle(s) (Pomeroy *et al.*, 2000b; Worthington Wilmer *et al.*, 2000) therefore such fine-scale site fidelity may eventually reduce the gene pool and lower fitness, i.e. inbreeding depression (Bean *et al.*, 2004). Therefore mate fidelity provides an inbreeding avoidance strategy enabling a female to mate only with a specific unrelated male in successive years (Amos *et al.*, 2001). Since female grey seals mate 2.9 times, on average, with more than one male per season another strategy is required to reduce inbreeding (Amos *et al.*, 2001). Amos *et al.* (2001) revealed maternal half-sibling pups from different fathers were more genetically diverse than expected from random mating and speculated that mothers mate with genetically dissimilar males by way of individual recognition (e.g. MHC olfactory/vocal cues) or sperm selection (anti-sperm antibody production resulting in weak immunotolerance of previous partner's sperm which reduces potential fertilization by a relative.

Molecular analyses have roused suspicion regarding traditional polygynous mating system of grey seals which necessitates females give birth on land and invest in pre-weaning parental care whereas males contribute sperm. The degree of polygyny is determined by annual synchrony and female spatial clustering (Mesnick & Ralls, 2002); the latter establishing distribution and behaviour of males (Twiss *et al.*, 1994, 2000a). Typical female defence polygyny occurs when male grey seals' reproductive success is determined by number of sired offspring, creating intense inter-male competition whereby males move ashore to directly defend females (rather than territories) to obtain exclusive access (Greenwood, 1980; Bonner, 1989; Baker *et al.*, 1995; Coltman *et al.*, 1999; Amos *et al.*, 2001; Mesnick & Ralls, 2002). Subsequently, mating is presumed to occur solely on land with dominant males expected to sire most offspring therefore more likely to form a long-term mate associations. Some males observed along CMHC exhibit sequential polygyny, directly defending a lactating female and her vicinity until the mother becomes receptive, typically a group is formed comprising mother, pup and male (Mesnick & Ralls, 2002).

Although many full-sibling pups exist at the North Rona breeding site indicative of mate fidelity, the realisation that they were not sired by dominant males as expected (Amos *et al.*, 1995; Worthington Wilmer *et al.*, 1999, 2000; Bean *et al.*, 2004) undermined traditional theory. Moreover, the majority of full-sibling pups were sired by subordinate/non-consort males that rarely venture ashore implying aquatic mating also occurs within the grey seal mating system (Amos *et al.*, 1995; Worthington Wilmer *et al.*, 1999, 2000; Bean *et al.*, 2004). Additionally, a female residing with a dominant male can leave his vicinity and be copulated by subordinate males elsewhere (*extraconsort copulation*, Ambs *et al.*, 1999). Subsequently, for North Rona breeding colony it was suggested polygyny, a degree of aquatic mating and mate fidelity were cooperating to reduce any potential inbreeding effects typical of polygynous systems (Twiss *et al.*, 1994; Amos *et al.*, 1995; Amos *et al.*, 2001; Bean *et al.*, 2004) and reduce aggression between dominant males in order for increased pup survival (Acevedo-Gutiérrez, 2002). Aquatically mating species are believed less polygynous than land mating species (Mesnick & Ralls, 2002).

Literature demonstrates differences in breeding behaviour between grey seal populations worldwide; notably levels of polygyny, site fidelity and sociality appear influenced by habitat, topography and ease of access to breeding sites (Anderson & Harwood, 1985; Pomeroy *et al.*, 1994; Twiss *et al.*, 2000a). Seals on Sable Island, a large uniform sandbank with unrestricted access to an excess of breeding sites demonstrate less developed polygyny (Anderson & Harwood, 1985) and little sign of site fidelity (Pomeroy *et al.*, 2005); the North Rona population restricted access to numerous breeding sites of varying quality yet individuals exhibit greater site fidelity and sociality than Sable Island. Individuals in the Isle of May population exhibit strong site fidelity related to topographic variation (Pomeroy *et al.*, 2000b, 2005).

Breeding sites are restricted along the Ceredigion coastline to a number of small cliff-bound beaches, intertidal caves and rocky outcrops to similar to Pembrokeshire (Bonner, 1972). Since male seals can only approach a Monarch Isle breeding site from the seaward side (Anderson & Harwood, 1985) infers that Cwmtydu may similarly demonstrate an intermediate degree of polygyny. Site fidelity in grey seals visiting the Ceredigion coastline is expected to be relatively strong to promote development of social/mate associations in order to reduce inbreeding depression within this relatively small population (Baines *et al.*, 1995; Westcott, 2002). Cwmtydu differs from the breeding sites discussed in that a colony does not form as such. Cwmtydu may comprise two or three isolated parturient females in any given season (compared to tens, North Rona, or hundreds, Sables Island, of females) for the dominant male to defend, probably a consequence of the dispersed nature of breeding sites along the CMHC.

9.6.4. Bird's Rock

14 seals identified at Bird's Rock comprised 10 females (3 pregnant), 2 males and 2 juveniles, and were sighted between 1 and 7 occasions. It is suspected male 008 was observed hauled-out on rock-C on 1st August 2005. Additionally, a juvenile identified by the aided eye via markings on its back, was hauled-out at Bird's Rock on two successive days in July and one day one month later. Therefore, it believed more seals were utilising the haul-out site during the study, however poor quality images obtained from the cliff prevented further reliable identifications.

Historically, pups have been born at Bird's Rock but its use as a pupping site appears infrequent compared to Cwmtydu. A female grey seal is believed to have been observed in initial stages of birth on rock-D on 1st September 2005 however a pup was not observed during subsequent days. Furthermore, 19 days later a bull and female were observed displaying potential aquatic mating behaviour left of Bird's Rock.

Therefore Bird's Rock primarily provides a temporary haul-out site for grey seals and given tendency for group-hauling, social associations could potentially form (Pomeroy *et al.*, 2005), as discussed above.

Repeated use of a specific temporary haul-out site has been attributed to the central place foraging theory (Sjöberg & Ball, 2000) such that it is beneficial for individuals to return to sites with reliable food resources (Pitcher & McAllister, 1981; Brown & Mate, 1983; Nordstrom, 2002). This may be the case at Bird's Rock since grey seals and more frequently bottlenose dolphins were observed foraging at Bird's Rock, particularly in the early morning. Juvenile 023 was often seen hauled-out on rock-A/C for several days, then not be seen for a short period but return to haul-out on the same rocks; this regular return to the same haul-out rock after a trip to sea was documented in Norwegian harbour seals (Bjørge *et al.*, 1995). Additionally, grey seals outside the moult-season spend approximately 40% of time near or on a haul-out site, a least 50km from the main foraging areas (McConnell *et al.*, 1999).

9.6.5. Rock Preference

Personal observations suggest grey seals rarely hauled-out at Bird's Rock when the tide was at its lowest and is attributed to the angular rocks which often protruded too high and/or were at an awkward angle for the seals to haul upon (e.g. rock-B/D). At such times, seals were often seen logging next to the rock on which they later hauled once the water had risen to an appropriate level to aid movement onto the rock.

Of the 13 major haul-out rocks, seals exhibited a preference by mainly hauling-out on rocks A, D, B and H, respectively. Rock-A gently slopes into the sea providing ease of access, however during high sea states would be swept by sea-spray and waves and is more exposed to passing vessels. Similarly, rock-H sloped easily into the sea whereas rock-D appeared difficult to haul-out on particularly at low tide given its steep, seaweed-covered side. Their popularity may be attributed to gradient, since hauling grounds are selected by topography and exposure, and large size enabling multiple seals to haul-out together, providing corporate vigilance. Rock-B is the smallest rock seals hauled-out on. Interestingly, when ample space was available on all other rocks, a seal would often haul-out on rock-B rather than the larger rocks. Furthermore, when a seal was already hauled-out on rock-B, typically new arrivals would also haul-out on rock-B; seal(s) would even attempt to haul-out onto rock-B when there clearly was no available space due to presence of three other seals, demonstrating their gregarious nature and preference of group protection. Rock-B, D and H tended to offer some shade on sunny occasions, perhaps influencing their appeal to seals for thermoregulatory reasons. Seals were not observed hauled-out on rocks-J/F; rock J has an incredibly steep gradient, however rock F appeared similar in topography to rock E therefore it is unknown why seals did not haul-out on this rock.

10. Implications for Management

10.1. Use of Haul-Out Counts for Population Estimates

In addition to annual pup censuses (Baines *et al.*, 1995; Lorentsen & Bakke, 1995: Westcott, 2002), general haul-out counts are used to estimate pinniped population size (Eberhardt *et al.*, 1979; Thompson *et al.*, 1996). An inherent limitation of the latter case results from a potentially large proportion of the population always at sea (Hindell & Burton, 1988). Similar to other studies (Eberhardt *et al.*, 1979; Terhune & Almon, 1983; Calambokidis *et al.*, 1987) the difficulty in estimating proportion of seals in water at any one time at Bird's Rock inherently leads to underestimated counts, since submerged seals were excluded.

Literature illustrates differing haul-out patterns within populations and between species (Grellier *et al.*, 1996; Lake *et al.*, 1997; Sjöberg *et al.*, 1999) consequently relationships revealed between environmental variables can not truly be attributed to all populations or species. Furthermore, this study demonstrates how undertaking haul-out counts at the overall theoretical time of maximum haul-out, i.e. midday (Schneider & Payne, 1983; Pauli & Terhune, 1987a,b; Watts, 1992, 1996; Nordstrom, 2002) may not be the best approach regarding population estimates for all populations/sub-populations. For instance, VPB data alone suggested maximum daily haul-out along the coastline occurred near midday. However, when focusing on one haul-out site, Bird's Rock, this is clearly not true since maximum daily haul-out count occurred in the early morning (06:00-09:00 hours), followed by a smaller peak in haul-out count between 15:30-16:00 hours. This may also be the case for other haul-out sites along the Ceredigion coast. Therefore, management decisions regarding the grey seal population estimates within CMHC/SAC based upon maximum haul-out count data from VPB trips only would be severely underestimated since the one-/two-hour VPB trips do not commence until after the maximum haul-out period, particularly at Bird's Rock. Similarly, population estimates for the entire CMHC/SAC based solely upon Bird's Rock direct observation data may lead to an overestimate. This study demonstrates the importance of ground-truthing prior to undertaking haul-out counts, to ensure counts occur when proportion of seals ashore is greatest (Sjöberg *et al.*, 1999) in order to obtain realistic population estimates. With additional data correction factor(s) can be derived (e.g. Thompson *et al.*, 1996) to further improve population estimates of grey seals along the CMHC/SAC.

10.2. Site Fidelity & Disturbance

Photo-identification of grey seals encountered along the Ceredigion Marine Heritage Coast revealed the nature of individuals to periodically return to a site, whether returning to a temporary haul-out site, Bird's Rock, for a few days interspersed with periods at sea, e.g. Juvenile 023, or annually returning to Cwmtydu for the breeding season e.g. Male 015, Female 007. This preliminary evidence suggests, like conspecifics of the Baltic (Sjöberg & Ball, 2000), grey seals of west Wales may also tend to concentrate most of their activity on and around a few specific haul-out grounds therefore posing important management implications for this seal population. There is concern regarding the effectiveness of the Ceredigion Marine Conservation Code of Conduct and its enforcement during the breeding season, particularly at pupping sites easily accessible and popular with tourists, e.g. Cwmtydu (*Refer to Figure 34 Appendix 7*).

In addition, this study demonstrated the majority of coastal-users abide the voluntary Ceredigion Marine Conservation Code of Conduct when passing Bird's Rock aboard a vessel. Consequently it appears a number of grey seals at Bird's Rock have become accustomed to such vessel conduct, displaying no major short-term negative response/disturbance. However, there is evidence of short-term disturbance to grey seals at Bird's Rock when directly approached by vessels, i.e. canoes. Future surveys at Bird's rock would provide further information regarding behavioural responses exhibited during seal-canoe interactions to enable adjustments to existing management plans/regulations to reduce their impact on seals in this area if necessary. Therefore, a precautionary approach to management of this coastline should continue to be implemented, particularly as long-term effects of disturbance to grey seals are unknown. To fully assess long-term affects of disturbance to the population, behavioural responses should be analysed in terms of individual fitness, focusing on parameters with known or expected links to reproductive success and subsequent survival (Gill & Sutherland, 2000; Gill *et al.*, 2001a,b; Engelhard *et al.*, 2002) and contribute towards maintaining or adjusting local management plans regarding Ceredigion Marine Heritage Coast, within the SAC, to protect the seals where necessary.

11.0. Conclusion

In corroboration with past pinniped literature (e.g. Terhune & Almon, 1983; Pauli & Terhune, 1987a,b; Yochem *et al.*, 1987; Moulton *et al.*, 2002), apart from intrinsic constraints on hauling-out during breeding and moult seasons, this study demonstrated haul-out behaviour of grey seals cannot be determined by one single environmental variable. Rather, haul-out behaviour is influenced in varying degrees by a complex interaction of numerous environmental variables. The consistency between the multiple regressions indicate tide, time of day, disturbance, adjusted air temperature and date were predominant factors underlying the haul-out behaviour of grey seals at Bird's Rock. Maximum numbers of grey seals were observed in the early morning (06:00-09:00 hours) at Bird's Rock as opposed to the typical midday peak described in other pinniped species (*See Section 8.2)*. A considerably smaller peak in maximum haul-out count occurred in early afternoon (15:30-16:00), corresponding with the warmest time of day. However, general absence of a midday peak in haul-out numbers may be attributed to a thermoregulatory mechanism ensuring seals do not suffer hyperthermia. Overall sightings of seals at Bird's Rock declined as the day progressed, the initial decline in numbers coincided with an increase in vessel traffic; a maximum early morning haul-out count observed in Harbour seals was attributed to disturbance by vessel traffic (Calambokidis *et al.*, 1987; Henry & Hammill, 2001) and this may be the case for grey seals at Bird's Rock, being a designated Site of Special Scientific Interest it attracts many tourists either passing by on local visitor passenger boats or personal watercraft. It is speculated that the early morning haul-out observed could be a behavioural modification over time, resulting from repeated exposure to vessel traffic, particularly prior to implementation of the Ceredigion Marine Conservation Code of Conduct, therefore potentially gaining cumulative negative experience of vessel activity/disturbance consequently resulting in seals becoming sensitized to vessel traffic. Early morning haul-out would therefore be beneficial in terms of energy budgets by maximising rest whilst maintaining corporate vigilance in case of danger. Although vigilant behaviour towards vessels is deemed synonymous with that towards natural predators, haul-out behaviour cannot be attributed to predator avoidance in this study since grey seals do not have any natural predators within Cardigan Bay.

Interesting research suggested grey seals elsewhere exhibited a maximum early morning haul-out (Lydersen *et al.*, 1994; Sjöberg *et al.*, 1995; Sjöberg *et al.*, 1999) indicating that such haul-out behaviour found in grey seals at Bird's Rock may actually be attributed to the diurnal behaviour of their main prey items.

As highlighted by Moulton *et al.* (2002) in using multivariate analyses it is extremely difficult to separate the diverse influences when dealing with many interrelated variables; to a degree the cause and effect aspect of behavioural studies can make results difficult to comprehend. This study shows that vessel traffic and its apparent disturbance may actually be masking the natural diurnal activity patterns of grey seals in this area, i.e. hauling-out from duck to early morning and actively foraging during the day (except during the breeding season). Further investigation is warranted but it is suspected that behaviour of prey species is most likely the key factor influencing early morning haul-out.

Fortunately the code of conduct appears successful in minimising extent of short-term impacts of disturbance, since many seals displayed no apparent behavioural response, seemingly tolerant, to vessels passing Bird's Rock abiding the code of conduct. However, when vessels violated the code of conduct and approached seals directly or in an unpredictable manner, seals tended to permanently modify their behaviour, becoming more vigilant. Escape-responses were also observed. However, the disturbance aspect of this study only provides preliminary evidence of a level of short-term disturbance and requires further quantitative data collection in terms of measure vigilance and analysing data combined with measurable individual fitness parameters with known or expected links to reproductive success and survival (Gill & Sutherland, 2000; Gill *et al.*, 2001a,b; Engelhard *et al.*, 2002) in order to obtain a realistic evidence regarding long-term disturbance as a result of vessel traffic.

Photo-identification was successful in determining site fidelity of individual grey seals. 27 individuals were identified in total, nine seals demonstrated intraseasonal site fidelity to Bird's Rock, being sighted at least twice in 2005 and two individuals showed inter-seasonal fidelity to Cwmtydu during the breeding season. Although photo-identification failed to reveal any definitive evidence of social/mate associations between the seals known to Cwmtydu, this study incites the necessity of continued photo-identification in the future, particularly at Cwmtydu and Bird's Rock, to obtain further knowledge on the mating systems and sociality of grey seals within the Ceredigion Marine Heritage Coast.

Given the knowledge that some coastal-users violate the code of conduct, whether unwittingly or purposefully, it is evident that ongoing education of tourists is paramount in raising awareness of the code of conduct, the importance of abiding such regulations and importantly providing clear-cut reasons why not to approach/harass wild seals, particularly pups. Since the long-term physiological or behavioural effects of vessel disturbance are unknown, the continuation of a precautionary approach to management is required. Furthermore, it is important this is achieved by a multi-agency approach, utilising the combined efforts of Ceredigion Local Authority, Countryside Council for Wales and volunteer-based charities/organisations, such as *Sea Watch Foundation* and *Cwmtydu Bay Wildlife Organisations* to work simultaneously in reaching effective management strategies in order to protect and conserve the grey seals utilising the West Wales coastline. Further research regarding long-term effects of vessel/human disturbance on grey seals on individual fitness (Gill *et al.* 2001) is warranted at Cwmtydu and Bird's Rock to ensure that further modifications to regulations are necessary for their conservation.

12.0. Evaluation of Study & Recommendations for Future Research

Aspects of this study were hindered. Improvements in study design and future research aims are recommended.

12.1. Environmental Variables & Haul-Out Behaviour

Accuracy of ambient air temperature during direct observation of Bird's Rock was doubted throughout the study; the temperature gauge was extremely sensitive such that despite being kept out of direct sunlight between intervals it would absorb heat given off the rocks and take much time to reach ambient air temperature. Consequently, erroneously high temperature values were recorded. The gauge was then placed on an ice-box between intervals and allowed to reach ambient air temperature every 15 minutes. Furthermore, the temperature variables will be inherently biased towards higher temperatures, since on sunny days the cliff was exposed to direct sunlight yet the rocks below were often shaded by the shadow cast by the cliff when the sun was situated south, behind the observer overlooking the haul-out site. Therefore the air temperature and substrate on which the seals' hauled in shaded areas would be cooler than that experienced on the cliff. Although air temperatures between cliff and sea-level (onboard VPB) differed marginally, when taking temperatures the VPB was also in direct sunlight. For future reference collection of sea-surface temperatures in addition to ambient air temperatures would be useful in assessing whether there is a threshold water-air temperature which would elicit haul-out response.

Prevailing wind direction was not always possible to determine; on the exposed cliff the wind frequently instantly changed direction. The higher level cliff behind where observations were taken shielded wind from the south. Correctly measured wind direction would be useful investigate whether seals behaviourally adjust to onshore/offshore winds via orientation (e.g. Finley, 1979).

A time lapse video system with night-vision (thermal-imaging) attached to the cliff overlooking the haul-out area at Bird's Rock would provide a non-invasive method of investigating behaviour, particularly regarding haul-out numbers between 21:00-06:00 hours. Combined with continued direct observation surveys ay Bird's Rock and other haul-out sites along CMHC, ample ground-truthing could be achieved in determining maximum daily haul-out for acquisition of realistic population estimates. Following Sjöberg *et al.* (1999), this system would also aide investigation of haul-out duration, since there was difficult to follow during direct observation surveys.

Although the study produced interesting information regarding the factors influencing haul-out behaviour at Bird's Rock, it also highlighted the need for further data collection in order to lessen effects of the outliers, i.e. occasions when a high number (>7) of seals hauled-out together. In retrospect, perhaps stepwise multiple regression was not the best multiple regression technique to be employed since it did not investigate any interactions between variables; hidden interactions between certain variables may accelerate the proportions of seals hauled-out given specific circumstances. Given further data collection, multiple regression analysis involving interactions between variables would be recommended to gain greater understanding of underlying reasons of haul-out behaviour. Many years of data could be analysed using time-series analysis.

The importance of Bird's Rock as a haul-out site may have been underestimated in the past since direct observation of seal behaviour was relatively unknown. Therefore, continuation of non-invasive direct observational data collection in this area is recommended to obtain further information on behavioural habits of grey seals.

12.2. Potential Disturbance Induced by Vessel Traffic

As discussed, pre-/post-interaction seal counts do not provide direct evidence that vessel traffic/disturbance is causing the numbers of seals utilising the haul-out site to decline overall. Furthermore, although most seals appeared to have become highly tolerant to the passing vessels abiding the code of conduct, a section of seals showed varying degrees of lowered tolerance. Since the data involved qualitatively recording categories of behavioural responses before, during and after the interaction the results did not provide substantial evidence regarding short-term disturbance. Bird's Rock is an ideal vantage point to conduct long-term future research involving measurement of vigilance displayed by the seals in presence and absence of vessel activity, i.e. counting head-lifts and scans/inter-scan intervals over set periods of time. This would provide quantitative evidence regarding variations in vigilance from which effects of vessel traffic can be assessed. Furthermore, dynamics of group haul-out behaviour can be investigated to find whether peripheral seals exhibit greater vigilance levels than central seals and whether larger groups and/or time since haul-out results in lowered individual vigilance as documented in other studies (*DaSilva* & Terhune, 1988; Quenette, 1990; Terhune & Brillant, 1996). Weather and disturbance variables should be simultaneously analysed as some species are more likely to enter water when disturbed when experiencing uncomfortable weather conditions (Quenette, 1990; Born *et al.*, 1999; Ronconi & St. Clair, 2002).

During the research vessel-seal interaction discussed the bull remained hauled-out and intensely increased vigilance whereas females and juveniles immediately fled their haul-out site may indicate sex- and/or age-related responses to vessel activity/disturbance (Quenette, 1990; Constantine, 2001) and warrants further investigation.

12.3. Photo-identification

Although photo-identification was proved a successful method inherent problems encountered undoubtedly limited its success. Often it was difficult to obtain images of the required profiles (Hiby & Lovell, 1990; Westcott, 2002) from the VPB trips, particularly when acquiring photographs of hauled-out seals. Frequently seals would be hauled-out facing the cliff as opposed to the seaward side, reducing opportunity of obtaining at least one adequate image. Furthermore, when seals were hauled-out in a group efforts generally failed to acquire images of all individuals in the group (to record associations) since one hauled-out seal would obscure the view of another.

As the maximum number of seals tended to haul-out during early morning opportunities of acquiring images of many seals and recording their associations were lost since VPB trips did not commence until 10:30 hours thus affecting the true representation of individuals using the area. An individual may only haul-out at Bird's Rock in the early morning and therefore may never be identified. Furthermore, given an early low tide, by the time the first VPB trip of the day would reach Bird's Rock seals that remained hauled-out since the early hours would have a dry pelage, resulting in poor quality identification images since patterns on a dry pelage are less recognisable (Westcott, 2002). Conversely, when images were obtained of recently hauled-out seals either from VPBs or the cliff, sunlight often reflected off the wet pelage making it impossible to determine any individual pelage patterns due to glare. Also the southerly position of the sun made it difficult to obtain high quality images of seals at Bird's Rock without experiencing glare from sun or shadow from the cliff.

Difficulty was experienced photographing seals in the water during VPB trips, given the unexpected brief surfacing behaviour. When trying to obtain images on passing Bird's Rock, seals would swim closer to cliff or submerge, reducing opportunities of obtaining good quality images.

Photo-identification to assess individual use of the coast in terms of site fidelity and associations is a useful, non-invasive technique however its value depends on the effort taken to obtain high-quality images. For instance, juvenile 023 was identified on three different days at Bird's Rock. This individual was identified using binoculars by the author and her assistant during direct observation surveys. Notes written on survey forms suggest juvenile 023 was present at Bird's Rock on at least 23 days, often sighted for four successive days at a time. Unfortunately many images obtained from the cliff of Juvenile 023 were of too poor a quality to be included in the catalogue. However, it demonstrates how the degree of intra- and inter-seasonal site fidelity of an individual using photo-identification may be underestimated due to a lack of high quality images and/or reduced effort.

In terms of social associations, photo-identification and direct observation provides adequate information, however accurate information of all associations will not be obtained as it is difficult to observe associations/behaviour underwater. Furthermore limitations of behavioural observations/photo-identification to determine mate fidelity exist in light of molecular research demonstrating paternity cannot be inferred from observed copulations, social associations or male dominant hierarchies (Amos *et al.*, 1995; Coltman *et al.*, 1999; Worthington Wilmer *et al.*, 1999; 2000; Amos *et al.*, 2001; Zeh & Zeh, 2001; Bean *et al.*, 2004). Although invasive, genetic studies appear the only method to date capable of revealing whether mate fidelity occurs in grey seals.

Photo-identification of grey seals from Bird's Rock was severely hampered by available camera equipment, however it is maintained that this is an ideal location to obtain images of individuals using the area and should be continued. For images to be of sufficient quality to form a catalogue, it is advised a digital camera with a large telescopic (polarising) lens is used, given the height of the cliff. Images should ideally be taken in the early morning when maximum numbers of seals are hauled-out, tide permitting, and/or between three hours prior to four hours post low tide. One would be able to obtain left and right profiles of head since individuals often shifted positions on the rocks. Furthermore, identification could be aided by side/underside profiles of females as they also had distinctive patterns which could be used in matching images with pupping females photographed by *Cwmtydu Bay Wildlife Organisation*. All images obtained and catalogued by Sea Watch Foundation could be compared with existing databases, such as *EIRPHOT* & CYMRUPHOT to further increase knowledge of habitat utilisation of grey seals in West and South-west Wales. Since Vincent *et al.* (2005) found a number of seals travelled from France to Wales it would be of interest to compare images of grey seals from west Wales with the French catalogue.

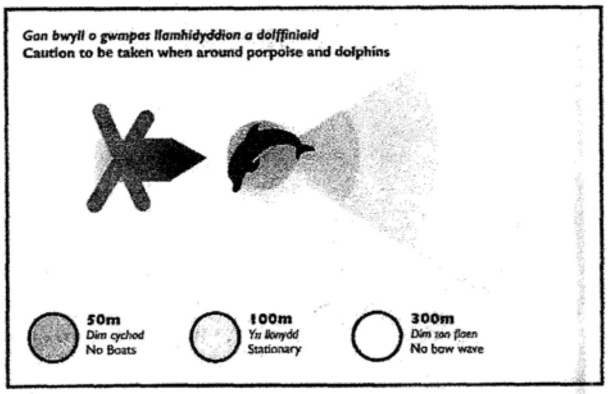
13.0. Appendices

Appendix 1: Ceredigion Marine Conservation Code of Conduct. Courtesy of *Ceredigion County Council*

Ceredigion Marine Conservation Code of Conduct

Dolphins/Porpoise:

If these marine mammals are encountered at sea:



- **Maintain a steady speed** and course, or **slow down gradually**
  Do **not exceed 8knots inside the yellow marker buoys** between **New Quay Head and Ynys Lochtyn**
- **Do not chase**, manoeuvre erratically, turn towards or attempt to feed or touch them
- **Take extra care to avoid dolphins with their young**
- **Do not attempt to swim** with these mammals

Seals:

Do not interfere with seals or their pups on the beach and control your dog. Please leave alone as any attempt to approach may cause distress.

Birds:

Keep 100m out from cliffs in the breeding season, 1 March to 31 July. Please keep clear of rafts of birds on the sea and avoid unnecessary noise close to cliffs

Penalties: The Harbourmaster is authorised to withdraw launching and mooring permits from vessels that do not observe the Marine Conservation Code of Conduct or byelaws. Vessels that break the byelaws or recklessly disturb dolphins, porpoise or seals are also liable to prosecution with a maximum penalty of £20,000.

Cyngor Cefn Gwlad Cymru
Countryside Council for Wales

Ceredigion County Council,
Department of Environmental Services & Housing

Appendix 2: Visitor Passenger Boat Data Collection Forms.

One-/two hour trip form 1: for general marine mammal sightings. Courtesy of *Sea Watch Foundation.*

One / Two hours trip

Date:_________ Time start: ______Time end: ________ Observers: __________
Ebb: High water_____ Low water______ or Flood: Low water_____ High water_____

Effort

Leg	Time	Lat.	Long.	Precipitation Type		Precipitation Inten		Visibility (km)	Sea state B	Sea state S	Sighting ref.
S C E		NQ pier N52°	W004°	N F	R	I C	L M H	0-1__ 1-10__ >10__			
S C E		N52°	W004°	N F	R	I C	L M H	0-1__ 1-10__ >10__			
S C E		N52°	W004°	N F	R	I C	L M H	0-1__ 1-10__ >10__			
S C E		N52°	W004°	N F	R	I C	L M H	0-1__ 1-10__ >10__			
S C E		NQ pier N52°	W004°								

Sightings

Enter all dolphin and porpoise sightings in the table below. All seal sightings should be entered in the attached 'Seals along the coast' table and map.

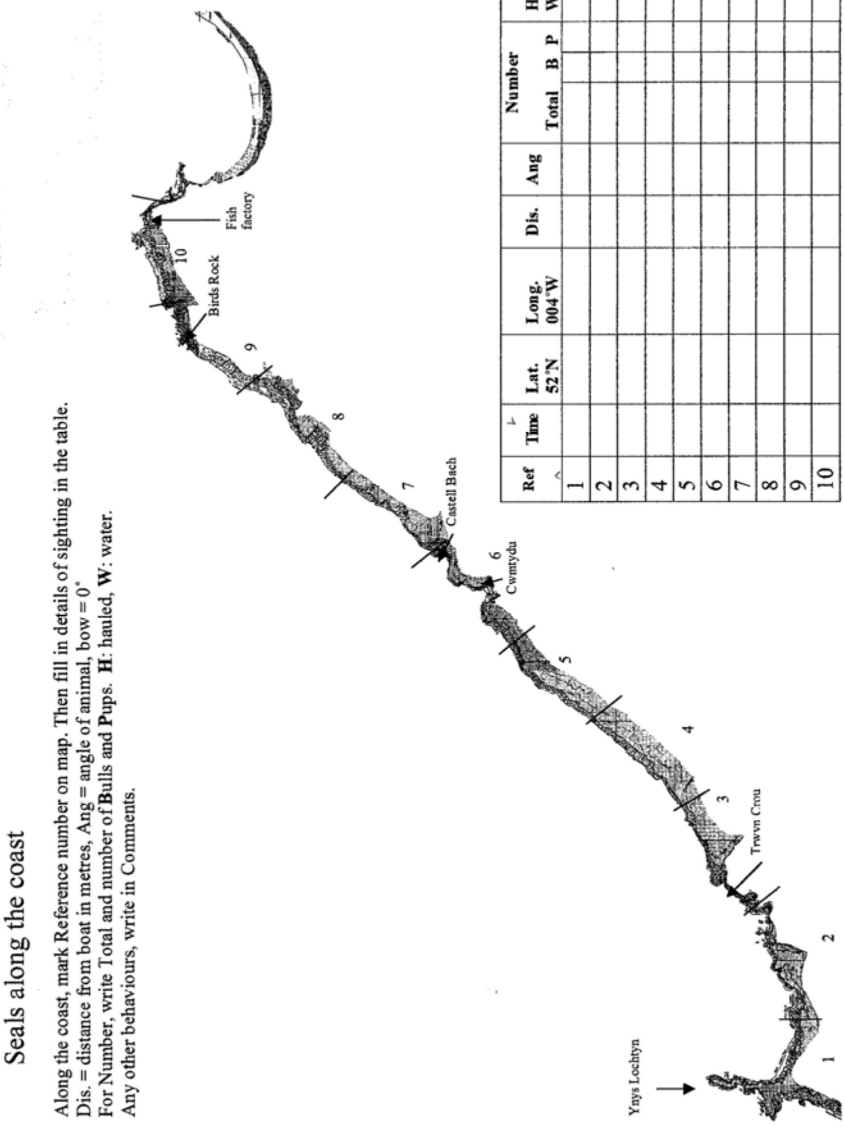
S	Time	Sp.	Total no.	A	C	NB	Cue	Lat	Long	Beh / Dir.	Seen by	Dist.	Dir. Ang.
1		D HP						N52°	W004°				P - S
2		D HP						N52°	W004°				P - S
3		D HP						N52°	W004°				P - S
4		D HP						N52°	W004°				P - S
5		D HP						N52°	W004°				P - S
6		D HP						N52°	W004°				P - S

Behaviours
Cue: F: fin / fluke / part of body, L: leaping (body out of water), S: splash, B: blow, U: unknown
Cetaceans: SF: suspected feeding / FF: feeding, fish seen / TR: travel / O: other / N: not known
Seals: H: Seals hauled out / W: Seals in water

One-/two hour trip form 2: for grey seal sightings. Courtesy of *Sea Watch Foundation*.

Seals along the coast

Along the coast, mark Reference number on map. Then fill in details of sighting in the table.
Dis. = distance from boat in metres, Ang = angle of animal, bow = 0°
For Number, write Total and number of **B**ulls and **P**ups. **H**: hauled, **W**: water.
Any other behaviours, write in Comments.



Ref	Time	Lat. 52°N	Long. 004°W	Dis.	Ang	Number Total	B	P	H/ W	Comments
1										
2										
3										
4										
5										
6										
7										
8										
9										
10										

Appendix 3: Direct Observation Data Collection.

Direct observation form 1: environmental/behaviour/vessel data collection at Bird's Rock; adapted from Pierpoint & Allen, 2004 (also refer to Lamb, 2004).

Name: **Location:** **Date:** **Sheet No: /**

		WEATHER					GS Count(B/P)		Human/Boat Encounter				
MAP/ REF	(15-Min) Start Time	General	Wind Direction	Wind Speed (mph)	Sea State	Air Temp. (°C)	No. GS hauled out	No. GS in adjacent water	Type (Boat/ Human)	Distance (m)	Total No. Boats within 300 m	Code of Conduct	Notes

The Number of Different Boats/Walkers Seen in 3 Hours

Boat Type		Tally	Total
MB	Recreational motorboat, cabin cruisers, dinghies with outboard		
SB/SS	Racing type speedboat/ RIB/Water-skier		

Boat Type		Tally	Total
SAIL	Any boat under sail incl. windsurfer		
CF	Commercial fishing boat		

Boat Type		Tally	Total
VPB	Visitor Passenger Boat		
C	Canoe		
W	Walker		

Boat Type		Tally	Total
J	Jet ski/ personal watercraft		
R	Cetacean research boat (please specify boat)		

Direct observation form 2: to collect information regarding grey seal-vessel interactions.

Grey Seal Direct Observations from Birds Rock

Date:

Data Sheet # : …./…..

Entire Survey Start/Finish: ……… - ……… (BST)

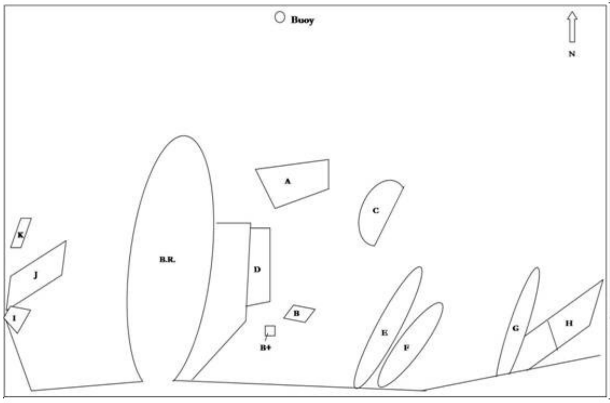
TIDAL INFORMATION

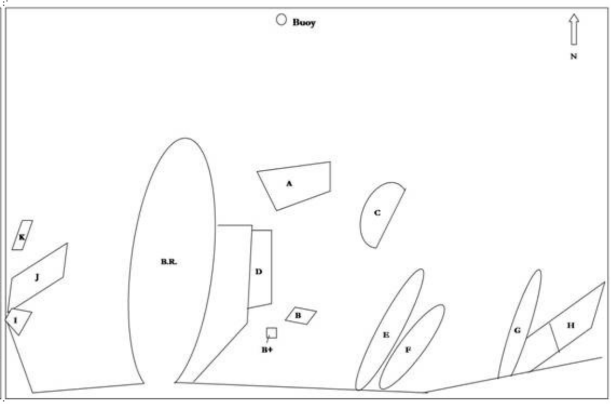
HW Aberystwyth (BST): ………… Tidal Height (m): …………

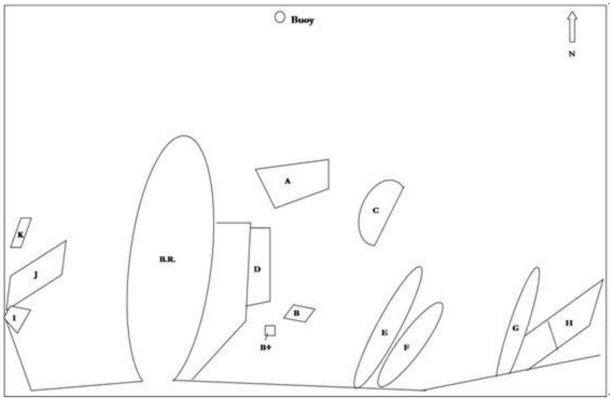
LW Aberystwyth (BST): ………… Tidal Height (m): …………

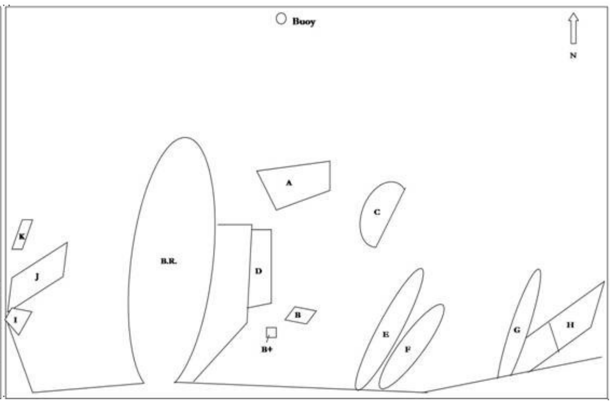
MAP /REF	Interaction Time		No. Grey Seals (Start)	Closest Distance of Boat to Seal (m)	Bearing	Behaviour Related to Human Proximity						NOTES
	Start	Finish				BEFORE (at 300 m dist.)	DURING	Reaction of seal(s) when boat/human at closest distance.	Human Conduct to Seals	AFTER (at 300 m dist.)	No. Grey Seals (After)	

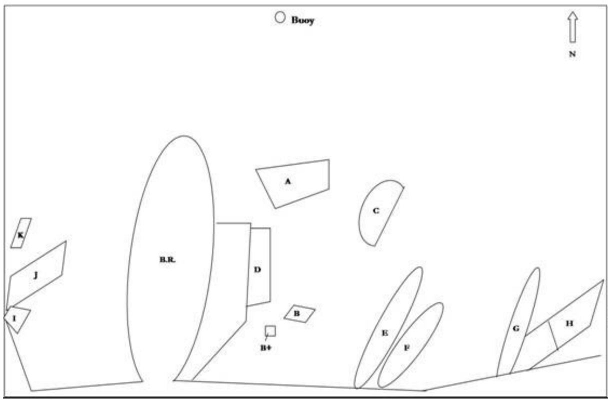
Direct observation form 3: plan view maps of Bird's Rock. Map is not to scale.

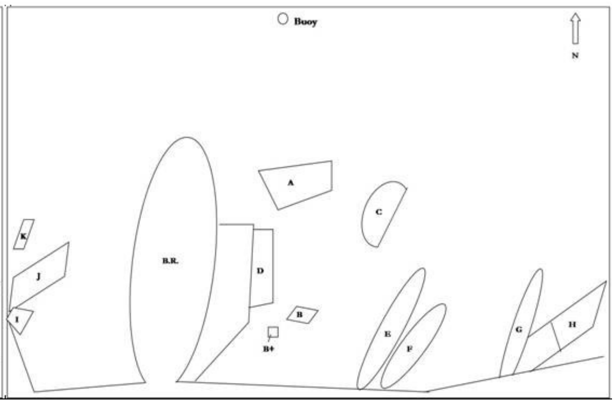












Direct observation form 4: key to codes used during data collection. Grey seal behaviour codes adapted from Westcott (2002); environmental and vessel conduct codes courtesy of *Sea Watch Foundation*.

Direct Observation: Key to Codes

GENERAL WEATHER	
1	Fair
2	Sunny
3	Overcast/Dull
4	Rain
5	Mist; Visibility < 2 km
6	Sun & Showers

VESSEL CONDUCT WITHIN 300 METRES	
Y1	No wake speed & no erratic changes in course when passing seals & cetaceans.
Y2	Slowed down gradually & stopped.
N1	Too fast: bow/wake speed, white water visible.
N2	Erratic course to approach/avoid/or follow seals (cetaceans).
N3	Attempted to touch/feed/play with seals and cetaceans.
N4	Exceeded 8 knots inside yellow buoys (N. Q. Harbour only).
R	Research vessel photographing individual animals (specify vessel name please).

SEA STATE			
0	Calm, glassy; mirror sea	4	Longer waves (1-1.5m high); frequent whitecaps
1	Calm, rippled surface	5	Many white horses; waves (~ 2m high)
2	Wavelets; glassy, crests do not break	6 +	Rough; white foam crests everywhere; waves > 2.5 m high
3	Small wavelets (< 1m); occasional whitecaps		*NB: Wind Direction as compass points please (N, NW, etc.)*

GREY SEAL BEHAVIOUR TO HUMAN/VESSEL PROXIMITY

HAULED-OUT		*IN SEA*					
GR	Resting on rocks, infrequent movement of head.	S	Swimming	B	Bottling	L	Logging
		1F	Foraging/suspected feeding	2F	Known Feeding	SC	Scanning
1L	Awareness (looking directly at source of disturbance without lifting head).	1S	Vigilance (looking directly at source of disturbance).				
2L	Intense vigilance (head up, looking directly at source of disturbance).	2S	Periscoping (rising upright as high out of the sea as possible & looking toward source of disturbance)				
3La	Moving some distance across the rocks then pausing to look again towards the source of disturbance.	3Sa	Slowly diving under but does not emerge to resume vigilance				
3Lb	Same as 3La, plus some other/similar movements to neighbouring seals and/or bickering where they stray into areas of other seals.	3Sb	Diving then emerging farther away from source of disturbance to resume vigilance.				
3Lc	Same as 3Lb but seals enter the adjacent sea.	3Sc	Diving then emerging closer to source of disturbance to resume vigilance.				
4L	Slipping (alone) off rocks into sea.	3Sd	Diving then emerging in same place to resume vigilance				
		4S	Crash dive by one seal				
5L	Hastening fast across rocks into the sea, simulating a general stampede of seals into the sea.	5S	Most or all other seals react by crash diving and/or submerging. Some seals emerge farther away, others leave the locality.				
6L	No apparent reaction.	6S	No apparent reaction.				

Appendix 4: Photo-Identification Filename System.

The designation of image filenames follows the system used by Westcott (2002).

1. For all images relating to a sighting recorded on a one-/two-hour form, a specific sighting reference number was assigned to it in the *Sea Watch Foundation* database, such as SO23; this reference constitutes the initial section of the filename of the image.

2. The second section of the filename is the initials of where the image was taken, for instance BR – Bird's Rock; CI – Cardigan Island; CT – Cwmtydu; YL – Ynys Lochtyn; MT – Mwnt, etc.

3. The filename is then given a six digit number corresponding to the date it was taken, e.g. 090805, followed by a number relating to the seal; where there are multiple images of the same seal from the same sighting, images are numbered in sequence for the site and date, such that the first image of the seal is given the original number, then additional images of the same seal could have a, b, c, d, and so on, after the number, e.g.: 45, 45a, 45b etc.

4. The next segment of the filename relates to the profile taken of the seal, for instance left (L), right (R), head on (H) and for the underside of body (U). This is then followed by a code for the sex of the individual: female (F), bull (B), juvenile (J), pup (P).

5. Finally, if a female is known to be a mother of a pup, the filename sequence should end with an M. If a bull is in the vicinity of the nursery site, the filename should end with F since the bull is a potential father of the subsequent years' pup.

Example of a filename is as follows:

SO23_BR_09.06.05_RF_26b.jpg

It is sighting #23 at Bird's Rock on 9th June 2005. It is an image of the right profile of a female. It is the 3rd image of individual #26.

Note: Images from Cwmtydu during the pupping/breeding season do not have a specific sighting reference number (i.e. SO23 is absent) since the data does not correspond with the current *Sea Watch Foundation* database. Therefore an example of a filename of a seal from Cwmtydu would simply be as follows:

CT_23.09.05_LF_032_M.jpg.

It was taken at Cwmtydu on 23rd September 2005. It is an image of the left profile of a female – individual #032. It is known to have pupped this year.

Appendix 5: Example Images of 27 Grey Seals Identified.

ID Number: 001
Sex: Female
Associations: Pup, 002, 015
Location: Cwmtydu
Date of First Sighting: 15.09.03
Date of Last Sighting: 26.09.03
Total Sightings Within Period: 7

ID Number: 002
Sex: Female
Associations: Pup, 001, 015
Location: Cwmtydu
Date of First Sighting: 15.09.03
Date of Last Sighting: 23.09.03
Total Sightings Within Period: 8

ID Number: 007
Sex: Female
Associations: Pup, 008, 009, 015
Location: Cwmtydu
Date of First Sighting: 13.09.04
Date of Last Sighting: 19.09.04
Total Sightings Within Period: 7
Date of Last Re-sighting: 20.08.05

ID Number: 008
Sex: Male
Associations: 007, 009, 015
Location: Cwmtydu
Date of First Sighting: 13.09.04
Date of Last Sighting: 25.09.04
Total Sightings Within Period: 10

ID Number: 009
Sex: Female
Associations: Pup, 007, 008, 015
Location: Cwmtydu
Date of First Sighting: 14.09.04
Date of Last Sighting: 25.09.04
Total Sightings Within Period: 11

ID Number: 015
Sex: Male
Associations: 001, 002, 007, 008, 009, 032
Location: Cwmtydu & Bird's Rock
Date of First Sighting: 19.09.03
Date of Last Sighting: 24.09.03
Total Sightings Within Period: 3
Dates of First Re-Sighting:13.09.04/16.09.04
Date of Last Re-Sighting: 18.09.05

ID Number: 016
Sex: Female
Associations: 019, 020, 021, 022, 027, 028, 029
Location: Bird's Rock
Date of First Sighting: 09.06.05 *(S019)*
Date of Last Sighting: 09.06.05 *(S021)*
Total Sightings Within Period: 1

ID Number: 018
Sex: Female
Associations: 016, 019, 020, 021, 022, 027, 028, 029
Location: Bird's Rock
Date of First Sighting: 09.06.05
Date of Last Sighting: 23.06.05
Total Sightings Within Period: 2

ID Number: 019
Sex: Female
Associations: 016, 020, 021, 022, 027, 028, 029
Location: Bird's Rock
Date of First Sighting: 09.06.05
Date of Last Sighting: 02.08.05
Total Sightings Within Period: 7

ID Number: 020
Sex: Female
Associations: 016, 019, 021, 022, 027, 028, 029
Location: Bird's Rock
Date of First Sighting: 09.06.05
Date of Last Sighting: 09.06.05
Total Sightings Within Period: 1

ID Number: 021
Sex: Female
Associations: 016, 019, 020, 022, 027, 028, 029
Location: Bird's Rock
Date of First Sighting: 09.06.05
Date of Last Sighting: 09.06.05
Total Sightings Within Period: 1

ID Number: 022
Sex: Juvenile
Associations: 016, 019, 020, 021, 027, 028, 029
Location: Bird's Rock
Date of First Sighting: 09.06.05
Date of Last Sighting: 16.08.05
Total Sightings Within Period: 3

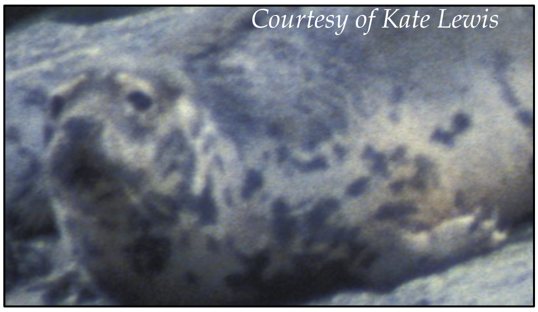
ID Number: 023
Sex: Juvenile
Associations: 024
Location: Bird's Rock
Date of First Sighting: 02.08.05
Date of Last Sighting: 09.08.05
Total Sightings Within Period: 3

ID Number: 024
Sex: Male
Associations: 023
Location: Bird's Rock
Date of First Sighting: 02.08.05
Date of Last Sighting: 09.08.05
Total Sightings Within Period: 2

ID Number: 025
Sex: Female
Associations: 026
Location: Bird's Rock
Date of First Sighting: 02.06.05
Date of Last Sighting: 16.08.05
Total Sightings Within Period: 2

ID Number: 026
Sex: Female
Associations: 025
Location: Bird's Rock
Date of First Sighting: 02.06.05
Date of Last Sighting: 09.06.05
Total Sightings Within Period: 2

ID Number: 027
Sex: Female
Associations: 016, 019, 020, 021, 022, 028, 029
Location: Bird's Rock
Date of First Sighting: 09.06.05
Date of Last Sighting: 09.06.05
Total Sightings Within Period: 1



ID Number: 028
Sex: Female
Associations: 016, 019, 020, 021, 022, 027, 029
Location: Bird's Rock
Date of First Sighting: 09.06.05
Date of Last Sighting: 02.08.05
Total Sightings Within Period: 6

ID Number: 029
Sex: Female
Associations: 016, 019, 020, 021, 022, 027, 028
Location: Bird's Rock
Date of First Sighting: 02.08.05
Date of Last Sighting: 02.08.05
Total Sightings Within Period: 1

ID Number: 030
Sex: Female
Associations: Pup & 015
Location: Near Mwnt
Date of First Sighting: 10.08.05
Date of Last Sighting: 10.08.05
Total Sightings Within Period: 1

ID Number: 031
Sex: Female
Associations:
Location: Unknown
Date of First Sighting: 10.08.05
Date of Last Sighting: 10.08.05
Total Sightings Within Period: 1

ID Number: 032
Sex: Female
Associations: Pup 3 *(Cwmtydu, 2005)*
Location: Cwmtydu
Date of First Sighting: 13.09.05
Date of Last Sighting: 20.09.05
Total Sightings Within Period: 4

ID Number: 033
Sex: Female
Associations:
Location: Cwmtydu
Date of First Sighting: 23.08.05
Date of Last Sighting: 23.08.05
Total Sightings Within Period: 1

ID Number: 034
Sex: Female
Associations:
Location: Cwmtydu
Date of First Sighting: 23.08.05
Date of Last Sighting: 23.08.05
Total Sightings Within Period: 1

ID Number: 035
Sex: Female
Associations: 036
Location: Cwmtydu
Date of First Sighting: 23.08.05
Date of Last Sighting: 23.08.05
Total Sightings Within Period: 1

ID Number: 036
Sex: Male
Associations: 035
Location: Cwmtydu
Date of First Sighting: 23.08.05
Date of Last Sighting: 23.08.05
Total Sightings Within Period: 1

ID Number: 037
Sex: Juvenile
Associations:
Location: Cwmtydu
Date of First Sighting: 23.08.05
Date of Last Sighting: 23.08.05
Total Sightings Within Period: 1

Appendix 6: Tidal Phase & Behaviour Results from VPB & Direct Observation data.

Total numbers and percentages of grey seals (*H. grypus*) sighted in ebb and flood tidal phases from visitor passenger boat trips during 10th April – 10th September 2004 and 1st May – 7th October 2005. *behaviour not recorded for three sightings. Combined data for both years is also shown.

2004		**Total Number (n)**	**Percentage (%)**
Tidal Phase	**Ebb**	286	82.90
Behaviour	Hauled Out	96	27.83
	In Water	190	55.07
Tidal Phase	**Flood**	59	17.10
Behaviour	Hauled Out	29	8.41
	In Water	30	8.70
2005		**Total Number (n)**	**Percentage (%)**
Tidal Phase	**Ebb**	169*	64.26
Behaviour	Hauled Out	99	37.64
	In Water	70	26.62
Tidal Phase	**Flood**	94	35.74
Behaviour	Hauled Out	49	18.63
	In Water	45	17.11
2004 + 2005		**Total Number (n)**	**Percentage (%)**
Tidal Phase	**Ebb**	455*	74.84
Behaviour	Hauled Out	195	32.07
	In Water	260	42.76
Tidal Phase	**Flood**	153	25.16
Behaviour	Hauled Out	78	12.83
	In Water	75	12.34

Number and percentage of grey seals and their behaviour as observed from Bird's Rock between 8th June and 1st September 2005.

Bird's Rock 2005		**Total Number (n)**	**Percentage (%)**
Tidal Phase	**Ebb**	709	42.78
Behaviour	Hauled Out	375	22.12
	In Water	334	20.66
Tidal Phase	**Flood**	801	57.22
Behaviour	Hauled Out	489	24.83
	In Water	312	32.38

Appendix 7: Violation of the Ceredigion Marine Conservation Code of Conduct.

The pup on Cwmtydu beach was fortunately weaned when this group approached it on 25th August 2005. However, if the pup had been approached during its weaning period there is every chance the unsuspecting group of people would have caused the pup to be abandoned by its mother, similar to the abandonment of the pup born on Dolau beach, New Quay. Education of tourists regarding the Ceredigion Marine Conservation Code of Conduct and the reasons why not to approach wild seals appears essential in the prevention of unnecessary disturbance to grey seal pups along the Ceredigion Marine Heritage Coast, particularly at Cwmtydu beach during the pupping season.

14.0. References

Abt, K.F., Hoyer, N., Koch, L. & Adelung, D. (2002). The dynamics of grey seals (*Halichoerus grypus*) off Amrum in the south-eastern North Sea - evidence of an open population. *Journal of Sea Research*, **47**: 55 – 67.

Acevedo-Gutiérrez, A. (2002). Group behaviour. pp: 537 – 544. In: Encyclopedia of Marine Mammals (Editors: Perrin, W.F., Würsig, B. & Thewissen, J.G.M.). pp: 1414. Academic Press. ISBN: 0-12-551340-2.

Alldredge, A.L. & Hamner, W.M. (1980). Recurring aggregation of zooplankton by a tidal current. *Estuarine and Coastal Marine Science*, **10**(1): 31-37

Allen, S.G., Ainley, D.G., Page, G.W. & Ribic, C.A. (1984). The effect of disturbance on harbor seal haul out patterns at Bolinas Lagoon, California. *Fishery Bulletin*, **82**(2): 493 – 500.

Ambs, S.M., Boness, D.J., Bowen, W.D., Perry, E.A. & Fleischer, R.C. (1999). Proximate factors associated with high levels of extraconsort fertilization in polygynous grey seals. *Animal Behaviour*, **58**: 527 – 535.

Amos, B., Twiss, S., Pomeroy, P. & Anderson, S. (1995). Evidence for mate fidelity in the gray seal. *Science*, **268**(5219): 1897 – 1899.

Amos, W., Worthington Wilmer, J. & Kokko, H. (2001b). Do female grey seals select genetically diverse mates? *Animal Behaviour*, **62**: 157 – 164.

Anderson, S.S. & Fedak, M.A. (1987). Grey seal, *Halichoerus grypus*, energetics: females invest more in male offspring. *J. Zool., Lond.*, **211**: 667 – 679.

Anderson, S.S. & Harwood, J. (1985). Time budgets and topography: how energy reserves and terrain determine the breeding behaviour of grey seals. *Animal Behaviour*, **33**: 1343 – 1348.

Anon. (1984). Grey Seals: Coastal Colonists. *In: Secrets of the Seashore: The Living Countryside.* Hall, D. (consultant) pp: 182 – 185. Readers Digest. ISBN: 0-276-374-363.

Anon. (Unknown Date). *Cardigan Bay Special Area of Conservation Management Plan*. Ceredigion County Council; the Countryside Council for Wales; Environment Agency Wales; North Western and North Wales Sea Fisheries Committee; Pembrokeshire Coast National Park Authority; Pembrokeshire County Council; South Wales Sea Fisheries Committee; Trinity House & Dŵr Cymru Welsh Water. pp: 197.

Backhouse, K.M. & Hewer, H.R. (1957). Behaviour of the grey seal (*Halichoerus grypus* FAB.) in the spring. *Proc. Zool. Soc. Lond.*, **129**: 450.

Baines, M.E., Earl, S.J., Pierpoint, C.J.L. & Poole, J. (1995). The west Wales grey seal census. CCW Contract Science Report 131. Countryside Council for Wales. pp: 238.

Baker, J.D.; Antonelis, G.A.; Fowler, C.W.; York, A.E. (1995). Natal site fidelity in northern fur seals, *Callorhinus ursinus*. *Animal Behaviour,* **50***:* 237 - 247.

Barraclough, R.K. (2000). Distance sampling. A discussion document produced for the Department of Conservation. Science & Research Internal Report 175. pp: 26.

Bean, K., Amos, W., Pomeroy, P.P., Twiss, S.D., Coulson. T.N. & Boyd, I.L. (2004). Patterns of parental relatedness and pup survival in the grey seal (*Halichoerus grypus*). *Molecular Ecology*, **13**: 2365 – 2370.

Beck, C.A., Bowen, W.D., McMillan, J.I. & Iverson, S.J. (2003). Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal. *Animal Behaviour*, **66**: 777 – 789.

Bejder, L., Fletcher, D. & Bräger, S. (1998). A method for testing association patterns of social animals. *Animal Behaviour,* **56**: 719-725.

Benoit, D. & Bowen, W.D. (1990). Seasonal and geographic variation in the diet of grey seals (Halichoerus grypus) in eastern Canada. In: Population Biology of Sealworm (Pseudoterranova decipiens) in Relations to its Intermediate and Seal Hosts. Pp: 215-226. (Ed. Bowen, W. D.). Canadian Bulletin of Fisheries and Aquatic Science, Ottawa, 222.

Berta, A. & Sumich, J.L. (1999) Marine Mammals: Evolutionary Biology. San Diego: Academic Press. ISBN: 0120932253. pp: 494

Boily, P. & Lavigne, D.M. (1996). Thermoregulation of juvenile grey seals, *Halichoerus grypus*, in air. *Canadian Journal of Zoology*, **74**: 201 – 208.

Bjørge, A. (2002). Summer home range and habitat selection of harbor seal (*Phoca vitulina*) pups. *Marine Mammal Science*, **18**(2): 439 – 454.

Bonner, W.N. (1972). The Grey Seal and Common Seal in European Waters. *Oceanogr. Mar. Biol. Ann. Rev.,* **10**: 461 – 507.

Bonner, W.N. (1989). The Natural History of Seals. Christopher Helm Publishers Ltd. pp: 196. ISBN: 0-7470-0203-7.

Boness, D.J. & Bowen, W.D. (1996). The evolution of maternal care in pinnipeds. *BioScience*, **46**(9): 645 – 654.

Boness, D.J., Clapham, P.J. & Mesnick, S.L. (2002). Chapter 10: Life history and reproductive strategies. pp: 278 – 324. In: *Marine Mammal Biology: An Evolutionary Approach.* Hoelzel, A.R. (Ed.); pp: 432. Blackwell Science Publishing. ISBN: 0-632-05232-5.

Boness, D.J. & James, H. (1979). Reproductive behaviour of the grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. *J. Zool., Lond.*, **188**: 477 – 500.

Born, E.W., Riget, F.F., Dietz, D.A. (1999). Escape responses of hauled out ringed seals (*Phoca hispida*) to aircraft disturbance. *Polar Biology*, **21**: 171 – 178.

Boskovic, R., Kovacs, K.M., Hammill, M.O. & White, B.N. (1996). Geographic distribution of mitochondrial DNA haplotypes in grey seals (*Halichoerus grypus*). *Canadian Journal Zoology*, **74**: 1787 – 1796.

Bowden, K.F. (1950). Processes affecting the salinity of the Irish Sea. *Monthly Notices of the Royal Astronomical Society. Geophysical Supplement,* **6**: 63 – 90.

Bowen, W.D., Beck, C.A. & Austin, D.A. (2002a). Pinniped Ecology. pp: 911 – 921. In: Encyclopedia of Marine Mammals (Editors: Perrin, W.F., Würsig, B. & Thewissen, J.G.M.). pp: 1414. Academic Press. ISBN: 0-12-551340-2.

Bowen, W.D. & Harrison, G.D. (1994). Offshore diet of grey seals *Halichoerus grypus* near Sable Island, Canada. *Marine Ecology Progress Series*, **112**: 1 – 11.

Bowen, W.D., Lawson, J.W. & Beck, B. (1993). Seasonal and geographic variation in the species composition and Size of Prey Consumed by Grey Seals (Halichoerus grypus) on the Scotian Shelf. *Canadian Journal of Fisheries and Aquatic Sciences,* **50**: 1768 – 1778.

Bowen, W. D., McMillan, J. & Mohn, R. (2003). Sustained exponential population growth of grey seals at Sable Island, Nova Scotia. *ICES Journal of Marine Science*, **60**: 1265 – 1274.

Bowen, W.D., Stobo, W.T. & Smith, S.J. (1992). Mass changes of grey seal *Halichoerus grypus* pups on Sable Island: differential maternal investment reconsidered. *J. Zool. Lond.,* **227**: 607 – 622.

Boyd, I.L. (1985). Pregnancy and ovulation rates in grey seals (*Halichoerus grypus*) on the British coast. J. *Zool. Lond.,* **205**: 265 – 272.

Boyd, I.L. (2000). State-dependent fertility in pinnipeds: contrasting capital and income breeders. *Functional Ecology*, **14**: 623 – 630.

Boyd, I.L. (2002). Pinniped Life History. pp: 929 – 934. In: Encyclopedia of Marine Mammals (Editors: Perrin, W.F., Würsig, B. & Thewissen, J.G.M.). pp: 1414. Academic Press. ISBN: 0-12-551340-2.

Boyd, J.M. & Laws, R.M. (1962). Observations on the Grey Seal (*Halichoerus grypus*) at North Rona in 1960. *Proceedings of the Zoological Society of London,* **139**: 249 – 260.

Boyd, J.M., Lockie, J.D. & Hewer, H.R. (1962). The Breeding Colony of Grey Seals on North Rona, 1959. *Proceedings of the Zoological Society of London*, **138**: 257 – 277.

Brasseur, S., Creuwels, J., Vanderwerf, B. & Reijnders, P. (1996). Deprivation Indicates Necessity for Haul-Out in Harbour Seals. *Marine Mammal Science*, **12**(4): 619 – 624.

Brazier, D.P., Holt, R.H.F., Murray, E. & Nichols, D.M. (1999). *Marine Nature Conservation Review Sector 10. Cardigan Bay and north Wales: area summaries*. Peterborough, Joint Nature Conservation Committee. (Coasts and seas of the United Kingdom. MNCR series). pp: 232.

Brown, J., Carillo, L., Fernand, L., Horsburgh, K.J. & Hill, A.E., (2003). Observations of the physical structure and seasonal jet-like circulation of the Celtic Sea and St. George's Channel of the Irish Sea. *Continental Shelf Research*, **23**: 533 – 561.

Browne, P., Laake, J.L. & DeLong, R. L. (2002). Improving pinniped diet analyses through identification of multiple skeletal structures in fecal samples. *Fisheries Bulletin,* **100**: 423–433.

Brown, R.F. & Mate, B.R. (1983). Abundance, movements, and feeding habits of harbor seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon. *Fishery Bulletin*, **81**(2): 291 – 301.

Burger, J. (1981). The effect of human activity on birds at a coastal bay. *Biological Conservation*, **21**: 231 – 241.

Burger, J. (1994). The effect of human disturbance on foraging behavior and habitat use in piping plover (*Charadrius melodus*). *Estuaries*, **17**(3): 695 – 701.

Burger, J. & Leonard, J. (2000). Conflict resolution in coastal waters: the case of personal watercraft. *Marine Policy*, **24**: 61 – 67.

Calambokidis, C., Taylor, B.L., Carter, S.D., Steiger, G.H., Dawson, P.K. & Antrim, L.D. (1987). Distribution and haul-out behavior of harbor seals in Glacier Bay, Alaska. *Canadian Journal of Zoology*, **65**: 1391 – 1396.

Cameron, A.W. (1970). Seasonal movements and diurnal activity rhythms of the grey seal (*Halichoerus grypus*). *J. Zool. Lond.,* **161**: 15 – 23.

Cassini, M. H. (2001). Behavioural responses of South American fur seals to approach by tourists – a brief report. *Applied Animal Behaviour Science*, **71**: 341 – 346.

Caudron, A.K., Kondakov, A.A. & Siryanov, S.V. (1998). Acoustic structure and individual variation in grey seal (*Halichoerus grypus*) pup calls. *Journal of the Marine Biological Association, U.K.,* **78**: 651 – 658.

Ceredigion County Council (2005). Website. http://www.ceredigion.gov.uk

Cézilly, F., Dubois, F. & Pagel, M. (2000). Is mate fidelity related to site fidelity? A comparative analysis in Ciconiiforms. *Animal Behaviour*, **59**: 1143 – 1152.

Coltman, D.W., Bowen, W.D. & Wright, J.M. (1999). A multivariate analysis of phenotype and paternity in male harbour seals, *Phoca vitulina*, at Sable Island, Nova Scotia. *Behavioural Ecology*, **10**(2): 169 – 177.

Constantine, R. (2001). Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. *Marine Mammal Science*, **17**(4): 689 – 702.

Constantine, R., Brunton, D.H. & Dennis, T. (2004). Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. *Biological Conservation*, **117**: 299–307.

Coulson, J.C. (1981). A study of the factors influencing the timing of breeding in the Grey Seal *Halichoerus grypus*. *J. Zool. Lond.*, **194**: 553 – 571.

Crowley, S.M., Kelly, B.P., Daniel, R. (2001). Individual identification of harbor seals for application to population and behavioural studies. pp: 161 – 168. In: Harbor Seal Investigations in Alaska. Annual Report for NOAA Award NA87FX0300. Alaska Department of Fish and Game. Division of Wildlife Conservation. Anchorage. AK. 356 pp.

Cruwys, E. & Davis, P. (1995). The effect of local weather conditions on the behaviour of moulting southern elephant seals, *Mirounga leonina* (L). *Polar Record*, **31**: 427-430.

Davies, J.L. (1949). Observations on the grey seal (*Halichoerus grypus*) at Ramsey Island, Pembrokeshire. *Proc. Zool. Soc. Lond.*, **119**: 673 – 692.

Dobson, M.R. & Whittington, R.J. (1987). The geology of Cardigan Bay. *Proc. Geol. Ass.*, **98**(4): 331 – 353.

Dyck, M.G. & Baydack, R.K. (2004). Vigilance behaviour of polar bears (*Ursus maritimus*) in the context of wildlife-viewing activities at Churchill, Manitoba, Canada. *Biological Conservation*, **116**: 343 – 350.

Eberhardt, L. L., Chapman, D. G. & Gilbert, J. R. (1979). A review of marine mammal census methods. *Wildlife Monographs*, **63**: 1 – 46.

Engelhard, G.H., Baarspul, A.N.J., Broekman, M., Creuwels, J.C.S. & Reijnders, P.J.H. (2002). Human disturbance, nursing behaviour, and lactational pup growth in a declining southern elephant seal (*Mirounga leonina*) population. *Canadian Journal of Zoology*, **80**: 1876 – 1886.

Erickson, A.W., Bledsoe, L.J. & Hanson, M.B. (1989). Bootstrap correction for diurnal activity cycle in census data for Antarctic seals. *Marine Mammal Science*, **5**(1): 29 – 56.

Evans, C.D.R. (1995). Chapter 2, Geology and physical environment. In: Barne, J.H., Robson, C.F., Kaznowska, S.S. & Doody, J.P. (Eds). Coast and Seas of the United Kingdom. Region 12: Wales. Margon to Little Orme, 23. Joint Nature Conservation Committee, Peterborough. pp: 239.

Fay, F.H. & Ray, C. (1968). Influence on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). I. Evidence from thermoregulatory behavior. *Zoologica*, **53**: 1 – 18.

Finley, K.J. (1979). Haul-out behaviour and densities of ringed seals (*Phoca hispida*) in the Barrow Strait area, N.W.T. *Canadian Journal of Zoology*, **57**: 1985 – 1997.

Fogden, S.C.L. (1971). Mother-young behaviour at grey seal breeding beaches. *J. Zool., Lond.,* **164**: 61 – 92.

Forcada, J. & Aguilar, A. (2000). Use of photographic identification in capture-recapture studies of Mediterranean monk seals. *Marine Mammal Science*, **16**: 767 – 793.

Fowler, G.S. (1999). Behavioral and hormonal responses of Magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitation. *Biological Conservation*, **90**: 143 – 149.

Frid, A. & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6**(1): 11 [online: http://www.consecol.org/vol6/iss_1/art11].

Freeman, S., Mackinson, S. & Flatt, R. (2004). Diel patterns in the habitat utilisation of sandeels revealed using integrated acoustic surveys. *Journal of Experimental Marine Biology and Ecology*, **305**(2): 141-154.

Gaggiotti, O.E., Jones, F., Lee, W.M., Amos, W., Harwood, J. & Nichols, R.A. (2002). Patterns of colonization in a metapopulation of grey seals. *Nature*, **416**: 424 – 427.

Galicia, E. & Baldassarre, G.A. (1997). Effects of motorized tourboats on the behavior of nonbreeding American flamingoes in Yucatan, Mexico. *Conservation Biology*, **11**(5): 1159 – 1165.

Garrigue, C., Dodemont, R., Steel, D. & Baker, C.S. (2004). Organismal and 'gametic' capture-recapture using microsatellite genotyping confirm low abundance and reproductive autonomy of humpback whales on the wintering grounds of New Caledonia. *Marine Ecology Progress Series*, **274**: 251-262.

Gauthier, G. (1990). Philopatry, nest-site fidelity, and reproductive performance in Buffleheads. *The Auk*, **107**: 126 – 132.

Gill, J.A., Norris, K. & Sutherland, W.J. (2001a). The effects of disturbance on habitat use by black-tailed godwits, *Limosa limosa*. *Journal of Applied Ecology*, **38**: 846 – 856.

Gill, J.A., Norris, K. & Sutherland, W.J. (2001b). Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*, **97**: 265 – 268.

Gill, J.A., Sutherland, W.J. & Watkinson, A.R. (1996). A method to quantify the effects of human disturbance on animal populations. *Journal of Applied Ecology*, **33**(4): 786 – 792.

Gill, J.A. & Sutherland, W.J. (2000). Predicting the consequences of human disturbance from behavioural decisions pp: 51 – 65; In: Behaviour and Conservation, Conservation Biology Series 2 Edited by Gosling, L.M. & Sutherland, W.J. pp: 438. Cambridge University Press. ISBN: 0-521-66539-6.

Godsell, J. (1988). Herd formation and haul-out behavior in harbour seals (*Phoca vitulina*). *Journal of Zoology*, **215**: 83-98.

Gope, C., Kehtarnavaz, N., Hillman, G. & Würsig, B. (2005). An affine invariant curve matching method for photo-identification of marine mammals. *Pattern Recognition*, **38**: 125 – 132.

Goulet, A.-M., Hammill, M.O. & Barrette, C. (1999). Quality of satellite telemetry locations of gray seals (*Halichoerus grypus*). *Marine Mammal Science*, **15**(2): 589 – 594.

Gregory, P.R. & Rowden, A.A. (2001) Behaviour patterns of bottlenose dolphins (*Tursiops truncatus*) relative to tidal state, time-of-day, and boat traffic in Cardigan Bay, West Wales. *Aquatic Mammals,* **27**(2): 105-113.

Gunnlaugsson, T. & Sigurjónsson, J. (1990). A note on the problem of false positives in the use of natural marking data for abundance estimation. pp: 143 – 145, i*n* P.S. Hammond, S.A. Mizroch & G.P. Donovan, editors. Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. Volume Special Issue 12. International Whaling Commission, Cambridge.

Hall, A. (2002). Gray Seal, *Halichoerus grypus*. pp: 522 – 524. In: Encyclopedia of Marine Mammals (Editors: Perrin, W.F., Würsig, B. & Thewissen, J.G.M.). pp: 1414. Academic Press. ISBN: 0-12-551340-2.

Hammill, M.O. (2002). Earless Seals, Phocidae. pp: 352 – 358. In: Encyclopedia of Marine Mammals (Editors: Perrin, W.F., Würsig, B. & Thewissen, J.G.M.). pp: 1414. Academic Press. ISBN: 0-12-551340-2.

Hammill, M.O., Stenson, G.B., Myers, R.A. & Stobe, W.T. (1998). Pup production and population trends of the grey seal (*Halichoerus grypus*) in the Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.,* **55**: 423 – 430.

Hammond, P.S., Hall, A.J. & Prime, J.H. (1994a). The diet of grey seals around Orkney and other island and mainland sites in north-eastern Scotland. *Journal of Applied Ecology*, **31**: 340 – 350.

Hammond, P.S., Hall, A.J. & Prime, J.H. (1994b). The diet of grey seals in the Inner and Outer Hebrides. *Journal of Applied Ecology*, **31**: 737 - 746.

Hart, A. & Lendrem, D.W. (1984). Vigilance and scanning patterns in birds. *Animal Behaviour*, **32**: 1216 – 1224.

Harwood, J. & Prime, J.H. (1978). Some factors affecting the size of British grey seal populations. *Journal of Applied Ecology*, **15**: 401 – 411.

Hastings, K.K., Small, R.J. & Hiby, L. (2001). Use of computer-assisted matching of photographs to examine population parameters of Alaskan harbour seals. pp: 146 – 160. *In:* Harbor Seal Investigations in Alaska. Annual Report for NOAA Award NA87FX0300. Alaska Department of Fish and Game. Division of Wildlife Conservation. Anchorage. AK. 356 pp.

Haug, T., Henriksen, G., Kondakov, A., Mishin, V., Nilssen, K. T. & Røv, N. (1994). The Status of Grey Seals *Halichoerus grypus* in North Norway and on the Murman Coast, Russia. *Biological Conservation*, **70**: 59 – 67.

Hauksson, E. & Ólafsdóttir, D. (1995). Grey Seal (*Halichoerus grypus* Fabr.), population biology, food and feeding habits, and importance as a final host for the life-cycle of sealworm (*Pseudoterranova decipiens* Krabbe) in Icelandic waters. In: Whales, Seals, Fish And Man pp: 565 – 571. Proceedings of the International Symposium on the Biology of Marine Mammals in the North East Atlantic, Tromsø, Norway, 29 November-1 December 1994. (Ed: Blix, A. S., Walløe, L. & Ulltang, Ø.). Elsevier. pp: 734. ISBN: 0-444-82070-1

Henry, E. & Hammill, M. O. (2001). Impact of small boats on the haulout activity of harbour seals (*Phoca vitulina*) in Métis Bay, Saint Lawrence Estuary, Québec, Canada. *Aquatic Mammals*, **27**(2):140-148.

Hewer, H.R. (1957). A Hebridean breeding colony of grey seals, Halichoerus grypus (FAB.), with comparative notes on the grey seals of Ramsey Island, Pembrokeshire. *Proc. Zool. Soc. Lond.*, **128**: 23 - 66.

Hewer, H.R. (1964). The determination of age, sexual maturity, longevity and a life-table in the grey seal (*Halichoerus grypus*). *Proc. Zool. Soc. Lond.*, **142**: 593 – 624.

Hewer, H.R. & Backhouse, K.M. (1959). Field identification of bulls and cows of the grey seal, *Halichoerus grypus* Fab. *Proc. Zool. Soc. Lond.*, 132: 641 - 645.

Hiby, L. & Lovell, P. (1990). Computer Aided Matching of Natural Markings: A Prototype System for Grey Seals. pp: 57 – 61 *in* P.S. Hammond, S.A. Mizroch & G.P. Donovan, editors. Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. Volume Special Issue 12. International Whaling Commission, Cambridge.

Hickling, G. (1962). Grey Seals & the Farne Islands. pp: 180. Routledge & Kegan Paul Ltd., London.

Hillman, G.R., Würsig, B., Gailey, G.A., Kehtarnavaz, N., Drobyshevsky, A., Araabi, B.N., Tagare, H.D. & Weller, D.W. (2003). Computer-assisted photo-identification of individual marine vertebrates: a multi-species system. *Aquatic Mammals,* **29**(1): 117 - 123.

Hind, A.T. & Gurney, W.S.C. (1998). Are there thermoregulatory constraints on the timing of pupping for harbour seals? *Canadian Journal of Zoology*, **76**: 2245 – 2254.

Hindell, M.A. & Burton, H.R. (1988). Seasonal haul-out patterns of the southern elephant seal (*Mirounga leonina* L.) at Macquarie Island. *Journal of Mammalogy*, **69**(1): 81 – 88.

Hindell, M.A. & Little, G.J. (1988). Longevity, fertility and philopatry of two female southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Marine Mammal Science*, **4**(2): 168 – 171.

Hoelzel, A.R. (Ed) (2002). Marine Mammal Biology: An Evolutionary Approach. Blackwell Publishing. ISBN: 0-632-05232-5. pp: 432.

Horsburgh, K.J., Hill, A.E. & Brown, J. (1998). A summer jet in the St. George's Channel of the Irish Sea. *Estuarine, Coastal and Shelf Science*, **47**: 285 – 294.

Irons, D. B. (1998). Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology*, **79**(2): 647 – 655.

Irving, L. & Hart, J.S. (1957). The metabolism and insulation of seals as bare-skinned mammals in cold water. *Canadian Journal of Zoology*, **35**(4): 497 – 511.

Jemison, L.A. & Kelly, B.P. (2001). Pupping phenology and demography of harbour seals (*Phoca vitulina richardsi*) on Tugidak Island, Alaska. *Marine Mammal Science*, **17**(3): 585 – 600.

Kelly, C., Glegg, G.A. & Speedie, C.D. (2004). Management of marine wildlife disturbance. *Ocean & Coastal Management*, **47**: 1 – 19.

Kiely, O., Lidgard, D., McKibben, M., Connolly, N. & Baines, M. (2000). Grey Seals: Status and Monitoring in the Irish and Celtic Seas. Maritime Ireland / Wales INTERREG Report No. 3. pp: 77. ISSN: 1393-9025.

Klein, M. L., Humphrey, S. R. & Percival, H. F. (1995). Effects of ecotourism on distribution of waterbirds in a wildlife refuge. *Conservation Biology*, **9**(6): 1454 – 1465.

Knauss, J.A. (1997). Introduction to physical oceanography. 2nd Edition. Prentice Hall Inc. ISBN: 0-13-238155-9. pp: 309.

Knopper, L.D. & Boily, P. (2000). Relationship between apnea duration and rate of oxygen consumption in captive female grey seals while sleeping or resting on land. *Marine Mammal Science*, **16**(3): 676 – 681.

Kovacs, K.M. & Innes, S. (1990). The impact of tourism on harp seals (*Phoca groenlandica*) in the Gulf of St. Lawrence, Canada. *Applied Animal behaviour Science*, **26**: 15 – 26.

Kreiber, M. & Barratte, C. (1984). Aggregation behaviour of harbour seals at Forillon National Park, Canada. *The Journal of Animal Ecology*, **53(3)**: 913 – 928.

Kvadsheim, P. H. & Folkow, L. P. (1997). Blubber and flipper heat transfer in harp seals. *Acta Physiol. Scand.,* **161**: 385 – 395.

Lafferty, K.D. (2001). Disturbance to wintering western snowy plovers. *Biological Conservation*, **101**: 315 – 325.

Lake, S. E., Burton, H. R. & Hindell, M. A. (1997). Influence of time of day and month on Weddell seal haul-out patterns at the Vestfold Hills, Antarctica. *Polar Biology*, **18**: 319 – 324.

Lamb, J. (2004). Relationships between presence of bottlenose dolphins, environmental variables and boat traffic; visual and acoustic surveys in New Quay Bay, Wales. *University of Wales, Bangor*. Masters of Science Thesis, Marine Mammal Science. pp: 80.

Lavigne, D.M. (1982). Pinniped thermoregulation: Comments on the "effects of cold on the evolution of pinniped breeding systems". *Evolution*, **36**(2): 409 – 414.

Lendrem, D.W. (1984). Sleeping and vigilance in birds, II. An experimental study of the Barbary dove (*Streptopelia risoria*). *Animal Behaviour*, **32**: 243 – 248.

Lesage, V., Hammill, M.O. & Kovacs, K.M. (1999). Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Canadian Journal of Zoology*, **77**: 74 – 87.

Leseberg, A., Hockey, P.A.R. & Loewenthal, D. (2000). Human disturbance and the chick-rearing ability of African black oystercatchers (*Haematopus moquini*): a geographical perspective. *Biological Conservation*, **96**: 379 – 385.

Lockley, R. M. (1966). A 'Survival' Book: Grey Seal, Common Seal: An account of the life histories of British seals. White Lion Publishers Ltd. pp: 175.

Lorentsen, S.-H. & Bakke, Ø. (1995). Estimation of grey seal *Halichoerus grypus* pup production from one or more censuses. pp: 47 – 51. In: Whales, Seals, Man & Fish. pp: 47 - 51. Proceedings of the International Symposium on the Biology of Marine Mammals in the North East Atlantic, Tromsø, Norway, 29 November-1 December 1994. (Ed: Blix, A. S., Walløe, L. & Ulltang, Ø.). Elsevier. pp: 734. ISBN: 0-444-82070-1

Lydersen, C., Hammill, M. O. & Kovacs, K. M. (1994). Activity of lactating ice-breeding grey seals, *Halichoerus grypus*, from the Gulf of St. Lawrence, Canada. *Animal Behaviour*, **48**: 1417 – 1425.

Lydersen, C. & Kovacs, K.M. (2000). Reversed molting patterns in starveling gray (*Halichoerus grypus*) and harp (*Phoca groenlandica*) seal pups. *Marine Mammal Science*, **16**(2): 489 – 493.

McConkey, S.D. (1999). Photographic identification of the New Zealand sea lion: a new technique. *New Zealand Journal of Marine and Freshwater Research*, **33**: 63 – 66.

McConnell, B.J., Fedak, M.A., Lovell, P. & Hammond, P.S. (1999). Movements and foraging areas of grey seals in the North Sea. *Journal of Applied Ecology*, **36**: 573 – 590.

McCulloch, S., Pomeroy, P. P. & Slater, P. J. B. (1999). Individually distinctive pup vocalizations fail to prevent allo-suckling in grey seals. *Canadian Journal of Zoology*, **77**: 716 – 723.

Martin, A.R. & Reeves, R.R. (2002). Chapter 1: Diversity and Zoogeography. pp: 1 – 37. In: Marine Mammal Biology: An Evolutionary Approach. Hoelzel, A.R. (Ed.); pp: 432. Blackwell Science Publishing. ISBN: 0-632-05232-5.

Matthiopoulos, J., Harwood, J. & Thomas, L. (2005). Metapopulation consequences of site fidelity for colonially breeding mammals and birds. *Journal of Animal Ecology*, **74**: 716 – 727.

Meddis, R. (1975). On the function of sleep. *Animal Behaviour*, **23**: 676 – 691.

Mesnick, S. L. & Ralls, K. (2002). Mating Systems. pp: 726 – 733. In: Encyclopedia of Marine Mammals (Editors: Perrin, W.F., Würsig, B. & Thewissen, J.G.M.). pp: 1414. Academic Press. ISBN: 0-12-551340-2.

Mikkelsen, B., Haug, T. & Nilssen, K.T. (2002). Summer diet of grey seals (Halichoerus grypus) in Faroese waters. *Sarsia*, **87**: 462 – 471.

Miller, E. H. (2002). Territorial Behaviour. pp: 1235 – 1243. In: Encyclopedia of Marine Mammals (Editors: Perrin, W.F., Würsig, B. & Thewissen, J.G.M.). pp: 1414. Academic Press. ISBN: 0-12-551340-2.

Mills, J.P., Newton, I. & Twiss, S.D. (1997). Photogrammetry from archived digital imagery for seal monitoring. *Photogrammetric Record*, **15**(89): 715 – 724.

Moore, P.G. (2003). Seals and fisheries in the Clyde Sea area (Scotland): traditional knowledge informs science. *Fisheries Research*, **63**: 51 – 61.

Moulton, V.D., Richardson, W.J., McDonald, T.L., Elliott, R.E. & Williams, M.T. (2002). Factors influencing local abundance and haulout behaviour of ringed seals (*Phoca hispida*) on landfast ice of the Alaskan Beaufort Sea. *Canadian Journal of Zoology*, **80**: 1900 – 1917.

Murie, D.J. & Lavigne, D.M. (1992). Growth and feeding habits of grey seals (*Halichoerus grypus*) in the northwestern Gulf of St. Lawrence, Canada. *Canadian Journal of Zoology*, **70**: 1604 – 1613.

Newton, I. (1993). Age and site fidelity in female sparrowhawks, *Accipiter nisus*. *Animal Behaviour*, **46**: 161 – 168.

Nikon Scan 4, Copyright 1998-2003 Nikon Inc. and Nikon Corporation.

Nisbet, I. C. T. (2000). Disturbance, habituation, and management of waterbird colonies. *Waterbirds*, **23**(2): 312 – 332.

Nordstrom, C.A. (2002). Haul-out selection by Pacific harbor seals (*Phoca vitulina richardsi*): isolation and perceived predation risk. *Marine Mammal Science*, **18**(1): 194 – 205.

Nowacek, S.M., Wells, R.S. & Solow, A.R. (2001). Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science*, **17**(4): 673 – 688.

Øien, N. & Øritsland, T. (1995). Use of mark-recapture experiments to monitor seal populations subject to catching. Whales, Seals, Fish & Man. pp: 35 – 45. Proceedings of the International Symposium on the Biology of Marine Mammals in the North East Atlantic, Tromsø, Norway, 29 November-1 December 1994. (Ed: Blix, A. S., Walløe, L. & Ulltang, Ø.). Elsevier. pp: 734. ISBN: 0-444-82070-1

OSPAR Commission 2000. Quality Status Report 2000, Region III – Celtic Seas. OSPAR Commission, London. 116 + xiii pp.

Parsons, E.C.M. (2003). Seal Management in Scotland: Tourist perceptions and the possible impacts on the Scottish tourism industry. *Current Issues in Tourism*, **6**(6): 540 – 546.

Patenaude, N.J (2003). Sightings of southern right whales around 'mainland' New Zealand. *Science for Conservation,* **225**: 1-35. New Zealand Department of Conservation. ISBN: 0–478–22454–0.

Pauli, B. D. & Terhune, J. M. (1987a). Tidal and temporal interaction on harbour seal haul-out patterns. *Aquatic Mammals*, **13**(3): 93 – 95.

Pauli, B. D. & Terhune, J. M. (1987b). Meteorological influences on harbour seal haul-out. *Aquatic Mammals*, **13**(3): 114 – 118.

Perrin, W.F. (2002). Coloration. *In*: Encyclopedia of Marine Mammals. pp: 236-244. Eds: Perrin, W.F., Würsig, B. & Thewissen, J.G.M. ISBN: 0-12-551340-2.

Peters, K.A. & Otis, D.L. (2005). Using the risk-disturbance hypothesis to assess the relative effects of human disturbance and predation risk on foraging American oystercatchers. *The Condor*, **107**: 716 – 725.

Pfister, C., Harrington, B.A. & Lavine, M. (1992). The impact of human disturbance on shorebirds at a migration staging area. *Biological Conservation*, **60**: 115 – 126.

Pierce, G.J., Miller, A., Thompson, P.M. & Hislop, J.R.G. (1991). Prey remains in grey seal (*Halichoerus grypus*) faeces from the Moray Firth, north-east Scotland. *Journal of Zoology, London*, **224**: 337 – 341.

Pierpoint, C. & Allan, L. (2004). Bottlenose dolphins and Boat Traffic at New Quay on the Ceredigion Marine Heritage Coast, West Wales, 2002-2003. Ceredigion County Council.

Pingree, R. D. & Le Cann, B. (1989). Celtic and Armorican slope and shelf residual currents. *Progress in Oceanography,* **23**: 303 – 338.

Pomeroy, P.P., Anderson, S.S., Twiss, S.D. & McConnell, B.J. (1994). Dispersion and Site Fidelity of Breeding Female Grey Seals (Halichoerus grypus) on North Rona, Scotland. *Journal of Zoology, London*, **233** (3): 429 – 447.

Pomeroy, P. P., Redman, P. R., Ruddell, S. J. S., Duck, C. D. & Twiss, S. D. (2005). Breeding site choice fails to explain interannual associations of female grey seals. *Behavioural Ecology and Sociobiology*, **57**: 546 – 556.

Pomeroy, P.P., Twiss, S.D. & Duck, C.D. (2000a). Expansion of a grey seal (*Halichoerus grypus*) breeding colony: changes in pupping site use at the Isle of May, Scotland. *Journal of Zoology, London*, **250**: 1 – 12.

Pomeroy, P.P., Twiss, S.D. & Redman, P. (2000b). Philopatry, Site Fidelity and Local Kin Associations within Grey Seal Breeding Colonies. *Ethology*, **106**: 899 – 919.

Pugh, D.T. & Thompson, K.R. (1986). The subtidal behaviour of the Celtic Sea - I. Sea level and bottom pressures. *Continental Shelf Research,* **5**(3): 293 – 319.

Quenette, P.-Y. (1990). Functions of vigilance behaviour in mammals: a review. *Acta Ecologica*, **11**(6): 801 – 818.

Reeves, R.R., Stewart, B.S., Clapham, P.J. & Powell, J.A. (2002). Sea Mammals of the World: A Complete Guide to Whales, Dolphins, Seals, Sea Lions and Sea Cows. A & C Black Publishers, London. pp: 528. ISBN: 0-7136-6334-0.

Reilly, J.J., Fedak, M.A., Thomas, D.H., Coward, W.A.A. & Anderson, S.S. (1996). Water balance and the energetics of lactation in grey seals (*Halichoerus grypus*) as studied by isotopically labeled water methods. *J., Zool., Lond.*, **238**: 157 – 165.

Rendall, D., Rodman, P. S. & Emond, R. E. (1996). Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour*, 51: 1007 – 1015.

Ridgway, S. H., Harrison, R. J. & Joyce, P. L. (1975). Sleep and cardiac rhythm in the gray seal. *Science*, **187**: 553 – 555.

Roen, R. & Bjørge, A. (1995). Haul-out behaviour of the Norwegian harbour seal during summer. In: Whales, seals, fish and man. pp: 61 – 67. Proceedings of the International Symposium on the Biology of Marine Mammals in the North East Atlantic, Tromsø, Norway, 29 November-1 December 1994. (Ed: Blix, A. S., Walløe, L. & Ulltang, Ø.). Elsevier. pp: 734. ISBN: 0-444-82070-1

Rogers, T.L. & Bryden, M.M. (1997). Density and haul-out behavior of leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Antarctica. *Marine Mammal Science*, **13**(2): 293 – 302.

Ronconi, R.A., St. Clair, C.C., (2002). Management options to reduce boat disturbance on foraging black guillemots (*Cepphus grylle*) in the Bay of Fundy. *Biological Conservation*, **108**: 265 – 271.

Samuels, A. & Tyack, P.L. (2000). Flukeprints: a history in studying cetacean societies. In: Cetacean Societies: Field Studies of Dolphins and Whales. pp: 9-44. Eds.: Mann, J., Connor, C., Tyack, P.L. & Whitehead, H. ISBN: 0-226-50341-0.

Schneider, D.C. & Payne, P.M. (1983). Factors affecting haul-out of harbor seals at a site in southeastern Massachusetts. *Journal of Mammalogy*, **64**(3): 518 – 520.

Schweigert, F.J., Luppertz, M. & Stobo, W.T. (2002). Fasting and lactation effect fat-soluble vitamin A and E levels in blood and their distribution in tissue of grey seals (H*alichoerus grypus*). *Comparative Biochemistry and Physiology Part A*, **131**: 901–908.

DaSilva, J. & Terhune, J.M. (1988). Harbor seal grouping as an anti-predator strategy. *Animal Behaviour*, **36**: 1309 – 1316.

Sjöberg, M. & Ball, J. P. (2000). Grey seal, *Halichoerus grypus*, habitat selection around haulout sites in the Baltic Sea: bathymetry or central-place foraging? *Canadian Journal of Zoology*, **78**:1661–1667.

Sjöberg, M., McConnell, B. & Fedak, M. (1999). Haulout patterns of grey seals Halichoerus grypus in the Baltic Sea. *Wildlife Biology*, **5**(1): 37 – 47.

Slooten, E. & Dawson, S.M. (1992). Survival rates of photographically identified hector's dolphins from 1984 to 1988. *Marine Mammal Science,* **8**(4): 327-343.

Smith, E.A. (1966). A review of the world's grey seal population. *J. Zool. Lond.*, **150**: 463 – 489.

Smith, T.S., Herrero, S. & DeBruyn, T.D. (2005). Alaskan brown bears, humans, and disturbance. *Ursus*, **16**(1): 1 – 10.

SPSS for Windows. Release 11.5.0 (2002). Copyright © SPSS Inc., 1989 – 2002.

Stevens, M. A. & Boness, D. J. (2003). Influences of habitat features and human disturbance on use of breeding sites by a declining population of southern fur seals (*Arctocephalus australis*). *J. Zool. Lond.*, **260**: 145 – 152.

Stevick, P. T., McConnell, B. J. & Hammond, P. S. (2002). Chapter 7: Patterns of Movement. Pp: 185 – 216. In: Marine Mammal Biology: An Evolutionary Approach. Hoelzel, A.R. (Ed.); pp: 432. Blackwell Science Publishing. ISBN: 0-632-05232-5.

Stevick, P. T., Palsbøll, P. J., Smith, T. D., Bravington, M. V. & Hammond, P. S. (2001). Errors in identification using natural markings: rates, sources, and effects on capture-recapture estimates of abundance. *Canadian Journal of Fisheries & Aquatic Science*, **58**: 1861 – 1870.

Sullivan, R.M. (1980). Seasonal occurrence and haul-out use in pinnipeds along Humboldt Country, California. *Journal of Mammalogy*, **61**(4): 754 – 760.

Summers, C. F. (1978). Trends in the Size of British Grey Seal Populations. *Journal of Applied Ecology*, **15**(2): 395 – 400.

Switzer, P. V. (1997a). Factors affecting site fidelity in a territorial animal, *Perithemis tenera. Animal Behaviour*, **53:** 865 – 877.

Switzer, P. V. (1997b). Past reproductive success affects future habitat selection. *Behavioural Ecology and Sociobiology*, **40**: 307 – 312.

Terhune, J.M. (1985). Scanning behaviour of harbour seals on haul-out sites. *Journal of Mammalogy*, **66**(2): 392 – 395.

Terhune, J. M. & Brillant, S. W. (1996). Harbour seal vigilance decreases over time since haul out. *Animal Behaviour*, **51**: 757 – 763.

Thomas, J.A. & DeMaster, D.P. (1983). Diel haul-out patterns of Weddell seal (*Leptonychotes weddelli*) females and their pups. *Canadian Journal of Zoology*, **61**: 2084 – 2086.

Thompson, D., Hammond, P.S., Nicholas, K.S. & Fedak, M.A. (1991a). Movements, diving and foraging behaviour of grey seals (*Halichoerus grypus*). *J. Zool. Lond.* **224**: 223 – 232.

Thompson, P. M., Pierce, G. M., Hislop, J. R. G., Miller, D. & Diack, J. S. W. (1991b). Winter foraging by common seals (Phoca vitulina) in relation to food availability in the Inner Moray Firth, N.E. Scotland. *The Journal of Animal Ecology*, **60**(1): 283 – 294.

Thompson, P.M., McConnell, B.J., Tollit, D.J., Mackay, A., Hunter, C. & Racey, P.A. (1996). Comparative distribution, movements and diet of harbour and grey seals from Moray Firth, N.E. Scotland. *Journal of Applied Ecology*, **33**: 1572 – 1584.

Tollit, D.J. & Thompson, P.M. (1996). Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. *Canadian Journal of Zoology*, **74**: 1110 – 1121.

Twiss, S. D., Caudron, A., Pomeroy, P. P., Thomas, C. J. & Mills, J. P. (2000a). Finescale topographical correlates of behavioural investment in offspring by female grey seals, *Halichoerus grypus*. *Animal Behaviour*, **59**: 327 – 338.

Twiss S. D. & Thomas C. J. (1999). Fine scale topographical influences on Environmental Potential for Polygamy (EPP) and male reproductive success in grey seals. pp. 191-195. In: *European Research on Cetaceans -13. Proc. 13th Ann. Conf. ECS, Valencia, Spain, 5-8 Apr, 1999.* (Eds. P.G.H. Evans, J.A. Raga, and J. Cruz). European Cetacean Society, Valencia, Spain. 484pp.

Twiss, S.D., Pomeroy, P.P. & Anderson, S.S. (1994). Dispersion and Site Fidelity of Breeding Male Grey Seals (Halichoerus grypus) on North Rona, Scotland. *J. Zool. Lond.*, **233**: 683 – 693.

Verhulst, S., Oosterbeek, K. & Ens, B.J. (2001). Experimental evidence for effects of human disturbance on foraging and parental care in oystercatchers. *Biological Conservation*, **101**: 375 – 380.

Walton, M. & Pomeroy, P. (2003). Use of blubber fatty acid profiles to detect inter-annual variations in the diet of grey seals *Halichoerus grypus*. *Marine Ecology progress Series*, **248**: 257 – 266.

Watts, P. (1992). Thermal constraints on hauling out by harbour seals (*Phoca vitulina*). *Canadian Journal of Zoology*, **70**: 553 – 560.

Watts, P. (1993). Possible lunar influence on hauling-out behavior by the Pacific harbor seal (*Phoca vitulina richardsi*). *Marine Mammal Science*, **9**(1): 68 – 76.

Watts, P., Hansen, S. & Lavigne, D. M. (1993). Models of heat loss by marine mammals thermoregulation below the zone of irrelevance. *Journal of Theoretical Biology*, **163**: 505 – 525.

Watts, P. (1996). The diel hauling-out cycle of harbour seals in an open marine environment: correlates and constraints. *J. Zool., Lond.*, **240**: 175 – 200.

Wells, R. S. (2002). Identification methods. *In*: Encyclopedia of Marine Mammals. pp: 601-608. Eds: Perrin, W.F., Würsig, B. & Thewissen, J.G.M. ISBN: 0-12-551340-2.

Wells, R. S. & Scott, M. D. (1990). Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. pp: 407 – 415 *in* P.S. Hammond, S.A. Mizroch & G.P. Donovan, editors. Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. Volume Special Issue 12. International Whaling Commission, Cambridge.

West, A.D., Goss-Custard, J.D., Stillman, R.A., Caldow, R.W.G., le V. dit Durrell, S.E.A. & McGrorty, S. (2002). Predicting the impacts of disturbance on shorebird mortality using a behaviour-based model. *Biological Conservation*, **106**: 319 – 328.

Westcott, S.M. (2002). The distribution of grey seals (*Halichoerus grypus*) and census of pup production in North Wales 2001. CCW Contract Science Report No. 499. Countryside Council for Wales. FC 73-02-183. pp: 163 – may need to recount.

Westcott, S.M. & Stringell, T.B. (2003). Field observations on the disturbance of grey seals in North Wales, 2003. Marine Monitoring Report No. 15. Countryside Council for Wales, pp: 49.

Westcott, S.M. & Stringell, T.B. (unpubl.). An evaluation of methods for generating images for photographic identification of grey seals; North Wales, 2002-2003. Marine Monitoring Report No. ?. Countryside Council for Wales, pp: 25.

White, N.A. & Sjöberg, M. (2002). Accuracy of satellite positions from free-ranging grey seals using ARGOS. *Polar Biology*, **25**: 629 – 631.

Whitehead, H., Christal, J. & Tyack, P.L. (2000). Studying cetacean social structure in space and time: innovative techniques. In: Cetacean Societies: Field Studies of Dolphins and Whales. pp: 65-90. Eds.: Mann, J., Connor, C., Tyack, P.L. & Whitehead, H. ISBN: 0-226-50341-0.

Wiig (1987). The grey seal, *Halichoerus grypus* (Fabricius), in Rogaland, Norway. *FiskDir. Skr. Ser. HavUnders.*, **18**: 303 – 309.

Williams, A.T. & Morgan, R. (1995). Aspects of physical and cultural parameters associated with coastal zone management along the Ceredigion Heritage Coast, Wales, UK. *Proc. Int. Conf. 'Coastal Change 95' Bordomer-IOC, Bordeaux, 1995*. pp: 850 – 863.

Williams, R., Trites, A.W. & Bain, D.E. (2002). Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches. *J. Zool. Lond.*, **256**: 255 – 270.

Worthington Wilmer, J., Allen, P. J., Pomeroy, P. P., Twiss, S. D. & Amos, W. (1999). Where have all the fathers gone? An extensive microsatellite analysis of paternity in the grey seal (*Halichoerus grypus*). *Molecular Ecology*, **8:** 1417 – 1429.

Worthington Wilmer, J., Overall, A.J., Pomeroy, P.P., Twiss, S.D. & Amos, W. (2000). Patterns of paternal relatedness in British grey seal colonies. *Molecular Ecology*, **9**: 283 – 292.

Würsig, B. (2002). Ecology, Overview. pp: 367 – 370. In: Encyclopedia of Marine Mammals (Editors: Perrin, W.F., Würsig, B. & Thewissen, J.G.M.). pp: 1414. Academic Press. ISBN: 0-12-551340-2.

Yochem, P.K., Stewart, B.S., DeLong, R.L. & DeMaster, D.P. (1987). Diel haul-out patterns and site fidelity of harbour seals (*Phoca vitulina richardsi*) on San Miguel Island, California, in autumn. *Marine Mammal Science*, **3**(4): 323 – 332.

Yochem, P.K., Stewart, B.S., Mina, M., Zorin, A., Sadovov, V. & Yablokov, A. (1990). Non-metrical analyses of pelage patterns in demographic studies of harbour seals. pp: 87 – 90 *in* P.S. Hammond, S.A. Mizroch & G.P. Donovan, editors. Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. Volume Special Issue 12. International Whaling Commission, Cambridge.

Yochem, P.K. & Stewart, B.S. (2002). Hair and Fur. pp: 548 – 549. In Encyclopedia of Marine Mammals, W.F. Perrin, B. Würsig, & J.G.M. Thewissen, editors. pp: 1414. Academic Press. ISBN: 0-12-551340-2.

Zeh, J.A. & Zeh, D.W. (2001). Reproductive mode and the genetic benefits of polyandry. *Animal Behaviour*, **61:** 1051–1063.

Guide Books Used

Corston, R. & Colman, A. (2003). A crash course in SPSS for Windows: versions 10 and 11, 2nd Edition. Blackwell Publishing. pp: 186. ISBN: 0-631-23206-0.

Fowler, J., Cohen, L. & Jarvis, P. (1998). Chapter 18: Multivariate Analysis, pp: 210 – 234. *In*: Practical Statistics for Field Biology, 2nd Edition. John Wiley & Sons. pp: 259. ISBN: 0-471-98296-2.

Websites

Cardigan Bay SAC: http://www.cardiganbaysac.org.uk
Last visited: 11th March 2006.

Office of Public Sector Information: http://www.opsi.gov.uk
Last visited: 5th February 2006 – to view Conservation of Seals Act (1970)