
Article:
Wilson, Susan C and Jones, Kayleigh A (2018) Behaviour of harbour seal (Phoca vitulina vitulina) mother-pup pairs in Irish Sea intertidal habitats. Biology and Environment, 118B (1). pp. 13-27. ISSN 0791-7945

DOI: 10.3318/BIOE.2018.02

BEHAVIOUR OF HARBOUR SEAL (*PHOCA VITULINA VITULINA*) MOTHER-PUP PAIRS IN IRISH SEA INTERTIDAL HABITATS

Susan C. Wilson and Kayleigh A. Jones

Susan C. Wilson (corresponding author; email: suewilson@sealresearch.org), Tara Seal Research, 14 Bridge Street, Killyleagh, N. Ireland, BT30 9QN, UK.

Kayleigh A. Jones. Environment Department, University of York, Wentworth Way, York YO10 5NG, UK. Present address: British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK.

Cite as follows: Wilson, S.C., and Jones, K.A., 2018. Behaviour of harbour seal (*Phoca vitulina vitulina*) mother-pup pairs in Irish Sea intertidal habitats. *Biology and Environment: Proceedings of the Royal Irish Academy* 2018. DOI: 10.3318/BIOE.2018.02

ABSTRACT

Information is sparse on harbour seal pupping dates and mother-pup behavioural ecology in Ireland. Here we define the pupping season and quantify the behaviour of mother-pup pairs in intertidal habitats of Dundrum Bay, north-east Ireland. Seals were counted and video footage was taken of mother-pup pairs at a rocky ledge site and a sandy beach site between 2002 and 2015. We recorded distances between pups and their mothers, filial social interactions, pup resting behaviours and mother scanning at three intertidal zones: the water, water's edge and dry ledge or beach.

The peak pupping time was 04–15 July at both sites, but the pup-to-adult ratio was higher at the rocky ledge site. Pups almost always remained less than 1m away from their mothers, and were closest while mother and pup rested in the dry zone. Filial social interactions were most frequent in the water, least frequent in the dry zone and intermediate at the water's edge; suckling occurred almost exclusively at the water's edge. Our findings highlight the essential features of a harbour seal pup's social and physical environment. We suggest how these features could be incorporated into the design and procedures of rehabilitation centres for 'orphan' pups.

INTRODUCTION

Harbour seals, *Phoca vitulina*, are one of two phocid species native to the British Isles; the other species being the grey seal, *Halichoerus grypus*. The approximate minimum number of harbour seals in the British Isles has been estimated at 28,400, with about 4,100 of those around the island of Ireland (Duck and Thompson 2009). The distribution around Ireland is very uneven, however, with main concentrations in the southwest, west, northwest and northeast, but very few harbour seals on the Irish east coast south of Carlingford Lough (Cronin *et al*. 2004). Our present study of harbour seal pupping dates, pup numbers and mother-pup behaviour was located in Dundrum Bay, County Down (Plate 1), within the northeast concentration.

Harbour seals in Ireland give birth in early summer and undergo their annual moult in late summer. Single counts of pups and adults have previously been made during the July pupping season in County Down, north-east Ireland in 1977 and 1978 (Nairn 1979) and at thirteen principal harbour seal breeding sites in the west of Ireland in 1978–79 (Warner 1983). A further study of pup numbers in July 1993–2000 in Strangford Lough and two other sites in north-east Ireland focused on the instability of pupping groups during the latter part of this period (Wilson and Montgomery-Watson 2002). However, more recent surveys of harbour seals in Ireland have typically taken place during August, when the maximum number of seals is usually present inshore during their moult (Cronin *et al*. 2004; 2007). There have been no published data for Ireland on the timing—that is, the beginning, peak and ending—of the pupping season. In the present study we derive a pupping curve for our study site in Dundrum Bay, based on pup counts over several years; these data on the timing of pupping should represent all of the breeding population in north-east Ireland.

The seals occupy two types of inshore intertidal habitat: rocky ledges and sandbanks or beaches. While it is known that some inshore sites may be more suitable for pupping while others are more appropriate for moulting (Joint Nature Conservation Committee 2007), previous surveys in Ireland have not considered individual sites or site types for either pupping or moulting. There is only incidental information on inshore habitat use by mothers and pups, with published studies referring to tidal ledge sites in County Down (Wilson 1974; Wilson and Montgomery-Watson 2002). The principal objective of our study is to assess quantitatively how mothers with pups use the intertidal areas of a rocky ledge site and a beach site, both within Dundrum Bay (Plate 1), with a particular emphasis on mother-pup social behaviour.

In this study we focus on the behaviours relating to social contact and bonding between mother and pup as they occur in the three intertidal zones of their nursery habitat: in the water, at the water's edge and on the dry shore. Harbour seal pups are highly precocial among northern phocid species. They are active in the water immediately after birth, with nursing pups spending about 60% of their time in the water (Bowen *et al*. 1999; Skinner 2006). Pups follow their mothers in the water and on to the shore to suckle and rest (Venables and Venables 1955; Wilson 1974; 1978; Renouf *et al*. 1983; Wilson 2001). The mother is primarily responsible for maintaining contact with her pup by leading and chaperoning it and by controlling the timing

and location of haul-out on to the shore, with nursing typically immediately following haul-out (Newby 1973; Wilson 1974; Groothedde 2011). Pups play beside their mothers in the water and at the water's edge, sometimes with solo locomotor movements (Wilson and Kleiman 1974; Wilson 1978; Renouf and Lawson 1986; 1987) and sometimes with body contact and nose-to-body contact, particularly with the muzzle and neck regions (Wilson 1974; 1978; Wilson and Kleiman 1974). These behaviours may be accepted as species-typical, since they have been recorded in *P. vitulina vitulina* at different sites in north-east Ireland, north-east England, west of Scotland, Shetland and the Netherlands (Wilson 1974; 2001; Venables and Venables 1955; Groothedde 2011), in *P.v. concolor* in Maine (Wilson 1978), Sable Island (Wilson and Kleiman 1974; Bowen *et al*. 1999) and at the Grand Barachois in Canada (Renouf et al. 1983; Renouf and Lawson 1986; 1987) and in *P. v. richardsi* in Washington State and Vancouver (Newby 1973; Skinner 2006).

Although these behaviours are ubiquitous to the species, the way in which mother-pup suckling, social contact and proximity may be influenced by different intertidal habitat areas and constraints has previously been unclear. However, the modern availability of low-cost digital camcorders with powerful zoom lenses has enabled us for the present study to record simultaneous activities by pup and mother in greater detail than was possible in the earlier studies that relied on field check-sheets or voice recorders. In this study we have used video recordings to quantify levels of social contact and interaction in different parts of the intertidal habitat.

We suggest how data recorded in this way may be used to compare quantitatively mother-pup behaviour and pup socialisation between different habitat types and populations. Improved understanding of the amount of social contact normally experienced by pre-weaning pups in different parts of their intertidal habitat could also lead to evidence-based recommendations to help rehabilitation centres design appropriate captive environments to facilitate species-appropriate levels of pup social contact and activity.

STUDY SITES AND METHODS

STUDY PERIOD AND SITES

Harbour seals were counted and filmed at two sites, located at Ballykinler (Bk) and Minerstown (Mt) approximately 7km apart in Dundrum Bay, north-east Ireland (Pl. 1). Seals were counted between 26 June and 17 August between the years 2002 and 2015 and filmed between the same dates between the years 2005 and 2015.

The Mt site (54.2483°N, -5.7042°W) is a group of tidal rocky ledges where seals can haul out when exposed by the tide but still surrounded by water. Rocky outcrops with *Laminaria* forest extend directly from the haul-out ledges to the subtidal area in the eastern

half of Dundrum Bay (Plate 1; Clements and Service 2015). The Bk site (54.2429°N, -5.8217°W) is a sandy beach bordering an estuarine channel with wide beach areas available for seals to haul-out at all but the highest tides. The mouth of the channel opens out into an open sandy bay, with an extensive intertidal sandy area and a largely sandy subtidal zone in the western half of Dundrum Bay (Plate 1; Clements and Service 2015). The Bk haul-out group during the summer harbour seal pupping season also included a relatively small number of grey seals, *Halichoerus grypus*, whereas grey seals were almost never seen at Mt during the time periods of this study.

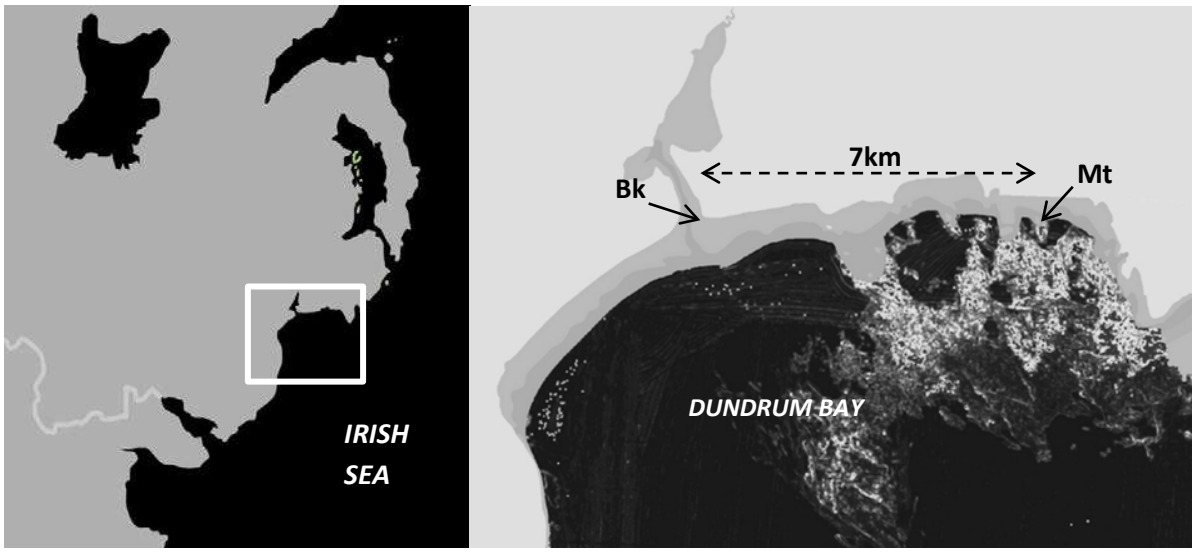

Plate 1. Location of the study sites in Northern Ireland (left) showing Ballykinler (Bk) and Minerstown (Mt) within Dundrum Bay (right). Rocky terrain ruggedness shown in white (Clements and Service 2015).

The tidal height range in Dundrum Bay is approximately 3–4.5m. Seals haul out at both sites at all stages of the tide, but maximum numbers of seals are closest to the shore and most clearly visible from the shore for counting and behaviour filming during the first 2.5 hours of the ebbing tide.

SEAL COUNTS

Harbour seals were counted as the tide ebbed between about 1–2.5h after high tide at both sites, when seals were most easily visible from the shore observation point. For Mt there were thirteen years of pupping season count data between 2002 and 2015, and for Bk there were eight years. We divided the pupping season into time periods I–VI between 26 June and 17 August (Table 1). A mean pup count (with standard error) was obtained for each time period for all seasons combined. For adults and subadults (i.e. all seals over one-year old), counts were analysed per season (over all six time periods).

Table 1. Dates, duration and the total (and mean) number of daily harbour seal counts for each time period during pupping seasons between 2002 and 2015 at Minerstown (Mt) (n=13 seasons) and Ballykinler (Bk) (n=8 seasons).

Time period	Dates	Duration	Total (x) no. counts 2002–2015	
			Mt n=13	Bk n=8
I	Jun 26–Jul 03	8 days	51 (3.9)	28 (3.5)
II	Jul 04–09	6 days	50 (3.8)	17 (2.1)
III	Jul 10–15	6 days	50 (3.8)	17 (2.1)
IV	Jul 16–21	6 days	30 (2.3)	18 (2.3)
V	Jul 22–31	10 days	45 (3.5)	30 (3.8)
VI	Aug 01–17	18 days	71 (5.5)	30 (3.8)

Shortly before mid-ebb the seals at Mt dispersed to ledges further offshore, when they were more difficult to count. The seals at Bk also moved location on the beach or sandbank as the tide ebbed after mid-tide and were sometimes more difficult to see. Due to limited access (through a Ministry of Defence base) at Bk, counts there were sometimes made from the other side of the estuary, where they were sufficiently visible at all stages of the ebbing tide for counts to be made by telescope and from digital camera stills. The final maximum count was recorded on each observation day at approximately mid-ebb, or lower tide if the seals were still visible. This study did not attempt to record factors influencing numbers at the haul-out sites, although behavioural observations and counts were only made during reasonably calm and dry weather.

Since not all seals frequenting the haul-out sites during the pupping season were present or visible on each tide-based visit, the average proportion of adults and subadults within the seal haul-out group at each site was estimated by the bounded count method (Olesiuk *et al*. 1990) for all years, with at least five separate counts using the following formula:

$$P_{av} = C_x / [C_{max} + (C_{max} - C_{max-1}\}]$$

where P_{av} is the average proportion of seals that were hauled out and C_x, C_{max} and C_{max-1} are the mean, the highest and the second highest counts respectively. The estimated abundance of seals (over one year old) was then calculated at each site for each year using C_x/P_{av} (see also Thompson *et al*. 1997; Wilson 2002).

VIDEO CLIP SHOOTING

Video clips were taken of mother-pup pairs between the hours of high tide and mid-to-low ebb tide in the 2005, 2008, 2009, 2010 and 2015 pupping seasons. Seals were filmed during settled weather and while there was no human disturbance. A Panasonic digital camcorder was used—initially (2005–10) with a 30x zoom lens and a 2.5x multiplier, recording on to mini-dv tapes, and later (2010–15) with a 70x zoom lens recording on to a memory card. Filming was conducted from a vantage point on the shore, out of sight of the seals. Video clips were taken opportunistically, attempting to select a different focal pup for each clip and filming each pup

in turn, regardless of its activity or location. The aim was to film each pup with its mother and other neighbouring seals for approximately five minutes. A pup's mother was identified as an adult female beside a pup and showing attention exclusively to it (looking at it, nosing it, leading it, suckling it) throughout the observation period. A pup's mother was also identified as the nearby adult to which the pup exclusively responded. Each video clip was given a pup ID, although individual mothers and pups could only be identified if they did not change position during the course of an observation. Individuals could not be re-identified on subsequent days.

VIDEO CLIP PROCESSING

In order to quantify behaviours in different intertidal habitats per unit time, each clip was divided into sequential 15-second segments. Each 15-s segment was classified according to one of three habitat zones: **water** (i.e. observed at or near the water surface in the shallow intertidal zone), **water's edge** (i.e. wet beach, rock or seaweed, splash and wavelet zone), and **dry zone** (i.e. beach or rock above water level). The location of the zones was dynamic according to the state of the tide.

A spreadsheet was created in which activities by pup and its mother were recorded (Table 2). Activities were recorded in binary format according to whether they did or did not occur in a 15-s segment, although a verbal narrative for each segment was also made for further reference. For each segment the distance between a pup and its mother or nearest neighbour was also estimated in approximate adult or pup body lengths (ABL or PBL). Some clips of behaviour in the water included 15-s segments where the pup was invisible underwater and therefore contained no data. Any clip with fewer than four 15-s segments containing data was discarded from the record.

Table 2. Behaviours recorded and analysed.

Behaviour recorded	Description
Behaviour of Pup	
Rest	Lying on shore or at surface of water, no voluntary forward movement, may be asleep or alert, comfort movements may occur
Comfort movements during rest	Face wiping, scratching, body rubbing on surface; at least two* of: fore or hind-flipper stretching or curling, yawning
Suckling	Nuzzles, nudges, suckles at mother's nipple area
Directed movement	Moves forward
Pup follows/mother directed movement	Follows mother when she moves forward
Play	Exaggerated body or locomotor movement
Behaviour of mother and pup	
Nosing exchange	Nose-to-nose contact between mother and pup; pup noses any part of mother's body (except nipple area); mother noses any part of pup's body
Body contact	Any part of the body in contact with mother in addition to nosing contact
Behaviour of Mother	
Rest	Lying on shore or at surface of water, no voluntary forward movement, may be asleep or alert
Scan	Mother raises head and looks around
Checks pup	Mother looks directly at pup

*at least two instances in order to filter out every involuntary twitch while the pup is asleep

VIDEO CLIP ANALYSIS

All statistical analyses were carried out using the XLSTAT-pro statistical package. Altogether 230 clips of mother-pup behaviour including 4,197 15-s segments were used in the analysis. The range of the number of usable 15-s segments from each video clip was 4–38 and averaged 7.3 (SD=7.7).

Inter-individual distances between a pup and its nearest neighbour were translated from estimated adult or pup body lengths to approximate metres (1ABL ≈ 1.5m, 1PBL≈ 0.9m). For each clip the inter-individual distance was assigned an overall value calculated from the mean (with standard error) from all 15-s segments within that clip. Statistical comparisons of inter-individual distances between pupping sites (Mt or Bk) and between intertidal zones (water, water's edge, dry zone) were made using the non-parametric Kruskal-Wallis or Mann-Whitney U tests.

Activities were recorded as present or absent in each 15-s segment, and were described according to the proportion (k-proportions or 2-proportions test) of the total usable 15-s segments in which each activity occurred, at each site and in each habitat category. Because several activities could occur during a 15-s segment, the proportions of the different behaviours in each row add up to more than 1.0 (Table 5). Where one or more behaviours could not be recorded as present or absent in a 15-s segment owing to either mother or pup not being visible, this resulted in the number of 15-s segments not always being the same across zone categories (Table 5).

RESULTS

PUP COUNTS

The peak number of pups counted each year from 2002–15 averaged 12±1 pups at the Minerstown (Mt) rocky ledge site and 9±1 pups at the Ballykinler (Bk) sandy beach site. Pupping at both sites generally began in the last week of June, with half the season's pups born by 03 July (end of time period I) and most of the remainder born between 04–09 July (time period II). Average peak counts in each time period were greatest in periods II–III (04–15 July) at both Mt and Bk (Fig. 1). The number of pups visible at both haul-out sites declined after mid-July during periods IV and V, with only a few pups still observed in August (period VI) (Fig. 1).

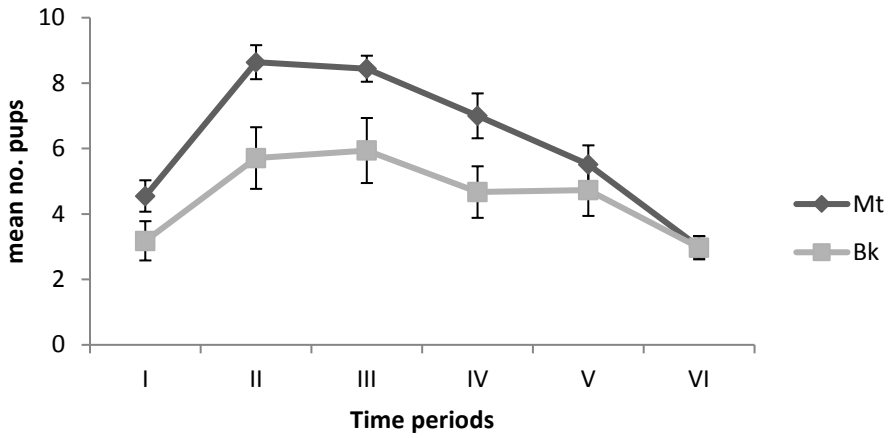

Figure 1. Mean harbour seal pup counts at Minerstown and Ballykinler sites in each time period, for all years recorded from 2002–2015.

ADULT/SUBADULT COUNTS

The average proportion of the estimated total number of adult and subadult harbour seals at the haul-out site averaged 0.54±0.04 over 13 late June/July seasons at Mt and 0.55±0.05 over 8 seasons at Bk. The estimated abundance of adult and subadult harbour seals at Bk (88±16 seals) was generally more than twice that of Mt (40± 4 seals) (Fig. 2). The grey seals present (usually < 30 individuals, maximum 78 recorded in 2014) tended to form a tight cluster close to the water's edge and were loosely surrounded by more widely spaced harbour seals resting on the dry zone.

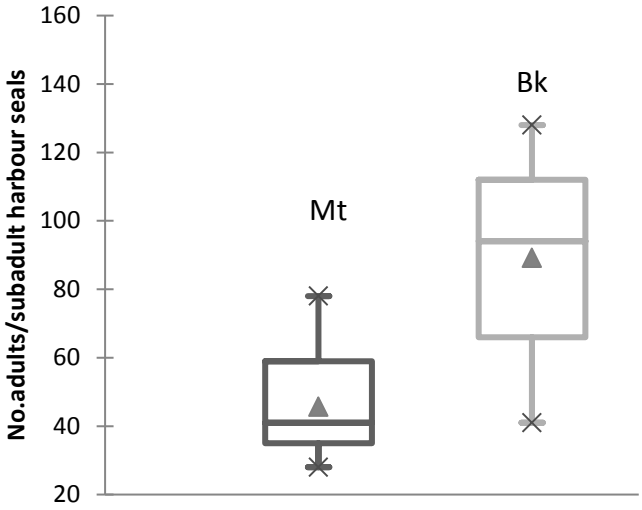

Figure 2. Abundance estimate summaries for adult and subadult harbour seals in the period June 15–July 31 at Minerstown (n= 13 seasons) and Ballykinler (n=8 seasons) from 2002–2015. X = maximum and minimum counts; horizontal lines = 1st quartile, median and 3rd quartile; shaded Δ = mean counts.

GENERAL BEHAVIOUR OF MOTHERS AND PUPS AT THE HAUL-OUT SITES

Mother-pup pairs were observed in all six observation periods in the present study, with the last record on 12 August. The first date on which an (apparently healthy) unattended 'lone' pup was recorded in the haul-out group was 05 July (period II), when the oldest pups would have been approximately 10 days old. Three further instances of 'lone' pups were recorded on 11–14 July (period III), and frequent instances from 16 July (period IV) onwards. The following descriptions of behaviour apply only to pups with attendant mothers.

Mother-pup pairs at Mt tended to congregate into discrete groups. At the start of the season these groups consisted only of pregnant females, mothers and newborn pups (Plate 2a) with the 'maternity' group using the same ledges in successive years. As the season progressed mothers and pups tended to haul-out as a 'nursery group' on a ledge closer to the main haul-out of other seals. By contrast, at Bk the mother-pup pairs hauled out more randomly amongst other seals and discrete clusters of mothers and pups were not seen (Pl. 2b).

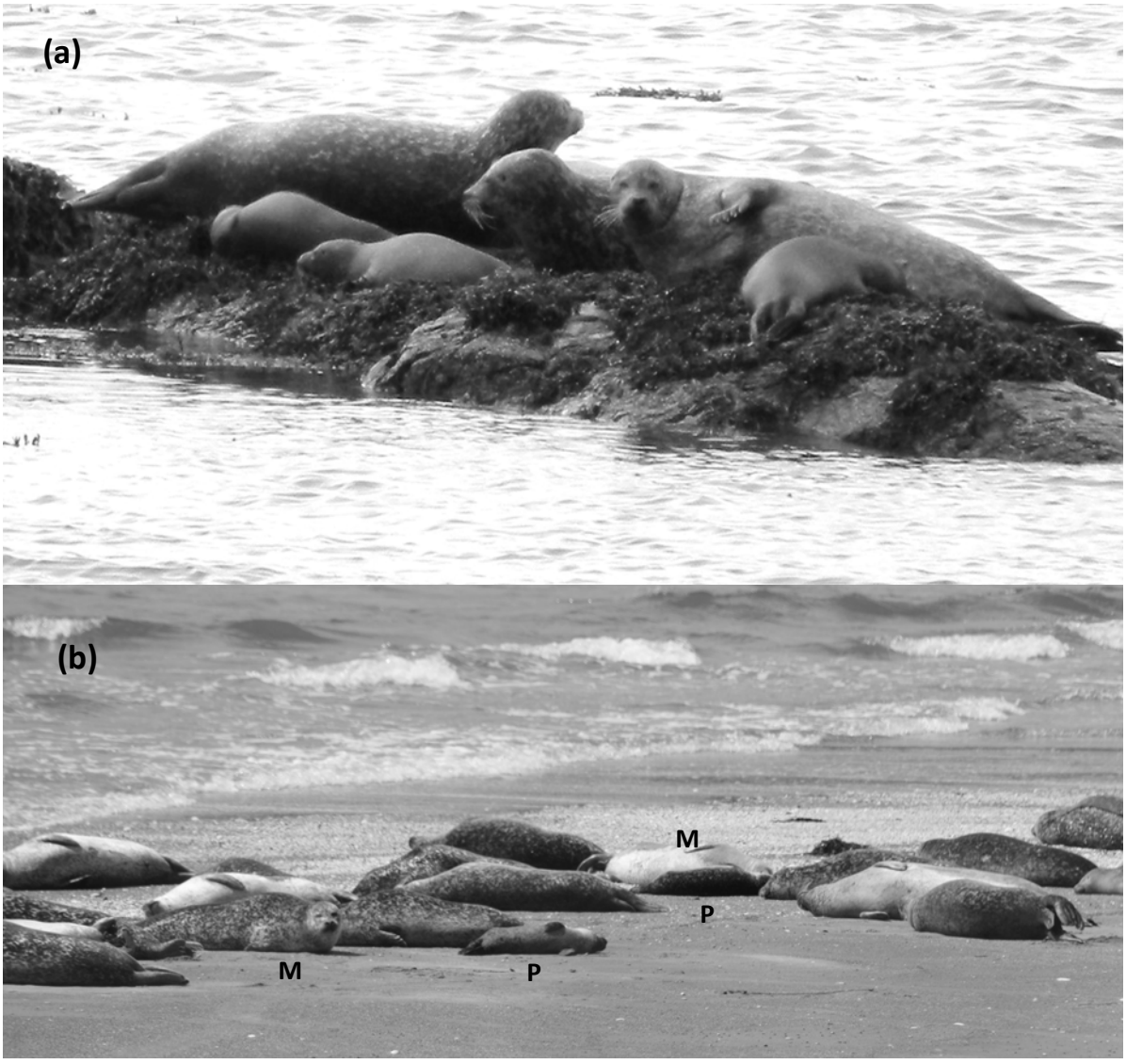

Plate 2. Harbour seal mother-pup pairs at Minerstown and Ballykinler

(a) Nursery group of three mothers with newborn pups at Minerstown
(b) Two mother-pup pairs within the haul-out group of adults at Ballykinler

All seals, including mother-pup pairs at both sites, moved between different parts of the occupied site as the tide ebbed. At Mt some ledges were covered at high tide and colonised by seals as the ledges emerged during the first hours of the ebb. These in turn were vacated in favour of further newly emerging ledges as the tide ebbed further and the initial sites were no longer surrounded by water. At Bk seals moved as a group from the original haul-out spot at high tide to a freshly emerging sandbank. Thus mother-pup pairs rarely stayed on any one part of either haul-out site for more than 2–3 hours.

Mothers and pups stayed together whether moving or resting within the colony. The distance between the pup and its nearest neighbour averaged < 1m in all intertidal zones, with the exception of an average distance of 1.3m and more variable distance in the water at Bk (Table 3). Over all records from both sites and all zones, the mother was the pup's nearest neighbour in > 90% of 15-s segments (Table 4). There were twelve separate instances recorded where mothers defensively repelled any other seal that approached too closely, by lunging and flippering and also splashing when in the water.

Table 3. Mean distance (x dist.) between harbour seal pups and with the accompanying mother or nearest neighbour. P indicates significance of difference between sites by Mann-Whitney U test.

Intertidal zones	*Site*	*n (no. pairs)*	*x dist. (m)*	*SE*	*P*
	Bk and Mt combined				**(Kruskal-Wallis)**
Water		44	0.73	0.16	
Water's edge		114	0.34	0.05	P<0.001
Dry zone		71	0.51	0.11	
	Bk and Mt separately				**(Mann-Whitney U)**
Water					
	Mt	34	0.73	0.16	
	Bk	10	1.26	0.42	P=0.32
Water's edge					
	Mt	71	0.34	0.05	
	Bk	43	0.49	0.07	P=0.06
Dry zone					
	Mt	41	0.51	0.11	
	Bk	30	0.36	0.07	P=0.75

Table 4. Proportion of 15-s video segments in which the harbour seal mother (M) was her pup's nearest neighbour (NN).

Intertidal zones	*Site*	*n (no. 15-s)*	*No. M NN*	*Prop. M NN*	*P*
	Bk and Mt combined				**(k-proportions)**
Water		*635*	614	0.967	
Water's edge		*1985*	1864	0.939	P<0.001
Dry zone		*1362*	1242	0.912	
	Bk and Mt separately				**(2-proportions)**
Water					
	Mt	*476*	457	0.960	
	Bk	*159*	157	0.987	P=0.073
Water's edge					
	Mt	*1260*	1186	0.941	
	Bk	*725*	678	0.935	P=0.664
Dry zone					
	Mt	*819*	708	0.864	
	Bk	*543*	534	0.983	P<0.0001

The behaviour of mother-pup pairs in the vicinity of the haul-out sites involved moving in the water between different parts of the haul-out site, hauling out, playing, suckling, resting and scanning (Pl. 3 a–j). Pups only interacted with their mothers. The dominant behaviour of pups was the following response to their mother's movement (Pl. 3 c, d), with young pups sometimes actually riding on the mother's back and thus in close body contact (Pl. 3 e, f). Mothers typically watched over their pups closely (Pl. 3h), guided them when moving from one location to another, and encouraged them to follow by exchanging nosing contacts, mainly in the muzzle, face and neck regions (Pl. 3b). Mothers would lead their pups to selected haul-out locations and there permit the pup to suckle (Pl. 3i–j). When a pup failed to follow its mother, the mother would rapidly re-establish contact and instances were not seen during the study when this failed to happen.

Harbour seal mother-pup behaviour

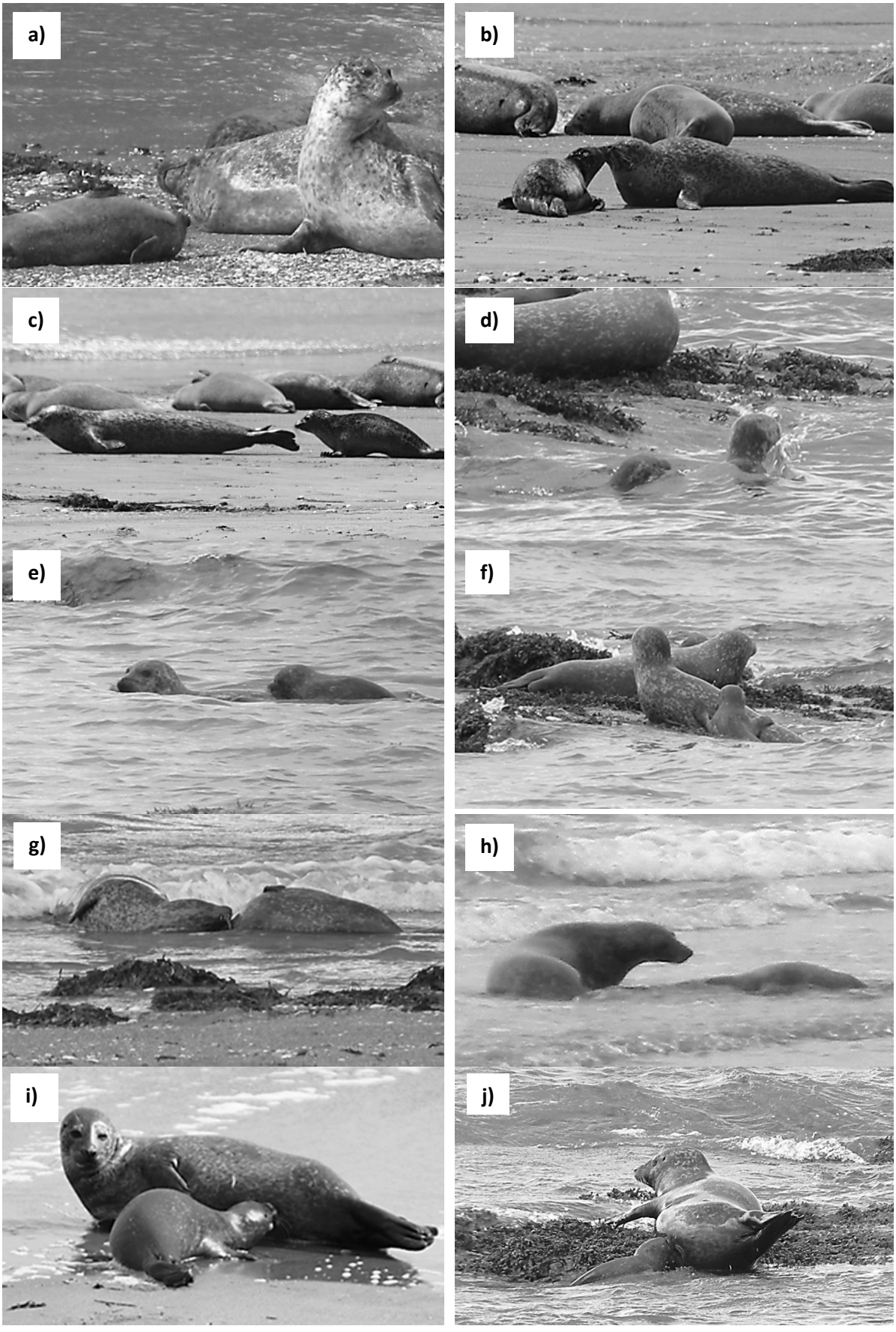

Plate 3. Examples of harbour seal mother-pup activities recorded

(a) Pup resting, supine position; mother scanning (Ballykinler – dry zone)
(b) Mother and pup nose-to-nose contact (nosing exchange) (Ballykinler – dry zone)
(c) Mother directed movement, pup directed movement, pup follows (Ballykinler – dry zone)
(d) Mother directed movement, pup directed movement, pup follows (Minerstown – water)
(e) Mother directed movement, pup follows, body contact (pup riding on mother's back) (Minerstown – water)
(f) Mother directed movement (hauling out), pup follows, body contact (Minerstown – water's edge)
(g) Mother and pup play, body contact (Ballykinler – water's edge)
(h) Mother looks directly at ('checks') pup in wavelets (Ballykinler – water's edge)
(i) Pup suckles (Ballykinler – water's edge)
(j) Pup suckles (Minerstown – water's edge)

MOTHER-PUP BEHAVIOUR – COMPARISON BETWEEN INTERTIDAL ZONES

The mean distance between a pup and its nearest neighbour varied significantly between the zones and was greater in the water (0.7m) than either at the water's edge (0.3m) or in the dry zone (0.5m; Table 3). Combining the data from both sites, the mother was her pup's nearest neighbour most often in the water (97% of 15-s segments; n= 635), less often at the water's edge (94%, n=1,985) and least often in the dry zone (91%, n=1,362, Table 4). When the data were separated according to site, the mother was significantly more likely to be her pup's nearest neighbour at Bk than at Mt when they were hauled out in the dry zone, but there was no site difference in the other zones (Table 4).

Activities of pups and their mothers varied significantly according to the intertidal zone (Table 5). Over all records from both sites combined, nosing contacts occurred between mother and pup in 25% and 18% of 15-s segments in the water and at the water's edge respectively, compared to only 11% in the dry zone. Body contact occurred in 13% and 5% of 15-s segments in the water and at the water's edge respectively compared to only 2% in the dry zone, and play occurred in 14% and 5% of 15-s segments respectively compared to 0% in the dry zone (Table 5). Pups also followed their mother when she moved more often in the water and at the water's edge (62% and 65% respectively) than in the dry zone (33%; Table 5). The predominant activities in the dry zone were resting by both mother and pup, and scanning by the mother (Table 5).

Table 5. Proportions of 15-s segments in which each activity by pups (P) and their mothers (M) occurred in each intertidal zone at Ballykinler (Bk) and Minertown (Mt). Numbers in italics are the number of 15-s video segments in each zone; numbers in bold indicate significant differences between shore zones or sites (P≤0.02; k- or 2-proportions test).

Intertidal zones	Site	Behaviour of pup					Behaviour of mother and pup		Behaviour of mother		
		Resting	Suckling	Directed movement	P follow/M directed movement	Play	Nosing exchange	Body contact	Rest	Scan	Checks pup
	Bk and Mt combined										
WATER		**0.22**	**0.00**	**0.59**	**0.62**	**0.14**	**0.25**	**0.13**	**0.06**	**0.19**	**0.70**
		671	*712*	*670*	*352*	*671*	*682*	*651*	*684*	*644*	*636*
WATER'S EDGE		**0.30**	**0.24**	**0.23**	**0.65**	**0.05**	**0.18**	**0.05**	**0.43**	**0.63**	**0.35**
		1966	*1968*	*1968*	*232*	*1968*	*1978*	*1967*	*1927*	*1916*	*1921*
DRY ZONE		**0.77**	**0.02**	**0.07**	**0.33**	**0**	**0.11**	**0.02**	**0.60**	**0.60**	**0.19**
		1422	*1422*	*1422*	*139*	1422	*1422*	*1422*	*1305*	*1303*	*1305*
	Bk and Mt separately										
WATER	Mt	**0.27**	0.00	**0.54**	0.64	**0.08**	0.26	**0.06**	**0.07**	0.18	0.68
		501	*501*	*500*	*250*	*501*	*488*	*498*	*476*	*473*	*460*
	Bk	**0.07**	0.00	**0.74**	0.58	**0.29**	0.27	**0.31**	**0.02**	0.20	0.74
		170	*170*	*170*	*102*	*170*	*194*	*170*	*172*	*171*	*176*
WATER'S EDGE	Mt	**0.35**	0.24	**0.18**	**0.61**	**0.02**	**0.14**	**0.03**	**0.47**	**0.72**	**0.26**
		1245	1245	*1245*	*85*	*1245*	*1248*	*1244*	*1219*	*1211*	*1217*
	Bk	**0.20**	0.24	**0.32**	**0.68**	**0.09**	**0.24**	**0.08**	**0.36**	**0.48**	**0.52**
		721	723	*723*	*147*	723	*730*	*723*	*708*	*705*	*704*
DRY ZONE	Mt	**0.75**	**0.00**	**0.04**	**0.14**	0.00	0.10	0.02	**0.57**	**0.64**	**0.52**
		858	*858*	*858*	*72*	*858*	*858*	*858*	*748*	*750*	*704*
	Bk	**0.80**	0.03	**0.11**	**0.54**	0.00	0.13	0.03	**0.63**	**0.54**	**0.13**
		564	*564*	*564*	*67*	*564*	*564*	*564*	*557*	*553*	*556*

Almost all suckling occurred at the water's edge: a total of 42 suckling bouts or partial bouts were filmed at the water's edge, but only two mother-pup suckling bouts were filmed in the dry zone. Of the 12 recorded cases of a mother defensively repelling another seal that came too close to her pup, five occurred in the water, six at the water's edge and one in the dry zone.

Although pups most often lay on their side while resting, they more often rested in the prone position at the water's edge than in the dry zone, while the supine position (suggesting deeper sleep) was more common in the dry zone and rarely occurred at the water's edge (Table 6).

Table 6. Comparison of harbour seal pup resting positions and comfort movements at the water's edge and in the dry zone (proportion of 15-s resting).

Intertidal zone	**n 15-s**	**Proportion of 15-s**			
		On side	**Supine**	**Prone**	**Comf. mov.**
WATER'S EDGE	*582*	0.625	0.012	0.361	0.093
DRY ZONE	*1098*	0.791	0.108	0.100	0.079
k-prop. test		*P*<0.0001	*P*<0.0001	*P*<0.0001	*P=0.379*

MOTHER-PUP BEHAVIOUR – COMPARISON BETWEEN SITES

Average distances between pups and their nearest neighbours did not differ significantly between the Mt tidal ledge and Bk beach sites (Table 3). However, mothers were their pups' nearest neighbour less often at Mt than at Bk in the dry zone (Table 4).

Levels of some activities differed significantly between the two sites. In the water pups showed more directed movement, more body contact and play at Bk than at Mt (Table 5). At the water's edge there was more body contact, more pup following when the mother moved, more play, more nosing exchange and more mother pup-checking at Bk, whereas mothers scanned more and both mother and pup rested more at Mt (Table 5). In the dry zone there was more pup directed movement at Bk, but significantly less following the mother when she moved at Mt and more mother scanning and pup checking at Mt (Table 5). The only two instances of suckling in the dry zone were filmed at Bk.

DISCUSSION

PUP COUNTS AT EACH SITE

Our total pup counts from the Minerstown and Ballykinler sites together from July 2002–15 suggest about 21 births annually and a total abundance of about 128 adult/subadult seals in Dundrum Bay. Our total counts are indeed very similar to those obtained for Dundrum Bay in 1977–78 (Nairn 1979), indicating overall stability of this breeding group of harbour seals over this period of about 35 years.

Our pup counts provide a well-defined pupping curve for Dundrum Bay, indicating that almost all pups in the bay were born over a two-week period from late June to the second week in July. They suckled, were weaned and then dispersed over a further five-week period to mid-August. Our records of a gradual disappearance of pups from the haul-out sites in early August is consistent with the results of an earlier radio-tracking study in which pups were caught and tagged at the Minerstown site between 19 July and 3 August, 1995. For the first three weeks after tagging, pups were located diving in waters close to the haul-out site, but thereafter through late October dispersed to offshore foraging sites and rarely hauled out (S. Wilson and H. Corpe, unpublished data).

Knowledge of the pupping curve can be very helpful to target the optimum time to conduct surveys on pup production in a particular area of coastline. Our pupping curve suggests that the optimum time to obtain a maximum pup count in Dundrum Bay is over a twelve-day period between 4 and 15 July. This is similar to a multi-year record of pup counts for a population of harbour seals in Alaska, in which peak pupping was defined as a nine-day period centred around the maximum pup count (Jemison and Kelly 2001) and also similar to a population in the Netherlands, where peak pupping in a single year occurred over a fifteen-day period (Groothedde 2011).

The peak pupping time for harbour seals in a given locality may shift by 10–12 days over a period of 10–20 years (Jemison and Kelly 2001), or by 25 days over a period of 35 years, possibly due to changes in food availability (Reijnders *et al*. 2010). Peak pupping time may also vary between populations. For example, on the Swedish Skagerrak coast, pupping peaked on June 19 (Härkönen and Harding 2001) and around 15 June at the Dollard in the Netherlands (Groothedde 2011), about three weeks earlier than in Dundrum Bay. It is likely that the pupping curve we have obtained for Dundrum Bay applies approximately to other adjacent populations in north-east Ireland, such as those in Strangford Lough (Wilson and Montgomery Watson 2002) and Carlingford Lough. However, peak pupping should be monitored in future years to detect any shift, and may differ in regions of the west of Ireland, where a separate series of counts would be required.

Protecting harbour seals from disturbance is most critical during the pupping season, in particular the immediate post-natal period when the mother-pup bond is being formed. For purposes of effective conservation management, knowledge of the locations of pupping groups and the pupping curve is essential. Our study has shown that in a particular area the haul-out group with the highest seal numbers is not necessarily the largest pupping group. Because recent harbour seal surveys in the UK and Ireland have tended to focus on population counts during the late summer moulting period (Cronin *et al*. 2004; 2007; Duck and Thompson 2009), published data on harbour seal pup locations and numbers is sparse in the British Isles, and our present study represents the only pupping curve data for any part of Ireland.

RELATIVE SUITABILITY OF THE TWO STUDY SITES FOR PUPPING

The differences between the two sites in counts of both pups and adults/subadults during the pupping season indicated that the two sites had different haul-out group compositions, with a pup to adult/subadult ratio of approximately 1:10 at Ballykinler but only 1:3 with a higher average pup count at Minerstown. This suggests that the Minerstown rocky ledge site was more suitable for pupping, whereas the sandy beach site at Ballykinler was more suitable for adult/subadult haul-out. Our study was unable to detect any differences between Minerstown and Ballykinler in mother-pup behaviour in the intertidal zones which might explain a greater suitability of Minerstown for pupping. The immediate subtidal area at Minerstown consists of rocky terrain with *Laminaria* forest, whereas at Ballykinler mother-pup pairs need to traverse an extensive intertidal sandy area, often with breaking waves, to reach the subtidal area, in which rocks and *Laminaria* are sparse (Plate 1; Clements and Service, 2015). We cannot therefore rule out the possible explanation of the readily accessible rocky terrain being a more suitable subtidal environment for mother-pup pairs, although this could not be assessed in the present study.

Harbour seal sub-populations <10 km apart have been shown to differ in composition by sex and age, partly due to the tendency of adult females to return to their natal sites to give birth (Härkönen and Harding 2001). Since females may continue to pup into their mid-30s (Härkönen and Heide-Jørgensen 1990), it is likely that the discrete birth and nursery group at Minerstown has developed as a tradition among familiar females over successive years, and may be part of the reason influencing parturient female choice of Minerstown for giving birth. The mothers in these groups were often hauled out very close together (as in Plate 2a) without visible stress or conflict – of the twelve instances we recorded of mothers defensively repelling other mother-pup pairs approaching too closely, only one instance was observed when hauled out in the dry zone.

Our finding that mothers at Minerstown were least often (only 86%) their pups' nearest neighbours while hauled out in the dry zone is likely explained by those mothers apparently having chosen to join the perinatal 'maternity' group or subsequent "nursery" group of other mother-pup pairs. These mothers are therefore highly tolerant of neighbouring mothers or pups being close beside their pup. Such distinct mother-pup groups, slightly separate from the other

seals at the haul-out site, were also recorded at a gravel beach site on Gertrude Island, British Columbia (Newby 1973).

MATERNAL VIGILANCE

Disturbance was not quantified in the present study but pedestrian and water-craft disturbance does occur erratically at both sites, although apparently more often at Ballykinler (S. Wilson and H. Corpe, unpublished data; I. Trukhanova, pers. com.). We considered the possibility that disturbance levels might affect female choices of birthing location. In our study, however, mothers scanned more when hauled out at Minerstown (with more pup births) than at Ballykinler (with the larger haul-out group). This is consistent with relatively higher vigilance levels typically occurring in relatively smaller groups of seals (Terhune 1985).

Mothers scanned more often at the water's edge than in the dry zone at Minerstown, but not at Ballykinler. Therefore our records at Minerstown are consistent with the usual pattern that scanning levels decline within 30 minutes of haul-out (Terhune and Brillant, 1996). However, scanning behaviour by mothers at Ballykinler did not decline while resting in the dry zone. This may be consistent with a greater perceived threat of pedestrian disturbance at Ballykinler, as harbour seals in Iceland are known to increase their vigilance in the presence of tourists (Granquist and Sigurjonsdottir, 2014).

Harbour seal mothers displayed no evident wariness of grey seals and there was no indication during our observation periods that grey seals disturbed or harassed pups or any harbour seals. There was a single isolated incident of grey seal predation on a harbour seal pup at Ballykinler recorded on Ministry of Defence CCTV in 2008 (C. Orchard, pers. comm.). A freshly-dead new-born pup carcase was recovered from the beach, with the soft organs having been removed through a ventral opening (S.Wilson, pers. obs.). However, there has been no known grey seal predation at Ballykinler in any subsequent year.

MOTHER-PUP DISTANCE

Our study has shown how the dependent pup is in a continual state of close social proximity in all three intertidal zones, with the mother almost always being within 1m of its pup, and usually being its nearest neighbour. The mother is therefore her pup's primary social contact as well as chaperone and source of nutrition. Thus a pup attended by its mother is always within immediate visual, olfactory and tactile contact with her.

The slightly greater average distance between mother and pup in the water (1.3m at Ballykinler), is due largely to the pup's increased scope for mobility and energetic swimming and diving. Mothers were their pups' nearest neighbour most often in the water and least often when they were resting in the dry zone, reflecting the greater need for close maternal chaperoning to ensure the pup does not become separated from her when swimming and diving.

MOTHER-PUP BEHAVIOUR IN EACH INTERTIDAL ZONE

Different frequencies of mother and pup behaviour shown in this study indicate the importance of all three intertidal zones for different aspects of maternal care and pup behaviour.

Water: Our results indicated that nosing, body contacts and pup following the mother when she moved were all much more frequent when mother-pup pairs were swimming in the water than when they were at the water's edge or on the dry part of the shore. Much of this enhanced contact and pup following occurred when mothers were guiding their pups as they moved between haul-out areas, but also when mothers chaperoned their pups as they dived and engaged in play behaviours. Earlier studies have also qualitatively considered harbour seal mother-pup filial interaction and play to be water-dependent (Wilson 1974; Wilson and Kleiman 1974; Renouf and Lawson 1986; 1987). We conclude that water is at least a facilitator and probably requisite for the expression of species-typical affiliative social interaction in harbour seals.

Mothers looked directly at (checked) their pups, and were their pup's nearest neighbour, most often when they were in the water, undoubtedly due to the critical need for a mother to avoid losing her pup. This greater 'concern' by mothers when the pair was in the water was also noted by Lawson and Renouf (1987). In this study we could not identify individual harbour seal mothers but nevertheless observable individual variation in maternal care was not apparent in spite of a large visual sampling dataset. Rather the increased levels of harbour seal mothers directing their gaze at their pup in the water compared with the dry zone suggests that in harbour seals maternal attentiveness changes dynamically according to the situation, reflecting the need to respond rapidly to circumstances involving a highly mobile but vulnerable pup in a potentially hazardous environment.

Water's edge: Much active social interaction also took place at the water's edge, where the frequencies of nosing and body contacts and play were intermediate between frequencies in the water and in the dry zone, and pups followed the mother when she moved as often as when they were completely in the water. This reinforces our conclusion that water—even a few centimetres—facilitates pup filial interaction and the following response in this species. The greater frequency of mother-pup activities in the water's edge zone at Ballykinler—including directed movement, following, play, body contact and nosing exchange—and maternal pup checking were probably at least partially due to the greater scope for movement and extensive space around the water's edge at this beach site.

Almost all (95%) of suckling bouts took place immediately after haul-out at the water's edge, confirming quantitatively earlier observations from other sites (Newby 1973; Wilson 1974; Groothedde 2011). The assumption that mother-pup pairs typically lie ashore (i.e. in the dry zone) for as long as possible in order to maximise the total daily nursing time (Osinga *et al*. 2012) was not true of our study sites, where mothers and pups swam to new locations as the tide height varied (usually about every 2 hours), often suckling when newly hauled out. In Shetland, harbour seal pups were frequently observed suckling in the water, but this was

believed to be a reaction to human disturbance and hunting pressure (Venables and Venables 1955; Wilson 1974).

Dry zone: The dry intertidal zone was used only for resting and sleeping by both mother and pup and only rarely for suckling. Pups in Strangford Lough (north-east Ireland) were observed sleeping at the water surface while their mother dived (presumably foraging) for a few minutes at a time (Wilson 1974). However, it is likely that for the mother to be able to sleep, the mother-pup pair need to be hauled out on shore. In the dry zone, the average distance between mother and pup was less than in the other intertidal zones and the mother checked her pup least often, potentially allowing her more opportunity to rest. In the dry zone pups also rested more often on their sides and supine than at the water's edge, suggesting more settled or deeper sleep than when lying prone.

PUP FILIAL BONDING AND SOCIALISATION

Pups, after about 10 days of age, are sometimes left behind within the haul-out group for some hours while their mother makes foraging trips offshore (Boness *et al*. 1994; Wilson and Montgomery-Watson 2001). By this age, the pups' following response to its mother will have been well-rehearsed and be transferable to neighbouring mother-pup pairs or other seals, whom they tend to follow as the haul-out group moves with the tide between different areas of the haul-out site. Hence such 'lone' pups avoid becoming isolated or lost during the mother's temporary absence (Wilson 1978; S. Wilson and K. Jones, unpublished data).

Further, harbour seal pups from the Minerstown site have been shown (by a radio-tagging study) to disperse to individual foraging areas post-weaning at around four weeks of age, returning only occasionally to the haul-out site (S. Wilson and H. Corpe, unpublished data). Since there is little opportunity for socialisation to continue during this dispersal period, it is likely that pup primary socialisation—to enable it to respond functionally to conspecifics—should occur during the 3–4 week period while the pup is with its mother.

IMPLICATIONS OF THIS STUDY FOR CARING FOR 'ORPHAN' PUPS IN REHABILITATION FACILITIES

Occasionally harbour seal pups become separated from their mothers at, or shortly after, birth and these 'orphan' pups eventually strand along the shoreline. If found in time, such pups stranded on the Irish coast will usually be taken to a rehabilitation facility in Ireland, where they are fed and cared for over a number of weeks until they are considered fit for release back to sea (e.g. Wilson, 1999). Amongst the challenges of rearing an orphan harbour seal pup is the pup's captive environment. One purpose of our study is to highlight what appear to be the essential features of the young harbour seal's natural social and physical environment in order to offer guidance to rehabilitators as to how they may mimic these features in the captive environment.

Rehabilitation facilities in the British Isles and N. America are often designed to maintain young 'orphan' harbour seal pups in isolation and in dry pens for some weeks after admission (e.g. Larmour 1989; Robinson 1995; Macrae 2011). By quantifying, in the present

study, the typical levels of social contact experienced by pups when in the shallow inter-tidal water and water's edge, we are able to provide an evidence-based explanation of why such an isolated, dry, captive environment will suppress normal behavioural expression, sensory input and hence development of pre-weaning pups. Although some disruption of social development of orphan pups in a rehabilitation environment is inevitable, this may be minimised by providing pups with a companion pup for reciprocal conspecific sensory input and access to a shallow water pool to facilitate affiliative social interaction (e.g. Wilson, 1999). Video-recording behaviour and contact levels of pups in rehabilitation for comparison with pups in the wild, as in the present study, may enable objective measurement of the degree of success of rehabilitation procedures in mimicking the pups' natural development.

ACKNOWLEDGEMENTS

We would like to thank Philip Nye for his help with seal counts at Minerstown. We are very grateful to the staff at the Ballykinler Ministry of Defence base, especially Kerry Orchard, Dennis O'Flaherty and Major Tony Canniford, for facilitating access to the seal observation site. Thanks also to Julie Hawkins at the University of York for her support of Kayleigh Jones' MSc studies in 2015, of which the fieldwork for the present study formed part. We thank Robert Fagen for his very helpful comments on the manuscript. We would also like to thank two anonymous reviewers for their very helpful and constructive comments to the original submitted manuscript.

REFERENCES

Boness, D.J., Bowen, W.D. and Oftedal, O.T. 1994. Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbour seal. *Behavioural Ecology and Sociobiology* **34**, 95–104.

Bowen, W.D., Boness, D.J. and Iverson, S.J. 1999. Diving behaviour of lactating harbour seals and their pups during maternal foraging trips. *Canadian Journal of Zoology* **77**, 978–988.

Clements, A.J. and Service, M. 2015. Bathymetric and habitat map for Murlough Special Area of Conservation and offshore, Northern Ireland. Technical Report, October 2015. Agriculture, food and Biosciences Institute, Northern Ireland. https://www.researchgate.net/publication/283498815_Bathymetric_and_Habitat_Map_for_Murlough_Special_Area_of_Conservation_and_offshore_Northern_Ireland.

Cronin, M., Duck, C., Ó Cadhla, O., Nairn, R., Strong, D. and O'Keefe, C. 2004. Harbour seal population assessment in the Republic of Ireland: August 2003. Irish Wildlife Manuals, No. 11. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin, Ireland.

Cronin, M., Duck, C., Ó Cadhla, O., Nairn, R., Strong, D. and O'Keefe, C. 2007. An

assessment of population size and distribution of harbour seals in the Republic of Ireland during the moult season in August 2003.

Duck, C.D. and Thompson, D. 2009. The status of the British common seal population in 2008. SCOS briefing paper 09/03. Scientific advice on matters related to the management of seal populations: 2009. http://www.smru.st-andrews.ac.uk/files/2016/08/SCOS-2009.pdf

Granquist, S.M. and Sigurjonsdottir, H. 2014. The effect of land based seal watching tourism on the haul-out behaviour of harbour seals (Phoca vitulina) in Iceland. *Applied Animal Behaviour Science* **156**, 85–93. http://dx.doi.org/10.1016/j.applanim.2014.04.004

Groothedde, J. 2011. Mother-pup interaction and the impact of anthropogenic disturbance in wild harbour seals (*Phoca vitulina*). MSc thesis, Linköpings University, Sweden.

Härkönen, T. and Heide-Jørgensen, M-P. 1990. Comparative life histories of East Atlantic and other harbour seal populations. *Ophelia* **32**, 211–235. http://dx.doi.org/10.1080/00785236.1990.10422032

Härkönen, T. and Harding, K.C. 2001. Spatial structure of harbour seal populations and the implications thereof. *Canadian Journal of Zoology* **79**, 2115–2127.

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

Joint Nature Conservation Committee. 2007. Second Report by the UK under Article 17 on the implementation of the Habitats Directive from January 2001 to December 2006. Peterborough: JNCC. Available from: www.jncc.gov.uk/article17

Larmour, L.J. 1989. Hand-rearing and rehabilitation of common seal pups *Phoca vitulina* at the Oban Sea Life Centre. *International Zoo Yearbook* **28**, 272–279.

Lawson, J.W. and Renouf, D. 1987. Bonding and weaning in harbor seals, *Phoca vitulina*. *Journal of Mammalogy* **68**, 445–449.

Macrae, A.M., Haulena, M. and Fraser, D. 2011. The effect of diet and feeding level on survival and weight gain of hand-raised harbour seal pups (*Phoca vitulina*). *Zoo Biology* **30**: 532–541.

Nairn, R.G.W. 1979. The status and conservation of the common seal *Phoca vitulina* (L.) in Northern Ireland. *Irish Naturalists' Journal* **19**, 360–263.

Newby, T.C. 1973. Observations on the breeding behaviour of the harbor seal in the State of Washington. *Journal of Mammalogy* **54**, 540–543.

Olesiuk, P. 1990. Recent trends in abundance of harbour seals, *Phoca vitulina*, in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 992–1003.

Osinga, N, Nussbaum, S.B., Brakefield, P.M. and de Haes, H.A.U. 2012. Response of common

seals (*Phoca vitulina*) to human disturbances in the Dollard estuary of the Wadden Sea. *Mammalian Biology* **77**, 281–287.

Reijnders, P.J.H., Brasseur, S.M.J.M. and Meesters, E.H.W.G. 2010. Earlier pupping in harbour seals, *Phoca vitulina*. *Biology Letters* **6**, 854–857.

Renouf, D., Lawson, J. and Gaborko, L. 1983. Attachment between harbour seal (*Phoca vitulina*) mothers and pups. *Journal of Zoology* **199**, 179–187.

Renouf, D. and Lawson, J.W. 1986. Play in harbour seals (*Phoca vitulina*). *Journal of Zoology* **208**, 73–82.

Renouf, D. and Lawson, J.W. 1987. Quantitative aspects of harbourseal (*Phoca vitulina*) play. *Journal of Zoology* **212**, 267–273.

Robinson, I. 1995. The rehabilitation of seals at the RSPCA Norfolk wildlife hospital. *The Journal of the British Veterinary Zoological Society*, **1**: 13–17

Skinner, J.P. 2006. Physical and behavioural development of nursing harbour seal (*Phoca vitulina*) pups in Maine. MSc thesis, University of Maine.

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

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

Thompson, P.M., Tollit D.J., Wood, D., Corpe, H.M., Hammond, P.S. and Mackay, A. 1997. Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland. *Journal of Applied Ecology* **34**, 43–52.

Venables, U.M. and Venables, L.S.V. 1955. Observations on a breeding colony of the seal *Phoca vitulina* in Shetland. *Proceedings of the Zoological Society, London* **125**, 521–532.

Warner, P. 1983. An assessment of the breeding populations of common seals (*Phoca vitulina vitulina* L.) in the Republic of Ireland during 1979. *Irish Naturalists' Journal* **21**, 24–26.

Wilson, S. 1974. Mother-young interactions in the common seal, *Phoca vitulina vitulina*. *Behaviour* **48**, 23–36.

Wilson, S. 1978. Social organization and behavior of harbor seals, *Phoca vitulina concolor*, in Maine. Report to the U.S. Marine Mammal Commission PB-280 188. Xi + 103pp.

Wilson, S.C. 1999. Radiotelemetry study of two rehabilitated harbour seal pups released close to the natural time of weaning in the wild. *Journal of Wildlife Rehabilitation* **22**: 5–11.

Wilson, S. 2001. Population growth, reproductive rate and neo-natal morbidity in a re-establishing harbour seal colony. *Mammalia* **65**, 319–334.

Wilson, S. and Kleiman, D.G. 1974. Eliciting play: a comparative study (*Octodon*,

Octodontomys, Pediolagus, Phoca, Choeropsis, Ailuropoda). *American Zoologist* **14**, 341–370.

Wilson, S.C. and Montgomery-Watson, J. 2002. Recent changes in the pattern of harbour seal pupping in Co. Down, north-east Ireland. *Irish Naturalists' Journal*. **27**: 89–100.