



Variability in haul-out behaviour by male Australian sea lions *Neophoca cinerea* in the Perth metropolitan area, Western Australia

Sylvia K. Osterrieder^{1,2,*}, Chandra Salgado Kent¹, Randall W. Robinson²

¹Centre for Marine Science and Technology, Curtin University, Bentley, Western Australia 6102, Australia

²Institute for Sustainability and Innovation, College of Engineering and Science, Victoria University, Footscray Park, Victoria 3011, Australia

ABSTRACT: Pinnipeds spend significant time hauled out, and their haul-out behaviour can be dependent on environment and life stage. In Western Australia, male Australian sea lions *Neophoca cinerea* haul out on Perth metropolitan islands, with numbers peaking during aseasonal (~17.4 mo in duration), non-breeding periods. Little is known about daily haul-out patterns and their association with environmental conditions. Such detail is necessary to accurately monitor behavioural patterns and local abundance, ultimately improving long-term conservation management, particularly where, due to lack of availability, typical pup counts are infeasible. Hourly counts of *N. cinerea* were conducted from 08:00 to 16:00 h on Seal and Carnac Islands for 166 d over 2 yr, including 2 peak periods. Generalised additive models were used to determine effects of temporal and environmental factors on *N. cinerea* haul-out numbers. On Seal Island, numbers increased significantly throughout the day during both peak periods, but only did so in the second peak on Carnac. During non-peak periods there were no significant daytime changes. Despite high day-to-day variation, a greater and more stable number of *N. cinerea* hauled out on the significantly smaller beach of Seal Island during 1 peak. Overall, numbers hauled out were associated with temperature and tidal height, but not wind speed. Relative percentages of age classes hauled out also varied with time of breeding cycle. Due to high variability in haul-out behaviour in space and time, and its association with environmental conditions, we conclude that counts for monitoring relative abundance in management decisions should be conducted systematically, using robust survey designs with relatively large sample sizes.

KEY WORDS: Haul-out pattern · Australian sea lion · *Neophoca cinerea*

INTRODUCTION

Hauling out is a behaviour displayed by pinnipeds where animals temporarily leave the water to spend time on land between periods of activity. Hauling out onto land is important for pinnipeds during specific periods of their life cycle, such as breeding and moulting, but most pinniped species also haul out for other reasons. For example, they may travel considerable distances to foraging grounds and may forage at their aerobic dive limits (e.g. Arnould & Hindell 2001, Costa & Gales 2003, Chilvers et al. 2005), thus

hauling out may help conserve energy and contribute to recuperation (Riedman 1990). Pinnipeds may also haul out to avoid predation (LeBoeuf et al. 1982), as shown by an inverse relationship between successful great white shark (*Carcharodon carcharias*) attacks and distance from a haul-out island (Hammerschlag et al. 2006) or increased instances of haul-out behaviour in the presence of killer whales *Orcinus orca* (London et al. 2012). Haul-out sites are also commonly used for social interactions and thermoregulation (e.g. Ling et al. 1974, Marlow 1975, Krieber & Barrette 1984, Riedman 1990).

*Corresponding author: sylvia.osterrieder@gmail.com

© The authors 2015. Open Access under Creative Commons by Attribution Licence. Use, distribution and reproduction are unrestricted. Authors and original publication must be credited.

The duration and frequency of hauling out can be specific to species, population or individual. Duration of haul out may be longer during the breeding and pupping season of some pinniped species (e.g. Lake et al. 1997, Southwell 2005), which may be related to variations between female and male haul-out duration and pattern (Thompson et al. 1989, Reder et al. 2003, Southwell 2003). Accordingly, within a population of the same species, age and sex, as well as timing within the breeding, pupping or moulting cycles, can influence haul-out patterns (Thompson et al. 1989, Reder et al. 2003, Bengtson & Cameron 2004).

Previous studies of seals and sea lions have shown considerable differences between species in diurnal and seasonal fluctuations in haul-out numbers (Thompson et al. 1989, Sepúlveda et al. 2001, 2012, Reder et al. 2003). Some phocids and otariids have shown lower numbers in the morning, with peaks in the afternoon (Stirling 1968, Lake et al. 1997, Carlens et al. 2006), though the timing of the peaks can vary between seasons (Lake et al. 1997). Some seals, for example, hauled out more over midday in some seasons, but less at the same time of day during others, such as harbour seals *Phoca vitulina* in Scotland, where there was a greater probability of hauling out around midday in summer (Cunningham et al. 2009). Diurnal haul-out patterns can also vary between locations (Cunningham et al. 2009), a trait observed in South American sea lions *Otaria flavescens* (Rosas et al. 1994, Sepúlveda et al. 2001, 2012).

Several studies have shown that variations in numbers of pinnipeds hauled out can be affected by weather conditions, such as temperature, cloud cover or wind speeds (Schneider & Payne 1983, Watts 1992, Carlens et al. 2006, Andrews-Goff et al. 2010). Additionally, oceanographic factors, such as tidal heights, times or currents may play a significant role in haul-out patterns (Stirling 1968, Pauli & Terhune 1987b, Thompson et al. 1989, Watts 1992). There may also be a combined effect of several environmental conditions combined with time of day and season (e.g. Schneider & Payne 1983, Pauli & Terhune 1987a,b, Thompson et al. 1989, Lake et al. 1997, Reder et al. 2003, Carlens et al. 2006, Mogren et al. 2010).

Australian sea lions *Neophoca cinerea* have been listed as Endangered on the IUCN Red List and are endemic to South and Western Australia (Goldsworthy 2015). *N. cinerea* have an unusual breeding cycle, unique among pinnipeds. Breeding takes place aseasonally on average every 17.4 mo (range: 16.0–19.9 mo) and asynchronously between breeding locations, during a period of 5 to 9 mo (Ling & Walker 1978, Gales et al. 1992, 1994, Higgins 1993, Goldswor-

thy et al. 2008). Haul-out sites in the Perth metropolitan area (Western Australia), approximately 250 km south of the closest breeding islands at Jurien Bay, are known to be used exclusively by males (Gales et al. 1992). Male *N. cinerea* travel significant distances away from breeding colonies, presumably to maximise foraging success and efficiency (Gales et al. 1992). Thus, access to these non-breeding haul-out sites is critical to the health of male sea lions and successful reproduction of the species. Management to reduce human impacts at key haul-out sites where animals rest is often implemented (e.g. Gales 1995, Lovasz et al. 2008), especially in areas of high human visitation such as the Perth metropolitan area. To determine the effectiveness of management guidelines, monitoring of animals using the islands is often undertaken by conducting counts over time (Cassini et al. 2004, Salgado Kent & Crabtree 2008). These counts can be used as estimates of relative abundance on which to base trends. Male numbers at the Perth haul-out islands peak aseasonally, aligned with the non-breeding season (Ling & Walker 1978, Gales et al. 1992, 1994, Higgins 1993, Goldsworthy et al. 2008). While these peaks can be predicted, little is known about the extent and variability in daily use of these islands, or how they vary with environmental conditions. Variation in the proportion of age classes on these islands is also unknown.

Counts are often used for management purposes to monitor numbers of animals hauled-out on islands over time. Based on the resulting counts, measures, such as establishing sanctuary zones in areas used by large number of animals, may be implemented to minimise human disturbance (e.g. Gales 1995, Cassini et al. 2004). However, single counts used as an indicator of numbers of animals using a haul-out site can be subject to significant inaccuracies when there is large day-to-day variability (Southwell 2005). Consequently, information on the extent of use of these islands and its associated variability with environmental conditions is critical for accurately monitoring changes in behaviour and relative abundance and is essential for the long-term conservation management of *N. cinerea* in the region.

To enhance current knowledge and thereby improve future monitoring practices and conservation management of *N. cinerea*, we aimed to identify whether *N. cinerea* had a consistent pattern in daily haul-out behaviour. We recorded haul-out numbers over a 2 yr period on 2 main haul-out islands in the Perth metropolitan area, and assessed whether hauling out was associated with local environmental conditions.

MATERIALS AND METHODS

Study sites

Male *Neophoca cinerea* are known to regularly haul out on 6 islands off the Perth metropolitan coast in Western Australia (WA, Fig. 1). On these 6 male-only haul-out islands, Seal (32.29° S, 115.69° E) and Carnac (32.12° S, 115.66° E) Islands are used by the largest number of *N. cinerea*, with up to 28 and 45 ind. hauled out during the Perth peak season,

respectively (Gales et al. 1992), and were therefore chosen as the field sites for this study. Approximately 15 *N. cinerea* can be found hauled out at Burns Rocks and Little Island combined, mostly less than 10 at Dyer Island during the Perth peak season, and 1 or 2 can be found infrequently on Penguin Island (Department of Parks and Wildlife [DPaW] unpubl. data). It is highly likely that sea lions move between the haul-out islands given their proximity; however, this has rarely been documented (Gales et al. 1992).

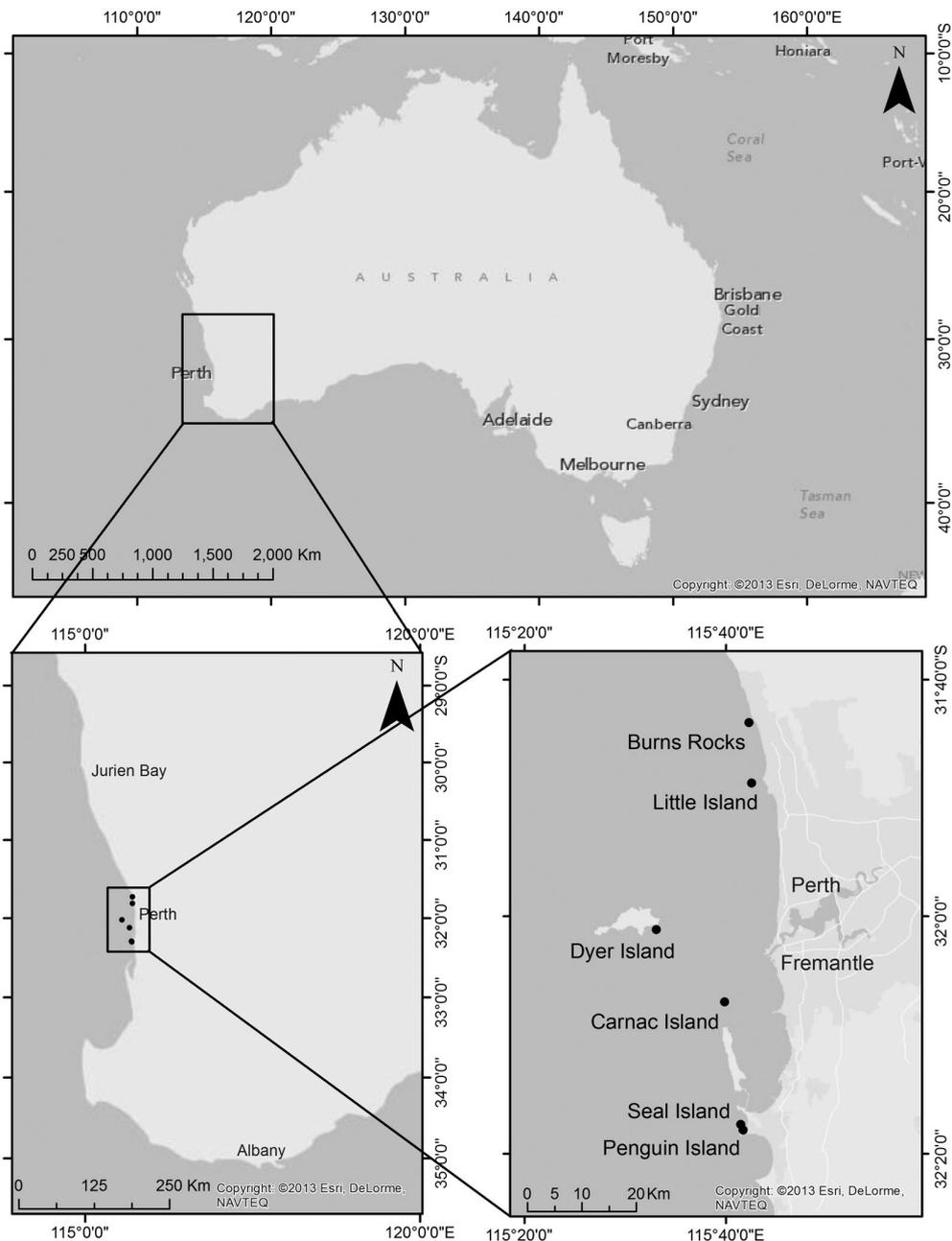


Fig. 1. Haul-out sites of *Neophoca cinerea* in the Perth metropolitan area

Seal Island is located in the Shoalwater Islands Marine Park, approximately 0.9 km offshore from Shoalwater (ca. 45 km south of Perth, capital city of WA, Fig. 1). Seal Island is a sanctuary zone, managed as a 'look, but don't take' area and, as such, landing on the island is prohibited (Department of Environment and Conservation [DEC] 2007, DEC & Fisheries 2011). The island provides a sandy beach of approximately 0.27 ha on the eastern side of the island (estimated from a Google Earth, 2014 image from 1 January 2014) with shrubs at the edges, small rocky overhangs and caves north and south of the beach, as well as along the southern bay. Apart from the beach area, the shores of the island are rocky. *N. cinerea* mainly use the beach and occasionally use adjacent shrubs or caves to haul out.

Carnac Island, approximately 10 km south-west of Fremantle (ca. 15 km south of Perth, Fig. 1) is classified as an A class nature reserve. Access to most of the island is prohibited, but the southern part of the eastern beach is available for public access during the day (Department of Conservation and Land Management [CALM] 2003). *N. cinerea* mainly haul out on the sandy beach of ca. 0.78 ha (estimated from a Google Earth, 2014 image from 1 January 2014) located on the east side of the island. The beach is fringed with shrubs and small bushes. There are some rocks, small rocky overhangs and caves to the north and south of the main beach where *N. cinerea* have been observed occasionally.

Data collection

Neophoca cinerea counts

Counts of *N. cinerea* on the main haul-out beaches of Seal and Carnac Islands were undertaken over 166 d between June 2012 and April 2014. The study was designed so that days on which counts were undertaken occurred approximately once or twice a week over most of the study period; however, on occasion, sampling was less frequent. During each day of counts, all *N. cinerea* within view of the observer were counted hourly, primarily between 08:00 and 16:00 h. *N. cinerea* not in view at the time of counting, but known to be present during the count (i.e. seen when entering a cave as well as when exiting) were also included in the counts. Counts were made every hour, except during inclement weather or when there were technical difficulties that caused some counts to be missed during the day or some days cut short. Counts on Seal Island were conducted over 78 d and on Carnac Island over 88 d.

On Seal Island, the observer was located strategically, where the entire beach was within view, and counts were conducted with the aid of binoculars (Nikon Eagleview 8–24 × 25). At Carnac Island, a live camera (AVT284 IP Camera with remote Pan, Tilt, and Zoom capability and 22× optical zoom), owned and serviced by DPaW, with a radio link to the local office (using a Proxim 8150 PTP microwave radio link), was used. This radio link allowed remote control over the camera's viewing direction and zoom (Salgado Kent & Crabtree 2008). The camera is located on a vantage point overlooking the eastern beach and was panned from north to south along the beach to count the *N. cinerea*. The zoom was used to aid counts when necessary, particularly to distinguish *N. cinerea* from some rocks on the far, southern part of the beach. This method was considered to accurately reflect counts that would have been made at a strategic vantage point at the site, based on the results of a study comparing simultaneous *in situ* beach counts and counts made with a previous model of this camera on the island (Salgado Kent & Crabtree 2008).

There were several cases when these methods were not used, due to logistical constraints (for example, in instances when a vessel was not available to travel to Seal Island or the live camera was not working at Carnac Island). On Seal Island, between July and August 2012 as well as on the 9 October 2012, a vantage point on the mainland (on the coast of Shoalwater, WA) with the entire beach area on Seal Island in view was used. Counts from this location were conducted using either a telescope (115 mm Tasco reflecting with either a 25, 20 or 10 mm eye piece with 36×, 45× or 90× magnification, respectively) or a spotting scope (Televid 77 with 20× to 60× zoom). The vantage point on the mainland (at 32.2855° S, 115.7035° E) was approximately 1.4 km away from Seal Island, and the telescope and spotting scopes were considered to give sufficient magnification to count *N. cinerea* easily and accurately. On Carnac Island, between the end of November 2013 and the end of April 2014 (with the exception of 8 and 13 January 2014), counts were conducted directly from the vantage point where the live camera was located.

During all counts (with the exception of the first 6 mo of the study; i.e. counts before 22 October 2012), animals were visually classified into age groups by S. K. O., either as juvenile, sub-adult, adult or otherwise unknown, following the description of Jefferson et al. (2011). Juvenile males were identified based on their silvery grey backs and light brown or fawn lower fronts. They are also lighter in colour than sub-

adults and adults. Sub-adult males are larger and darker than juveniles and most show a white ring around their eyes which diminishes as they grow into bulls. Bulls are usually dark brown with a light creamy coloured crown. A number of *N. cinerea* present in the Perth metropolitan area are in intermediate stages of becoming either a sub-adult or adult and it can be difficult to distinguish between the age classes. For classification purposes here, younger *N. cinerea*, with undersides darker in colouration than juveniles and showing darker spots, were classed as sub-adults. Distinguishing between sub-adults and adults was based on size and the light coloured crown. If the individual showed a pronounced white eye ring and the light coloured crown was at the initial stages of showing through, it was classified as a sub-adult; however, if a full white crown was visible it was classified as an adult. For most *N. cinerea*, the age classification was straightforward. However, if no decision could be made on an individual *N. cinerea* was obscured sufficiently so that no age class could be determined, the class was recorded as unknown. Counts and age classifications were made by the same observer to avoid observer variability (Udevitz et al. 2005).

Environmental data

Beaufort condition and cloud cover (in percentage) were recorded qualitatively at the time each count was made. Quantitative measures of air temperature, wind speed, wind direction, precipitation and atmospheric pressure at sea level were accessed through the Bureau of Meteorology (BOM) half-hourly weather station measurements made on Garden Island. This station was the closest to the study sites; located between Seal and Carnac Islands at a range of approximately 5.5 and 13.8 km from the islands, respectively. Weather station readings within 30 min from the start time of *N. cinerea* counts were taken to represent those at the time counts were made. Tide levels (from the lowest astronomical tide) at the start of counts were interpolated based on half-hourly tidal measurements from the tidal gauge at Fremantle, WA (provided by BOM). The times in which counts were conducted were recorded using a GPS set to local time (UTC +8) unless the remote-controlled camera was used, in which the current local time was accessed from www.timeanddate.com (which uses Australian Western Standard Time). The times were also expressed as decimal hours since sunrise in the final database by subtracting the time

of sunrise (accessed from www.timeanddate.com) from the local start time of counts (with minutes being divided by 60 to express decimal hours).

Statistical analysis

Modelling

Generalised additive models (GAM) with Poisson distribution and log link functions for count data were used to determine the relationship between temporal and environmental factors and numbers of *N. cinerea* hauled out at the 2 islands. GAMs were chosen to allow the inclusion of smoothers in the model as well as an autocorrelation structure to account for the dependency of subsequent counts in a short time period. Explanatory variables included survey interval (as a factor) with 8 levels (1 to 8), location as a factor with 2 levels (Seal and Carnac Islands), hours since sunrise (in decimal hours) in which the counts were made (as a continuous variable), and temperature, tide level and wind speed (as continuous variables). The entire survey time was split into 8 survey intervals, hereafter called 'periods'. Each period consisted of an average of 83.6 d (varying by a maximum of 3 d), with Period 1 starting on Day 1 of the study and Period 8 starting on Day 586 (corresponding to 6 July 2012 and 12 February 2014, respectively). Periods 1 and 7 were found to be the peak periods for *N. cinerea* counts, and Period 4 fell on the minima of the cycle. As not all intervals within the 17.4 mo breeding cycle of *N. cinerea* could be sampled multiple times, 'period' is treated as a sequential survey interval from 1 to 8 rather than a period relative to the aseasonal cycle. Thus, Periods 1 and 2 and Periods 7 and 8 represented intervals during sequential peak and post-peak periods in the aseasonal cycles, respectively. Each period included between 20 and 26 survey days (across both islands), except Period 6 (October 2013) which had 9 survey days. The autocorrelation structure used decimal days rescaled so that values were relative to the time since sunrise, reported as hours since sunrise from Day 1.

Interaction terms included time since sunrise by location and location by period. Correlation structures tested to account for temporal correlation among counts included autoregressive correlation of order 1 (AR-1), continuous AR(1), and exponential and spherical correlations (available in the R package 'mgcv' used for the GAMs, Wood 2006).

Variance inflation factors (VIF) were used to test for collinearity. All covariates showed VIFs < 3, indicating

no collinearity between covariates (Zuur et al. 2007, 2009). Sea level pressure, however, showed high non-linear correlation with air temperature and was excluded from the analysis to prevent model misfit. Air temperature was chosen as biologically more significant than sea level pressure because air temperature has shown significant influence on haul-out behaviour in previous studies (e.g. Carlens et al. 2006). Precipitation was excluded from the models because of the lack of rainy days and, therefore, the poorly balanced data set. Cloud cover was recorded as a percentage of the whole sky. This was removed from the analysis (to simplify an already complex model) as it was considered of low biological significance, since recorded clouds could have been far away and not impacting *N. cinerea* locally. Wind speed influences the sea conditions the Beaufort scale measures and we included wind speed as the more precise covariate in the model, excluding Beaufort from the analysis. Wind direction was excluded from the analysis to keep the model as simple as possible (and to avoid problems in convergence), since it was considered biologically of less significance than the other variables. The full model thus included air temperature, tide level and wind speed as environmental covariates. Temperature, wind speed and tide level showed some non-linear patterns with period, hence the validity and interpretation of models including these environmental factors were assessed carefully. Three counts lacked temperature and wind speed measurements and were thus removed from the analysis.

Data exploration and model validation

Data exploration was undertaken to identify and remove any outliers or any single exceptionally large or small values that would overly influence the model results, and to check general assumptions of GAMs. Counts from 2 days, Days 38 and 550 (within Periods 1 and 7, respectively) from Carnac Island were excluded from the model to avoid influential data in the analysis. Counts on Day 38 were exceptionally low and were made 2 d after an unusually large storm event. Day 550 had exceptionally high numbers of *N. cinerea*.

The general approach to model construction and validation was to begin with the most complex model, with all effects that were considered to be of relevance to the numbers of *N. cinerea* hauling out based on biological knowledge (Flom & Cassell 2007, Zuur et al. 2009). The model was restricted *a priori* to an acceptable level of complexity, based on a general rule of thumb of at least 20 samples per covariate

level (Harrell 2001), with the exception of Period 6 with 9 sampling days. Period 6 was included in the analysis to avoid a large data gap between Periods 5 and 7, and was interpreted carefully. To validate the model, residuals were plotted against each individual explanatory variable to ensure there were no obvious patterns. To test that the inclusion of a correlation structure accounted for dependency sufficiently with no persisting autocorrelated residuals, normalised residuals were inspected for remaining pattern using variograms (Zuur et al. 2009). Fewer counts were made before 08:00 h and after 16:30 h which appeared to influence the autocorrelation left in the normalised residuals. Therefore, only counts between 08:00 and 16:30 h (which included 0.7 until 10.9 h after sunrise) were included in the models.

Following this first complex model, submodels were created by removing insignificant explanatory terms ($p > 0.05$) with very small estimated variances one by one from the model, starting with the least significant term for model simplification (Wood 2006, Zuur et al. 2009). Each time, the resulting submodel was refitted and re-validated. Submodels were compared, and of these the final model was selected by finding the simplest validated model using Akaike's information criterion (AIC) as a guide. While identifying the simplest model that reduced the AIC by >2 units (Burnham & Anderson 2002) was the initial aim, because environmental variables were related (non-linearly) to period, selection of the lowest AIC reduced by >2 units would have meant removing significant terms from the model. We minimised AIC for model selection, while including all significant terms based on p -values for which to explain phenomena (de Valpine 2014). Smoothers fit to the variable 'time since sunrise' were straight lines, indicating linear relationships between response and explanatory variables, and did not improve the model from one using a non-smoothed 'time since sunrise' term according to the AIC. When adding a smoother to tide level in the final model selected the model could not converge; however, comparisons in previous submodels leading up to the final model fit better with tide as a non-smoothed function. Time since sunrise and tide level were therefore added without smoothing functions.

Finally, there were some submodels that could not be tested, for the simple reason that they did not converge. All submodels, regardless of which insignificant terms had been removed, showed the same explanatory variables as significant, providing confidence in the final model selected.

As a large number of *N. cinerea* used the islands during peak periods (i.e. Periods 1 and 7 in this

study), maximum counts were also compared between islands. Finally, models were not generated for identifying patterns associated with age class since data sets split by age class did not contain sufficient samples. These patterns were, however, investigated using exploratory analyses. The maximum numbers of juveniles, sub-adults, adults and unknowns counted for each day were averaged over each period. Percentages of each class were then calculated from the averages. All analyses and figures were produced using R version 3.1.1 (R Development Core Team 2014) run through RStudio Version 0.98.983 – © 2009–2013 RStudio.

RESULTS

Neophoca cinerea was observed on 163 of 166 survey days. There were 620 hourly counts made over 78 d on Seal Island and 712 counts over 88 d on Carnac Island, totalling 1332 hourly counts. Models were produced using 1227 counts, which covered all survey intervals (603 from Seal Island and 624 from Carnac Island).

The final GAM selected which produced the most parsimonious model followed the form:

$$\log(\mu_i) = \alpha + \beta_1 \times \text{TimeSinceSunrise}_i + \beta_2(\text{Period}_i \times \text{Location}_i) + \beta_3 \times \text{Tide}_i + s(\text{Temperature}_i) + e_i \quad (1)$$

where:

$$e_i = \text{Time} + \varepsilon_i \quad (2)$$

with μ being the number of *N. cinerea* observed at count i , α being the intercept, β the corrections of the slope for each covariate at count i , s the smoothing function, and e_i consisting of the correlation structure indicated by the Time + noise ε (with noise normally distributed with mean 0 and variance σ^2). Time here was expressed as decimal days, rescaled so that

values were relative to the time the sun rises (rather than relative to GMT). A spherical correlation structure resulted in the best fit, and was given by the equation in Pinheiro & Bates (2000), their Table 5.2:

$$\gamma(s, \rho) = 1 - \left[1 - 1.5 \left(\frac{s}{\rho} \right) + 0.5 \left(\frac{s}{\rho} \right)^3 \right] I(s < \rho) \quad (3)$$

with $\gamma(s, \rho)$ as the correlogram with correlation parameters ρ as the range and s as the time, and where function ' $I(s < \rho)$ ' denotes a binary variable taking value 1 when $s < \rho$ and 0 otherwise' Pinheiro & Bates (2000, p. 231). The greatest variation in numbers of *N. cinerea* on Seal and Carnac Islands was from the 17.4 mo aseasonal cycle in arrival at and departure of animals from breeding grounds. Peak numbers at both islands occurred between July and August 2012 and December 2013 and January 2014 (Periods 1 and 7, respectively, Fig. 2). The trough in numbers was between April and May 2013 (Period 4). This was reflected in the model by 'Period' being the most influential variable ($p < 0.001$, see Table S1 in the Supplement at www.int-res.com/articles/suppl/n028/p259_supp.pdf). There was a significant difference in numbers of *N. cinerea* hauling out on Seal and Carnac Islands ($p < 0.001$, Table S1), with overall numbers greater at Seal than at Carnac Island (Fig. 2). The interaction between period and location was significant ($p < 0.001$, Table S1), showing that the greater numbers at Seal Island than at Carnac occurred during Periods 1, 2, 5 and 6 (Fig. 2). Numbers of *N. cinerea* present did not show any significant difference between the 2 islands in Periods 3, 4 and 7, but numbers on Carnac Island were greater than on Seal Island in Period 8 (Fig. 2). A small increase with time since sunrise was observed for Carnac Island in the second peak season, but not in the first peak season (Fig. 3). The time since sunrise and its interaction with period significantly influenced the number of *N.*

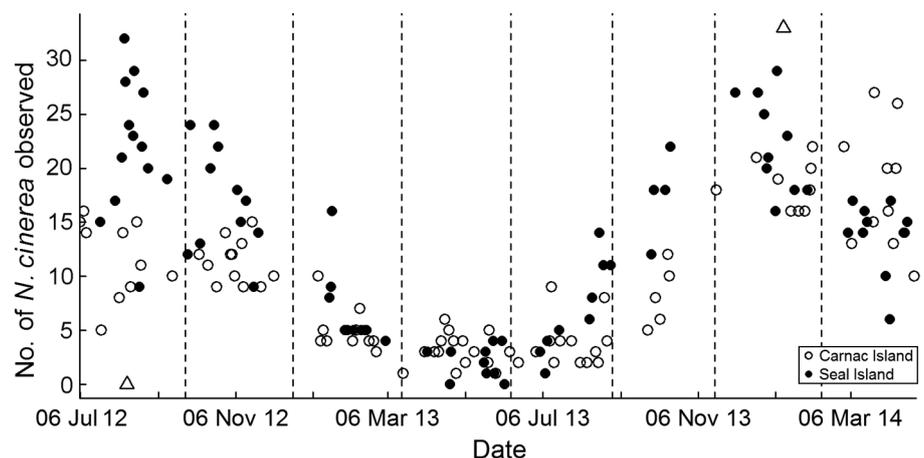


Fig. 2. Maximum number of *Neophoca cinerea* observed on Carnac (O) and Seal Islands (●) over 166 survey days between June 2012 and April 2014, including the exceptionally high and low observations (Δ) on Carnac Island. Dashed lines mark the survey periods (survey intervals 1 to 8)

cinerea ($p < 0.001$, Table S1), with increasing numbers of *N. cinerea* hauled out over the course of a day during certain periods (Fig. 3). On Seal Island, this trend occurred during Periods 1, 6 and 7 with a slight increase during Period 2. On Carnac Island, the trend occurred during Period 7 and to a lesser extent during Periods 2 and 8. No increase over the course of a day was observed at either location during Periods 3, 4 and 5, which were the periods with the lowest numbers of *N. cinerea* present. Additionally, no trend was observed during Periods 1 and 6 on Carnac Island (Fig. 3). The interaction term between location and time since sunrise did not show any significant effect on the number of *N. cinerea* hauled out and was thus removed from the final model.

Air temperature and tide level had significant effects on the number of *N. cinerea* hauled out on Seal and Carnac Islands (Figs. 4 & 5). The numbers of *N. cinerea* on the islands decreased with increasing tide level ($p = 0.003$, Table S1, Fig. 5). The pattern was more pronounced on Seal Island than on Carnac Island (Fig. 5). On Carnac Island, a steeper decrease in *N. cinerea* numbers hauled out was only observed when the tide had reached 1.0 m above the lowest astronomical tide (Fig. 5). The numbers of *N. cinerea* increased with air temperature up to approximately 21°C ($p < 0.001$, Table S1), at which point they became comparatively stable. Smoothing function confidence intervals (95%) at temperatures below 15°C and above 27°C were large; thus, interpretation at these temperatures is unreliable (Fig. 4). Wind speed did not have a significant effect on numbers of *N. cinerea* hauled out ($p > 0.1$).

Peak periods

There were 308 counts conducted in the peak periods, 174 on Seal Island and 134 on Carnac Island over 21 and 23 d, respectively. More *N. cinerea* were observed on Seal than on Carnac Island during this period. The maximum numbers counted were 32 and 29 on Seal Island and 16 and 33 on Carnac Island in the first and second peaks, respectively. The maximum numbers of animals hauling out in each peak

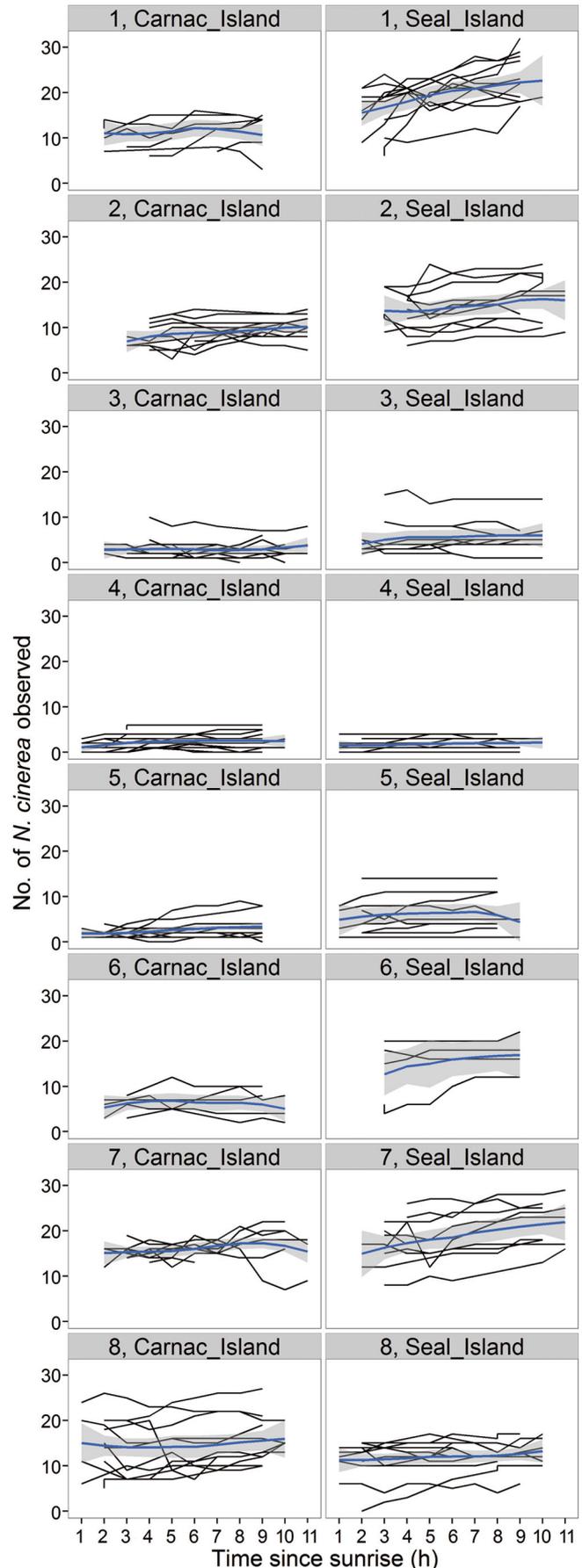


Fig. 3. Number of *Neophoca cinerea* observed during hourly counts on Carnac and Seal Islands during survey Periods 1 to 8. Each line represents counts conducted on a single sampling day represented in hours since sunrise. A LOESS smoother (blue line) with 95% confidence intervals (grey) has been added as a visual aid. (The 2 exceptionally high and low observation days on Carnac Island were excluded)

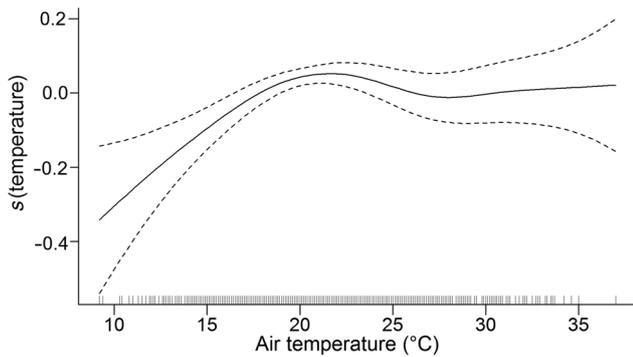


Fig. 4. Smoothing function (solid line) with 95% confidence intervals (dashed lines) fitted to air temperature ($^{\circ}\text{C}$) estimated in the final generalised additive model (GAM). The small ticks above the x-axis represent air temperature values of the observations

season were counted on Days 35 and 550 on Seal Island and Days 3 and 556 on Carnac Island, and were 515 (16.9 mo) and 553 d (18.3 mo) apart, respectively. However, excluding the highest and most influential count, the highest count was conducted on Day 578 (19.0 mo after Day 3) with 22 ind. counted on Carnac Island. More *N. cinerea* hauled out on Carnac Island in the second than in the first peak season (Fig. 2). There was a high variation in numbers counted on different days in the peak seasons, more so on Seal than on Carnac Island (Figs. 2 & 3).

Age classes

The majority of animals on Seal and Carnac Islands consisted of sub-adults and adults, with a maximum

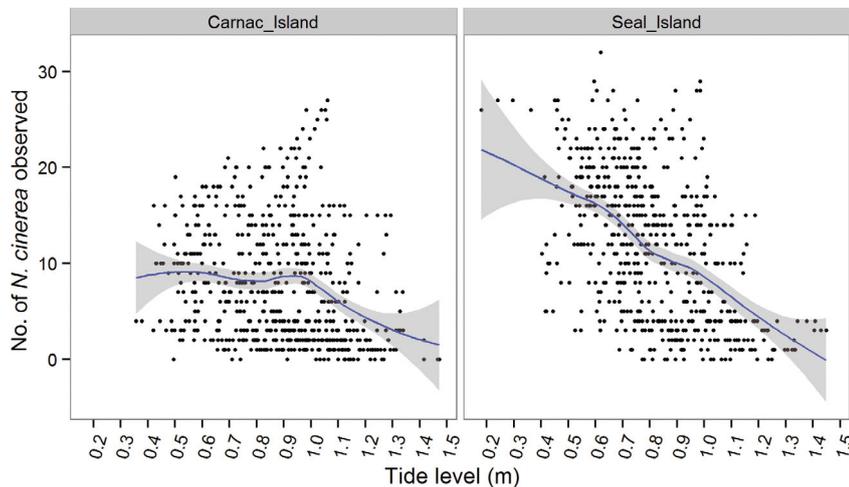


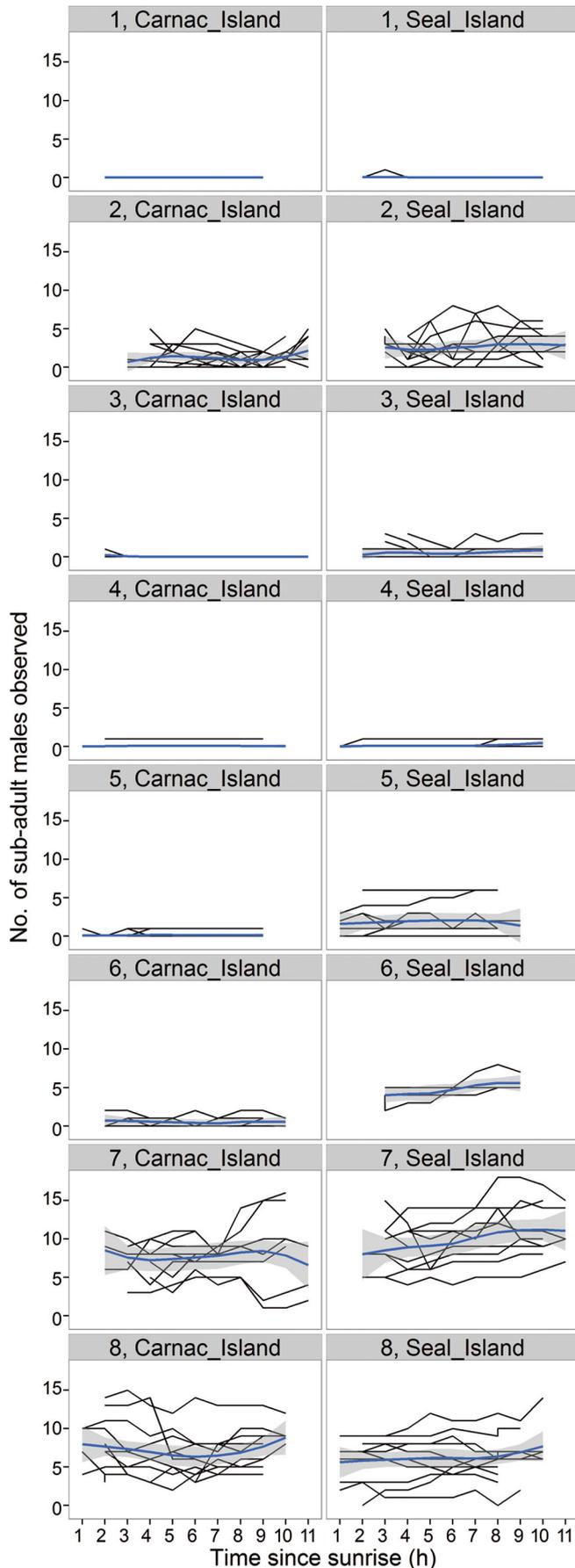
Fig. 5. Relationship between number of *Neophoca cinerea* and tide level (m) observed on Seal and Carnac Islands. A LOESS smoother (blue line) with 95% confidence intervals (grey) has been added to aid visual interpretation

of 18 sub-adults and 24 adults hauled out at any one time (Figs. 6 & 7). Juveniles were present on both Seal and Carnac Islands, but were low relative to overall numbers, not exceeding 8 ind. at any time. Juveniles did not show any visible variation in hauled out numbers throughout the day. Sub-adults increased throughout the day during Periods 6 and 7, and slightly increased during Period 8 on Seal Island. A similar increasing pattern was observed during Periods 7 and 8 on Carnac Island. An increase in numbers of *N. cinerea* was evident in Period 7 between 2 and 9 h after sunrise, but numbers decreased between 10 and 12 h after sunrise. However, the variability in these last 3 h of observations was visibly greater. Sub-adults on Carnac Island during Period 8 showed a slight decrease in numbers until 6 h after sunrise, but numbers thereafter increased. With few *N. cinerea* remaining in the area during the non-peak period, a small variation in *N. cinerea* numbers had a large influence in their percentages (indicated by the large standard deviations). Thus, patterns in haul-out behaviour of different age classes could only be detected in plots when *N. cinerea* numbers were high. Adult *N. cinerea* came ashore throughout the day during Periods 2 and 7 on both Seal and Carnac Islands and also during Periods 5 and 8 on Carnac Island. The sample size in Period 6 on Seal Island was too small and the variability of adult counts too high to identify a pattern.

The ratio of adult to sub-adult *N. cinerea* increased at both islands during the breeding season (i.e. the period with few individuals occurring around Perth). During the breeding season (Periods 2 to 6), the period-averaged, maximum daily percentage (\pm SD) of sub-adults on the islands ranged from 2% (\pm 8) to 32% (\pm 34), compared with the percentage of adults which ranged from 47% (\pm 23) to 92% (\pm 49) (Table S2 in the Supplement). When numbers of *N. cinerea* in the area increased, however, the ratio of adults to sub-adults was closer to parity, with adults ranging from 43% (\pm 26) to 47% (\pm 24) and sub-adults ranging from 49% (\pm 17) to 52% (\pm 20) (Table S2, Fig. 8).

DISCUSSION

Numbers of male *Neophoca cinerea* hauling out in Perth metropolitan waters display aseasonal cycles in



abundance, varying according to the approximately 17.4 mo breeding cycle of the species. Sampling period, in relation to the breeding season, was the most influential variable on numbers of *N. cinerea* hauled out, similar to other sea lion species (Sepúlveda et al. 2001, Marcotte 2006). Results here were similar to those of Gales et al. (1992) in that overall *N. cinerea* numbers on Perth metropolitan haul-out islands followed a 17 to 18 mo cycle, with troughs in Perth aligning with the peaks on breeding islands to the north (Jurien Bay).

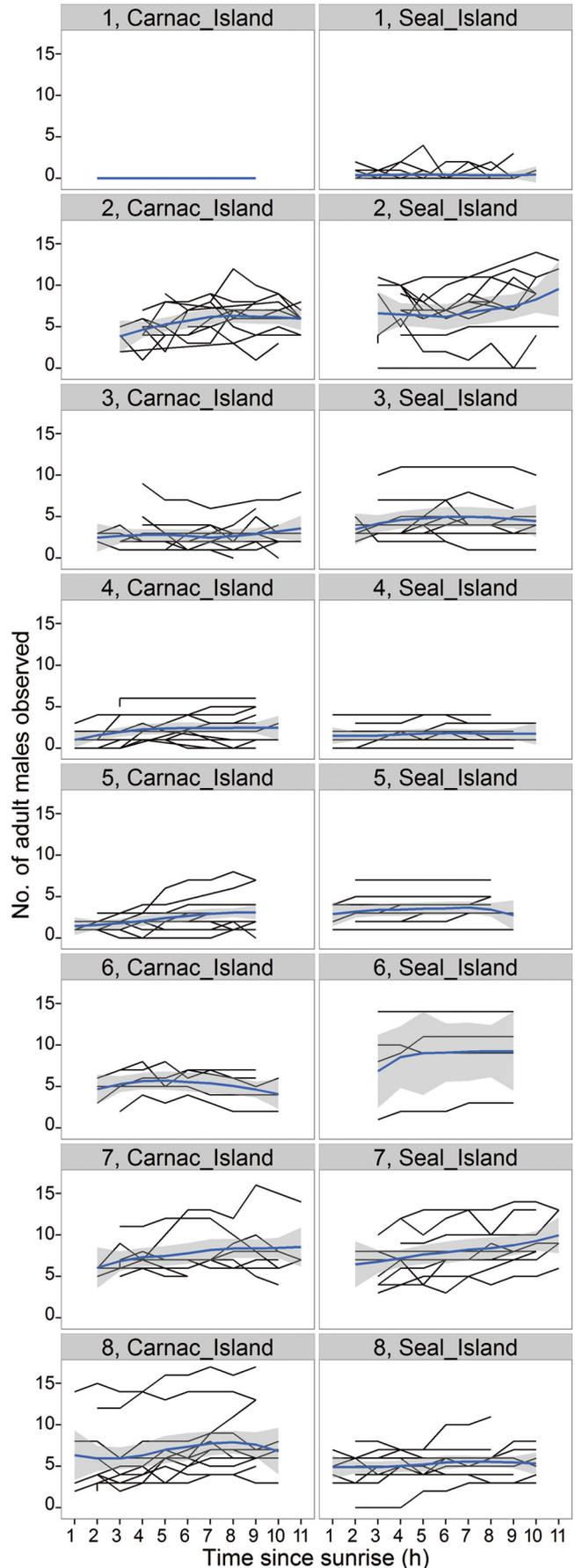
The numbers of hauled out *N. cinerea* at their peaks varied between peaks and islands; with greater numbers throughout all of the first peak and during part of the second peak at Seal Island than at Carnac Island. There are many possible reasons for these differences. While a larger beach size, potentially allowing more sea lions to haul out, has been suggested (Krieger & Barrette 1984), beach area available appeared to be unrelated in this study. The beach area on Carnac Island was estimated to be approximately 3 times larger than that at Seal Island. The intertidal region where animals hauled out at Carnac Island appeared to be equally as large as that on Seal Island. We suggest that other drivers, such as proximity to preferred foraging locations, influenced haul-out site choice. If there are shifting prey locations, we suggest that this may be reflected by changes in haul-out site selection. There is evidence of this behaviour in other pinnipeds, such as Steller sea lions *Eumetopias jubatus* in Alaska, suggested to depart to follow herring spawn and eulachon runs (Marcotte 2006), and Californian sea lions *Zalophus californianus* in California, responding to prey abundance (Ainley et al. 1982). Since breeding, and the resulting peak numbers in the Perth metropolitan area, follow a 17 to 18 mo cycle, successive peaks in the Perth area occur in different seasons. In this study, the first peak occurred in winter, and the second in summer. A seasonal change in targeted prey location is possible, and therefore a change in foraging location for the same prey or a change in target prey species in different seasons could be expected (Lowry et al. 1991, Sinclair & Zeppelin 2002, Sigler et

Fig. 6. Number of sub-adult male *Neophoca cinerea* observed during hourly counts on Carnac and Seal Islands during survey Periods 1 to 8. Each line represents counts conducted on a single sampling day represented in hours since sunrise. A LOESS smoother (blue line) with 95% confidence intervals (grey) has been added as a visual aid. (The 2 exceptionally high and low observation days on Carnac Island were excluded)

al. 2004, Womble et al. 2005, 2009, Winter et al. 2009). Such instances could have resulted in Carnac Island being relatively less favourable during the second peak than the first peak. A second plausible explanation is that the numbers using the islands are directly related to human use reflected by the differing management regulations at the 2 islands. Carnac Island has direct access for recreational use on most of the beach, and despite the presence of a sanctuary zone on a section of the beach, the entire beach is used for recreation. At Seal Island, recreational users are completely and effectively restricted from landing on any part of the island, including the beach.

In the present study, the percentage of adults to sub-adults increased at both islands from close to parity to above 90%, as the abundance of *N. cinerea* dropped from peak to trough in the cycle. A range of age class distributions have been observed among pinniped species at haul-out and breeding sites elsewhere. At a Steller sea lion (*E. jubatus*) breeding island in Southeast Alaska, for example, more bulls than sub-adults hauled out consistently across the survey period (Marcotte 2006). In contrast, sub-adult Subantarctic fur seals *Arctocephalus tropicalis* dominate during most of the year at a haul-out site where no breeding occurs as well as at a breeding site on the same island during the non-breeding season (at Marion Island, close to the Antarctic Convergence; Kerley 1983). Results that are more similar to those in this study were observed for *A. tropicalis*, with a sub-adult to adult ratio of approximately 5 to 3 at a haul-out site with occasional breeding on Amsterdam Island (6% females, Roux & Hes 1984). In the current study, the changes in the composition of different age classes were consistent between the 2 islands and appeared to follow the timing of the breeding season. It is not known if age classes depart at different times from the breeding sites in this species; however, staggered departures have been observed between females and pups in *E. jubatus* (Marcotte 2006). We suggest that observations here are likely a result of the following premise: as young males grow older, they increasingly travel longer distances and stay away for longer periods (Goldsworthy et al. 2009).

Fig. 7. Number of adult male *Neophoca cinerea* observed during hourly counts on Carnac and Seal Islands during survey Periods 1 to 8. Each line represents counts conducted on a single sampling day represented in hours since sunrise. A LOESS smoother (blue line) with 95% confidence intervals (grey) has been added as a visual aid. (The 2 exceptionally high and low observation days on Carnac Island were excluded)



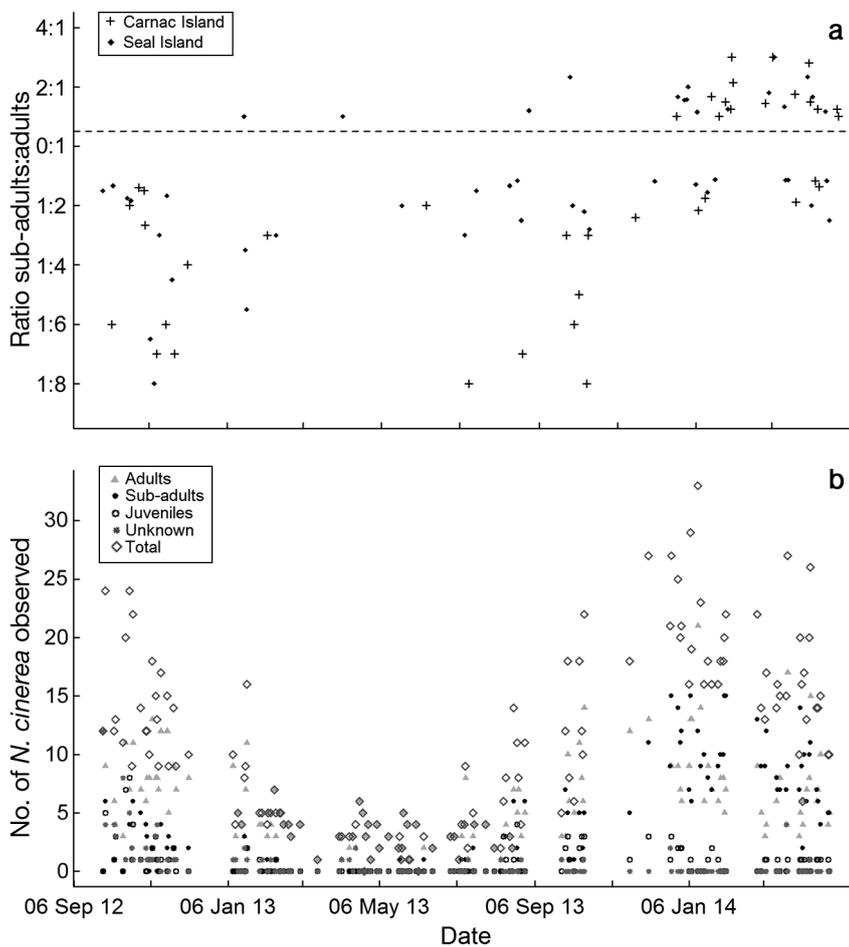


Fig. 8. Age classes of *Neophoca cinerea* observed at the time of maximum count on 166 days on Carnac and Seal Island between September 2012 and April 2014 (after the first non-breeding season, i.e. high numbers in Perth). (a) Ratio of sub-adults to adults on Carnac (black crosses) and Seal (diamonds) Islands. The dashed horizontal line marks the ratio of sub-adults to adults at 1:1. Three data points are missing due to zero sub-adults or adults present, and no ratio could be calculated. (b) Number of *N. cinerea* observed in each age classes: (grey triangles) adults; (black, solid circles) sub-adults; (white-filled circles) juveniles; (black asterisks) unknown

Day-to-day haul-out numbers of *N. cinerea* on Seal and Carnac Islands often fluctuated considerably, similar to South American *Otaria flavescens*, *E. jubatus* and Hooker's *Phocarctos hookeri* sea lions (Beentjes 1989, Rosas et al. 1994, Kucey 2005). The positive relationship between numbers of hauled out *N. cinerea* and time since sunrise each day, observed during periods of high numbers of *N. cinerea* in the study area, is not uncommon. Hooker's sea lions *P. hookeri* on the Otago Peninsula in New Zealand were found to increasingly arrive ashore mid-morning, with numbers reaching a plateau at midday before departing again around 18:00 h (Beentjes 1989). Similarly, studies of other otariids, of varying sex and age class, have

also shown a pattern of increasing numbers hauling out throughout the day, until mid-afternoon or early evening, when these numbers began to decrease (Stirling 1968, Harestad 1978, Ainley et al. 1982, Sepúlveda et al. 2001, 2012). On Carnac Island, this pattern was less prominent, and only occurred significantly during the second non-breeding season, where there were overall greater numbers of animals hauling out.

During a study of *N. cinerea* at Dangerous Reef in South Australia, animals mostly arrived and hauled out between 05:00 and 07:00 h, and departed between 18:00 and 20:00 h to forage mainly at night (Goldsworthy et al. 2009). The study, however, was on lactating adult females, rather than males. While there are variations in behaviour among species, there are also variations within different populations of the same species. This has been shown to be true for Steller sea lions *E. jubatus* which displayed no evidence of a diurnal pattern in hauling out at one site (Kucey 2005, Marcotte 2006), while Harestad (1978) indicated a clear diurnal pattern, dissimilar from the Perth findings, at another. Furthermore, *N. cinerea* in this study represent a unique cohort of juvenile, sub-adult, and adult males, reflecting the unique haul-out patterns observed. Adult male *N. cinerea* are known to forage further offshore, spend longer periods at sea, and have higher variations among individuals in

distances travelled than other age and sex classes (Goldsworthy et al. 2009). The large number of adult males at Carnac and Seal Islands likely influenced the arrival times, as *N. cinerea* travelling longer distances may return later in the day. Conversely, juvenile foraging behaviour is reportedly similar to the more restricted ranges of adult females, compared to the more distant and longer duration foraging by adult males (Goldsworthy et al. 2009). The low numbers of juveniles counted on Seal and Carnac Islands suggests that daily patterns in behaviour would be mostly due to sub-adults and bulls using the islands.

While the present study showed similarities and contrasts to findings elsewhere, studies referred to

here have reported haul-out timing in relation to local time rather than relative to the time of sunrise (e.g. Stirling 1968, Sepúlveda et al. 2001, Carlens et al. 2006). We suggest that by reporting haul-out patterns relative to sunrise and sunset rather than relative to GMT, studies will be more comparable and meaningful in terms of their biological significance. Circadian rhythms of wild animals are more closely related to daily solar patterns and seasonal changes than our clocks (Reebs 2002, McCauley 2012). Also, we note, that in this study, logistical constraints limited observations to before 07:00 h and after 17:00 h. It is possible that numbers at Seal and Carnac Island decrease at dusk or later, as has been observed for *N. cinerea* in South Australia (Goldsworthy et al. 2009). *P. hookeri* and *O. flavescens* have also been reported to depart haul-out islands in the evening, likely to forage (Beentjes 1989, Sepúlveda et al. 2001, 2012). Alternatively, numbers present at Seal and Carnac Islands later in the day after observations had been made could have remained constant if diurnal foraging patterns are absent, such as reported by Costa & Gales (2003) for female *N. cinerea* on Kangaroo Island, South Australia. The few counts conducted in this study before 07:00 h did not indicate a spike in numbers of *N. cinerea* returning ashore just after sunrise as reported by Goldsworthy et al. (2009).

During the breeding season, when overall numbers of *N. cinerea* were low, there was no distinguishable diurnal pattern. This was likely due to either too few numbers of *N. cinerea* present to detect a relatively small effect, or highly variable foraging patterns (and thus arrival times) of adult males.

In our study, numbers of *N. cinerea* hauled out increased with increasing temperature up to 21°C. This association has also been observed in harbour seals *Phoca vitulina* and Weddell seals *Leptonychotes weddellii* (Watts 1992, 1996, Andrews-Goff et al. 2010). In winter months, the local waters around Perth can drop to below 16°C (BOM). Immersion in water below 17°C is energetically costly and may stop cell growth in Steller sea lions (Feltz & Fay 1966). Thus, for winter months, temperature could be expected to be a contributing factor to haul-out patterns as it benefits cell growth and recovery. Hauling out also conserves energy, reducing heat loss by spending less time in a high temperature-conducting medium, such as water (Riedman 1990). When temperature on land increases, however, pinnipeds may return to water to support thermoregulation, which may explain why there were no further increases in association beyond 21°C. However, the effect of temperature on seals' diurnal haul-

out patterns has also been observed to vary at different times of the year in *P. vitulina* in Scotland and in captive harp seals *Pagophilus groenlandicus* (Grellier et al. 1996, Watts 1996, Moulton et al. 2000).

N. cinerea decreased in numbers in the present study when tidal height increased. While this pattern was similar to that reported for Steller sea lions *E. jubatus* on islands off Alaska, tide level did not have a significant influence at other locations in Alaska (Kastelein & Weltz 1991, Kucey 2005). Tidal heights have been reported to have variable effects in different seasons in *P. vitulina* (Reder et al. 2003), and other pinnipeds, regardless of season (Thompson et al. 1989). In *E. jubatus*, more adult males entered the water during low tides, despite the tide level having little to no impact on their preferred haul-out location (Kastelein & Weltz 1991). The variation observed in other studies is comparable to that seen in *N. cinerea* in the present study, where tide level was more influential on Seal Island than on Carnac Island. While Seal Island was, overall, a preferred site over the larger beach of Carnac Island, the decrease in the number of *N. cinerea* hauling out became more prominent when tidal heights were above 1.0 m. This increase in tide would have greater impact on available intertidal and overall beach area on Seal Island than Carnac Island because of the wider beach on Carnac Island. Variation in tidal heights in this study was small compared to the 4 m tidal heights that impact some *P. vitulina* haul-out sites. Where higher proportions of *N. cinerea* haul out and tides above 4 m constrain the available size of the haul-out sites, numbers hauled out reduce (Watts 1993). Extremely high tides, combined with strong winds, can push the water over the whole beach on Seal Island; however, a large proportion of the beach on Seal Island does not appear to be impacted during typical high tides, suggesting that the association between tidal height and numbers hauled out may not be simplistic. It is not only beach availability that is affected by lunar variation, however. Localised movement of fish species in relation to tides and lunar phase have been documented in the Perth metropolitan area (Wakefield 2010), which may also be true for prey species of *N. cinerea*. Some prey species may be influenced by tide and may become easier to target during low tide (Morrison et al. 2002, Ribeiro et al. 2006), implying that *N. cinerea* might follow their food source during a time when it is easier to catch, leaving lower numbers on the haul-out islands during lower tidal heights.

Wind speed did not have a significant effect on the numbers of *N. cinerea* hauling out in this study, similar to the case for *P. vitulina* in Scotland and

Norway (Grellier et al. 1996, Reder et al. 2003), although it has been observed to affect diurnal haul-out patterns of other pinniped species (e.g. Lake et al. 1997, Sato et al. 2003). One sampling day on Carnac Island was removed from the analysis because of the unusually low number (zero) of *N. cinerea* hauling out during the peak season. Within 3 d prior to this count, a storm including time-averaged winds of up to 54 km h⁻¹ and heavy rains with up to 10.2 mm d⁻¹ precipitation passed Carnac Island and may have affected the *N. cinerea* haul-out pattern. Extreme environmental conditions have been shown to alter sea lion behaviour, for example in *E. jubatus* during stormy weather (Kenyon & Rice 1961) or *O. flavescens* after an earthquake and tsunami (Sepúlveda et al. 2012).

Finally, different methods of sampling can often bias count data. It is unlikely that the different sampling methods used here would have caused significant variations in count numbers in this type of study (Balouin et al. 2014). Salgado Kent & Crabtree (2008) have previously shown that the remotely controlled camera on Carnac Island does not produce significantly different counts to those made by an observer on the island. Though considered infrequent, individuals may have remained undetected during the few surveys when counts were conducted from the vantage point at Shoalwater. On 1 occasion, rangers aboard a DPaW vessel, near Seal Island, conducted a count on Seal Island at the same time as counts were conducted from the Shoalwater vantage point. The authors observed 19 of the 21 observed from the vessel. Two were hidden from view from the vantage point.

While sub-models resulting in the same significant explanatory variables provided confidence in the final model selected, none of the sub-models accounted for absolutely all of the autocorrelation in the residuals. A smoother through numbers of *N. cinerea* observed versus normalised residuals still explained approximately 7.6% of the variation remaining in the residuals. Nevertheless, despite modelling constraints and convergence problems experienced in modelling these complex, longitudinal data, the models provided an improvement in our current knowledge of *N. cinerea*, which is needed for management and conservation.

The variability in numbers of *N. cinerea* hauling out at Carnac and Seal Islands within a day can affect the accuracy of trend in relative abundance over time if counts are undertaken at different times each day. For monitoring trends in relative abundance, counts would be best conducted between 9 and 11 h after sunrise if this is logistically possible. If this is not pos-

sible, a similar time of day across all survey days (in relation to the time of sunrise) should be targeted, so that they are comparable between sites and years. Conducting surveys only during periods of comparable temperature and tidal conditions, in addition to comparable times, would be logistically highly restrictive, resulting in a very small sample size. We have therefore suggested maintaining consistency in the most influential variable, the time of day. However, temperature and tidal heights can be recorded so that relative abundance can be adjusted using a correction factor to improve comparability over time (Seber 1986, Huber et al. 2001). Through the systematic collection of count data during periods when haul-out behaviour is expected to be comparable, more accurate trend estimations can be obtained to improve management outcomes.

Acknowledgements. This project was made possible with the significant support provided by the Department of Parks and Wildlife (Western Australia) who made the spotting scope available to use, provided substantial logistical support to and from islands, as well as local and scientific knowledge. The Department of Fisheries and Cockburn Volunteer Sea Search and Rescue also contributed transports to and from islands. The project was also supported by Malcom Perry through maintenance of the research vessel, and the Fremantle Sailing Club who provided access to their boat ramp. Mike Todd lent us his telescope. Many volunteers have allocated substantial time in assistance in the field and data entry. We are grateful to Sven Gestauer for helping with the R coding and to Alain Zuur who gave useful advice concerning initial models. Miles Parsons provided comments on multiple drafts of the manuscript, which significantly improved its quality. Finally, this project was supported by funding from the Holsworth Grant, and was conducted under a Department of Parks and Wildlife permit (number SF009371) and university animal ethics approvals (AEETH24/11 granted by Victoria University, Melbourne and AEC_2013_32 granted by Curtin University, Perth).

LITERATURE CITED

- Ainley DG, Huber HR, Bailey KM (1982) Population fluctuations of California sea lions and the Pacific whiting fishery off central California. *Fish Bull* 80:253–258
- Andrews-Goff V, Hindell MA, Field IC, Wheatley KE, Charassin JB (2010) Factors influencing the winter haulout behaviour of Weddell seals: consequences for satellite telemetry. *Endang Species Res* 10:83–92
- Arnould JPY, Hindell MA (2001) Dive behaviour, foraging locations, and maternal attendance patterns of Australian fur seals (*Arctocephalus pusillus doriferus*). *Can J Zool* 79:35–48
- Balouin Y, Rey-Valette H, Picand PA (2014) Automatic assessment and analysis of beach attendance using video images at the Lido of Sète beach, France. *Ocean Coast Manage* 102:114–122
- Beentjes MP (1989) Haul-out patterns, site fidelity and

- activity budgets of male Hooker's sea lions (*Phocarctos hookeri*) on the New Zealand mainland. *Mar Mamm Sci* 5:281–297
- Bengtson JL, Cameron MF (2004) Seasonal haulout patterns of crabeater seals (*Lobodon carcinophaga*). *Polar Biol* 27: 344–349
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY
- Carlens H, Lydersen C, Krafft BA, Kovacs KM (2006) Spring haul-out behavior of ringed seals (*Pusa hispida*) in Kongsfjorden, Svalbard. *Mar Mamm Sci* 22:379–393
- Cassini MH, Szteren D, Fernández-Juricic E (2004) Fence effects on the behavioural responses of South American fur seals to tourist approaches. *J Ethol* 22:127–133
- Chilvers BL, Wilkinson IS, Duignan PJ, Gemmill NJ (2005) Summer foraging areas for lactating New Zealand sea lions *Phocarctos hookeri*. *Mar Ecol Prog Ser* 304:235–247
- Costa DP, Gales NJ (2003) Energetics of a benthic diver: Seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecol Monogr* 73:27–43
- Cunningham L, Baxter JM, Boyd IL, Duck CD, Lonergan M, Boss SE, McConnell B (2009) Harbour seal movements and haul-out patterns: implications for monitoring and management. *Aquat Conserv* 19:398–407
- de Valpine P (2014) The common sense of *P* values. *Ecology* 95:617–621
- Department of Conservation and Land Management (CALM) (2003) Carnac Island Nature Reserve, Management Plan 2003. Department of Conservation and Land Management, Perth
- Department of Environment and Conservation (DEC) (2007) Shoalwater Islands Marine Park Management Plan 2007–2017. Department of Parks and Wildlife, Perth
- DEC, Fisheries (2011) Shoalwater Islands Marine Park. Marine parks. WA's submerged wonders. Recreation guide. Department of Environment and Conservation, Department of Fisheries, Perth
- Feltz ET, Fay FH (1966) Thermal requirements *in vitro* of epidermal cells from seals. *Cryobiology* 3:261–264
- Flom PL, Cassell DL (2007) Stopping stepwise: Why stepwise and similar selection methods are bad, and what you should use. NorthEast SAS Users Group 20th Annual Conference, 11–14 November 2007, Baltimore, MD
- Gales NJ (1995) Hooker's sea lion recovery plan (*Phocarctos hookeri*). Threatened species recovery plan series no. 17. Threatened Species Unit, Department of Conservation, Wellington
- Gales NJ, Cheal AJ, Pobar GJ, Williamson P (1992) Breeding biology and movements of Australian sea lions, *Neophoca cinerea*, off the west coast of Western Australia. *Wildl Res* 19:405–416
- Gales NJ, Shaughnessy PD, Dennis TE (1994) Distribution, abundance and breeding cycle of the Australian sea lion *Neophoca cinerea* (Mammalia: Pinnipedia). *J Zool (Lond)* 234:353–379
- Goldsworthy SD (2015) *Neophoca cinerea*. The IUCN Red List of Threatened Species Version 2015.2. www.iucnredlist.org (accessed 5 August 2015)
- Goldsworthy SD, Shaughnessy PD, McIntosh RR, Kennedy C, Simpson J, Page B (2008) Australian sea lion populations at Seal Bay and the Seal Slide (Kangaroo Island): continuation of the monitoring program. South Australian Research and Development Institute, Government of South Australia, Adelaide
- Goldsworthy SD, Page B, Shaughnessy PD, Hamer D and others (2009) Innovative solutions for aquaculture planning and management: addressing seal interactions in the finfish aquaculture industry. South Australian Research and Development Institute, Adelaide
- Grellier K, Thompson PM, Corpe HM (1996) The effect of weather conditions on harbour seal (*Phoca vitulina*) haulout behaviour in the Moray Firth, northeast Scotland. *Can J Zool* 74:1806–1811
- Hammerschlag N, Martin RA, Fallows C (2006) Effects of environmental conditions on predator-prey interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) at Seal Island, South Africa. *Environ Biol Fishes* 76:341–350
- Harestad AS (1978) Diurnal activity of Northern sea lions, *Eumetopias jubatus* (Schreber). *Syesis* 11:279–280
- Harrell FE Jr (2001) Regression modeling strategies. Springer, New York, NY
- Higgins LV (1993) The nonannual, nonseasonal breeding cycle of the Australian sea lion, *Neophoca cinerea*. *J Mammal* 74:270–274
- Huber HR, Jeffries SJ, Brown RF, DeLong RL, Vanblaricom G (2001) Correcting aerial survey counts of harbor seals (*Phoca vitulina richardsi*) in Washington and Oregon. *Mar Mamm Sci* 17:276–293
- Jefferson TA, Webber MA, Pitman RL (2011) Marine mammals of the world: a comprehensive guide to their identification. Academic Press, London
- Kastelein RA, Weltz FC (1991) Distribution and behaviour of Steller sea lions (*Eumetopias jubatus*) in Prince William Sound, Alaska, June 1989. *Aquat Mamm* 17:91–97
- Kenyon KW, Rice DW (1961) Abundance and distribution of the Steller sea lion. *J Mammal* 42:223–234
- Kerley GIH (1983) Comparison of seasonal haul-out patterns of fur seals *Arctocephalus tropicalis* and *A. gazella* on Subantarctic Marion Island. *S Afr J Wildl Res* 13:71–77
- Krieger M, Barrette C (1984) Aggregation behaviour of harbour seals at Forillon National Park, Canada. *J Anim Ecol* 53:913–928
- Kucey L (2005) Human disturbance and the hauling out behaviour of Steller sea lions (*Eumetopias jubatus*). MSc thesis, University of British Columbia, Vancouver
- Lake SE, Burton HR, Hindell MA (1997) Influence of time of day and month on Weddell seal haul-out patterns at the Vestfold Hills, Antarctica. *Polar Biol* 18:319–324
- LeBoeuf BJ, Riedman M, Keyes RS (1982) White shark predation on pinnipeds in California coastal waters. *Fish Bull* 80:891–895
- Ling JG, Walker GE (1978) An 18-month breeding cycle in the Australian sea lion? *Search* 9:464–465
- Ling JK, Button CE, Ebsary BA (1974) A preliminary account of grey seals and harbor seals at Saint-Pierre and Miquelon. *Can Field-Nat* 88:461–468
- London JM, Ver Hoef JM, Jeffries SJ, Lance MM, Boveng PL (2012) Haul-out behavior of harbor seals (*Phoca vitulina*) in Hood Canal, Washington. *PLoS ONE* 7:e38180
- Lovasz T, Croft DB, Banks P (2008) Establishing tourism guidelines for viewing Australian sea lions *Neophoca cinerea* at Seal Bay Conservation Park, South Australia. In: Lunney D, Munn A, Meikle M (eds) Too close for comfort: contentious issues in human-wildlife encounters. Royal Zoological Society of New South Wales, Mosman, p 225–232
- Lowry MS, Stewart BS, Heath CB, Yochem PK, Francis JM (1991) Seasonal and annual variability in the diet of Cal-

- ifornia sea lions *Zalophus californianus* at San Nicolas Island, California, 1981–86. *Fish Bull* 89:331–336
- Marcotte M (2006) Steller watch: timing of weaning and seasonal patterns in numbers and activities of Steller sea lions (*Eumetopias jubatus*) at a year-round haulout site in southeast Alaska. MSc thesis, University of British Columbia, Vancouver
- Marlow BJ (1975) The comparative behaviour of the Australasian sea lions, *Neophoca cinerea* and *Phocarcctos hookeri* (Pinnipedia: Otariidae). *Mammalia* 39:159–230
- McCauley RD (2012) Fish choruses from the Kimberley, seasonal and lunar links as determined by long term sea noise monitoring. Acoustics, Development and the Environment, 21–23 November 2012, Fremantle, Australian Acoustical Society. *Proc Acoustics* 2012:441–446
- Mogren HG, Lindstrøm U, Nilssen KT, Haug T (2010) Haulout behaviour of harbour seals (*Phoca vitulina*) during breeding and moult in Vesterålen, Norway. *NAMMCO Sci Publ* 8:303–312
- Morrison MA, Francis MP, Hartill BW, Parkinson DM (2002) Diurnal and tidal variation in the abundance of the fish fauna of a temperate tidal mudflat. *Estuar Coast Shelf Sci* 54:793–807
- Moulton VD, Miller EH, Ochoa-Acuña H (2000) Haulout behaviour of captive harp seals (*Pagophilus groenlandicus*): incidence, seasonality, and relationships to weather. *Appl Anim Behav Sci* 65:367–378
- Pauli BD, Terhune JM (1987a) Meteorological influences on harbour seal haul-out. *Aquat Mamm* 13:114–118
- Pauli BD, Terhune JM (1987b) Tidal and temporal interaction on harbour seal haul-out patterns. *Aquat Mamm* 13:93–95
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer, New York, NY
- R Development Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Reder S, Lydersen C, Arnold W, Kovacs KM (2003) Haulout behaviour of High Arctic harbour seals (*Phoca vitulina vitulina*) in Svalbard, Norway. *Polar Biol* 27:6–16
- Reeb SG (2002) Plasticity of diel and circadian activity rhythms in fishes. *Rev Fish Biol Fish* 12:349–371
- Ribeiro J, Bentes L, Coelho R, Gonçalves JMS (2006) Seasonal, tidal and diurnal changes in fish assemblages in the Ria Formosa lagoon (Portugal). *Estuar Coast Shelf Sci* 67:461–474
- Riedman M (1990) The pinnipeds: seals, sea lions, and walrus. University of California Press, Berkeley, CA
- Rosas FCW, Pinedo MC, Marmontel M, Haimovici M (1994) Seasonal movements of the South American sea lion (*Otaria flavescens*, Shaw) off the Rio Grande do Sul coast, Brazil. *Mammalia* 58:51–60
- Roux JP, Hes AD (1984) The seasonal haul-out cycle of the fur seal *Arctocephalus tropicalis* (Gray, 1872) on Amsterdam Island. *Mammalia* 48:377–389
- Salgado Kent CP, Crabtree B (2008) The effectiveness of an established sanctuary zone for reducing human disturbance to Australian sea lions (*Neophoca cinerea*) at Carnac Island, Western Australia. *Tourism Mar Environ* 5:29–42
- Sato K, Tsuchiya Y, Kudoh S, Naito Y (2003) Meteorological factors affecting the number of Weddell seals hauling-out on the ice during the molting season at Syowa Station, East Antarctica. *Polar Biosci* 16:98–103
- Schneider DC, Payne PM (1983) Factors affecting haul-out of harbor seals at a site in southeastern Massachusetts. *J Mammal* 64:518–520
- Seber GAF (1986) A review of estimating animal abundance. *Biometrics* 42:267–292
- Sepúlveda M, Oliva DP, Palma FJ (2001) Daily and annual circarhythms activity in the South American sea lion *Otaria flavescens* (Carnivora: Otariidae) at the central zone of Chile. *Rev Biol Mar Oceanogr* 36:181–187
- Sepúlveda M, Quiñones RA, Carrasco P, Álvarez-Pérez MJ (2012) Daily and seasonal variation in the haul-out behavior of the South American sea lion. *Mamm Biol* 77:288–292
- Sigler MF, Womble JN, Vollenweider JJ (2004) Availability to Steller sea lions (*Eumetopias jubatus*) of a seasonal prey resource: a prespawning aggregation of eulachon (*Thaleichthys pacificus*). *Can J Fish Aquat Sci* 61:1475–1484
- Sinclair EH, Zeppelin TK (2002) Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). *J Mammal* 83:973–990
- Southwell C (2003) Haul-out behaviour of two Ross seals off eastern Antarctica. *Antarct Sci* 15:257–258
- Southwell C (2005) Optimising the timing of visual surveys of crabeater seal abundance: haulout behaviour as a consideration. *Wildl Res* 32:333–338
- Stirling I (1968) Diurnal movements of the New Zealand fur seal at Kaikoura. *NZ J Mar Fresh* 2:375–377
- Thompson PM, Fedak MA, McConnell BJ, Nicholas KS (1989) Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). *J Appl Ecol* 26:521–535
- Udevitz MS, Jay CV, Cody MB (2005) Observer variability in pinniped counts: ground-based enumeration of walrus at haul-out sites. *Mar Mamm Sci* 21:108–120
- Wakefield CB (2010) Annual, lunar and diel reproductive periodicity of a spawning aggregation of snapper *Pagrus auratus* (Sparidae) in a marine embayment on the lower west coast of Australia. *J Fish Biol* 77:1359–1378
- Watts P (1992) Thermal constraints on hauling out by harbour seals (*Phoca vitulina*). *Can J Zool* 70:553–560
- Watts P (1993) Possible lunar influence on hauling-out behavior by the Pacific harbour seal (*Phoca vitulina richardsi*). *Mar Mamm Sci* 9:68–73
- 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
- Winter A, Foy RJ, Wynne K (2009) Seasonal differences in prey availability around a Steller sea lion haulout and rookery in the Gulf of Alaska. *Aquat Mamm* 35:145–162
- Womble JN, Willson MF, Sigler MF, Kelly BP, VanBlaricom GR (2005) Distribution of Steller sea lions *Eumetopias jubatus* in relation to spring-spawning fish in SE Alaska. *Mar Ecol Prog Ser* 294:271–282
- Womble JN, Sigler MF, Willson MF (2009) Linking seasonal distribution patterns with prey availability in a central-place forager, the Steller sea lion. *J Biogeogr* 36:439–451
- Wood SM (2006) Generalized additive models: an introduction with R. Chapman and Hall/CRC, Boca Raton, FL
- Zuur AF, Ieno EN, Smith GM (2007) Analysing ecological data. Springer, New York, NY
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY