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THEME SECTION

Acoustic determination of activity and flipper stroke rate in foraging northern fur seal females

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ABSTRACT: Foraging effort for lactating female otariid pinnipeds is largely a function of the energy expended swimming to a site and diving in search of prey. This is especially true for northern fur seal *Callorhinus ursinus* females, which predictably punctuate their suckling with 7 to 12 d foraging trips at sea, with swimming distances often exceeding 400 km. In the present study we tested a unique approach (flow noise from onboard acoustic dataloggers) to empirically measure swim effort in free ranging female northern fur seals, the first such field measurements on an otariid pinniped. We first measured behavioural activity budgets of seals from a combination of satellite telemetry, pressure (depth), and onboard acoustic data. From these data we were able to quantify the time spent in each of 4 mutually exclusive forms of behaviour: locomoting, diving, resting, and surface activity. Second, flipper stroke rates and stroke rate patterns were measured from the acoustic data for each seal during 3 dive types (i.e. locomoting, shallow and mid/deep dives) and during 3 dive parts (descent, bottom time and ascent). Although stroke rates during each of the 3 dive types were similar (ca. 0.5 Hz), they were distinct during the different parts of a dive. In each case, variation among individuals was significant. Stroke rate patterns were distinct for the different dive types and dive parts. Overall, in addition to applying a unique technique to measure foraging effort in a declining population, the results emphasize the importance of accounting for individual variation to obtain accurate estimates of foraging cost.

KEY WORDS: Flipper stroke rate · Effort · Activity budget · Diving behaviour · Foraging effort · Marine mammal · Pinniped · Otariid · Fur seal

INTRODUCTION

While caring for their young, female pinnipeds in the family Otariidae (i.e. sea lions and fur seals) are central place foragers, alternating between suckling on land and foraging at sea (Orians & Pearson 1979, Bowen et al. 2002). Foraging success during the period of lactation is therefore a key factor determining offspring survival and the female's reproductive success. Foraging effort is largely a function of the amount of energy expended while swimming, specifically locomoting to a site and diving in search of prey (Gentry & Kooyman

1986). While gravity is the primary force behind the energetic cost of locomotion in terrestrial mammals (Cavagna et al 1977, Taylor et al 1980), in marine mammals it is a combination of hydrostatic pressure, body drag, and buoyancy, all of which vary with depth (Williams 2001). In the present paper we investigate a novel method (flow noise combined with pressure and geo-location data) to measure the swimming effort of lactating female northern fur seals *Callorhinus ursinus* during foraging trips at sea.

Reliable measurements of swimming effort in aquatic mammals are difficult to obtain in nature (Boyd et

al. 1995). Two essential components are (1) the amount of time spent in each aquatic activity and (2) estimates of the energy expenditure for each. The first requirement can be satisfied with an accurate behavioural activity budget (Martin & Bateson 1993). Although activity budgets are basic to an understanding of an animal's behavioural ecology, they are logistically difficult and consequently rare for pelagic animals. Despite considerable recent advances in remote instrumentation techniques on free ranging animals, studies of pinniped pelagic activity are mostly restricted to location (using satellite transmitters, also referred to as platform terminal transmitters, PTTs) and diving behaviour (using time-depth recorders, TDRs; but see Bailleul et al. 2005 and Guinet et al. 2005).

A number of different techniques including swim speed, heart rate and swimming stroke rate have been used to satisfy the second requirement, accurate estimates of swimming effort (i.e. cost) by free ranging animals (Costa & Williams 1999). Of these methods, stroke rate appears to be the best predictor of swimming effort (Williams et al. 2004, Wilson et al. 2006). Stroke rate frequencies and patterns have been successfully measured in a number of free ranging marine animals, including phocid pinnipeds (Williams et al. 2000, 2004), cetaceans (Skrovan et al. 1999, Williams et al. 2000, Nowacek et al. 2001) and diving seabirds (van Dam et al. 2002, Watanuki et al. 2003, Wilson et al. 2006). More importantly, stroke rate appears to have a simple and predictable relationship to dive cost (Williams et al. 2004). Stroke rate, as mostly measured by video and acceleration data, is thus proving to be a standard metric for estimating energetic expenditure in many free ranging animals (Wilson et al. 2006).

We focused our attention on the foraging trips of lactating northern fur seal females from the Pribilof Island population in the Bering Sea, Alaska. In addition to the wealth of background data on this population of fur seals, their foraging ecology is of particular interest for 2 reasons. First, foraging trips of lactating females in this species are consistently the longest in duration of all the otariids (although single trips may be longer in *Arctocephalus* spp. during times of depleted prey; Gentry 1998). Females of the Pribilof population predictably alternate 7 to 12 d foraging trips at sea with 2 to 3 d nursing bouts on land, and while away may travel distances in excess of 400 km (Gentry & Kooyman 1986, Loughlin et al. 1987, Gentry 1998, Goebel 2002, Robson et al. 2004). As a result, the cost of swimming is clearly important in this species. Second, the Pribilof Island population is the largest colony of northern fur seals in the world. Although this population has been considered stable for the past 2 decades, it now appears to be declining at an accelerating rate (York et

al. 2002, Towel et al. 2006). The cause of the decline is currently unknown; however, decreased food availability, whether due to anthropogenic or heterospecific competition or climate change, is a principal suspect. If food availability has decreased, the effort or cost to find sufficient food may be increasing. Consequently, empirical measurement of foraging costs, particularly for lactating females, is needed.

The goal of this study was to determine whether we could combine flow noise from onboard acoustic dataloggers with pressure and geo-location data to empirically measure swim effort in free ranging female northern fur seals. To do so, we first produced behavioural activity budgets from the combined dataset to determine the time spent in each activity while at sea. We then measured flipper stroke rates and stroke rate patterns as a proxy for effort for each of the activities that involved swimming. The result is an empirical measurement of swim effort during different behavioural states combined with the amount of time spent in each state, the first such field measurements on an otariid pinniped.

MATERIALS AND METHODS

Subjects, location and equipment. Four lactating females located on St. Paul Island (area known as Reef Rookery, 57° 06.466' N, 170° 17.815' W), Alaska, were captured and instrumented during late August 2002. A set of 3 instruments was attached to the pelage on the dorsal surface of each female with 5-minute epoxy: an acoustic datalogger (Bioacoustic Probe, BP), a PTT, and a VHF radio transmitter. Each BP was mounted along the central axis of the dorsal surface of the seal, positioned to minimize any body contact during the spinal flexion associated with swimming. After the epoxy had set, females were released and returned to their offspring. Radio checks were then conducted twice daily in order to determine whether females had departed or returned from foraging trips at sea. Each female was subsequently recaptured after a single foraging trip, and all instruments were removed. The mass of each of the 4 seals was 37.5, 40.5, 47.5, and 38.0 kg at the time of deployment, and (in the same order) 38.0, 43.5, 50.5 kg at the time of recapture 11 to 12 d later (we were not able to get a return weight on the 4th seal).

Each BP (Greeneridge Sciences) is fully programmable and consists of a hydrophone potted in epoxy resin that records directly to a 288 MB flash memory chip. BPs (19.3 cm long × 3.2 cm diameter; 230 g) sampled at 16 bit acoustic resolution with a maximum sampling frequency of 20 kHz. Sampling frequency, which affects recording time and bandwidth, was set in 2 units to 1560 Hz and 2 at 2048 Hz. A sampling

frequency of 1560 Hz results in a Nyquist of 780 Hz and, after the anti-aliasing filter, an effective frequency bandwidth of 8 to 578 Hz, providing roughly 30 h of continuous recording. Sampling at 2048 Hz results in an effective frequency bandwidth of 8 to 759 Hz, providing roughly 20 h of continuous recording. Recording duty cycles were set at a 1:5 ratio, recording 1 min of every 5, providing coverage for approximately 5 d. In addition to the acoustic data, each BP also provided continuous pressure records for time-depth information (equivalent to a TDR).

Each seal was also fitted with a PTT (single battery Kiwisat 101 ARGOS Satellite transmitter manufactured by Sirtrack™) and a VHF radio transmitter (ATS™ model MM170B). The PTT provided position data for females while they were at sea; each was set to transmit continuously without duty cycle. PTTs (80 mm long × 60 mm wide × 18 mm high) were placed along the central axis of the dorsal surface of each seal, anterior to the scapula as far forward as possible, in order to maximize the number and quality of transmissions received by ARGOS satellites. The VHF tags (50 mm long × 30 mm diameter) were used for locating seals when they returned to shore. Each VHF tag was placed alongside or behind the BP so that its antenna would not make contact and cause acoustic interference.

Analysis of PTT data. Satellite telemetry studies of animal movements typically use filtering algorithms to detect implausible location fixes while retaining accurate locations (e.g. Keating 1994, Vincent et al. 2002, Austin et al. 2003). In our study, we used an interactive stage-based filtering process to evaluate the directionality and velocity at each step of the movement path. We also considered the Argos location class (LC) as an additional factor in determining which locations to remove. In the first stage, beginning with the third sequential location for a seal, we calculated the rate of movement to each of the previous 2 locations and to the subsequent 2 locations. If all 4 velocities exceeded 3.0 m s^{-1} the location was discarded (Austin et al. 2003). In the second stage we used both the Keating index (Keating 1994) and the iterative forward/ backward-averaging filter developed by McConnell et al. (1992) to evaluate the remaining locations. The Keating filter assumes that large location errors are indicated by a single large movement followed by an immediate return to a point near the origin (Keating 1994). It uses sequential sets of 3 movement vectors and associated angles to calculate an error index for comparison to a threshold value. The McConnell et al. (1992) filter derives an index value (V_i) from each set of 4 consecutive velocities calculated in stage one. We examined the Argos quality of locations in which the Keating index exceeded 3.0 or V_i exceeded a rate of

3 m s^{-1} to evaluate whether a location represented an implausible movement, or alternatively failed our filter due to an inaccurate adjacent location. We simultaneously plotted the movement path in ArcView™ 8.2 and at each movement step evaluated the Argos LC of a location relative to that of its neighbours. Through this process, we eliminated the propensity of non-interactive filtering algorithms to delete 'accurate' locations that are adjacent to locations of poor quality, and thereby retained the maximum number of acceptable locations.

Analysis of acoustic data. Analysis of acoustic data was conducted in stages. First, the data were sampled in real time using Spectra PLUS™ (16 384 point Fast Fourier Transform, FFT, using 16 bit processing and a 44.1 kHz sampling rate) while simultaneously being monitored aurally (NAD™ 3130 Stereo amplifier). Second, using a Macintosh™ OS-X command-line program, the large acoustic 'superfiles' from the BP were split into individual files that contained the 1 min segments of data recorded during each 5 min duty cycle. Pressure and temperature files were also split in the same manner. A second OS-X command-line program was then used to create intermediate FFT files from which the spectrograms of each 1 min acoustic record were built. Third, TIFF format images of the spectrograms were viewed using Graphics Converter (OS-X) and printed as needed in high-resolution gray scale.

Behavioural analysis. By combining the acoustic and pressure data, we identified and measured 4 mutually exclusive behavioural state categories. Three of these states, 'resting', 'surface active' and 'locomoting', listed in increasing order of activity, occurred at the water surface. The fourth behavioural state, 'diving', is divided further in the next section. Definitions of all behaviour state categories were as follows:

(1) Resting (Surface inactive): was identified by a noticeable and lasting reduction of noise in the acoustic record, while the pressure record indicated that the seal was at or near the surface; often unchanged for long time periods (i.e. >1 h). Steady breathing and at times heartbeats were often clearly audible due to the decrease in background noise level caused by the lack of movement.

(2) Surface active: defined as irregular non-dive related movements while the seal was at the surface that continued for more than 10 s at a time. Surface activity was evidenced by multiple noisy events in the acoustic record such as rhythmic rubbing-like sounds (likely caused by grooming activities) and broadband, i.e. acoustic energy spread over a wide frequency range, transient signals with high energy and fast onset times (likely caused by sudden movements) punctuated by reductions in flow noise.

(3) Locomoting: the acoustic record showed clear evidence of flipper strokes in the flow noise punctuated by regular surface intervals (visible as broadband transient signals with high energy and fast onset times). The pressure record indicated that the seal was at or near the surface and remained there. Locomoting dives were easily distinguished from shallow dives (see 'Stroke rate analysis' below) by their (1) short and consistent duration, (2) shallow and consistent depth, and (3) regularity over multiple dives.

(4) Diving: characterized by clearly defined dive events in the pressure record with less than 5 min surface intervals between dives. Three sub categories of diving were defined: (1) shallow (<20 m), (2) mid-depth (20 to 75 m), and (3) deep (>75 m). The resolution of depth was 5 m for Seal 01 and 10 m for Seals 03 and 07.

Activity budgets for each individual were calculated for the duration of the acoustic record (i.e. 3, 4, and 5 d) and were further divided into 12 and 24 h blocks for further analysis.

Stroke rate analysis. Verification that flow noise patterns were indeed flipper strokes (although aurally and visually obvious) was first conducted with a phocid pinniped (northern elephant seal *Mirounga angustirostris*; Fletcher et al. 1996) and more recently with an otariid pinniped (Antarctic fur seal *Arctocephalus gazella*; Hooker et al. 2005). In the latter case, flipper strokes were verified using a similar acoustic tag accompanied by an accelerometer and/or video recorder (Hooker et al. 2005). An example of a 60 s acoustic spectrogram with accompanying pressure record showing flipper strokes during the descending portion of a 50 m dive is shown in Fig. 1.

Measurement of stroke rate and stroke rate patterns began by dividing all swimming behaviour into the 3 categories of dive type: (1) locomoting, (2) shallow

dives, and (3) mid/deep dives. Dive category definitions were consistent with the behavioural state categories (see 'Behavioural analysis' above), with the exception that mid-depth and deep dives were combined into a single category to maintain reasonable sample sizes. The mid/deep dive category was further divided into 3 dive parts, as follows:

(1) Descent: the initial part of a dive; this began when pressure and acoustic records indicated that the seal had left the surface with depth consistently increasing (i.e. descending) and ended when 80% of the maximum dive depth was achieved.

(2) Bottom time: the middle part of a dive; this began when 80% of maximum depth was achieved and ended when the seal ascended above 80% of the maximum dive depth.

(3) Ascent: the final part of a dive; this began when the seal ascended above 80% of the maximum dive depth and ended when both the pressure and acoustic records indicated that the seal had reached the surface.

The average stroke rate (i.e. number of full stroke cycles s⁻¹ reported in Hz) and the stroke rate pattern (i.e. whether the rate was increasing, decreasing, constant, or variable) was recorded for each sample. Scores were automatically logged into an Access™ database using a customized PenDragon™ form. Strokes were counted in 2 manners. First, the total number of strokes was divided by the sample duration to give a stroke rate for each sample portion. Second, cycle times of individual strokes were measured for each sample to judge if and how the rate was changing (i.e. increasing, decreasing etc.). Sample durations were determined first by the acoustic sample (max. 1 min; constrained by the 1:5 min acoustic tag duty cycle), second by the portion of the acoustic sam-
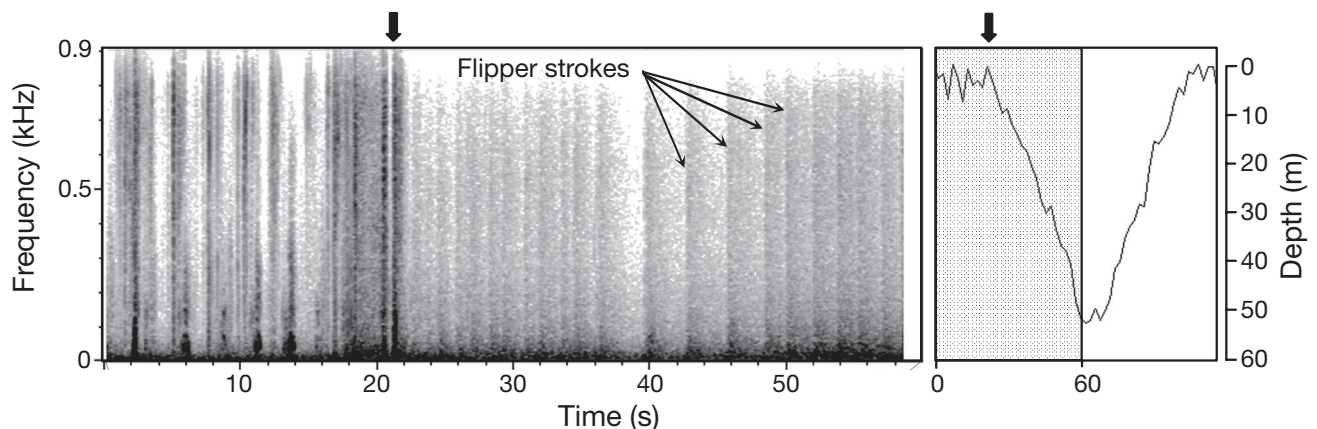

Fig. 1. A 60 s acoustic spectrogram with corresponding pressure record (stippled area) recorded from onboard a female northern fur seal while foraging at sea. The acoustic record shows ca. 20 s of surface time and the descent portion of a dive. The start of the dive is indicated in both records with an arrow, after which flipper strokes (initially rapid) are clearly evident. During the surface interval recorded here, the seal is very active and appears to have broken the surface several times just prior to descent

ple which fell into the respective category (e.g. descent portion of diving, etc.), and third by the portion of the sample which had clear unambiguous strokes for counting. Measurements of stroke rate were limited to acoustic records that covered at least 50% of the category (i.e. spectrogram covered at least 50% of the descent, bottom time or ascent). In nearly all cases, there were 10 acoustic samples per category, with each sample coming from a different dive bout. Stroke rates of locomoting dives were always estimated from the first 10 bouts of that behavioural state. For shallow and mid/deep dives, stroke rates were obtained from as many different bouts as possible, starting with the last bout in the record. Measurement began at the end of the record for these latter 2 categories because of the increased incidence of this type of diving behaviour later in the foraging trip.

Statistical analysis. Statistical analyses used Statistica™ and SPSS™ software. The effects of dive type (i.e. locomotion, shallow, mid/deep), and dive part (i.e.

descent, bottom time, and ascent) on stroke rate was analyzed using a mixed linear model with individual classified as a random factor. In this manner, individual variation was accounted for in the model. Test residuals were normally distributed. Stroke rate pattern (i.e. Constant, Increasing, Decreasing, or Variable) across the 3 dive types and 3 dive parts was a categorical variable and thus compared with chi-square tests. Relationships between stroke rate and maximum dive depth and dive duration were compared with Pearson correlation coefficients.

RESULTS

We obtained multi-day acoustic records from 3 of the 4 females instrumented during their foraging trips at sea. The recorded portion of each trip (3, 4, and 5 d for each female, respectively) in relation to the entire trip duration and location is shown in Fig. 2.
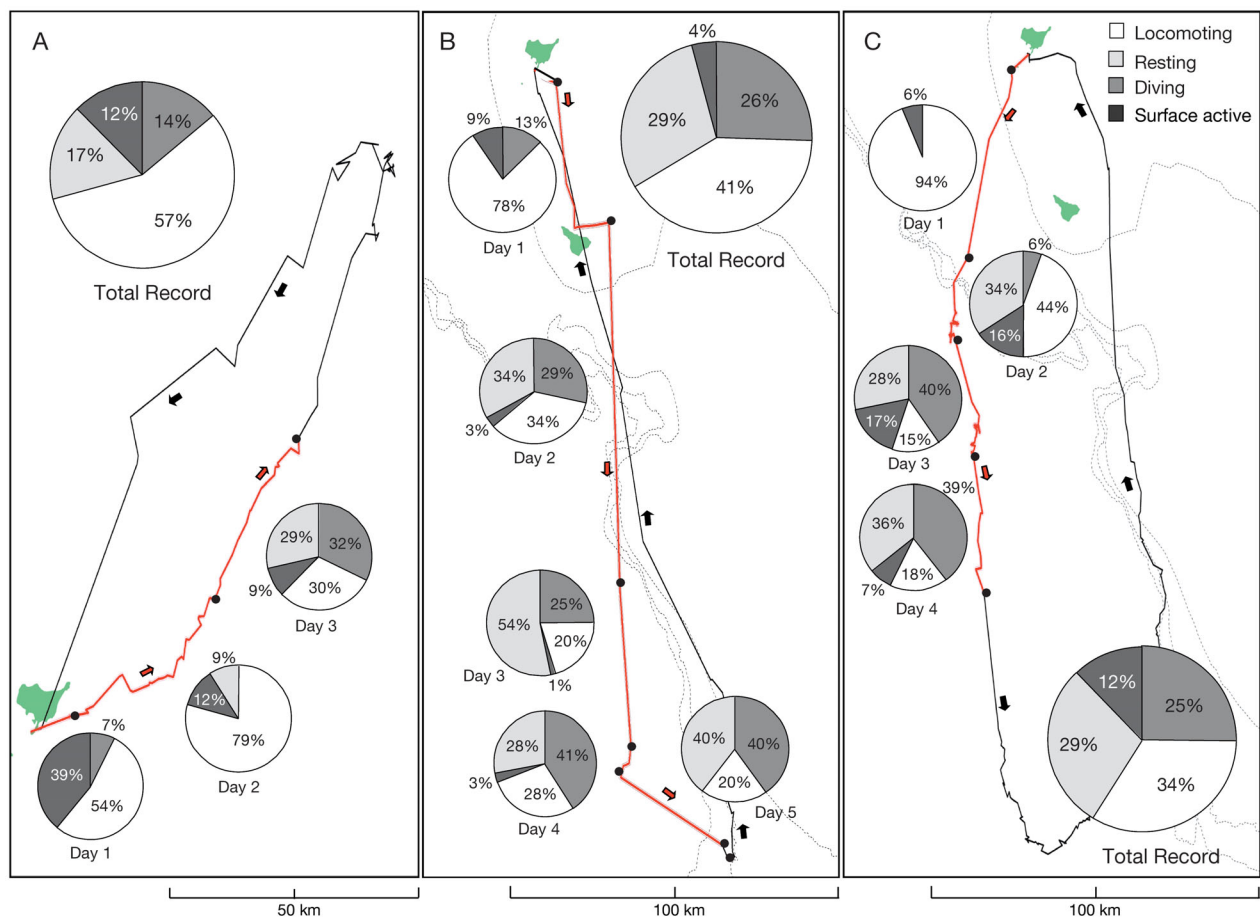

Fig. 2. *Callorhinus ursinus.* Satellite tracks of the 3 northern fur seal females (A–C) on foraging trips that began on the southernmost point of St. Paul Island, Alaska. (➡, red) Portion of each trip for which there are acoustic records; (➡) Portion of trip without acoustic records; Dotted lines are bottom contours (100 m intervals). (●) Estimated positions at 00:00 h local time each day (i.e. day marks). Activity budgets (%) for 4 mutually exclusive behavioural states (i.e. diving, locomoting, surface active, resting; see 'Materials and methods' for definitions and details) are summarized in pie charts for each 24 h period (or portion thereof) and for the total of each record

The combination of acoustic, pressure and PTT data gave clear behavioural activity budgets. The total activity budget for the recorded portion of each foraging trip for each seal is shown in Fig. 2. The data in Fig. 2 have also been divided into 1 d segments (or portions thereof), illustrating proportional changes of each activity over the course of a foraging trip.

There was no effect of dive type on stroke rate (mixed linear model: $F_{2,6.353} = 0.238$, p = 0.795); however, there was a significant difference in stroke rate among individuals ($F_{6,117} = 3.091$, p = 0.008). Average stroke rates for each dive type were very close to 0.5 Hz or 1 stroke every 2 s (Fig. 3).

Dive part had a significant effect on stroke rate (mixed linear model: $F_{2,6.383} = 6.567$, p = 0.028) in addition to there being significant differences among individuals ($F_{6,57} = 2.582$, p = 0.028). Stroke rates were fastest during descent and slowest during ascent (Fig. 3).

Stroke rate pattern, when compared using categorical variables (i.e. constant, increasing, decreasing or variable), showed significant differences across dive types (chi-square test: $\chi^2_6 = 35.784$, p < 0.0005) and dive parts ($\chi^2_6 = 19.36$, p = 0.004). Shallow and mid/deep dives were characterized by variable and decreasing stroke rates, respectively. The descents and ascents of mid/deep dives were characterized by decreasing stroke rates, while stroke rates typically increased during bottom times (Fig. 4).
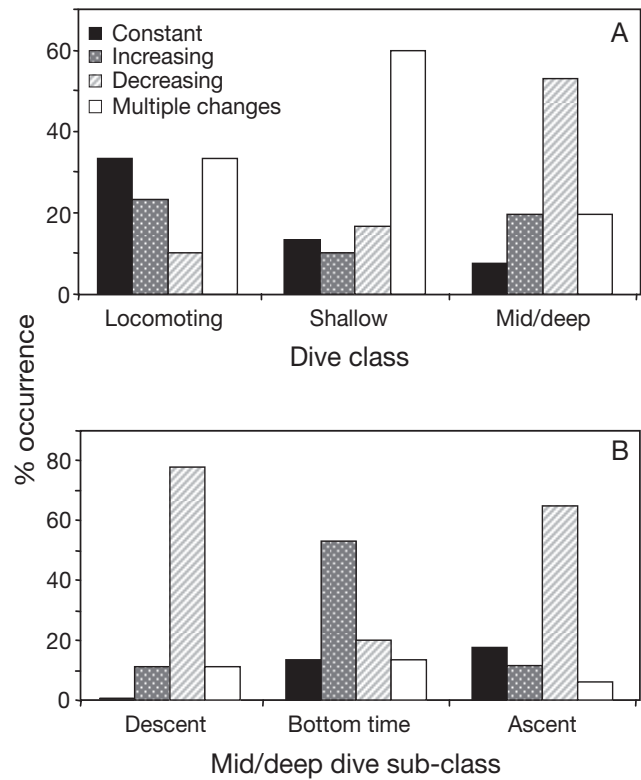

Fig. 4. *Callorhinus ursinus.* Stroke rate patterns for (A) the 3 dive types and (B) the 3 parts of mid/deep dives
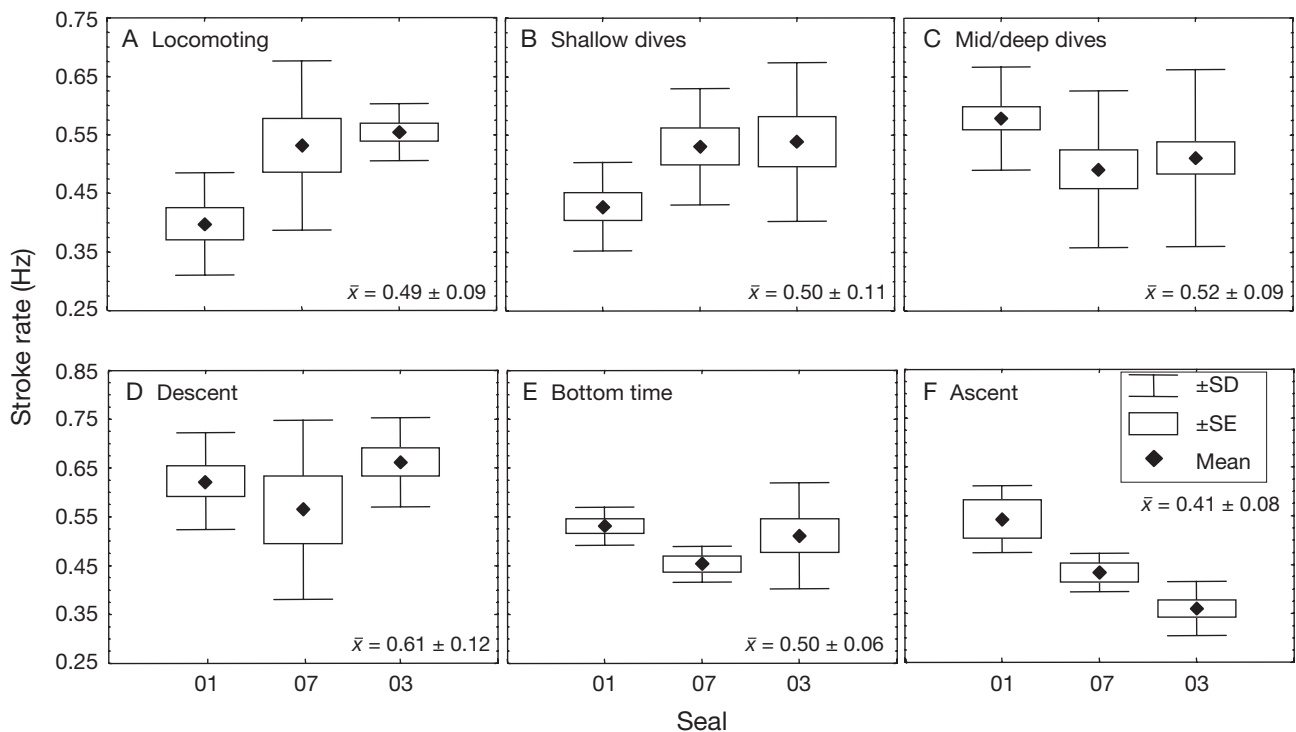

Fig. 3. *Callorhinus ursinus.* Measured stroke rate for the 3 dive types (A–C) and the 3 distinct dive parts of mid/deep dives (D–F) for 3 female northern fur seals. Seals are arranged in order of increasing mass (i.e. 37.5, 38, and 40.5 kg). Overall means ± SD for all 3 seals are also provided for each category

Finally, stroke rate did not vary consistently with either dive depth (Pearson correlation coefficient: r = 0.013) or dive duration (r = 0.083).

DISCUSSION

We examined whether a combination of acoustic, pressure and geo-location data could provide a more detailed and accurate accounting of at-sea behaviour and effort of female northern fur seals during lactation, a topic of particular interest given the present population decline. Possible broader application to other free-ranging large pelagic vertebrates is also important. We subjected the combined dataset to 2 complementary classes of analyses, activity budget and stroke rate, in order to measure the time and the effort that seals spent in different activities.

Pelagic activity budgets

Activity budgets were derived by subdividing and quantifying at-sea behaviour into 4 categories (see Fig. 2). Bailleul et al. (2005) found that Antarctic and sub-Antarctic fur seals (*Arctocephalus tropicalis* and *A. gazella*) were similar to one another in the time spent in each of 3 respective behaviour categories. Although limited, our activity proportions were comparable to the southern fur seal species; if our surface active and resting categories are combined for comparison, the proportion of time spent locomoting, diving, and resting, respectively, was 44, 22.7, and 33.3% compared to 54.3, 18.8 and 23.4% in an average for *A. tropicalis* and *A. gazella* (Bailleul et al. 2004). In all 3 species, the primary source of variation was individual seals.

Activity budgets can be measured with either TDRs or acoustic tags. TDRs that combined pressure and velocity data (e.g. Bailleul et al. 2004, Guinet et al. 2005) have a cost and memory advantage. In particular, TDRs use considerably less memory than acoustic tags, making it possible to record data over greater periods of time. This is less of a problem as memory technology advances (current BPs have 1 GB memory; the next generation should have 8 GB). The acoustic data are advantageous in that they allow additional layers of detail. For example, we could clearly differentiate between true resting behaviour (i.e. at the surface and not moving) and other surface active behaviours (e.g. grooming). It was also possible to quantify durations of specific behaviours within the 4 gross categories such as grooming bouts, vocalizations, and also external events such as ship noise (S. J. Insley, B. W. Robson & W. C. Burgess unpubl. data). In addition, the combination of acoustic and pressure data allowed detailed analysis of swimming behaviour, particularly stroke rate.

Pelagic stroke rate analyses

The data from our 3 northern fur seal females indicated that average stroke rates were similar throughout the 3 different dive types (i.e. ~0.5 Hz or 1 stroke every 2 s during locomoting, shallow and mid/deep dives). The only other stroke rate record for an otariid pinniped, a captive Australian sea lion *Neophoca cinerea*, was also 0.5 Hz (Wilson & Liebsch 2003). Our findings also fit the broad relationship found by Sato et al. (2007) between maximum stroke rate and body size. Maximum stroke rates in 4 phocid pinnipeds ranged from 0.63 (Weddell seal *Leptonychotes weddellii*) to 1.02 Hz (Baikal seal *Phoca sibirica*). The maximum stroke rates for the 3 individual northern fur seals (otariid pinnipeds) sampled here were 0.76, 0.84 and 0.89 Hz. Finally, while our sample was limited, we found significant individual variation in stroke rates. Similar intraspecific variation in stroke rates have also been observed in Weddell seals (Sato et al. 2003), Baikal seals (Watanabe et al. 2006), and sperm whales *Physeter macrocephalus* (Miller et al. 2004).

Buoyancy appears to be important in both the consistency and diversity of stroke rate patterns. During dives of mid-to-deep depth, we found that stroke rate was fastest during descent and slowest during ascent. This same pattern appears to hold true across a wide array of taxa (e.g. Emperor penguins *Aptenodytes forsteri*, van Dam et al. 2002; Magellanic penguins *Spheniscus magellanicus,* Wilson & Liebsch 2003). Related to this finding, we found that both dive descents and dive ascents were characterized by decreasing stroke rate patterns, likely driven by buoyancy acting in opposite directions (Watanabe et al. 2006). For example, during descent, an animal is increasingly propelled with negative buoyancy and inertia. As depth increases, less energy output (i.e. stroking) is necessary to maintain a constant velocity, resulting in a decrease in stroke rate with depth. The opposite is true during ascent. In both cases, the point of neutral buoyancy becomes energetically significant. Factors such as the seal′s physical features (e.g. fat ratio, body size), the amount of internal residual gas, and environmental conditions (e.g. salinity, temperature) all interact to determine the depth of neutral buoyancy. This manifests as among-individual variation in the depth at which an ascending seal can begin to glide, and has direct implications for calculating how effort varies, for example across age classes. Exhalation during dive ascents, a behaviour found in Antarctic fur seals (Hooker et al. 2005), could also directly effect buoyancy but this was not observed in northern fur seals (S. K. Hooker & S. J. Insley unpubl. data).

In contrast, bottom times were characterized by increasing stroke rates, likely a function of bursts of speed correlated with foraging events. More detailed

analysis of the stroke rate patterns during bottom times in relation to dive shape may be a useful indictor of prey type (e.g. Baechler & Beck 2002, Pütz & Cherel 2005). Furthermore, prey capture and ingestion events may be quantifiable from the acoustic records, but such events would first need to be carefully calibrated in controlled settings to be reliable.

Energy budgets

Costa & Williams (1999) summarized energetic demands in marine mammals as: total energy costs = basal metabolic costs + locomotor costs + feeding costs. Feeding costs were found to be additive, representing a 30 to 67% increase over basal metabolic rates (Costa & Williams 1999, Williams et al. 2004). What was required was a good method of estimating locomotor costs, perhaps the most significant factor in the equation. Heart rate or swim speed have proven to be poor predictors of locomotor costs because of complicating factors (nonlinearities) such as bradycardia (McPhee et al. 2003) and behaviours such as prolonged gliding (Costa & Gales 2000, Williams et al. 2000, Davis et al. 2001) and buoyancy changes (Williams et al. 2000, Sato et al. 2003). Further, it appears as though the use of gliding and buoyancy changes to save energy during dives is widespread in aquatic vertebrates (e.g. Lovvorn & Jones 1991, Skrovan et al. 1999, Nowacek et al. 2001, Sato et al. 2002). In comparison, swimming stroke rate appears to be a reliable predictor of locomotor costs (Williams et al. 2004, Wilson et al. 2006).

Measuring energy consumption in free ranging Weddell seals, Williams et al. (2004) found that stroke rate had a reasonably tight ($r^2 = 0.74$) linear fit with energy spent during dives. Each stroke had a predictable effect on O_2 reserves, allowing a reliable estimate of energy expenditure, and moreover, appeared to be relatively conserved among similar taxa (i.e. 1.44 to 2.87 J kg^{-1} $stroke^{-1}$ for 5 phocid pinniped species; Williams et al. 2004). If correct, this suggests that the total number of strokes during a dive is a good predictor of the energetic cost of the dive. Foraging events caused a predictable cost increase (44.7% for Weddell seals; Williams et al. 2004). However, counting the total number of strokes at sea, not to mention individual foraging events, is not an insignificant task. Furthermore, it is not clear whether all strokes are equal in cost.

At the species level we found a surprising degree of concordance in the overall flipper stroke rates across behaviour categories (~0.5 Hz). Furthermore, stroke rates (at least maximum stroke rates) appear to be highly predictable across a wide size range of aquatic diving taxa (Sato et al. 2007).

The implication is that a reasonable approximation of the total cost of locomotion during a foraging trip at sea, at least for a diving northern fur seal, should be possible from the simple product: stroke rate × (time diving + time travelling). These data are relatively simple to collect; total diving time can be taken from basic TDR records, while time spent travelling would need both a TDR and velocity transducer (e.g. flow meter; combined in some TDRs). It may be possible to refine the estimate further by gathering and calibrating the covarying data of seal mass, a regular procedure during instrumentation, although more data are first necessary to adequately describe this relationship. Finally, of interest as more activity budget data are collected showing complete trips, is whether the proportions of time spent swimming (total time diving + total time travelling) remain at ~70% (present study), as was also observed for 2 of the southern fur seals (Bailleul et al. 2004). This would suggest that roughly 70% of total trip length × stroke rate might serve as a reasonable first approximation of the total cost of locomotion. The similarities across taxa may suggest a widespread energy optimum or constraint.

In conclusion, we were able to quantify flipper stroke rates from acoustic records of female northern fur seals during foraging trips at sea, a critical life-history period in a species whose population is currently in decline. Combined with activity budgets, these data provide a reliable empirical measure of foraging effort that could be broadly applied.

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