Sex differences in diving at multiple temporal scales in a size-dimorphic capital breeder

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Summary

1. Air-breathing marine predators can modify their diving behaviour to accommodate different patterns of prey abundance and distribution and may do so at multiple temporal scales (individual dives, bouts of dives and foraging trips).

2. The grey seal, *Halichoerus grypus*, is a size-dimorphic, capital breeding species in which sex differences in foraging ecology have previously been found at the scale of individual dives. In this study, diving behaviour of male and female adult grey seals was examined at the temporal scales of dive bouts (41 males/46 females) and foraging trips (7 males/9 females) during the 8-month prebreeding foraging period between 1992 and 1999 to investigate whether sex differences were evident at longer temporal scales.

3. Foraging trip duration did not differ between males and females. However, females (the smaller sex) spent significantly more time diving and less time hauled-out on land between trips than males. This suggests that females are more selective than males when searching for prey. These differences are consistent with the effects of body-size dimorphism on diving behaviour.

4. Virtually all dives occurred in bouts. At this scale, males and females showed significantly different seasonal patterns of most bout characteristics, including bout duration, percentage of bout spent at depth and effort (hours spent in bouts day^{-1}).

5. Grey seals used four different types of bouts, differing in duration, depth, percentage bout spent at depth and the shape of individual dives within the bout. Males and females differed in the proportion of each bout type used and in the seasonal and day–night distribution of bout types.

6. Few bout characteristics varied significantly among years, despite interannual variation in prey abundance. Where interannual differences did occur, both sexes behaved in a similar way.

7. Different seasonal patterns in bouts of diving by males and females could not be accounted for by body-size dimorphism or niche divergence, but were consistent with the hypothesis that females must recover condition earlier in the year than males to support the energetic costs of reproduction.

Key-words: bouts, foraging trips, grey seals, seasonal patterns.

Introduction

To understand the ecology of apex predators in marine ecosystems, information is needed on the scales at which individuals forage. Environmental variation at different temporal and spatial scales may affect the foraging success, survival and reproductive success of individuals and thus defines evolutionary selection pressures (e.g. Whitehead 1996). In addition to characteristics of their prey (i.e. patchiness, abundance and predictability), the foraging decisions of animals are influenced by their current physical state, the risk of predation and reproductive status (Schoener 1971; Orians & Pearson 1979; Abram 1991). As a result, predators are expected to make foraging decisions at varying

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spatial and temporal scales to maximize fitness (Clutton-Brock, Guinness & Albon 1982; Allan & Hoekstra 1992). Large-bodied, long-lived species with low reproductive rates, such as marine mammals, must therefore have evolved adaptations that enable them to deal with environmental variability over a variety of temporal scales (Whitehead 1996).

There are basically three ways to study how air-breathing aquatic predators (marine mammals, seabirds and reptiles) make foraging decisions: by studying predator behaviour relative to prey abundance and distribution, by determining what the behaviour of the predator indicates about the abundance and distribution of prey, or by examining individual behavioural patterns and interpreting them relative to each other (this study). The first approach is still not practical in many cases because we are unable to sample prey in the ocean at scales that are likely relevant to the predator. However, the other two approaches have been useful in understanding the foraging ecology of these taxa (e.g. Boyd 1996; Springer, Platt & VanViet 1996).

Individuals can modify their diving behaviour to accommodate different patterns of prey abundance and distribution and may do so at multiple temporal scales (i.e. individual dives, the number and characteristics of repeated dives within a bout of diving, the organization of bouts in time). In the case of pinnipeds and seabirds, these behaviours are nested within trips to sea and might vary seasonally and interannually. Within foraging trips, pinnipeds and seabird species usually cluster individual dives into bouts of activity (e.g. Watanuki *et al.* 1993; Boness, Bowen & Oftedal 1994; Boyd *et al.* 1994). Animals should organize their behaviour for optimal patch use, subject to the constraints of other vital activities. This means that divers must optimize both the time budget of individual dives and the number of dives within a bout. Recent theoretical and empirical studies suggest that characteristics of bouts of dives may provide insight into how predators forage that is not captured at the level of individual dives (Boyd *et al.* 1994; Mori 1998).

In otariid pinnipeds and seabirds, it is reasonably assumed that dive bouts represent periods of foraging and that the duration of a bout, as well as other characteristics, reflects the quality and size of a prey patch (Feldkamp, DeLong & Antonelis 1989; Boyd 1996). This is because these predators are known to swim at the surface between bouts of diving or fly between foraging locations. Thus, bouts probably represent a more informative unit of behaviour with which to examine foraging than do individual dives. Although it is clear that many phocid pinniped species also organize their diving behaviour into bouts (Nordoy, Folkow & Blix 1995; Kelly & Wartzok 1996), telemetry data have shown that phocid seals do not travel at the surface to any significant degree (Thompson *et al.* 1991; Le Boeuf *et al.* 2000). Therefore, unlike otariids and seabirds, bouts of diving in phocids are used both to forage and travel (Thompson et al. 1991; Asaga, Leboeuf &

Sakurai 1994; Schreer & Testa 1996). Nevertheless, we expect that the temporal pattern and characteristics of bouts should provide insight into how these animals forage, since much of diving behaviour is necessarily associated with foraging.

In birds and mammals, the differing roles of males and females during reproduction often lead to sex differences in foraging behaviour and diet during the breeding season (Williamson 1971; Petit *et al.* 1990). However, the extent to which sex differences in foraging behaviour persist outside the breeding season has received less attention (e.g. ungulates – Barboza & Bowyer 2000; elephant seals – Le Boeuf *et al.* 2000). Foraging behaviour during the non-breeding period should have particularly important consequences on the fitness of capital breeders since little or no foraging occurs during the breeding season. Thus, the energy needed for successful reproduction must be stored prior to the period of expenditure. Shortfalls in stored energy may negatively affect fitness either through direct effects on adults or indirectly through effects on offspring (White, Rowell & Hauer 1997).

In this study, we examined how adult male and female grey seals, *Halichoerus grypus* (Family Phocidae), organize bouts of diving behaviour during the 8-month foraging period prior to breeding. The grey seal is a polygynous, size-dimorphic species, with adult males being approximately 1·5 times heavier than adult females in the north-west Atlantic population (Beck 2002). Females are capital breeders, using stored body energy accumulated over the previous 8-month period to support the high energetic cost of lactation and their own metabolic expenditures during the breeding season. Females with low body mass (and hence energy stores) at parturition tend to wean smaller pups (Iverson *et al.* 1993; Mellish, Iverson & Bowen 1999; Pomeroy *et al.* 1999), increasing the probability of juvenile mortality (Coulson 1960; Coulson & Hickling 1964; Hall, McConnell & Baker 2001). Male grey seals use a variety of mating strategies (e.g. tenure on land, alternating short foraging trips with mate acquisition on land; Boness & James 1979; Lidgard, Boness & Bowen 2001) but rely on energy stores accumulated prior to breeding to compete for and acquire mates. As a result males may also be considered capital breeders. Godsell (1991) and Lidgard *et al.* (2001) found that for adult male grey seals on Sable Island, the correlation between body mass at the start of the breeding season and mating success is weak, although this does not appear to be the case in all colonies of grey seals (Anderson & Fedak 1985). This suggests that in the north-west Atlantic population, the reproductive success of males may be less dependent than that of females on the amount of stored body energy at the beginning of the breeding season.

Three non-mutually exclusive hypotheses have been advanced to explain sex differences in foraging behaviour outside the breeding season. The size-dimorphism hypothesis predicts sex differences in foraging due to

the larger sex requiring more energy per unit time than the smaller sex to meet energy requirements (Klieber 1961). This may result in the larger sex consuming greater quantities of the same prey, consuming different prey types or foraging more efficiently (e.g. African elephants, *Loxodonta africana*, Stokke & du Toit 2000; red deer, *Cervus slsphas*, Clutton-Brock, Guinness & Albon 1983; northern elephant seals, *Mirounga angustirostris*, Le Boeuf *et al*. 2000). In the case of grey seals, where males are larger than females, we might expect males to exhibit greater foraging effort than females, and therefore different bout characteristics, simply because they require more food. The niche-divergence hypothesis (Schoener 1969; Hughes 1980) predicts that sex differences in foraging result from natural selection for different resource use such that intraspecific competition between males and females is reduced (e.g. downy woodpecker, *Picoides pubescens*, Williams 1980; northern elephant seals, Leboeuf *et al*. 2000). If this applies to grey seals, we might expect males and females to use different habitats, which might be reflected in the depth of bouts, as grey seals are known to forage at the sea bottom (Thompson *et al*. 1991). Finally, the fitness-maximizing hypothesis predicts sex differences in foraging ecology because males and females differ in the way foraging is balanced with other activities to maximize reproductive success (e.g. isopod, *Idotea baltica*, Merilaita & Jormalainen 2000; Jormalainen *et al*. 2001; guppies, *Poecilia reticulata*, Griffiths 1996). Under this hypothesis, we would expect sex-specific seasonal differences in grey seal foraging behaviour, as females must commit to reproduction earlier in the year than males owing to the dependence of successful pregnancy on body condition (Boyd 1984; Albon *et al*. 1986; Pitcher, Calkins & Pendleton 1998).

Adult male and female grey seals differ both in the characteristics and seasonal pattern of individual dives (Beck *et al*. 2003a). However, these differences could not be explained by the size dimorphism hypothesis alone. Rather they appeared better explained as sex-specific fitness-maximizing strategies to the trade-off between storing body energy for reproduction and the costs associated with the long-term storage of energy. By examining foraging behaviour at the longer temporal scales of bouts and foraging trips, we hoped to gain further insight into the sex differences in grey seal foraging behaviour and the causes underlying these differences. We used data collected using electronic time–depth recorders (TDRs) to study the diving behaviour of adult grey seals during the prebreeding period in each of 8 years.

Methods

The study was carried out between May 1992 and January 2000 on Sable Island (43°55′N, 60°00′W), a partially vegetated sandbar approximately 300 km south-east of Halifax, Nova Scotia, Canada. Animals congregate in large numbers on the island in May and June to moult, in late December and January to rear offspring and mate, and in smaller numbers throughout the year between foraging trips.

Known-age, adult grey seals (8–27 years) were captured on-shore following the spring moult (May and June) or in the autumn (late September and early October) using hand-held nets (Bowen, Oftedal & Boness 1992). Seals were weighed to the nearest 0·5 kg on Salter spring balances suspended from an aluminium tripod. Males and females were anaesthetized with an intramuscular injection of Telazol (equal parts of tiletamine and zolazepam) at an average dose of $0·45$ mg kg^{-1} body mass and $0·90$ mg kg^{-1} body mass, respectively (Bowen, Beck & Iverson 1999), to allow data loggers to be fastened to the animals and to take body measurements. Roughly equal numbers of males and females were instrumented in each year (Table 1).

To study diving behaviour, we used TDRs manufactured by Wildlife Computers (Redmond, Washington; models: Mk3e, Mk5, Mk6 and Mk7). TDRs were secured to netting, which was then attached to the pelage of the animal just posterior to the shoulders along the midline using 5-min epoxy. Instruments weighed between 65 and 300 g (< 0·3% of initial body

Table 1. Number of adult grey seals instrumented each year and had ≥ 3 months of diving data for seasonal and interannual analysis

Year	No. of animals instrumented		No. of animals used in seasonal analysis		No. of animals with data from October to December	
	Males	Females	Males	Females	Males	Females
1992	2	4	1	2	2*	1*
1993	4	6	4	5	3	3
1994	5	6	2	3	2*	1*
1995	7	12	6	8	6	8
1996	18	17	11	10	8	9
1997	13	12	6	7	6	7
1998	9	8	6	5	5	4
1999	8	9	5	6	4	6
Total	66	74	41	46	36	39

*Not included in analysis of interannual variation.

mass) depending on the model used. TDRs were programmed to sample depth every 20 s and a wet/dry sensor indicated when the animal was hauled out on land. Most instruments were duty-cycled to prolong the period of data collection. Given the duty cycle schedules used, between 33% and 100% of diving behaviour was sampled. Instruments were recovered the following January when animals returned to Sable Island for the breeding season. Between May 1992 and October 1999, 140 animals (66 males, 74 females) were fitted with TDRs (Table 1). Overall, 81·4% (58 males, 56 females) of these animals returned to Sable Island the following January

DIVE ANALYSIS

TDR data were processed using software supplied by the manufacturer (Wildlife Computers). Zero-offset correction software was used to correct for shifts in the calibration of the pressure transducer of the instrument over the period of data collection. Dive analysis software was then used to calculate a number of variables describing individual dives (see Boness *et al.* 1994 for details).

Transducer drift and sea surface conditions introduce noise in depth measurements that cannot be completely removed by the zero-offset correction program. Therefore, we excluded dives < 5 m in depth from the analysis. Dives of longer than 30 min were also excluded from analysis as visual inspection of these long dives indicated that they generally represented two dives that were not properly separated by the zero-offset correction software. These erroneous 'dives' accounted for < 0·05% of the total number of dives sampled.

DIVE BOUTS

Bouts were defined using a modification of an iterative statistical method presented in Boyd *et al.* (1994). We considered a bout to have started when three or more dives occurred within 35 min. This 35-minute start window allowed for three dive cycles to be completed based on the 80th percentile of dive duration and surface interval between dives for this species (Beck 2002). Once a bout had begun, subsequent dives were added to the bout if the next surface interval was not significantly greater than the mean of the previous surface intervals within the bout (*t*-test, $P > 0.05$). If the subsequent surface interval did not meet this criterion, the bout was ended. Bouts that were truncated by the TDR's duty cycle were omitted from the analysis.

Several statistical methods were used to determine the accuracy of bout identification (Boyd *et al.* 1994). We examined the distribution of significant *P*-values that resulted in bout termination. This analysis indicated that 92·8% of defined bouts ended with *P*-values < 0·01 and 83·5% of bouts ended with *P*-values < 0·001, suggesting that surface intervals ending a bout

represented genuine changes in behaviour and were not the result of random variation in surface intervals. Bouts were also examined to determine if there was a systematic increase in surface interval as the bout progressed, resulting in overestimation of bout length. Linear regressions of surface interval against dive number within bout indicated no systematic trend in the duration of surface intervals as a bout progressed that should have affected our identification of bouts.

Each dive within a bout can be characterized by depth, duration and percentage of time spent at the bottom of the dive. In addition to these characteristics, the time/depth profile or 'shape' of each dive > 1 min in duration was determined. Dives less than 1 min are necessarily V-shaped as only three samples could be taken at the 20-s sampling rate used in this study. Five dive shapes were classified using supervised, discriminate function analysis (DFA; Schreer & Testa 1996) as described in Beck, Bowen & Iverson (2000). In four of these shapes, seals spent a large fraction of time at the bottom of the dive and these dives differed mainly in symmetry of rates of travel to and from the surface. In the fifth shape, so-called V-shape dives, less than 20 s was spent at the bottom of the dive. Two of the shapes (square and V-shaped dives) accounted for > 70% of all dives (Beck *et al.* 2000; Beck *et al.* 2003a). Square dives are symmetrical; bottom-time dives characterized by similar rates of travel to and from the surface. We used these two shapes to investigate possible bout functions because they have been associated with different behaviours, including foraging, in other phocid species (e.g. Le Boeuf *et al.* 2000).

Linear mixed-effects models (LME; S-Plus 4·5) were constructed to examine the influence of covariates (body size, sex and month) on bout characteristics. These models account for the serial correlation of dive variables measured over time within individual and are able to handle missing cells that standard repeated-measures designs cannot. Specifically, we examined the following six bout characteristics: bout duration, bout depth (i.e. mean depth of dives within bout), percentage of bout spent at depth, percentages of square and V-shape dives/bout and the duration of post-bout surface intervals. Age had little influence on the diving behaviour of males and females at the level of individual dives (Beck *et al.* 2003a), presumably because all of the animals studied were adults. Therefore, we did not include age in the present analysis to limit the number of LME models to be examined. The males and females used in this study did not overlap in body length or mass. Body size was a significant covariate only when sex was not included in the model. Once sex was entered, body size did not account for significant variation in diving behaviour. As a result, body size was not considered further in the statistical analysis, but was considered in the interpretation of our results. LME models were fitted using maximum-likelihood parameter estimation. We assumed an auto-regressive (i.e. AR1) variance-covariance matrix for the within-

subject error terms. All possible models with two–way interactions were examined and all models were compared to the mean model: $y = \mu + \varepsilon$. Variables included in each model were entered simultaneously. To select the best predictive model, the five models with the lowest Akaike's information criterion (AIC) were compared using a log-likelihood ratio test. We used this approach, rather than relying only on the lowest AIC, because of the non-orthogonal nature of our data (i.e. not all animals were measured in each month). The explained variance was calculated using Cox & Snell's (1989: 208–209) generalized coefficient of determination (R^2), modified to incorporate the effective degrees of freedom (edf) using the following formula:

$$R^2 = 1 - (\text{log-likelihood mean model}/\text{log-likelihood of best model})^{2/edf}$$

where edf = the number of observations $\times (1 - $ serial correlation parameter of the model) (W. Blanchard personal communication). Eighty-seven (41 males, 46 females) individuals with dive data in ≥ 3 months were included in the seasonal analysis. May was excluded from all statistical analyses because only one male was sampled during this month. However, May data were included in the figures because they provide additional insight into female diving behaviour.

We used MANOVA to examine interannual variability in bout characteristics. Univariate tests were used to locate differences if the overall MANOVA was significant. To standardize the data for seasonal effects, but to maximize sample size of both males and females, we used only animals with diving data from October to December (Table 1). Data from 1992 and 1994 were excluded from analysis of interannual variation due to insufficient sample size in these years.

Most of the bout characteristics were positively skewed within individual. As a result, the median value of individual bout characteristics was a better representation of the central tendency of an individual's diving behaviour. Thus, we used the median bout characteristics of each individual to examine the influence of sex, month and year on bout characteristics. The percentage of square and V-shaped dives within a bout were arcsine-transformed and other bout variables were $\log_e$-transformed as necessary to meet the assumptions of parametric analyses.

CLASSIFICATION OF DIVE BOUT TYPES

Bouts may differ in predictable ways such that the analysis of different types of bouts may provide insight about how predators organize their behaviour (Boyd *et al.* 1994). Bout types were determined using cluster analysis (based on Euclidean distances) following Boyd *et al.* (1994). This method uses both the characteristics of individual dives within a bout (dive duration, surface interval and depth) and characteristics of the bout itself (number of dives, bout duration, per-
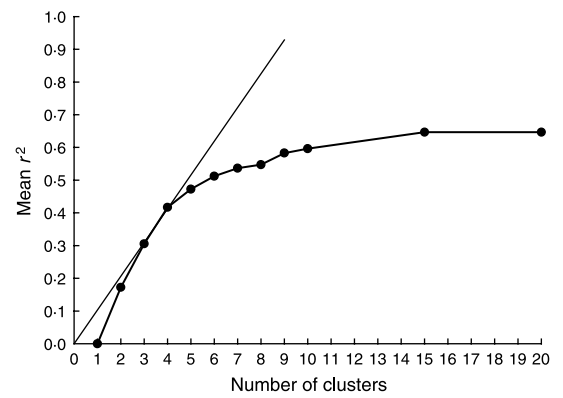
Fig. 1. Relationship between explained variation (mean r^2) of cluster groupings (i.e. bout types) vs. the number of bout type clusters used. Optimum number of clusters indicated by the intersection of the tangent from the origin and curve (Boyd *et al*. 1994).

centage of the bout spent at depth and the percentages of square and V-shape dives/bout). To determine the optimal number of clusters representing different types of dive bouts, the mean r^2 value for cluster analyses with 1–10, 15 and 20 clusters (weighted for the variance of the original variables) was plotted against the number of clusters (Fig. 1). The point where the tangent from the origin met with the resulting curve was defined as the optimum number of clusters (Boyd *et al*. 1994). Using this method, four bout types appeared optimal. We then used DFA to determine the accuracy of bout classifications. DFA indicated that 97·5% of dive bouts were classified correctly with a cross-validation error rate of 2·5%. Repeated-measures MANOVAs were used to examine the effects of sex, month and year on the use of different bout types.

FORAGING TRIPS

We examined sex differences in trip characteristics using 16 seals ($n = 7$ males and 9 females) that were equipped with non-duty cycled TDRs and thus had continuous records covering between 2 and 4 months of diving behaviour. The duration of foraging trips was estimated as follows: a trip started when a period of haulout (i.e. extended dry time) was followed by five or more dives and ended when > 20 min of accumulated dry time was recorded between successive dives. We examined only the effect of sex on trip characteristics because there were too few individuals with uninterrupted dive records to examine month and year effects.

Results

BOUT CHARACTERISTICS

A total of 30 451 bouts was identified from the dive records of 87 grey seals. Of these, 8·2% were truncated by duty cycling and omitted from statistical analyses. Omitted bouts were equally distributed between males

Table 2. Bout characteristics of male and female adult grey seals. Values are the means of median values of each bout characteristic for individual animals with the 95% confidence intervals in brackets

Bout characteristic	Males ($n = 32$)*	Females ($n = 37$)*	Univariate test values
Bout duration (h)	1·21 (1·11, 1·33)	2·19 (1·79, 2·68)	$F_{1,57} = 23·46$ $P < 0·001$
Bout depth (m)	57 (51·9, 62·0)	44 (38·3, 49·8)	$F_{1,57} = 14·10$ $P < 0·001$
% bout spent at depth	38·5 (36·0, 41·1)	49·8 (47·6, 52·0)	$F_{1,57} = 49·65$ $P < 0·001$
% square dives/bout	81·1 (76·6, 85·2)	73·4 (64·9, 81·0)	$F_{1,57} = 4·107$ $P = 0·047$
% V-dives/bout	0·8 (0·2, 1·8)	0·40 (0·08, 0·96)	$F_{1,57} = 1·63$ $P = 0·207$
No. dives/bout	12·0 (11·2, 12·9)	20 (16·8, 23·9)	$F_{1,57} = 28·05$ $P < 0·001$
Post-bout surface interval (min)	4·8 (4·5, 5·1)	6·2 (4·9, 7·9)	$F_{1,57} = 3·04$ $P = 0·086$

*Only individuals with dive data from October through December were used in this comparison.

and females. Overall, 99·3 ± 0·08% of dives by an individual were contained within dive bouts. Thus, essentially all diving by males and females was organized into temporal clusters.

Overall bout characteristics of males and females differed significantly (2-way MANOVA of bout characteristics by sex and year: sex: $F_{7,51} = 12·35$, $P < 0·001$), but did not differ significantly among years (year: $F_{35,275} = 1·30$, $P = 0·128$) and there was no significant sex by year interaction (sex by year: $F_{35,275} = 1·11$, $P = 0·310$). Males had significantly deeper bouts than females, but females had significantly longer bouts, spent a significantly higher percentage of the bout at depth, and had more dives per bout than males (Table 2).

All models accounting for variability in bout characteristics had significant month or month by sex effects (Table 3). Variation in bout duration was best explained by a model that included a significant month² by sex interaction (Fig. 2a), indicating that males and females exhibited different seasonal patterns in bout duration. The percentage of time in a bout spent at depth included significant sex and year effects and sex by month and sex by year interactions (Table 3). Thus, males and females differed in the both the seasonal (Fig. 2b) and interannual pattern of time spent at the bottom of bouts. Over the 8 years of the study, males consistently spent an average of 41 ± 0·7% of each bout at depth. Females showed more interannual variability in this bout characteristic. In 1992 and 1998 the average proportion of an individual bout spent at depth by females peaked at > 55%, whereas only 41 ± 3·6% and 37 ± 5·2% of each bout was spent at depth in 1993 and 1994, respectively.

Mean bout depth was best described by a model that included a cubic month effect, year, sex and a month³ × year interaction (Table 3). Although the mean depth of bouts by males was significantly greater than that of females, both sexes followed the same seasonal pattern. Bout depth decreased from June to September (males: 54 ± 2·7 m to 49 ± 3·36 m; females: 44 ± 3·3 to

30 ± 3·2 m) but increased from September to December (peak: males = 62 ± 2·8 m; females = 51 ± 3·3 m). Bout depth then decreased in January to a mean of less than 40 m for both sexes. Although males and females exhibited the same seasonal pattern of bout depth, this differed among years. In the last three years of the study (1997–99), bout depth showed less seasonal variation with a more consistent mean bout depth of 40–45 m in all months for both sexes.
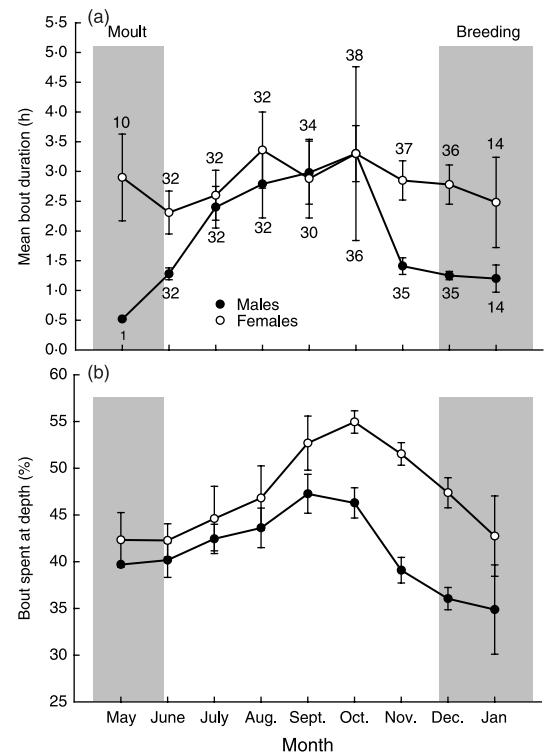

Fig. 2. Seasonal changes in (a) bout duration (h) and (b) the percentage of bout spent at depth by male and female grey seals. Values are means ± 1 SE. Numbers above or below each mean represent number of individuals in each month and are the same for both panels. May was not included in statistical analyses since only one male was sampled.

Table 3. Linear mixed effects models of individual bout characteristics

Bout variable ($n = 87$)	Source	Coefficient	SE	z-score	P-value	d.f.	Pseudo R^2
Bout duration (ln transformed)	Constant	−3·424	2·766	−1·238	0·108		0·089
	Month	1·095	0·943	1·161	0·123	406	
	Month^2	−0·090	0·104	−0·866	0·192	406	
	Month^3	0·002	0·004	0·578	0·281	406	
	Sex	0·040	0·078	0·519	0·301	85	
	Month$^2 \times$ Sex	$1·3 \times 10^{-4}$	$6·2 \times 10^{-5}$	2·185	0·014	398	
% bout at depth (arcsine transformed)	Constant	−2294·6	1295·4	−1·771	0·384		0·180
	Month	−4·011	9·682	−0·414	0·341	406	
	Month^2	0·879	1·065	0·826	0·209	406	
	Month^3	−0·046	0·004	−1·224	0·111	406	
	Sex	−23·930	14·221	−1·683	0·047	85	
	Year	48·410	27·048	1·79	0·037	79	
	Year^2	−0·251	0·141	−1·78	0·038	70	
	Month$^3 \times$ Sex	$1·4 \times 10^{-4}$	$7·4 \times 10^{-4}$	1·91	0·028	398	
	Sex $\times$ Year^2	$2·6 \times 10^{-3}$	$1·5 \times 10^{-3}$	1·71	0·044	77	
Mean bout depth	Constant	11·884	4·078	2·01	0·002		0·132
	Month	−4·210	0·829	−5·08	< 0·001	406	
	Month^2	0·420	0·091	5·19	< 0·001	406	
	Month^3	−0·011	0·004	−2·49	< 0·006	406	
	Sex	−0·192	0·039	−4·92	< 0·001	85	
	Year	0·039	0·033	1·16	0·145	79	
	Month$^3 \times$ Year	$−6·3 \times 10^{-5}$	$3·0 \times 10^{-5}$	−2·09	0·018	350	
% square dives/bout (arcsine transformed)	Constant	−9339·8	2610·3	−3·58	0·002		0·232
	Month	−169·2	20·35	−8·32	< 0·001	406	
	Month^2	18·79	2·24	8·41	< 0·001	406	
	Month^3	−0·67	0·079	−8·38	< 0·001	406	
	Sex	−4·88	1·701	−2·87	0·002	85	
	Year	250·50	54·500	3·77	0·001	79	
	Year^2	−1·069	0·284	−3·76	0·001	79	
	Month$^3 \times$ Sex	$2·3 \times 10^{-3}$	$1·3 \times 10^{-3}$	1·71	0·043	398	
% V-dives/bout (ln transformed)	Constant	4165·56	1926·34	2·16	0·015		0·199
	Month	90·30	15·028	6·00	< 0·001	406	
	Month^2	−10·17	1·653	−6·15	< 0·001	406	
	Month^3	0·368	0·059	6·27	< 0·001	406	
	Sex	4·155	1·374	3·03	0·001	85	
	Year	−91·967	40·225	−2·29	0·011	79	
	Year^2	0·479	0·210	2·29	0·011	79	
	Month$^3 \times$ Sex	$−3·5 \times 10^{-3}$	$1·1 \times 10^{-3}$	−3·08	0·001	398	
Post-bout surface interval (ln transformed)	Constant	−24·478	4·837	−5·06	< 0·001		0·148
	Month	8·799	1·647	5·34	< 0·001	396	
	Month^2	−0·934	0·181	−5·16	< 0·001	396	
	Month^3	0·032	0·006	4·93	< 0·001	396	
	Sex	0·658	0·123	5·35	< 0·001	83	
	Month$^3 \times$ Sex	$−3·0 \times 10^{-4}$	$1·0 \times 10^{-4}$	−3·37	< 0·001	388	

Seasonal analysis did not include animals sampled in May, as only one male was sampled.

The percentage of square dives and V-shaped dives within a bout were best described by predictive models that included a cubic month effect, a quadratic year effect, sex and a month^3 by sex interaction term (Table 3). Thus, the seasonal pattern in the percentage of these dive shapes within bouts differed in males and females (square dives see Fig. 3), but interannual changes where similar for both sexes. In the case of the percentage of square dives, both sexes had higher levels in 1995 and 1996 and low levels in 1993 compared with other years. As might be expected, the percentage of V-shaped dives showed the reciprocal annual pattern.

Post-bout surface interval was best described by a model that included a cubic month effect, sex and month^3 by sex interaction term (Table 3). For both sexes, mean post-bout surface interval increased from June through September and then declined through the fall and winter. The magnitude of increase in the duration of post-bout surface intervals was greater for females than for males during the summer months resulting in the significant month by sex interaction term. Thus, for a number of bout characteristics, there was evidence that males and females organized bouts of diving differently at monthly and interannual time scales.
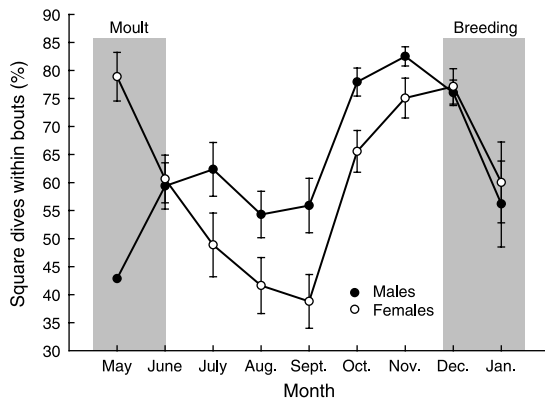
Fig. 3. Seasonal changes in the percentage of square dives within bouts for male and female grey seals. Values are means ± 1 SE. Sample sizes are given in Fig. 2. May was not included in statistical analyses since only one male was sampled.

BOUT TYPES

The four types of bouts identified by cluster analysis differed in a number of characteristics (Table 4, Fig. 4). Type-1 bouts (30·1% of all bouts) were deep and long with few V-shape dives, a high percentage of square dives and a short post-bout surface interval. Type-2 bouts were the most common type of bout (40·7% of all bouts). These were the deepest bouts with a high percentage of square shaped dives, but were considerably shorter in duration than type-1 bouts. Type-3 bouts (16·5% of all bouts) were shallow and short with few square shape dives and relatively long (i.e. > 10 min) post-bout surface intervals. The final bout type (type-4, 12·7% of all bouts, was the shortest and shallowest and was composed of 50% V-shaped dives. During type-4

bouts individuals spent < 15% of the bout at depth and had long post-bout surface intervals. In terms of bout duration and diving depth, bouts 1 to 4 could be characterized as long and deep, medium and deep, medium and shallow, and short and shallow, respectively. These characteristics and the large differences in time spent at depth suggest that different bout types may represent quite different behaviours.

SEX, SEASON AND YEAR EFFECTS ON BOUT TYPES

The percentage of each bout type exhibited by male and female grey seals differed significantly (repeated-measures analysis of percentage bout type by sex, month and year: sex – $F_{2,31} = 16·52$, $P < 0·001$), but did not vary interannually (year – $F_{10,114} = 1·11$, $P = 0·366$). Females exhibited significantly more bouts of type-1 and -3 and less of type-2 than males. There was no difference in the proportion of type-4 bouts used by males and females (Table 4). The percentage of bout types also varied seasonally (month – $F_{12,21} = 7·95$, $P < 0·001$; Fig. 5) and the seasonal pattern differed between males and females (month × sex – $F_{12,21} = 2·70$, $P = 0·022$; Fig. 5a,b). There was no month × sex × year interaction ($F_{60,125} = 1·147$, $P = 0·259$), indicating that the seasonal differences between males and females were consistent across the 8 years of the study.

TIME OF DAY EFFECTS ON BOUT TYPES

Bout types used by grey seals also differed by time of day. The percentage of each bout type by time period (3-h time periods) was examined using a double

Table 4. Characteristics of four different bout types identified from 87 grey seal dive records. Values are means with 95% confidence intervals in brackets

|	Type 1	Type 2	Type 3	Type 4
Bout duration (h)	5·50	0·91	0·87	0·42
	(5·40, 5·60)	(0·90, 0·92)	(0·85, 0·89)	(0·41, 0·43)
Mean bout depth (m)	50·8	61·5	19·0	15·5
	(50·3, 51·3)	(61·1, 62·0)	(18·6, 19·4)	(15·1, 15·9)
% bout spent at depth	50·1	39·3	48·5	13·9
	(49·9, 50·4)	(39·1, 39·6)	(48·1, 49·0)	(13·6, 14·3)
% square dives	76·0	87·5	28·1	10·3
	(75·5, 76·6)	(87·1, 87·8)	(27·3, 29·0)	(9·6, 11·0)
% V-dives	1·4	1·4	6·8	50·4
	(1·3, 1·5)	(1·3, 1·5)	(6·4, 7·2)	(48·9, 52·0)
Dives/bout	49·7	9·1	10·0	5·9
	(48·9, 50·4)	(9·0, 9·2)	(9·8, 10·2)	(5·8, 6·1)
Mean dive duration (min)	5·80	4·79	4·77	2·56
	(5·76, 5·84)	(4·76, 4·81)	(4·70, 4·82)	(2·52, 2·60)
Mean surface interval between dives (min)	1·07	1·49	0·86	2·09
	(1·06, 1·08)	(1·48, 1·50)	(0·85, 0·88)	(2·04, 2·14)
Post-bout surface interval (min)	7·20	6·30	10·90	17·61
	(6·90, 7·40)	(6·21, 6·46)	(10·30, 11·50)	(16·69, 18·57)
% of bouts	30·1	40·7	16·5	12·7
% of bout by males	28·4 ± 1·79	48·8 ± 3·24	11·9 ± 1·50	10·9 ± 1·48
% of bouts by females	38·9 ± 3·37	20·7 ± 2·51	26·6 ± 3·16	13·8 ± 2·44
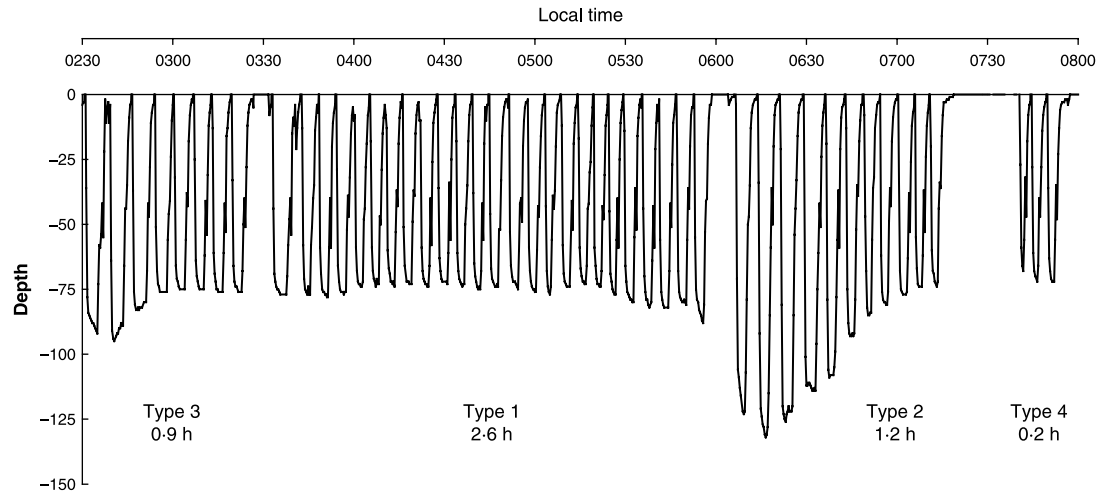
Fig. 4. A sample of an individual male grey seal dive record measured over a period of 6-h period and illustrating bout duration and dive shape within bout for each bout type. The brief inversion of depth, at about 50 m, on the ascent of some dives is not an artefact of the data collection but is also not typical of most diving.
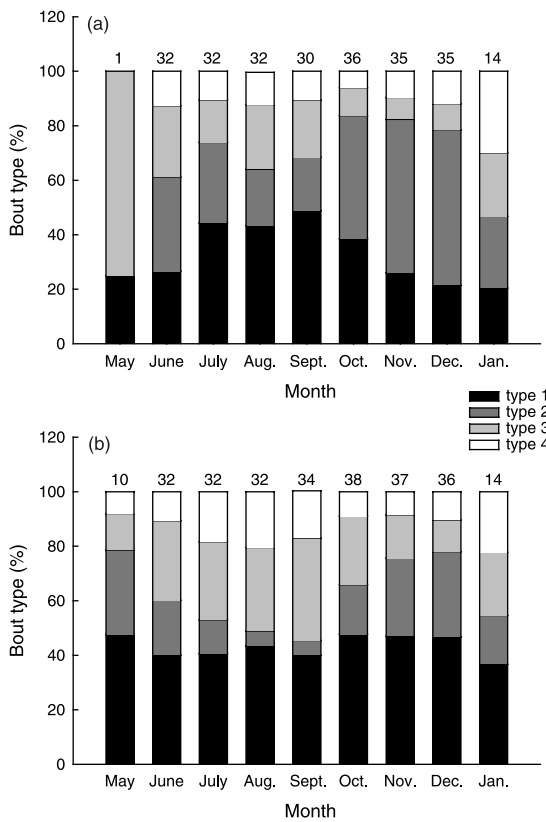

Fig. 5. Seasonal variation in the distribution of bout types use by male (a) and female (b) grey seals. Numbers above each bar represents sample size.

Fig. 6. Diurnal pattern of bout type use. Solid line represents an even distribution of each bout type throughout the eight daily time periods.

repeated-measures analysis that included both month and time period as within-subject factors and sex as the between subject factor. All bout types showed statistically significant day–night patterns (Table 5); however, these patterns were most prominent for type-3 and type-4 bouts with over 60% of these bouts performed between 18:00 and 06:00 hours local time (Fig. 6a). Type-1 and 2 bouts occurred more evenly throughout the 24-h period (Fig.
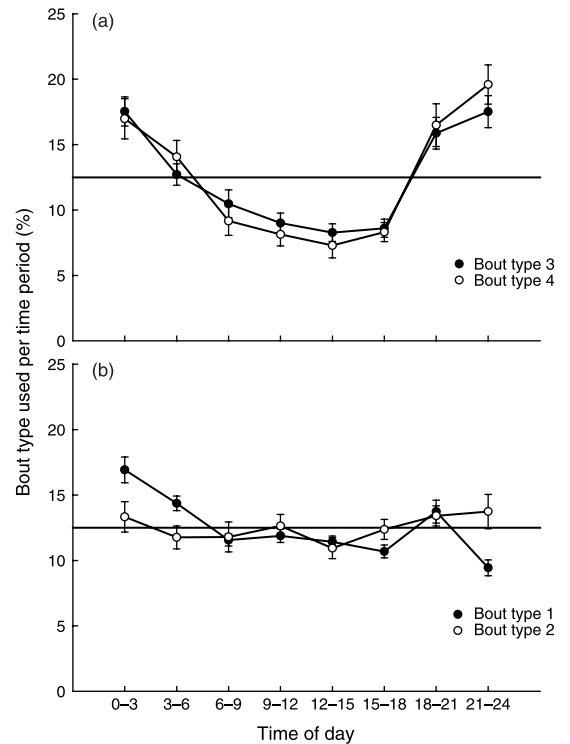
6b). The day–night pattern of type-1 and 3 bouts differed by month (Table 5). In the case of type-1 bouts, the general pattern was consistent throughout the prebreeding foraging period; however, the magnitude of difference between time periods changed slightly from month to month. The day–night pattern of type-3 bouts changed more dramatically by month. Whereas the pattern of type-3 bouts shown in Fig. 6(a) was dominant throughout the summer and autumn, by November and December type-3 bouts were distributed more evenly throughout the daily cycle. Only type-1 bouts exhibited a day-night

Table 5. Repeated-measures analysis of bout type by time of day, month and sex

Source	Type 1	Type 2	Type 3	Type 4
Month				
$F_{4\cdot1,183\cdot7}$*	2·667	8·951	1·466	1·968
P-value	0·003	< 0·001	0·190	0·070
Month × Sex				
$F_{4\cdot1,183\cdot7}$	1·334	1·203	0·730	1·279
P-value	0·242	0·310	0·626	0·273
Time period				
$F_{2\cdot7,121\cdot5}$	8·518	2·526	12·718	10·907
P-value	< 0·001	0·036	< 0·001	< 0·001
Time period × Sex				
$F_{2\cdot7,121\cdot5}$	2·853	1·105	0·501	0·728
P-value	0·043	0·357	0·713	0·591
Month × Time period				
$F_{11\cdot8,531\cdot7}$	3·711	1·212	2·296	1·340
P-value	< 0·001	0·258	0·003	0·159
Month × Time period × Sex				
$F_{11\cdot8,531\cdot7}$	1·568	1·023	0·911	0·978
P-value	0·098	0·429	0·557	0·482

*The repeated-measures analysis assumption of sphericity was violated in this analysis. As a result the Greenhouse–Geisser correction was applied resulting in fractional degrees of freedom for this analysis.

pattern that differed significantly between males and females (Table 5). Males had slightly more type-1 bouts during the afternoon period (12:00–18:00 hours) compared with females; however, this difference was minor and likely has little biological significance.

TEMPORAL PATTERN OF BOUT TYPES

Although we cannot explicitly specify the function of each bout type, it is likely that there are functional differences among the four types. Thus the temporal sequence of bout types may contain information on how seals organized their diving or foraging behaviour. The four bout types can be broadly categorized into deep (bout types-1 and 2) and shallow (bout types-3 and 4). To test whether these two categories of bouts were randomly distributed in time, we conducted a non-parametric Runs test on the sequence of deep and shallow bout types for each animal. For 77 of the 87 animals (88·5%), the pattern of deep/shallow bouts was significantly non-random (*P*-value < 0·05), indicating that there is a temporal structure to the use of different bout types.

To examine more closely the pattern of bout type use and the factors that influenced the temporal organization of bout types, we calculated transition probabilities (i.e. the probability that each bout type was followed by each of the four bout types) for each individual. Overall, bouts were most often followed by bouts of the same type (Table 6), suggesting that animals often performed a series of one bout type before changing their behaviour. Transition probability matrices differed by sex (repeated-measures MANOVA: $F_{3\cdot02,105\cdot6} = 16\cdot76$, $P < 0\cdot001$), but not by year (repeated-measures MANOVA: $F_{15\cdot08,105\cdot6} = 1\cdot39$, $P = 0\cdot164$), and there

was no significant sex × year interaction ($F_{15\cdot08,105\cdot6} = 0\cdot54$, $P = 0\cdot915$). The most common transition among male grey seals was from a type-2 bout to another type-2 bout, with type-1 to type-1 transitions being the second most common. Among females, type-1 to type-1 transitions occurred twice as often as any other transition type (Table 6).

Given the pronounced seasonal effects in other aspects of bout use by grey seals, we would have liked to examine the monthly variation in transition probabilities. However, there were many empty cells in the transition matrices at this temporal scale. Thus, to examine larger temporal-scale changes in the pattern of bout type use, transition matrices were re-calculated for the period from June through September and for October to December. Repeated-measures MANOVA indicated strong seasonal effects ($F_{2\cdot2,50\cdot8} = 9\cdot59$, $P < 0\cdot001$) with fewer transitions involving type-3 and 4 bouts from October through December compared to June to September, but more transitions involved type-1 and 2 bouts. These seasonal changes in transition probabilities did not differ between males and females (repeated-measures MANOVA: $F_{2\cdot2,50\cdot8} = 2\cdot41$, $P = 0\cdot095$) or among years (repeated-measures MANOVA: $F_{11\cdot1,50\cdot8} = 0\cdot86$, $P = 0\cdot581$).

DIVE EFFORT

Males and females organized their behaviour differently in terms of bout characteristics and the seasonal pattern of diving. However, these measures do not incorporate the total effort that individuals spend foraging. To investigate this, we calculated the amount of time spent in type-1, 2 and 3 bouts day^{-1} as an index of effort for each individual. There is evidence that grey

Table 6. Transition probabilities (probability of each bout type being followed by each of the four bout types) of bout types for 41 male and 46 female adult grey seals

Current/next	Type 1	Type 2	Type 3	Type 4
Males				
Type 1	0·12 ± 0·012	0·11 ± 0·006	0·04 ± 0·005	0·02 ± 0·003
Type 2	0·10 ± 0·005	0·32 ± 0·025	0·02 ± 0·002	0·03 ± 0·003
Type 3	0·04 ± 0·005	0·02 ± 0·002	0·06 ± 0·011	0·02 ± 0·003
Type 4	0·02 ± 0·002	0·03 ± 0·003	0·02 ± 0·003	0·05 ± 0·009
Females				
Type 1	0·23 ± 0·021	0·09 ± 0·008	0·06 ± 0·006	0·02 ± 0·003
Type 2	0·10 ± 0·009	0·12 ± 0·018	0·01 ± 0·002	0·01 ± 0·002
Type 3	0·07 ± 0·007	0·01 ± 0·002	0·11 ± 0·015	0·04 ± 0·007
Type 4	0·03 ± 0·003	0·01 ± 0·002	0·03 ± 0·006	0·06 ± 0·017

Table 7. Linear mixed-effects model of dive effort* for adult grey seals ($n = 87$)

Source	Coefficient	SE	z-score	P-value	d.f.	Pseudo R^2
Constant	208·261	25·676	8·11	< 0·001		0·183
Month	−51·214	6·570	−7·80	< 0·001	406	
Month^2	5·660	0·721	7·85	< 0·001	406	
Month^3	−0·206	0·026	−7·89	< 0·001	406	
Sex	−2·652	1·024	−2·59	0·008	85	
Year	−0·477	0·172	−2·78	0·001	79	
Month^3 × Sex	0·002	0·001	2·21	0·020	398	

*Measured as hours spent in type 1, 2 and 3 bouts day^{-1}.

seals forage near the ocean floor and thus increasing the time spent at depth should increase the probability of encountering prey (Thompson *et al.* 1991). Thus, the characteristics of these three bout types suggested that they were more likely to represent foraging behaviour (i.e. a high percentage of the bout was spent at the depth) than type-4 bouts.

We used LME models to examine seasonal effects over the entire period from June to December. This analysis showed significant monthly variation in the amount of time spent in these bout types day^{-1}. A model that included a significant cubic month effect, year, sex and month^3 by sex interaction best explained 'foraging' effort (Table 7). Female effort was relatively high immediately following the spring moulting period (May–June), but showed a marked decrease from June to September before increasing again through the autumn and then declining in January (Fig. 7). In contrast, male effort increased more variably from June to November before decreasing abruptly in December and January. Among years, average foraging effort was higher during the early years of the study (13·0 ± 00·85 h day^{-1} in 1993), relatively consistent at 11·0 ± 00·51 h day^{-1} through the mid-1990s, but decreased to a low in 1998 (8·0 ± 00·53 h day^{-1}) before increasing again in 1999 (11·4 ± 0·79 h day^{-1}).

FORAGING TRIPS

In total, 147 trips were recorded from the seven males and nine females whose TDRs were not duty cycled,
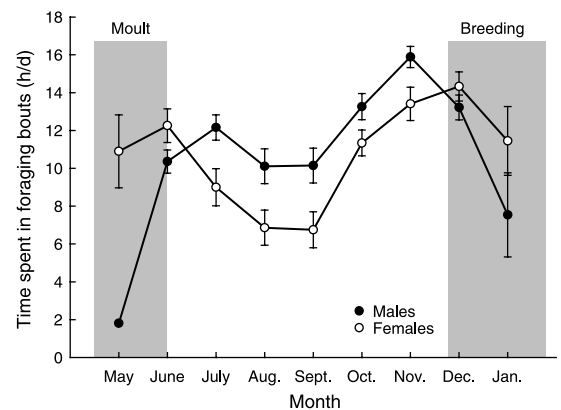

Fig. 7. Seasonal changes in dive effort (h day^{-1} spent in bouts) of male and female grey seals. Values are means ± 1 SE. Sample sizes are given in Fig. 2. May was not included in statistical analyses since only one male was sampled.

with an average of 9·2 ± 1·03 trips per seal. Trips ranged between 1 h and 78·3 days with a mean duration of 8·3 ± 1·25 days. Haulout periods following foraging trips ranged from 3·6 to 37·5 h with a mean of 16·2 ± 02·09 hours. Although male and female trip durations did not differ ($t_{14} = 0·12$, $P = 0·904$), males had significantly longer post-trip haulout periods than females (20·8 ± 02·98 hours vs. 12·5 ± 02·38 hours, $t_{14} = 2·19$, $P = 0·046$). The percentage of time spent diving while on foraging trips also differed, with females spending significantly more time diving than males (58·7 ± 3·56% vs. 36·8 ± 5·91%; $t_{14} = −3·33$, $P = 0·005$).

Discussion

Air-breathing marine carnivores represent a challenging group of species in which to study the foraging behaviour of individuals since most feeding takes place underwater and at highly variable spatial and temporal scales. Among pinnipeds, the temporal characteristics of foraging behaviour are well studied only in lactating females (Boyd & Croxall 1992; Boness *et al.* 1994; Boyd *et al.* 1994; Boyd 1996; McCafferty *et al.* 1998; Bowen *et al.* 2001). Diving behaviour at the temporal scale of bouts and trips has also been studied in several seabird species, but again, data are limited to foraging during the breeding season when parents are provisioning young (Williams *et al.* 1992; Watanuki *et al.* 1993; Watanuki, Kato & Naito 1996; Mori 1997; Jodice & Collopy 1999). Foraging behaviour of adults may differ substantially when not constrained by provisioning or otherwise caring for offspring. Therefore studies during the non-breeding season are needed to fully understand sex differences in the foraging strategies of marine carnivores.

During the prebreeding foraging period, adult male and female grey seals make different decisions about the allocation of time to diving compared with other behaviours (e.g. resting at the surface, hauled out on land). These differences are evident at multiple temporal scales: individual dives (minutes; Beck *et al.* 2003a), bouts (hours; this study) and trips (days; this study). At the scale of bouts, males and females exhibit significantly different seasonal patterns of dive effort, bout type use, as well as several bout characteristics (e.g. bout duration, percentage bout spent at depth). Although mean trip duration did not differ, the amount of time spent diving during trips and the duration of rest periods between trips differed significantly between males and females. In grey seals, all foraging occurs while diving and the prebreeding period is known to be a time of substantial mass and energy gain (Beck, Bowen & Iverson 2003b). Thus, differences in diving behaviour of males and females during this period undoubtedly reflect sex differences in foraging ecology. Although males are larger than females, we conclude that sex rather than body size accounts for variability in diving behaviour because body size was not a significant variable once sex was included in any of the models.

FUNCTION OF BOUT TYPES

Grey seals organize their diving behaviour into temporal clusters, with few dives (< 1%) performed outside bouts. Functional interpretation of single dives outside bouts is difficult given their rarity and variable characteristics. We identified four types of diving bouts differing primarily in duration, depth, the percentage of square and V-shaped dives/bout and the percentage of bout spent at depth. These bout types also differed in their day–night and seasonal distribution. In another apex marine predator, the Antarctic fur seal, *Arctocephalus gazella*, different bout types are thought to represent different aspects or types of foraging (Boyd *et al.* 1994). Thus, it is tempting to conclude that different bout types also represent different behaviours in grey seals. However, as noted earlier, functional interpretation of different bout types is more complex in phocid seals since phocids dive both during foraging and to travel to and among prey patches.

Although functional interpretations of bout types may be less clear in phocids, there is evidence that grey seals usually forage at or near the seabed, at depths between 30 and 70 m in the North Sea (Thompson *et al.* 1991). Thus, we suggest that most foraging in grey seals is associated with type-1, 2 and potentially 3 bouts because a large fraction of these bouts is spent at depth (see Table 4). Sex differences in the seasonal pattern of energy storage in adult grey seals (Beck *et al.* 2003) coincide with the seasonal distribution of these bout types (Fig. 5), lending support for this hypothesis. Day–night patterns of diving have also been used to infer dive function in other pinniped species (Boyd *et al.* 1994; Le Boeuf *et al.* 2000). Among elephant seals, females exhibit a strong diurnal pattern of dive depth that has been interpreted as foraging on pelagic prey species. In contrast, male elephant seals do not exhibit diurnal patterns in dive depth, which is consistent with foraging on benthic species. The relatively weak day–night pattern in bout types-1 and 2 further support the hypothesis that these bout types probably represent benthic foraging in grey seals.

Type-4 bouts differ considerably from the other three bout types. Not only are they much shorter in duration, these bouts also are composed of 50% V-shaped dives and therefore a relatively small proportion of the bout is spent at shallow depths. In the two species of elephant seals, V-shaped dives are clearly associated with travel (Hindell, Burton & Slip 1991; Le Boeuf *et al.* 1992, 2000) and we suggest that a similar function might be assigned to our type-4 bouts. Support for this hypothesis again comes from the seasonal distribution of bout types (Fig. 5). Both males and females exhibited a higher level of type-4 bouts in January, a time when animals may be travelling greater distances to return to the breeding colony. Although V-shape dives within type-4 bouts may represent travel, satellite data (W. D. Bowen unpublished data) indicate that all bout types are associated with movement. Given the small proportion of V-shape dives in the more common bout types, travel must be associated with other dive shapes as well.

INTERANNUAL VARIATION IN DIVE BOUTS

Interannual variation in prey abundance and distribution can affect the diving behaviour of seabirds and marine mammals (e.g. Boyd *et al.* 1994). During the period of this study, there was interannual variability in both the ocean temperatures and prey abundance on the eastern Scotian Shelf (Zwanenburg *et al.* 2002), the main foraging area for this population. In general, this

time period was characterized by colder than average bottom temperatures, declining abundance of large gadoid fishes and increased abundance of small pelagic fishes, such as sandlance (*Ammodytes dubius*) and capelin (*Mallotus villosus*) (Zwanenburg *et al*. 2002), both of which are known to be important prey items for adult grey seals (Bowen & Harrison 1994; Beck 2002). However, this interannual environmental variability generally was not reflected in the characteristics or seasonal patterns of dive bouts, with one exception. Males showed relatively little interannual variation in the percentage of bouts spent at depth; however, in females this bout characteristic ranged from 37 to 60%. Given that most foraging by adult grey seals is expected to occur at depth, this suggests that females may be more sensitive than males to interannual changes in prey availability.

SEX DIFFERENCES IN THE TEMPORAL
ORGANIZATION OF DIVING

Male and female grey seals showed considerable differences in the characteristics of foraging trips. At this scale (days), although males and females had trips of similar duration, males spent almost twice as long hauled-out on land between trips and spent less time diving while on a trip relative to females. This suggests that females are either more selective when searching for food and thus spend more time searching, or simply require more energy than males. We can eliminate this latter explanation given the relationship between body mass and absolute energy requirement. Although females expend more energy than males during the breeding season (Beck *et al*. 2003b), during the rest of the year, males require more energy than females given their larger body size. The former option seems more likely, particularly in light of the sex differences seen in the foraging ecology of several size-dimorphic ungulate species (e.g. giraffes – Ginnett & Demment 1997; bighorn sheep – Ruckstuhl 1998; Mysterud 2000; red deer – Clutton-Brock *et al*. 1983). In these species, females (the smaller sex) have been showed to spend more time foraging than males in order to search for and obtain food of higher quality. In contrast, males forage on a wider variety of lower-quality food in order to increase overall intake (Clutton-Brock *et al*. 1983). Preliminary data on diet composition, based on quantitative fatty acid signature analysis (Iverson *et al*. in press), suggest that while the diets of male and female grey seals overlap considerably, males have a more diverse and lower energy-density diet than females (Beck 2002). Thus it seems reasonable to suggest that the higher level of foraging effort in female grey seals is at least partially the result of females being more selective in their choice of prey.

Sex-specific seasonal patterns of bout characteristics and effort could be explained by the seasonal differences in body mass of males and females, which in turn would generate seasonal differences in energy requirements.

However, this seems unlikely as the ratio of male to female body mass is rather constant during the prebreeding foraging period (Beck *et al*. 2003b). Similarly, the niche divergence hypothesis seems an unlikely explanation for the sex-specific seasonal patterns of foraging behaviour evident in adult grey seals. Although one could interpret the deeper bouts of males as evidence of niche divergence in grey seals, both sexes showed the same seasonal pattern of bout depth. Furthermore, both satellite telemetry and geolocation data indicate that males and females have broadly overlapping at-sea distributions (W. D. Bowen unpublished data; Beck 2002) and therefore would be similarly influenced by seasonal variability in their environment.

Thus, we interpret our findings as primarily reflecting differences in the magnitude and timing of the reproductive costs of males and females (i.e. sex-specific fitness-maximizing strategies; Clutton-Brock *et al*. 1983; Gittleman & Thompson 1988; Perrigo 1990; Wilkinson & Barclay 1997). Beck *et al*. (2003b) suggested that the reproductive requirements of each sex results in different behavioural solutions to the trade-off between the costs (Jönsson 1997) and benefits of long-term energy storage for reproduction. Owing to the higher relative importance of stored body energy to female reproductive success, females commit to reproduction earlier than males by showing high levels of diving effort and energy gain early in the prebreeding foraging period (Beck *et al*. 2003b). In contrast, male grey seals increase dive effort gradually and gain mass at a higher rate during the last few months prior to breeding. Presumably, this is because males do not benefit from the early storage of body energy to the same degree as females and therefore are unwilling to pay the costs associated with long-term storage (Beck *et al*. 2003b).

Most bout characteristics showed significant sex-specific seasonal patterns. These patterns are similar to those seen at the level of individual dives (Beck *et al*. 2003a), as might be expected since most dives occur in bouts. These findings strengthen our previous conclusions that males and females commit to reproductive costs at different times of the year. Females exhibited a higher level of foraging effort (h in bouts day^{-1}) immediately following the moult and again in the 3 months prior to the breeding season (Fig. 7) than during the summer months and had long bouts throughout the foraging period (Fig. 2a). In contrast, bout duration and foraging effort among males increased gradually through the summer and early autumn. These sex-specific seasonal patterns of dive bout characteristics and effort are similar to the seasonal pattern of mass and energy gain in adult grey seals (Beck *et al*. 2003b).

Conclusions

Virtually all dives by grey seals occurred within four types of bouts. These bouts types differed in ways that suggest they represent different behaviours (e.g. foraging vs. travel). Diving bouts exhibited by males and

females differed significantly. The effects of body size dimorphism on diving behaviour may be evident both in the deeper bouts and shorter foraging time of males relative to females. However, the significant sex differences in the seasonal pattern of bout characteristics and effort are unlikely to be the result of sexual size dimorphism or niche divergence, given that males and females forage in the same habitats and on the same prey species. Rather, we suggest that our results are better explained by the sex-specific fitness-maximizing hypothesis, with females committing to energy storage for reproduction earlier in the year than males because they need to attain a minimum body condition to support early pregnancy and to minimize the risk of not storing sufficient energy for lactation. Males, whose reproductive success is less dependent on stored body energy in this population, forgo the costs of storing energy until just prior to the breeding season. We suggest that these differing trade-off solutions result in the different seasonal patterns of diving and foraging behaviour in this capital breeding species.

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