Haulout behaviour of harbour seals (*Phoca vitulina*) during breeding and moult in Vesterålen, Norway

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ABSTRACT

Haulout behaviour of harbour seals (*Phoca vitulina*) in Vesterålen, Norway, was investigated from 1 July to 23 August 2003 using a combination of high- and low-tide counts performed from boat and elevated land positions, and hourly counts from the land positions through 12- or 24-h cycles at specific haulout sites. There were obvious contrasts in haulout patterns of the seals throughout the period. The number of seals hauled-out was considerably higher in the area in July (the pupping period) than during August when the moulting period started. Contrasting July, when numbers of seals hauled-out at low tide was clearly higher than at high tide, there were virtually no systematic differences in haulout numbers between high and low tides in August. Circadian patterns were weaker in August than in July as well. Low temperatures had significant adverse effects on haulout numbers both in July and August, whereas increased cloud cover resulted in fewer seals hauled-out in July, but more seals in August.

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INTRODUCTION

Under a new management regime for harbour seals (Phoca vitulina) in Norway (Anon. 1990), it has been recommended that a monitoring programme be established where the population should be surveyed approximately every 5 years (see Nilssen et al. 2010). The most feasible approach to estimating harbour seal abundance is to use aerial photographic surveys when the seals are hauled-out of the water. Understanding the timing of haulout behaviour, therefore, is of critical importance to survey design. Harbour seals are usually counted during pupping and/or moult, when a larger fraction of the population hauls-out (Heide-Jørgensen and Härkönen 1988, Thompson and Harwood 1990, Reijndeers et al. 1997, Huber et al. 2001, Boveng *et al.* 2003, Gilbert *et al.* 2005). In Norwegian coastal waters, 2 abundance estimate surveys have been performed to assess the size of the entire population, and both were conducted during moult in 1996-1999 (Bjørge *et al.* 2007) and in 2003-2006 (Nilssen *et al.* 2010), respectively.

Several factors have been identified as factors that affect the number of harbour seals hauling out. These include seasonal, meteorological, tidal and diurnal factors. However, relationships between these conditions and the numbers of seals hauled-out tend to be quite variable between years and locations indicating that population or site specific analyses of conditions may be required (*e.g.*, Stewart 1984, Thompson and Miller 1990, Roen and Bjørge

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1995, Grellier et al. 1996, Watts 1996, Reder et al. 2003). Conducting surveys at low tide (±2 h) has become standard as this is when most seals are expected to be hauled-out (Watts 1996, Gilbert et al. 2005). In addition to tidal state, time of the day and meteorological conditions have been shown to be important factors influencing haulout patterns of harbour seals at various sites along the coast of Norway (Roen and Bjørge 1995) and on Svalbard (Reder et al. 2003) during summer.

Previous studies have found haulout peaks both during the mid-summer pupping period and during late summer/early autumn when harbour seals moult (Boulva and McLaren 1979, Everitt and Braham 1980, Brown and Mate 1983, Stewart and Yochem 1984, Thompson 1989, Thompson *et al.* 1989, 1994, Jemison and Kelly 2001, Daniel *et al.* 2003, Reder *et al.* 2003). The aim of the present study was to gain a better understanding of harbour seal haulout behaviour during the potential periods when aerial surveys designed to assess the abundance of the stock in Norway would be flown. To do this we investigated how the

haulout patterns were influenced by (1) the annual cycle with particular reference to possible differences between the pupping period (June/July in Norway, Bjørge 1991) and the moulting period (August/September in Norway, Bjørge *et al.* 2007), and (2) other factors including diurnal changes, tidal state and environmental conditions.

MATERIALS AND METHODS

This study was conducted in a harbour seal colony in Stø, localized in the archipelago Vesterålen, Northern Norway (69°N, 15°E, see Fig. 1), during the period 1 July to 23 August 2003. Fieldwork was concentrated in a local archipelago including the centre Beinøya surrounded by different-sized skerries, which are typical haulout sites for harbour seals in this area (Fig. 1). The study area was surrounded by shallow waters in the immediate vicinity of the haulout areas (2-10 m), whereas outside the archipelago the coast is characterized by shelves that sloped down to 150-200 m within a few kilometres of the shore. The outer, western part

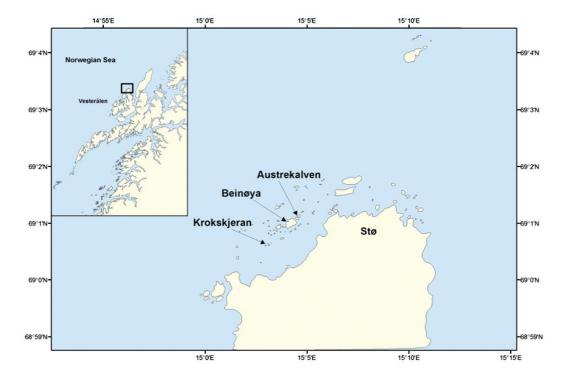


Fig. 1. The study area west of Stø in Vesterålen, North Norway.

of the studied archipelago is exposed to severe weather arriving from the open Norwegian Sea. Tidal amplitudes in Vesterålen were within the range of 1-1.5 m during the study period (Norwegian Mapping Authority 2003), and the haulout sites in the study area included intertidal ledges as well as rocky outcrops which were accessible throughout the tidal cycle.

The impact of meteorological and tidal influences, as well as seasonal patterns, on haulout behaviour and distribution patterns were investigated by daily counts during 3 periods: 1-3 July, 16-18 July, and 12-23 August. The seals were monitored from 3 elevated view points at Beinøya, Austrekalven and Krokskjeran (Fig. 1). Observations were made using a 20x50 telescope. Hauled-out seals were counted hourly, either in 12-h bouts (N=8) from 08:00/09:00 hours to 20:00/21:00hours (local Norwegian time), or in 24-h bouts (N=2). On some days seals were only counted at low and high tide (N=2). Data on times of low and high tide were based on tide tables (Norwegian Mapping Authority 2003).

At every low and high tide, the haulout site use was also monitored via boat surveys which

included parts of the haulout sites which were concealed from the land-based observation posts. Small aggregations of seals were counted from an inflatable boat using binoculars (10x42 and 7x50). Meteorological variables were measured at the observation sites: (1) wind speed in m/s (using a hand-held anemometer at approximately 1.5 m above the ground), (2) temperature in °C, (measured in the shade with a digital thermometer), (3) cloud cover (percentage of covered sky), (4) irradiation (sun presence or absence) and (5) precipitation (presence or absence). Any possible human disturbance (for example boat traffic) was also recorded.

Previous studies suggest that harbour seals have a periodic haulout behaviour where more animals haul out during low tide than during high tide (*e.g.* Reder *et al.* 2003). Therefore, a periodic model was used to analyze harbour seal haulout patterns over time in a given period of time (16-18 of July and 12-23 of August 2003):

$$N_t = a + b \cos \frac{2TC}{T} (t - t_0)$$

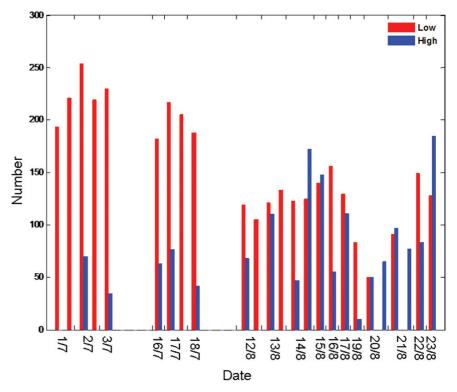


Fig. 2. Numbers of harbour seals hauled-out in the Stø colony in periods from 1 July to 23 August 2003. Data were derived from low (red) and high (blue) tide counts and included counts performed both from land and boat.

Table 1. Summary statistics of the GLM analysis. The residuals from the cos model were used as response variable and the metrological data (see text) as predictors. The significant variables were selected using forward selection. Res.dev. is the residual deviance.

Variables	Estimate	Std.error	t-value	P-value	Res.dev.	d.f.	AIC
July							
Temperature	1.13	0.30	3.69	< 0.001			
Cloudiness	-0.30	0.07	-4.53	< 0.001	533.5	27	238.4
August							
Intercept	-92.81	31.48	-2.95	0.004			
Temperature	5.70	2.09	2.72	0.007			
Cloudiness	0.18	0.08	2.28	0.024	93287	124	1206.5

where a, b, T and t_0 are parameters to be estimated. N_t is the number of seals observed on land at a given time t, a is the average number of seals hauling out in the period, b is the amplitude on the curve and t_0 indicates the top of the sinus curve or the phase component of the cosinus curve. Time (t) is a time index, a continuous variable, which includes year, month, day and time. The unit of the time index is decimal year; one hour corresponds to 11.43×10^{-5} hours. To examine if the tidal cycle had impact on the haulout pattern, a Spearman rank analysis of correlation was used.

The residuals from the model above were then used as response variables in a Generalized Linear Model (GLM) when examining the effect of tide and the meteorological variables on the number of seals hauled-out.

RESULTS

The total number of seals hauled-out, counted at high and low tide, indicated that there was a higher number of seals observed in the period 1-3 and 16-18 July than during 12-23 August (Fig. 2). In July there were clearly more seals hauled-out at low tide (182-254 seals) than at high tide (35-80 seals). Additional animals seemed to haul out at exposed reefs during low tide. In August, however, there were no significant differences between the low and high tide observations (50-185 seals at low tide, 10-180 seals at high tide); in some cases the

highest numbers of seals hauled-out were observed at low tide, in other cases at high tide. In August the seals hauled-out at fewer and larger islands than in July.

During the period 16-18 July, two 12-h series with hourly land based counts, followed by one high tide and one low tide count, were made in the colony (Fig. 3). The non-linear model, used to analyze the variation in haulout patterns for the seals over time, explained 85.6 % (R^2 =0.856, p < 0.05) of the observed variation. The parameter estimates of the model were as follows: a = 100.4 (SD=0.7), b = 58.1 (SD=0.9), T = 0.0014(SD=0.0001), $t_0 = 0.033$ (SD=0.002). A periodicity of 0.0014 decimal year correspond to 12.25 hours A Spearman rank Analysis of Correlation (ρ) between number of observed seals and the tidal cycle showed significant negative correlation between the variables, meaning that there were significantly higher numbers of seals hauled-out at low tide compared with high tide (ρ = – 0.79; p<0.05). The highest numbers of hauled-out seals were observed just before or after the lowest tide. Significant effects of temperature (more hauledout animals at higher temperatures; p < 0.01) and cloud coverage (more sun gave more hauledout animals; p<0.01) were detected via GLM analyses (Table 1).

The longest period of continuous observation throughout the study was from 12 to 23 August, *i.e.* during the harbour seal moulting period (Fig. 4). This period included 2 series with

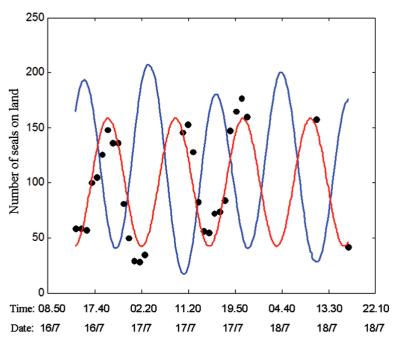


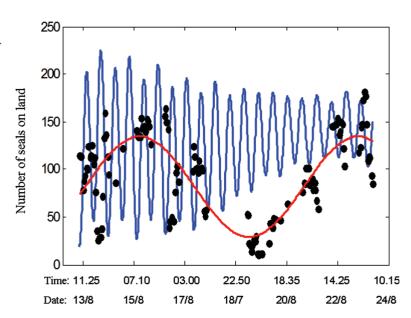
Fig. 3.
Total numbers of hauled-out harbour seals, observed in hourly counts from land at Stø in the period 16 to 18 July 2003, and plotted with the tidal cycle (blue line; tops are high tides, bottoms are low tides) and the non-linear model (red line).

24-h hourly counts and 6 series with 12-h hourly counts. Fitting the non-linear model to these data gave a much less conclusive result than in July. The Spearman rank correlation was not significant between the number of seals hauledout and the tidal cycle (ρ =0.009, p>0.05). The model explained only 58 % of the variations in the observed numbers of hauled-out seals in this period (R^2 =0.58, p<0.05). The parameter estimates of the model were as follows: a = 81.7 (SD=0.2), b = 52.6 (SD=0.3), T = 0.0214(SD=0.0001), t_0 = 0.1005 (SD=0.0013), implying a periodicity of 187.25 hours. Similar to the July analysis, the GLM analysis showed that temperature and cloud coverage contributed significantly to explain the variation in number of seals hauled-out in August (Table 1). In contrast to the analysis of the July data, however, the intercept was significant and cloud coverage coefficient was positive implying more clouds gave more hauled-out animals (Table 1).

DISCUSSION

This study of haulout behaviour of harbour seals in Vesterålen was conducted over a period which covered both breeding and moult, and there were obvious contrasts in haulout patterns of the seals throughout the period. The number of seals hauled-out was considerably higher in the area in July (the pupping period) than during August when the moulting period started. Previous studies have shown that the age-sex proportions of harbour seals hauledout varies substantially during summer, including the moulting period (Härkönen et al. 1999, Boveng et al. 2003, Daniel et al. 2003). Behavioural differences between the sexes and among the age classes indicate that the composition of the hauled-out fraction varies over time, and is not representative of the entire population at any time during the summer season (Härkönen et al. 1999). This may also have contributed to the observed changes in observed numbers of hauled-out seals. Härkönen et al. (1999) observed that juvenile harbour seals in Skagerrak, Sweden, hauledout more frequently during summer than older seals, whereas possible differences among age classes in the adult segment were unclear. In other studies of harbour seal moulting phenology, it has been observed that juveniles moulted first, then adult females, and finally adult males (Daniel et al. 2003, Reder et al. 2003). Available data do not permit a detailed sequence of the sex-age composition among hauled-out harbour seals during summer in

Fig. 4.
Total number of hauled-out harbour seals observed in hourly counts from land at Stø in the period 12 to 23 August 2003, and plotted with the tidal cycle (blue line; tops are high tides, bottoms are low tides) and the non-linear model (red line).



Vesterålen, but there was some evidence of a higher proportion of adults hauled-out by the end of August compared with mid August (Mogren 2006).

In general, the number of harbour seals hauling out to moult will increase and reach a peak at some point during the moulting period (Boveng et al. 2003, Reder et al. 2003). Since the timing of the moult varies among the sexes and age classes, and the relative timing among age classes may vary from year to year, the date of this peak may vary (Thompson and Rothery 1987, Boveng et al. 2003, Daniel et al. 2003, Small et al. 2003). In Norwegian coastal waters the harbour seal moulting period usually lasts from mid-August to mid-September (Bjørge and Øien 1999, Bjørge et al. 2007). The present study was terminated on August 23, i.e. only one week or so into the assumed moulting period, and may therefore have missed a possible peak that would have resulted in a larger number of hauled-out seals being observed in the colony. Supporting this is the observation of a considerable exodus of animals in the mid-August period (17-18 August), followed by an influx that builds up rapidly throughout the rest of the observation period.

In previous studies, time of day, tidal state and meteorological conditions have generally been shown to be important elements influencing haulout patterns of harbour seals during summer and autumn within the range of the species (e.g., Roen and Bjørge 1995, Thompson et al. 1997, Boveng et al. 2003, Reder et al. 2003). Most studies conducted in habitats consisting of rocks and intertidal ledges, as in Vesterålen, report peaks in the number of harbour seals hauledout around low tide (e.g., Schneider and Payne 1983, Terhune and Albon 1983, Thompson and Harwood 1990, Frost et al. 1999, Boveng et al. 2003, Reder et al. 2003), as was also observed in Vesterålen in July. Contrasting with this result, the August haulout behaviour showed an obvious lack of well defined tidal and circadian cycle influence, with virtually no systematic differences between high and low tide. The circadian patterns were also weaker in August than in July.

Roen and Bjørge (1995) noted a different influence of the tidal cycle between sites in Norway and suggested that the haulout behaviour of seals at sites with low tidal amplitudes was less influenced by tides than that of seals in areas with higher amplitude. When Boveng *et al.* (2003) investigated the influence of both height and time of the tides, they suggested that both might be good predictors of haulout behaviour, and that prevalence of one over the other was likely to vary among studies due to differences in data that might not necessarily be of biological significance. Local conditions at each site (*e.g.* for how long during each tidal cycle are the

potential haulout rocks submerged?) may contribute importantly to the realised patterns. The August studies in Vesterålen were performed in the first half of the assumed harbour seal moulting period. During moult, harbour seals change behaviour in that individuals spend more time hauled-out, possibly to elevate skin temperature and conserve energy (Boily 1995, Boveng *et al.* 2003). In the Stø archipelago, the local conditions also permit haulout outside the typical low tide period, and it is not unlikely that the otherwise strong correlations between haulout behaviour and tidal cycle may have become weaker and more blurred in August due to this.

Inclement meteorological conditions such as low temperatures and extensive cloud cover had significantly adverse effects on haulout numbers in July. None of the other monitored meteorological parameters (wind speed, irradiation and precipitation) contributed to explain variation in haulout numbers at all. In August there was still an adverse effect of temperature on haulout numbers, while the cloud coverage coefficient was positive implying more clouds gave more hauled-out seals. Generally, studies of haulout behaviour are based on censuses of hauled-out fractions of the population, assuming that the structure of the hauled-out population is stable during the study period. Consequently, if studies on the effect of tidal or circadian cycles or meteorological conditions on hauled-out seal numbers are carried out during any part of the summer period, results will be influenced by clines in haulout tendencies of various segments of the population (Härkönen et al. 1999). Small et al. (2003) have demonstrated that the influence of covariates on haulout behaviour can vary spatially at the site and regional scale, as well as temporally across years. Some of the detected changes in correlations in the Vesterålen studies could probably be attributed to changes in the structure of the studied haulout population (Mogren 2006). The lack of correlation between the haulout behaviour and meteorological parameters could also be due to the low variations in the latter since all manual counts performed in this period were performed under very stable weather conditions with low cloud coverage and a general absence of rain and strong winds. This was particularly the case in August.

The study area in Stø is located such that there is no physical obstruction impeding winds from the north and the west. Consequently, sea spray and waves during periods with strong wind can markedly impair the quality of haulout sites. Although no strong winds prevailed in the study period, even small changes in both strength and direction are likely to effect how seals select their haulout sites (e.g. on which side of the rocks they prefer to haul out). This may represent a potential sampling error in that the land based observations made did not cover all sides of all haulout rocks in the area, although there was little evidence from the boat - based observations that a shift or change in distribution of animals occurred around the haulout in the study period.

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REFERENCES

- Anon. 1990. Landsplan for forvaltning av kystsel. (National plan for management of coastal seals). *Norges Offentlige Utredninger 1990*(12):158 pp. (In Norwegian.)
- Bjørge, A. 1991. Status of the harbour seal, *Phoca vitulina* L., in *Norway. Biol. Conserv.* 58:229-238.
- Bjørge, A. and Øien, N. 1999. Statusrapport for Havforskningsinstituttets overvåkning av kystsel. (Status report for the Institute of Marione Research's monitoring of coastal seals). Havforskningsinstituttet. *Rapport SPS-9904*. 35 pp. (In Norwegian.)
- Bjørge, A., Øien, N. and Fagerheim, K.-A. 2007. Abundance of harbour seals, *Phoca vitulina*, in Norway based on aerial surveys and photographic documentation of hauled-out seals during the moulting season, 1996 to 1999. *Aquat. Mamm.* 33:269-275.
- Boily, P. 1995. Theoretical heat flux in water and habitat selection of phocid seals and beluga whales during the annual moult. *J. Theor. Biol.* 172:235-244.
- Boulva, J. and Mclaren, I. 1979. Biology of the harbour seal, *Phoca vitulina*, in eastern Canada. *Bull. Fish. Res. Bd. Can.* 200:1-24.
- Boveng, P., Bengtson, J.L., Withrow, D.E., Cesarone, J.C., Simpkins, M.A., Frost, K.J. and Burns, J.J. 2003. The abundance of harbour seals in the Gulf of Alaska. *Mar. Mamm. Sci.* 19:111-127.
- Brown, R.F. and Mate, B.R. 1983. Abundance, movements, and feeding habits of harbour seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon. *Fish. Bull.* 81:291-301.
- Daniel, R.G., Jemison, L.A., Pendleton, G.W. and Crowley, S.M. 2003. Molting phenology of harbour seals on Tugidak Island, Alaska. *Mar. Mamm. Sci.* 19:128-140.
- Everitt, R.D. and Braham, H.W. 1980. Aerial surveys of Pacific harbour seals in the southeastern Bering Sea. *Northwest Sci.* 54:281-288.
- Frost, K. J., Lowry, L.F. and Ver Hoef, J.M. 1999. Monitoring the trend of harbour seals in Prince William Sound, Alaska, after the Exxon Valdez oil spill. *Mar. Mamm. Sci.* 15:494-506.
- Gilbert, J.R., Waring, G.T., Wynne, K.M. and Guldager, N. 2005. Changes in abundance of harbour seals in Maine, 1981-2001. *Mar. Mamm. Sci.* 21:519-535.
- Grellier, K., Thompson, P.M. and Corpe, H.M. 1996. The effect of weather conditions on harbour seal haulout behaviour in the Moray Firth, northeast Scotland. *Can. J. Zool.* 74:1806-1811.
- Härkönen, T., Harding, K.C. and Lunneryd, S.G. 1999. Age- and sex-specific behaviour in harbour seals *Phoca vitulina* leads to biased estimates of vital population parameters. *J. Appl. Ecol.* 36:825-841.
- Heide-Jørgensen, M.P. and Härkönen, T. 1988. Rebuilding seal stocks in the Kattegat-Skagerrak. *Mar. Mamm. Sci.* 4:231-246.

- Huber, H.R., Jeffries, S.J., Brown, R.F., DeLong, R.L. and VanBlaricom, G. 2001. Correcting aerial survey counts of harbour seals (*Phoca vitulina richardsi*) in Washington and Oregon. *Mar. Mamm. Sci.* 17:276-293.
- Jemison, L.A. and Kelly, B.P. 2001. Pupping phenology and demography of harbour seals (*Phoca vitulina richardsi*) on Tugidak Island, Alaska. *Mar. Mamm. Sci.* 17:585-600.
- Mogren, H.-G. (MS) 2006. Steinkobbens adferd i kaste- og hårfellingsperioden i Vesterålen. (Harbour seal behaviour during breeding and moult in Vesterålen). [Master thesis], Norwegian College of Fishery Science, University of Tromsø, Norway, 41 pp. (In Norwegian.)
- Nilssen, K.T., Skavberg, N.-E., Poltermann, M., Haug, T. and Henriksen, G. 2010. Status of harbour seals (*Phoca vitulina*) in mainland Norway. *NAMMCO Sci. Publ.* 8:61-70.
- Norwegian Mapping Authority 2003. *Tide tables from the Norwegian Coast to Svalbard*. Sjøkartverket, Stavanger.
- Reder, S., Lydersen, C., Arnold, W. and Kovacs, K.M. 2003. Haulout behaviour of high Arctic harbour seals (*Phoca vitulina vitulina*) in Svalbard, Norway. *Polar Biol.* 27:6-16.
- Reijndeers, P.J.H., Ries, E.H., Tougaard, S., Nørgaard, N., Heidemann, G., Schwartz, J., Vareshi, E. and Traut, I.M. 1997. Population development of harbour seals *Phoca vitulina* in the Wadden Sea after the 1988 virus epizootic. *J. Sea Res.* 38:161-168.
- Roen, R. and Bjørge, A. 1995. Haul-out behaviour of the Norwegian harbour seal during summer. In: Blix, A.S., Walløe, L. and Ulltang, Ø. (eds.); *Whales, seals, fish and man*. Elsevier Science B.V., Amsterdam, 61-67.
- Schneider, D.C. and Payne, P.M. 1983. Factors affecting haul out of harbour seals at a site in southeastern Massachusetts. *J. Mammal.* 64:518-520.
- Small, R.J., Pendleton, G.W. and Pitcher, K.W. 2003. Trends in abundance of Alaska harbour seals, 1983-2001. *Mar. Mamm. Sci.* 19:344-362.
- Stewart, B.S. 1984. Diurnal hauling out patterns of harbour seals at San Miguel Island, California. *J. Wildl. Manage.* 48:1459-1461.
- Stewart, B.S. and Yochem, P.K. 1984. Seasonal abundance of pinnipeds at San Nicolas Island, California, 1980-1982. *Bull. South Calif. Acad. Sci.* 83:121-132.
- Terhune, J.M. and Albon, M. 1983. Variability in harbour seal numbers on haul out sites. *Aquat. Mamm.* 10:71-78.
- Thompson, P. and Rothery, P. 1987. Age and sex differences in the timing of moult in the common seal, *Phoca vitulina*. *J. Zool.* 212:597-603.
- Thompson, P.M. 1989. Seasonal changes in the distribution and composition of common seal (*Phoca vitulina*) haul out groups. *J. Zool.* 217:281-294.

- Thompson, P.M., Fedak, M.A., McConnell, B.J. and Nicholas, K.S. 1989. Seasonal and sexrelated variation in the activity patterns of common seals (*Phoca vitulina*). *J. Appl. Ecol.* 26:521-535.
- Thompson, P.M. and Harwood, J. 1990. Methods for estimating the population size of common seals, *Phoca vitulina*. *J. Appl. Ecol.* 27:924-938.
- Thompson, P.M. and Miller, D. 1990. Summer foraging activity and movement of radio-tagged common seals (*Phoca vitulina* L.). *J. Appl. Ecol.* 27:492-501.
- Thompson, P.M., Miller, D., Cooper, R. and Hammond, P.S. 1994. Changes in the distribution and activity of female harbour seals during the breeding season: implications for their lactation strategy and mating patterns. *J. Anim. Ecol.* 63:24-30.
- Thompson, P.M., Tollit, D.J., Wood, D., Corpe, H.M., Hammond, P.S. and Mackay, A. 1997. Estimating harbour seals abundance and status in an estuarine habitat in north-east Scotland. *J. Appl. Ecol.* 34:43-52.
- Watts, P. 1996. The diel hauling-out cycle of harbour seals in an open marine environment: correlates and constraints. *J. Zool.* 227:257-275.