

## RESEARCH ARTICLE

# Free-swimming northern elephant seals have low field metabolic rates that are sensitive to an increased cost of transport

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**ABSTRACT**

Widely ranging marine predators often adopt stereotyped, energy-saving behaviours to minimize the energetic cost of transport while maximizing energy gain. Environmental and anthropogenic disturbances can disrupt energy balance by prompting avoidance behaviours that increase transport costs, thereby decreasing foraging efficiency. We examined the ability of 12 free-ranging, juvenile northern elephant seals (*Mirounga angustirostris*) to mitigate the effects of experimentally increased transport costs by modifying their behaviour and/or energy use in a compensatory manner. Under normal locomotion, elephant seals had low energy requirements ( $106.5 \pm 28.2 \text{ kJ kg}^{-1} \text{ day}^{-1}$ ), approaching or even falling below predictions of basal requirements. Seals responded to a small increase in locomotion costs by spending more time resting between dives ( $149 \pm 44 \text{ s}$ ) compared with matched control treatments ( $102 \pm 11 \text{ s}$ ;  $P < 0.01$ ). Despite incurred costs, most other dive and transit behaviours were conserved across treatments, including fixed, rhythmic swimming gaits. Because of this, and because each flipper stroke had a predictable effect on total costs ( $P < 0.001$ ), total energy expenditure was strongly correlated with time spent at sea under both treatments ( $P < 0.0001$ ). These results suggest that transiting elephant seals have a limited capacity to modify their locomotory behaviour without increasing their transport costs. Based on this, we conclude that elephant seals and other ocean predators occupying similar niches may be particularly sensitive to increased transport costs incurred when avoiding unanticipated disturbances.

**KEY WORDS:** Accelerometer, Disturbance, Drag, Energetics, Field metabolic rate, Flipper stroking, Foraging, Locomotion, Translocation

**INTRODUCTION**

For aquatic animals, the cost of transport (COT; the energetic cost of covering a unit distance) is a substantial component of foraging efficiency; moving through water can be energetically expensive, as drag increases exponentially with increased swimming speed (Fish, 1994; Acevedo-Gutiérrez et al., 2002). Swimming behaviours should therefore contribute to an optimization of foraging strategies by reducing COT. Some marine mammals, for example, minimize energy invested in locomotion by swimming at optimal speeds and depths (Williams, 1989; Sato et al., 2007), and utilizing their

negative buoyancy to passively glide or drift during descent (Crocker et al., 1997; Skrovan et al., 1999; Costa and Gales, 2000; Williams et al., 2000; Crocker et al., 2001; Watanabe et al., 2006). In Weddell seals, the amount of time spent actively swimming shows a strong relationship with overall costs, such that each propulsive flipper stroke incrementally increases energy expenditure in a predictable manner (Williams et al., 2004b). This is likely the case for other aquatic animals (Wilson et al., 2006; Insley et al., 2007), but empirical measurements of swimming effort in highly migratory pelagic species are difficult to obtain due to the animals' elusive behaviours and far-ranging movements. Data logging instrumentation such as time-depth recorders and video cameras allow documentation of locomotory behaviours, but without an understanding of the associated energetic costs that would be necessary to quantitatively examine swimming effort.

Modification of energy-saving behaviours as a response to local disturbance or food stress can increase swimming effort by increasing the amount of time and energy spent in locomotion, resulting in lowered foraging efficiency and, therefore, lowered fitness (Costa, 2012). Marine mammals may be particularly vulnerable to disturbance as an increased COT would be superimposed on the already elevated energetic demands prescribed by endothermy in water and carnivory (McNab, 1986; Dejours, 1987; Nagy, 1987; Speakman and Król, 2010; Hudson et al., 2013). For example, northern elephant seals demonstrate increased foraging trip durations, increased travel time between foraging patches and reduced pup survivorship during severe El Niño years (Crocker et al., 2006). Similar effects on foraging economics can result as an avoidance response to anthropogenic disturbance. For example, avoidance of boat traffic was estimated to reduce energy intake by 18% for resident killer whales compared with individuals in a nearby vessel-exclusion marine protected area (Williams et al., 2006). As disruptive human ocean-based activities intensify, and as prey resources shift in response to climate change, understanding the efforts marine mammals make acquiring resources, and the behaviours that optimize these efforts, becomes increasingly important (Boyd et al., 2008). However, little is understood about the bioenergetics and routine behaviours of these cryptic animals in general, let alone how environmental change or anthropogenic disturbance might modify them.

One approach to addressing questions of disturbance to marine mammals is to measure behavioural and physiological responses to artificially increased transport costs (Boyd et al., 1997; Cornick and Horning, 2003). This concept was validated with captive Steller sea lions (*Eumetopias jubatus*), whereby increasing COT by increasing hydrodynamic drag had effects on foraging behaviour and efficiency comparable to a decrease in prey availability under standard locomotion (Cornick et al., 2006). Whether due to increased search time when prey encounter rates were low, or increased locomotion costs with added drag,

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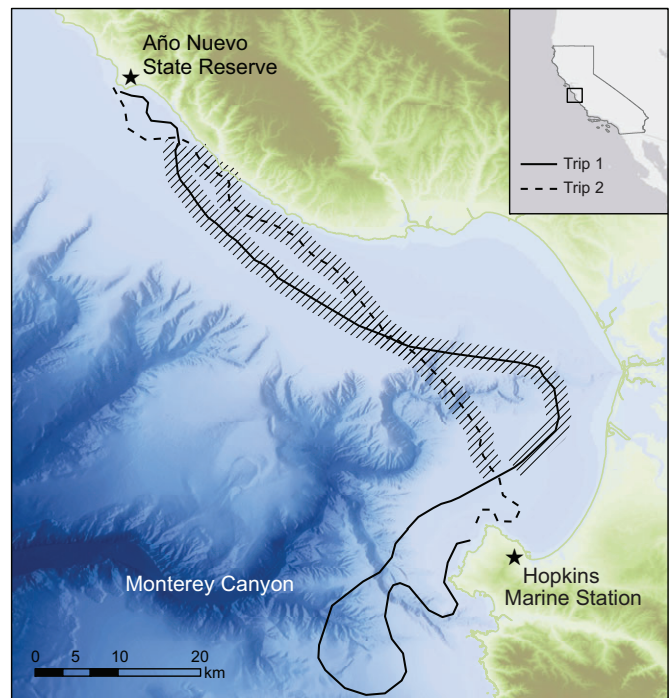
**List of symbols and abbreviations**

AIC <sub>c</sub>	corrected Akaike information criterion
BMR	basal metabolic rate (kJ kg <sup>-1</sup> day <sup>-1</sup> )
COT	cost of transport
CPS	cost per stroke (J kg <sup>-1</sup> stroke <sup>-1</sup> )
FMR	field metabolic rate (kJ kg <sup>-1</sup> day <sup>-1</sup> )
GAMM	generalized additive mixed-effects model
N <sub>s</sub>	total number of flipper strokes
OLS	ordinary least squares
<i>t</i>	time at sea (day <sup>-1</sup> )
TEE	total energy expenditure (kJ kg <sup>-1</sup> )
TBW	total body water

swimming effort increased because sea lions were working harder to find and capture prey (Cornick et al., 2006).

The logistical challenges of working with wild marine mammals have traditionally limited the use of this added-drag approach in studies of free-ranging animals. The northern elephant seal [*Mirounga angustirostris* (Gill 1866)], however, is an unusually tractable study species. Elephant seals have a life history schedule that, together with their large body size, facilitates the attachment and retrieval of archival tagging instrumentation, resulting in a rich database of information on the at-sea foraging success and migration behaviour of this species. In addition, northern elephant seals, like many marine predators (Polovina et al., 2001; Ayers and Lozier, 2010; Block et al., 2011), exploit resources throughout the northeast Pacific Ocean by tracking large-scale oceanographic features concentrating prey (Simmons et al., 2010; Robinson et al., 2012). Collectively, these factors make the northern elephant seal an ideal study system by which to gain insight into the effects of disturbance on less accessible marine species filling similar ecological niches.

The purpose of this study was to examine the impacts of increased transport costs on the swimming behaviours and bioenergetics of free-ranging northern elephant seals. Specifically, we aimed to determine: (1) the at-sea costs of locomotion for swimming seals; (2) which aspects of behaviour are measurably affected by increased locomotion costs and how seals might mitigate those costs; and (3) whether there are predictable relationships between these costs and the suite of diving and swimming behaviours most commonly measured in long-term tracking programs. To achieve these objectives, drag-inducing devices were deployed on seals to simulate disturbance and reduce performance, and potential behavioural changes were monitored using time-depth recorders (TDRs), GPS tracking devices and tri-axis accelerometers. Metabolic costs were measured simultaneously using the doubly-labelled water method (Nagy, 1983; Speakman, 1997), and a cost-per-stroke approach (Williams et al., 2004b) was used to model the relationship between individual strokes and total locomotion costs under both conditions (normal swimming, and with added drag). Using each seal as its own control, we used a short-term double translocation protocol (Andrews et al., 1997; Oliver et al., 1998; Webb et al., 1998b; Costa et al., 2003) in which elephant seals were relocated from their haul-out site along the northern side of Monterey Bay in central California to the southern side of the bay (Fig. 1). Seals captured and translocated just after returning from a long foraging trip will usually return to their rookery within 1 week. While crossing deep water, homing elephant seals demonstrate diving patterns similar to naturally migrating seals, providing valid insights into the swimming behaviours of free-ranging seals. To our knowledge, this study is the first to simultaneously measure, *in situ*, the behavioural and energetic responses of a wild marine mammal to at-sea disturbance.



**Fig. 1. Haul-out (Año Nuevo) and release (Hopkins) sites of translocated seals, ~50 km apart across Monterey Bay.** Surface tracks of one homing seal during both trips are shown as an example. For this seal, Trip 1 was under the control treatment, while Trip 2 was under the added drag treatment. Only portions of the tracks representing transit across the bay (hatched) were used in comparisons of diving behaviour and transit rates.

**RESULTS**

Table 1 summarizes the types of samples collected from the 12 seals involved in this study. In contrast to all other translocations, seal 6 was in positive energy balance after her second trip, which was indicative of foraging. In addition, 24% of her dives during this time were classified as foraging dives, compared with 0–6% (mean=1.5±0.02%) in all other translocations (Fig. 2). For these reasons, data for seal 6's second trip were excluded from energetics analyses.

**Effects of increased transport costs on metabolism, diving behaviour and swimming mechanics**

Field metabolic rates (FMRs) of free-ranging, control seals averaged 106.5±28.2 kJ kg<sup>-1</sup> day<sup>-1</sup> (mean ± s.d.), with younger seals generally having higher metabolisms than older seals (Table 2). Seals were working ~1.6 times harder with the added drag than without (Welch two-sample *t*-test, *t*=-4.8165, d.f.=16.619, *P*<0.001), with FMRs averaging 175.2 kJ kg<sup>-1</sup> day<sup>-1</sup>. This increased effort was reflected in some of the dive behaviours (Table 3). Results from generalized additive mixed-effects models (GAMMs) indicate that seals under the drag treatment increased time spent at the surface resting between dives by 46% (*P*<0.01). In addition, seals under the drag treatment ascended from their dives ~13% slower (*P*<0.05), and the magnitude of this effect decreased with increasing body size (i.e. the ascent rate of larger seals was less affected by added drag than that of smaller seals) (*P*<0.005). Likewise, seals under the drag treatment descended to depth ~10% slower (*P*<0.05), although with no interaction effect of mass.

To determine the cause of changes in ascent and descent rates, we compared swim speed and pitch angle between treatments for the

**Table 1. Summary of types of samples collected from the 12 northern elephant seals in this study**

Seal	Treatment		Behaviour			At-sea field metabolic rate
	Control	Drag	Diving	Tracking	Stroking	
1	x	x	x	x		x
2	x	x	x	x		x
3	x	x	x	x		x
4		x	x	x		x
5	x	x	x	x		x
6	x	x	x	x		x
7	x	x	x	x	x	x
8	x	x	x	x	x	x
9		x	x	x	x	x
10	x	x	x	x	x	x
11		x	x	x	x	x
12	x		x	x	x	x

Blank cells indicate no data collection. Under 'Treatment', 'Control' indicates seals swimming normally and 'Drag' indicates seals swimming with added drag.

three seals with matched treatments that were carrying accelerometers (paired Student's *t*-test; Table 4). For each dive, pitch was calculated using information from the acceleration sensor along the longitudinal axis of the seal, after correcting for the placement of the instrument on the seal (Sato et al., 2010). In combination with vertical speed from the TDR, pitch angle was used to calculate true swim speed (Sato et al., 2003) in 1 s intervals. Data were suggestive of slower swim speeds ( $P=0.07$ ) and shallower diving angles during descent ( $P=0.13$ ) under the drag treatment, with no clear effect of added drag on swim speed or diving angles during ascent ( $P=0.30$  and  $0.51$ , respectively). Individual responses varied, which, collectively with our small sample size, precludes firm conclusions in regards to changes in swim speed or pitch angle under the drag treatment. However, regardless of the specific mechanism, slower ascent and descent rates were likely an artefact of the hydrodynamic effects of the drag block on forward propulsion, rather than an actual behavioural response.

For the remaining dive variables tested, seals conserved many of their swimming behaviours across both treatments despite the elevated energetic costs of added drag. There were no differences in dive depth or duration, or time spent at depth (bottom time) relative to the entire dive duration (Table 3). Surprisingly, the elevated energetic effort

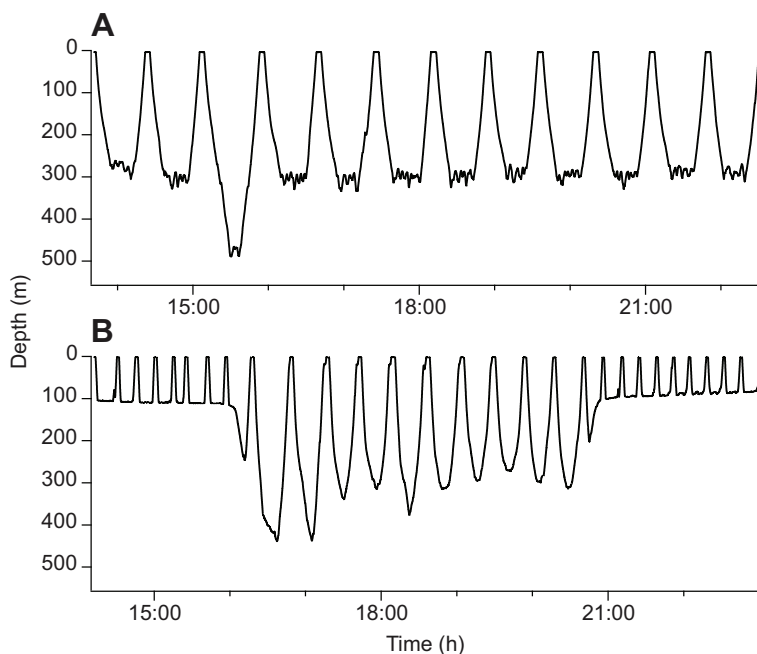
associated with the drag treatment did not measurably alter swim gait: neither flipper stroking frequency ( $1459\pm 117\text{ h}^{-1}$ ) nor amplitude differed across treatments. This result was consistent when stroking mechanics of different portions of the dive cycle (surface, descent, bottom and ascent) were compared across treatments, as well as when averages of entire dive cycles were compared.

#### Predicting costs during standard locomotion

As expected, total number of flipper strokes ( $N_S$ ) increased linearly with total time spent at sea ( $r^2=0.97$ ,  $F_{1,7}=330.3$ ,  $P<0.0001$ ; Fig. 3) according to the equation:

$$N_S = 38,629t - 10,331, \quad (1)$$

where  $t$  is time in days. There was no effect of treatment on this relationship ( $P=0.25$ ), so Eqn 1 includes data pooled from seals under both treatments. Using Eqn 1, we were able to approximate the total number of flipper strokes for the six seals in this study for which time-at-sea was measured but stroking information was not (Table 5), and compared the number of calculated strokes with the total energy expenditure measured for each. As expected, total at-sea energy expenditure (TEE;  $\text{kJ kg}^{-1}$ ) increased linearly with the



**Fig. 2. A comparison of dive types during similar time frames for two different translocations.** A shows putative foraging and was taken from the dive record of seal 6 during her second trip, which included a large proportion of foraging dives (24%) compared with all other translocations (mean= $1.5\pm 0.02\%$ ). B shows a more typical translocation dive record, with relatively deep U- and V-shaped transiting dives over the canyon flanked by shallow, benthic dives where the seal is following the bottom topography of Monterey Bay.

**Table 2. At-sea field metabolic rates (FMR) of the 12 seals in this study**

Seal	Age (years)	Mass (kg)	Treatment	At-sea FMR (kJ kg <sup>-1</sup> day <sup>-1</sup> )	Kleiber
1	1–1.5	149	Control	120.8	1.4
		140	Drag	201.6	2.4
2	1–1.5	177	Drag	156.7	1.9
		176	Control	123.2	1.5
3	1–1.5	154	Control	120.8	1.5
		154	Drag	197.9	2.4
4	1–1.5	138	Drag	202.0	2.4
5	1–1.5	138	Control	94.7	1.1
		134	Drag	181.7	2.2
6	1–1.5	156	Drag	232.5	2.8
7	2–2.5	211	Control	73.2	0.9
		210	Drag	170.9	2.2
8	2–2.5	229	Control	69.3	0.9
		225	Drag	174.6	2.2
9	2–2.5	204	Drag	156.0	2.0
10	2–2.5	197	Drag	106.3	1.3
		196	Control	96.9	1.2
11	1–1.5	147	Drag	147.1	1.8
12	1–1.5	174	Control	152.7	1.9
Mean ± s.d.	Yearlings		Control	122.5±20.6	1.5±0.3
			Drag	188.5±29.3	2.3±0.3
	2-year-olds		Control	79.8±14.9	1.0±0.2
			Drag	152.0±31.5	1.9±0.4
	All seals		Control	106.5±28.2	1.3±0.3
			Drag	175.2±33.9	2.1±0.4

Mass was measured just prior to release. 'Treatment' refers to seals swimming with and without (control) added drag. 'Kleiber' is a multiplier of Kleiber (Kleiber, 1975) predictions of mammalian basal metabolic rate.

number of flipper strokes ( $r^2=0.98$ ,  $F_{1,6}=342.1$ ,  $P<0.001$ ; Fig. 4) according to the equation:

$$TEE = 0.0039N_S - 87.62. \quad (2)$$

There was a significant effect of treatment on this relationship ( $P<0.01$ ), so Eqn 2 includes data from seals under the control treatment only. Eqn 2 also includes the six seals for which flipper stroke number was calculated using Eqn 1. When those six seals are excluded and only measured seals used, the relationship between total at-sea energy expenditure and the number of flipper strokes ( $r^2=0.99$ ,  $F_{1,2}=533.5$ ,  $P<0.005$ ) is similar (ANCOVA,  $F_{1,8}=3.901$ ,  $P=0.09$ ):

$$TEE = 0.0041N_S - 139.10. \quad (3)$$

Again, there was a significant effect of treatment on this relationship ( $P<0.05$ ), so Eqn 3 includes data from seals under the control treatment only. These results suggest that the magnitude of the effect of each flipper stroke on total energy costs (cost per stroke, CPS) is approximately  $4 \text{ J kg}^{-1} \text{ stroke}^{-1}$  in free-ranging control seals, although this is somewhat higher than measured (mean= $3.0 \pm 0.77 \text{ J kg}^{-1} \text{ stroke}^{-1}$ ,  $N=8$ ). In comparison, the CPS increased by approximately 71% for the seals under the drag treatment (mean= $5.1 \pm 0.78 \text{ J kg}^{-1} \text{ stroke}^{-1}$ ,  $N=11$ ). As was the case with the control seals (Eqns 2, 3), the relationship between total at-

sea energy expenditure and number of flipper strokes was similar under the drag treatment regardless of which seals were included in the regression (ANCOVA for slopes,  $F_{1,13}=0.53$ ,  $P=0.96$ ; ANCOVA for intercepts,  $F_{1,14}=0.57$ ,  $P=0.46$ ).

Under both treatments, CPS tended to decrease with body size (Fig. 5A), although this effect was not significant ( $P=0.08$  and  $0.36$  for seals under the control and drag treatments, respectively). While not statistically different (ANCOVA,  $F_{1,9}=0.3$ ,  $P=0.60$ ), the intercepts in Eqns 2 and 3, together with the low  $P$ -value comparing the two intercepts ( $P=0.09$ ), also support the idea of a lower CPS for larger individuals: seals whose flipper strokes were directly counted were, on average, larger and older than seals whose flipper strokes were only estimated using Eqn 2 (Tables 1, 2), again indicating a possible size effect on CPS. This trend was likely associated with the age of the animal rather than mass per se: the CPS for yearling control seals averaged  $3.45 \text{ J kg}^{-1} \text{ stroke}^{-1}$  compared with  $2.58 \text{ J kg}^{-1} \text{ stroke}^{-1}$  for 2- to 2.5-year-olds [ordinary least squares (OLS) linear regression,  $F_{1,6}=16.67$ ,  $P<0.01$ ,  $r^2=0.69$ ], suggesting increased costs in juveniles that may not be detectable with our small sample size.

This cost, however, is a whole-body cost and therefore incorporates the basal metabolic rates (BMRs) of the seals (and, therefore, gliding). After accounting for the contribution of predicted

**Table 3. Comparison of mean (±s.d.) values of various diving behaviours during directed transit across the bay for seals swimming under the control and drag treatments**

Treatment	Ascent rate (m s <sup>-1</sup> )	Bottom time: dive duration	Descent rate (m s <sup>-1</sup> )	Dive duration (s)	Maximum depth (m)	Surface interval (s)
Control	0.95±0.11	0.55±0.06	0.89±0.12	1083±123	266±43	102±11
Drag	0.82±0.19	0.55±0.07	0.80±0.12	1196±278	254±56	149±44
All	0.89±0.16*	0.55±0.06	0.84±0.13*	1139±216	260±49	125±39**

Behaviours are described in Materials and methods. Results are based on mixed effect models described in Materials and methods. Asterisks denote significant differences between treatments (\*\* $P<0.01$ , \* $P<0.05$ ).

**Table 4. Comparison of mean ( $\pm$ s.d.) values of dive ascent and descent behaviours for three seals swimming under both the control and drag treatments with accelerometers**

Seal	Treatment	Ascent				Descent			
		Pitch (deg)	Vertical rate ( $\text{m s}^{-1}$ )	Swim speed ( $\text{m s}^{-1}$ )	Relative drag	Pitch (deg)	Vertical rate ( $\text{m s}^{-1}$ )	Swim speed ( $\text{m s}^{-1}$ )	Relative drag
7	Control	29.0 $\pm$ 18.1	1.11 $\pm$ 0.34	1.51 $\pm$ 1.13		-41.0 $\pm$ 25.6	1.04 $\pm$ 0.25	1.49 $\pm$ 1.06	
	Drag	24.2 $\pm$ 20.5	0.83 $\pm$ 0.21	1.46 $\pm$ 1.10	1.06	-32.9 $\pm$ 28.6	0.89 $\pm$ 0.21	1.47 $\pm$ 1.09	0.99
8	Control	15.8 $\pm$ 24.3	0.88 $\pm$ 0.29	1.36 $\pm$ 1.00		-30.0 $\pm$ 28.2	0.79 $\pm$ 0.14	1.38 $\pm$ 1.02	
	Drag	15.0 $\pm$ 11.4	0.41 $\pm$ 0.06	1.19 $\pm$ 0.98	1.55	-25.9 $\pm$ 29.9	0.51 $\pm$ 0.10	1.22 $\pm$ 0.94	1.48
10	Control	21.6 $\pm$ 17.8	0.87 $\pm$ 0.19	1.63 $\pm$ 1.11		-33.7 $\pm$ 27.3	0.89 $\pm$ 0.16	1.61 $\pm$ 1.14	
	Drag	27.2 $\pm$ 19.2	0.89 $\pm$ 0.21	1.72 $\pm$ 1.18	0.87	-34.2 $\pm$ 24.8	0.81 $\pm$ 0.15	1.54 $\pm$ 1.09	1.33
Mean $\pm$ s.d.	Control	22.2 $\pm$ 6.6	0.95 $\pm$ 0.14	1.50 $\pm$ 0.14		-34.9 $\pm$ 5.6	0.91 $\pm$ 0.13	1.49 $\pm$ 0.12	
	Drag	22.1 $\pm$ 6.3	0.71 $\pm$ 0.26	1.46 $\pm$ 0.27	1.16	-31.0 $\pm$ 4.5	0.74 $\pm$ 0.20	1.39 $\pm$ 0.14	1.27

Behaviours are described in Materials and methods. There was a tendency for decreased swim speeds and shallower pitch angles during descent under the drag treatment, although these results were not statistically significant (paired Student's *t*-tests,  $P=0.06$  and  $0.12$ , respectively). 'Relative drag' is a drag multiplier, if optimal swim speed is proportional to  $(\text{BMR}/\text{drag})^{1/3}$ .

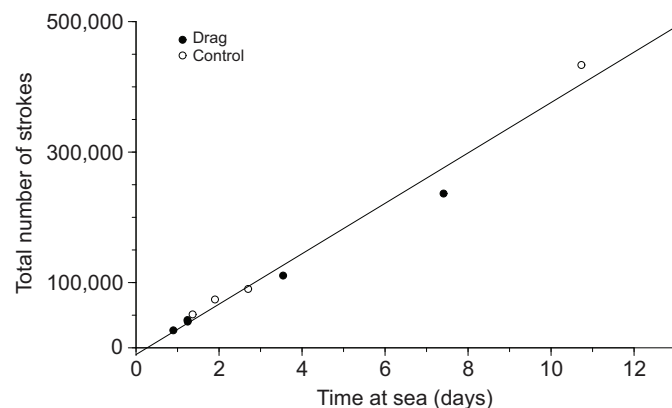
BMR (Kleiber, 1975) to FMR using Eqn 1, locomotion costs represented approximately one-quarter of the control seals' at-sea energy expenditure. There was no effect of body size on the CPS associated strictly with locomotion under the control treatment ( $P=0.35$ ), but there was a decreasing tendency under the drag treatment (Fig. 5B), although this effect was not statistically significant ( $P=0.13$ ). This suggests that locomotion costs during normal swimming are the same for each seal, regardless of body size (or age), and so the increased total CPS of younger seals is driven by elevated juvenile metabolism instead.

Total at-sea energy expenditure increased linearly with time spent at sea ( $r^2=0.98$ ,  $F_{1,6}=274.1$ ,  $P<0.0001$ ; Fig. 6) according to the equation:

$$\text{TEE} = 163.0t - 142.4. \quad (4)$$

There was a significant effect of treatment on this relationship ( $P<0.05$ ), so Eqn 4 includes data from seals under the control treatment only.

Finally, to explore the potential to use other, more commonly measured behaviours to predict the at-sea energy expenditure of wild northern elephant seals not instrumented with accelerometers, we compared the number of strokes calculated using time at sea (Eqn 1) with those calculated using a constant flipper stroking frequency of 1459 strokes  $\text{h}^{-1}$  (Table 5). The number of strokes calculated using time at sea and a constant stroke frequency were



**Fig. 3. Total number of flipper strokes increased linearly with total time spent at sea (entire measurement period).** This relationship was similar for seals regardless of treatment and can be described by the equation  $y=38,629x-10,331$  ( $r^2=0.97$ ,  $F_{1,7}=330.3$ ,  $P<0.0001$ ).

within  $11\pm 5\%$  and  $9\pm 5\%$  (absolute mean errors) of true values, respectively, demonstrating their effectiveness in estimating at-sea energy expenditure (Eqn 2) when stroking information is not directly available.

## DISCUSSION

The analyses presented here demonstrate the energetic requirements of free-ranging elephant seals, their behavioural responses to increased locomotion costs, and the predictive relationships between these costs and time spent swimming at sea – a simple metric commonly measured in long-term tracking programs. Data from this experiment specifically show that (1) free-swimming elephant seals have low field metabolic costs that approach predictions of mammalian basal metabolism with increasing age; (2) the effect of each individual flipper stroke on fuel reserves decreases as seals mature; (3) the amount of time spent at sea has a predictable effect on the total number of flipper strokes, overall field metabolic rate, and total energy expenditure of northern elephant seals; and (4) artificially increased transport costs are associated with longer resting periods between dives and slower dive descent and ascent rates, but are not associated with changes in dive duration, maximum dive depth, time spent at depth, or swimming mechanics (flipper stroking frequency and amplitude).

### Ecological implications: field metabolic rates and locomotion

An animal's FMR includes costs associated with both locomotion and basal maintenance. Thermoregulation can impose additional costs; however, these costs are expected to be trivial for elephant seals adapted to the range of water temperatures encountered in Monterey Bay (Noren, 2002). Feeding and digestion will also increase costs, but we assume these costs, if present, to be minor in their overall contribution to the total FMRs of the seals in this study. Seal 6 was likely foraging extensively during her second homing trip, but a comparison of her diving behaviour with that of the remaining seals indicates simple transiting and resting behaviours only during all other translocations (Le Boeuf et al., 1992; Crocker et al., 1997; Robinson et al., 2007; Robinson et al., 2010) (Fig. 2). For these reasons we are confident that our FMR measurements generally included only those associated primarily with locomotion and basal metabolism.

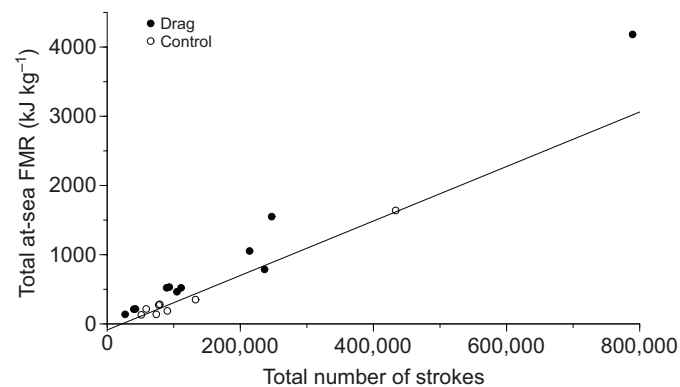
We report the mass-specific FMR of free-ranging seals to be  $106.5\pm 28.2 \text{ kJ kg}^{-1} \text{ day}^{-1}$ , a rate that is  $\sim 1.3$  times above predicted BMR (Kleiber, 1975) (Table 2). Locomotion costs were therefore responsible for approximately one-quarter of the total at-sea energy

**Table 5. Comparison of estimations of the total number of flipper strokes for each seal under each treatment (drag, control) during the entire measurement period**

Seal	Treatment	Strokes (A)	Strokes (B)	Strokes (C)	Error (A–B)	Error (A–C)	Error (B–C)
1	Control		58,665	61,513			-4.85
	Drag		89,407	88,921			0.54
2	Drag		104,590	102,457			2.04
	Control		79,052	79,689			-0.81
3	Control	77,362	78,182	78,182			-1.06
	Drag	93,350	92,436	92,436			0.98
4	Drag		789,236	712,849			9.68
	Control		132,704	127,522			3.90
5	Drag		213,878	199,892			6.54
	Drag		247,062	229,477			7.12
6	Control		47,291	51,372			-8.63
	Control	73,935	63,118	65,483	14.63	11.43	-3.75
7	Drag	40,017	37,741	42,858	5.69	-7.10	-13.56
	Control	90,292	93,914	92,939	-4.01	-2.93	1.04
8	Drag	42,478	37,633	42,762	11.41	-0.67	-13.63
	Drag	26,822	24,301	30,876	9.40	-15.11	-27.06
9	Drag	236,420	275,980	255,259	-16.73	-7.97	7.51
	Control	51,308	42,194	46,828	17.76	8.73	-10.98
10	Drag	110,902	126,561	122,045	-14.12	-10.05	3.57
	Control	433,514	404,180	369,554	6.77	14.75	8.57
Mean $\pm$ s.d. algebraic error					3.42 $\pm$ 12.3	-0.99 $\pm$ 10.4	-1.64 $\pm$ 9.3
Mean $\pm$ s.d. absolute error					11.17 $\pm$ 5.0	8.75 $\pm$ 4.8	6.79 $\pm$ 6.3

Strokes (A) includes the number of strokes measured directly from accelerometers; (B) includes values calculated based on the relationship between time at sea and total number of flipper strokes (Eqn 1); (C) includes values calculated based on a constant flipper stroking frequency of 1459 strokes  $h^{-1}$ , as presented in Results. Error columns represent percent differences in number of strokes estimated using the different approaches – for example, the Error (A–C) column represents the percent difference in strokes estimated between measured values and values calculated using a constant stroking frequency of 1459 strokes  $h^{-1}$ . The mean ( $\pm$ s.d.) error of each pairwise comparison is included below each error column.

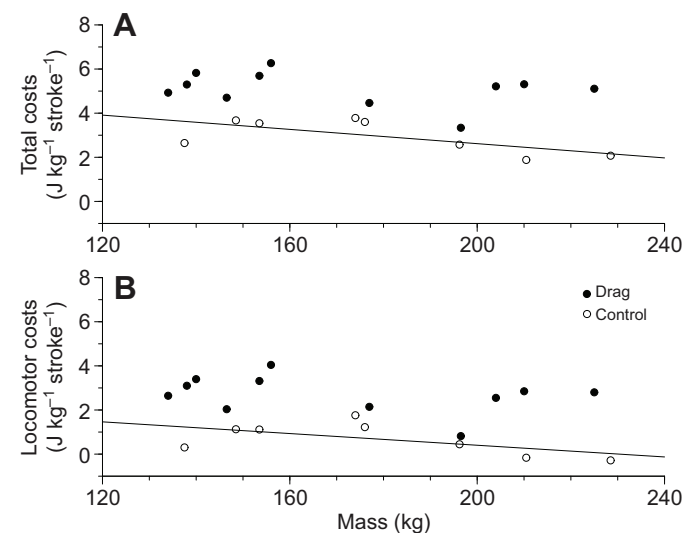
expenditure of juvenile elephant seals. As expected, when separated by age class, yearling seals had higher FMRs than older seals, averaging 1.5 and 1.0 times predicted BMR, respectively. Seals 7 and 8 showed FMRs lower than predicted BMR. They were the largest seals in this study (211 and 229 kg), suggesting that larger, adult elephant seals are capable of metabolic suppression while diving. FMR values reported here are also in agreement with those measured in captive juvenile elephant seals diving in a metabolic chamber (Webb et al., 1998a) but somewhat lower than the 1.9 times BMR reported by Williams et al. (Williams et al., 2004b) for adult Weddell seals diving for 18.35 min, the average dive duration of elephant seals in the present study. These results suggest that northern elephant seals, even as juveniles, have low metabolic costs relative to other seals, and indeed, relative to other carnivores that typically operate at 2.0–4.7



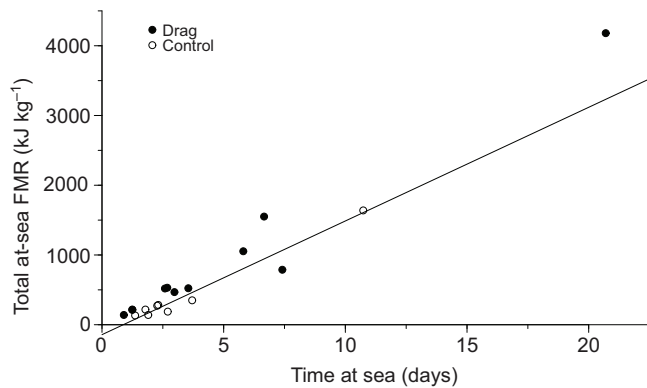
**Fig. 4. Total at-sea mass-specific energy expenditure increased linearly with total number of flipper strokes for seals swimming normally and for seals swimming with added drag.** This relationship differed between treatments so the regression line is for control seals only and can be described by the equation  $y=0.0039x-87.62$  ( $r^2=0.98$ ,  $F_{1,6}=342.1$ ,  $P<0.001$ ).

times predicted BMR on land and 4.9–6.4 predicted BMR in water (Reilly and Fedak, 1991; Costa, 1993; Nagy et al., 1999; Nagy, 2005; Costa, 2009; Speakman and Król, 2010).

Dividing total energy expenditure by the number of flipper strokes recorded gives us a predictable effect of each stroke on fuel stores:  $\sim 3.0$  J  $kg^{-1}$  stroke $^{-1}$ . We found no statistically significant effect of body size on stroke costs for elephant seals, although the data are suggestive of a decreasing trend with mass (Fig. 5) that may not have been detectable given the small sample size. However, Tift et al. (Tift et al., 2013) and Houser et al. (Houser et al., 2012)



**Fig. 5. Stroking costs had a tendency to decrease linearly with mass, although these relationships were not statistically significant.** A shows total costs, and B shows net locomotor costs. This relationship differed between treatments so the regression lines are shown for control seals only.



**Fig. 6. Total at-sea mass-specific energy expenditure [field metabolic rate (FMR)] increased linearly with time spent at sea.** This relationship was similar for seals regardless of treatment and can be described by the equation  $y = 163.0x - 142.4$  ( $r^2 = 0.98$ ,  $F_{1,6} = 2741$ ,  $P < 0.0001$ ).

measured a 7–10% reduction in resting metabolism between elephant seal pups 2 weeks (mass =  $119 \pm 18$  kg) and 7 weeks post-weaning (mass =  $81 \pm 20$  kg), indicating that the relationship between juvenile and adult metabolism is conditional on the age class of the animal if not actual body size. Indeed, when the two age classes in the present study are separated out, the CPS for yearling seals increases to  $3.45 \text{ J kg}^{-1} \text{ stroke}^{-1}$  and decreases to  $2.58 \text{ J kg}^{-1} \text{ stroke}^{-1}$  for 2- to 2.5-year-olds. This suggests that, for elephant seals, existence costs decline with age as growth costs decrease and that the true CPS for an adult northern elephant seal is likely at or below  $2.58 \text{ J kg}^{-1} \text{ stroke}^{-1}$ . This CPS value converges on those measured directly using open-flow respirometry on captive phocids (Innes, 1984; Davis et al., 1985; Fish et al., 1988) and on free-ranging Weddell seals (Williams et al., 2004b) ( $1.44$ – $2.87 \text{ J kg}^{-1}$ ).

#### Basal metabolic rates: marine mammals and juveniles

It is worth examining the assumption of Kleiber predictions (Kleiber, 1975) for BMR in the conclusions drawn thus far. There has been much discussion of the validity of measurements of BMR reported for marine mammals (Lavigne et al., 1986; Hurley and Costa, 2001; Williams et al., 2004b; Costa, 2009), with no conclusive results. Traditionally, marine mammals have been reported as having BMRs approximately two times higher than Kleiber predictions for a similarly sized terrestrial mammal (Lavigne et al., 1986; Williams et al., 2001), approaching values predicted for terrestrial, carnivorous mammals (McNab, 2000). Others have reported values approaching Kleiber predictions (Hurley and Costa, 2001; Williams et al., 2004b). Evidence suggests that much of this discrepancy can be accounted for to some degree by whether the animal is resting at the water surface or is submerged during measurements. For example, Hurley and Costa (Hurley and Costa, 2001) reported metabolic rates of two to three times expected for sea lions resting on the water surface, but approaching Kleiber predictions during prolonged submergence. Similarly, Weddell seals resting at the water surface are reported as having metabolic rates 1.8 times (Castellini et al., 1992) and 1.6 times (Williams et al., 2001; Williams et al., 2004b) higher than predicted for terrestrial mammals, but only 1.1 times higher when submerged and inactive (Williams et al., 2004b). Additionally, juvenile elephant seals resting at the water surface are reported as having metabolic rates 1.3 times higher than predicted BMR, but similar to predicted BMR while diving in a metabolic chamber (Webb et al., 1998a). As our study animals spent ~90% of their time at sea submerged, we chose to assume Kleiber predictions when factoring BMR into our

measurements of overall at-sea energy expenditure in northern elephant seals.

However, the seals in this study were juveniles, and it is typically the case that immature, growing animals have elevated mass-specific BMRs relative to adults. It is thus possible that the BMRs of the seals in this study were underestimated, which would result in an overestimation of locomotion (and therefore stroking) costs. Lavigne et al. (Lavigne et al., 1986) present evidence to suggest that the BMR of immature seals is actually 1.6 times that of Kleiber predictions for adult seals; however, it is not clear that the BMR values used in the Lavigne et al. review (Lavigne et al., 1986) were for individuals at rest, and thus we believe their estimates of BMR in juvenile seals to be overestimates. Indeed, recent studies report resting metabolic rates of newly weaned elephant seal pups of 0.9–1.4 Kleiber when submerged and 1.1–1.6 Kleiber in air (Noren, 2002; Houser et al., 2012; Tift et al., 2013), supporting the idea that basal costs of even the youngest elephant seals approach Kleiber predictions for adults during submergence.

#### Altered behaviour at sea

In this experiment, seals with added drag saw a 65% increase in FMR compared with seals under the control treatment (Table 2). The elevated cost under the drag treatment was reflected in only two major alterations to behaviour: time spent resting between dives, and descent and ascent rates while diving. Seals with added drag had longer, more variable inter-dive surface intervals ( $149 \pm 44$  s) than control seals ( $102 \pm 11$  s). This response is consistent with that of Antarctic fur seals, who demonstrated longer surface durations when their locomotion costs were artificially increased (Boyd et al., 1997). These results are not unexpected as seals diving with added drag would deplete more of their oxygen reserves during breath-hold, requiring longer recovery times at the surface. In contrast, surface intervals of the control seals in this experiment resembled those of adult elephant seals during natural migrations: short, consistent, and uncorrelated with dive duration or any other measured dive variable (Le Boeuf et al., 1988; Le Boeuf et al., 1992). For all free-ranging northern elephant seals, extended time spent resting at the surface is rare as it leaves the animal vulnerable to surface predators such as white sharks (*Carcharodon carcharias*) and killer whales (*Orcinus orca*) (Le Boeuf et al., 1998), making the response by the seals in this study noteworthy.

Seals with added drag also exhibited 10% slower descent and 13% slower ascent rates during diving (Table 3), perhaps because of shallower pitch angles and/or a reduction in swim speeds (Table 4). The reduced swim speeds measured here are indicative of a 16–27% increase in drag, if optimal speeds are proportional to  $(\text{BMR}/\text{drag})^{1/3}$  (Alexander, 1999; Motani, 2002; Sato et al., 2010). Our results are consistent with previous studies showing similar effects of instrumentation on these particular aspects of diving performance in various species (Littnan et al., 2004; Heaslip and Hooker, 2008; Latty et al., 2010). For the seals in the present study, the mechanisms behind slower descent and ascent rates, while unclear, were likely a physical artefact of the hydrodynamic drag added by the block, rather than a behavioural response per se.

None of the remaining dive variables tested here – dive duration, maximum depth, bottom time, stroke frequency or stroke amplitude – were affected by the increased costs associated with the drag treatment. Most surprising was the lack of an effect on stroking mechanics: regardless of effort, stroking amplitude (relative measure) and stroking frequency ( $1459 \text{ strokes h}^{-1}$ ) remained constant. This was surprising as we expected that, in response to increased drag, amplitude and/or frequency would either decrease in order to reduce costs or increase in order to maintain preferred swim speeds (Wilson

et al., 1986; Boyd et al., 1997; Cornick et al., 2006). The stroking mechanics of northern elephant seals appear to be relatively fixed; that is, composed of stereotypic movements coordinated by rhythmic pattern generators similar to the locomotor gaits of tetrapods and other animals (Grillner and Wallén, 1982; Grillner and Wallén, 1985; Duysens and Van de Crommert, 1998; Ijspeert, 2008). Fixed gaits allow for economy of energy expenditure (Schmidt-Nielsen, 1972; Hoyt and Taylor, 1981; Perry et al., 1988) and are 'hard-wired' components of animal locomotion subject to modulation via energetic input: once energy expenditure increases beyond some threshold value, animals will alter stride frequencies and mechanics (i.e. switch gaits) in order to maximize efficiency (Kar et al., 2003). Our results suggest that, despite the increased effort required for forward movement, alternative gaits were not attractive options for seals with added drag – seals either did not reach the inefficiency threshold necessary to trigger a gait switch, or alternative gaits did not improve energy economy. Either way, the stroking frequencies and amplitudes measured here were likely efficient under normal swimming conditions, but less so with the added drag, giving rise to the increased FMR under the drag treatment.

### Predicting the energy requirements of free-ranging animals

Marine mammals occupy high trophic positions and can have disproportionate, landscape-level effects on the structure and function of ecosystems (Bowen, 1997; Estes et al., 1998; Williams et al., 2004a; Estes et al., 2011). However, the cryptic behaviours and far-ranging movements of marine mammals make determination of energy requirements particularly challenging for this group. Studies of marine mammal foraging energetics are thus often limited to inferences about the ecology and physiology of free-ranging animals by extrapolation of measurements taken on individuals in captivity (Cornick et al., 2006; Williams et al., 2007; Liwanag, 2010). For most species, even captive studies are impossible and thus a variety of indirect approaches have been applied in trying to quantify at-sea energetics. These include the use of physiological variables such as heart rate (Williams et al., 1992; Boyd et al., 1995; Butler and Jones, 1997) and behavioural metrics such as swim speed (Kshatriya and Blake, 1988; Hind and Gurney, 1997) as proxies of metabolism, with inherent inaccuracies because of unvalidated or weak relationships and substantial variation between individuals (McPhee et al., 2003).

Our study adds to a very small body of work directly measuring energetic demands on free-ranging marine mammals, including Antarctic fur seals (Arnould et al., 1996) and Weddell seals (Castellini et al., 1992; Ponganis et al., 1993; Williams et al., 2004b); to our knowledge, it is the only one to do so for a species outside an Antarctic ecosystem. For the seals in our study, energy expenditure was predictably affected by flipper strokes (Fig. 4), the total number of which was directly and strongly correlated with time spent swimming at sea (Fig. 3). Because of these relationships, time-at-sea alone could be used as a predictor of total energy expenditure within ~10% of true values (Table 5), making it possible to estimate the energy requirements of free-ranging, cryptic seals in the absence of direct stroking information (Fig. 6).

In summary, northern elephant seals demonstrate low existence costs with field metabolic rates approaching and falling below estimates of basal metabolic requirements. This is particularly noteworthy given that the animals in this study were (1) marine mammals, (2) carnivores and (3) juveniles. Energy expenditure was strongly correlated with time spent at sea as swim gait was fixed and rhythmic, regardless of locomotion costs. Seals working harder during locomotion did not alter gait, resulting in elevated costs, with

consequent alterations in diving behaviour that did not mitigate these costs. These results indicate that elephant seals may be inflexible in their swimming behaviours, which are best suited for efficient locomotion given the mechanical constraints of movement in water. As present patterns of prey availability and distribution in the North Pacific Ocean shift in response to rapid climate change, elephant seals, like many marine predators, will need to travel farther to track prey fields with high energetic payoff, with predictable effects on energy expenditure and, ultimately, energy balance and foraging success.

## MATERIALS AND METHODS

### Experimental design and animal handling

We experimentally manipulated the COT for twelve 1- to 2.5-year-old northern elephant seals (mass range=135–230 kg) in March–May 2009 and 2010. Seals were chosen at random in an effort to randomize the sex of the study subjects; however, all seals but two (seals 2 and 4) were female. We chemically immobilized the seals for instrument attachment and recovery using established protocols (Le Boeuf et al., 1988; Le Boeuf et al., 2000). Each seal was weighed upon initial capture by suspension in a canvas sling from a tripod using a Dyna-Link scale (1000±1 kg). In most cases, seals were reweighed in subsequent handlings; for the remaining ( $N=7$  of 32 handlings), mass was estimated based on the average daily percent mass loss of weighed seals of 0.37% (OLS linear regression,  $F_{1,12}=4.465$ ,  $P=0.06$ ,  $r^2=0.24$ ), which did not differ between treatments (ANCOVA,  $F_{1,8}=0.294$ ,  $P=0.60$ ).

Using each seal as its own control, we performed double translocation experiments, transporting seals twice by truck from their haul-out rookery at Año Nuevo State Reserve in California, USA (37°6'N, 122°18'W), and releasing them into the southern end of Monterey Bay, near Hopkins Marine Station (36°37'N, 121°54'W; ~50 km straight distance across the bay; Fig. 1). Each seal was fitted with a wooden block ('drag block') representing an ~7% increase in cross-sectional area in order to elevate the cost of transport during one return trip. The blocks consisted of a 12×10×9 cm wooden cube wrapped with splicing tape, and filled with lead weights to ensure neutral buoyancy in water. The drag block was placed along the back in line with other instrumentation, at the position of the animal's maximum girth. The order of the treatments – control (no drag block) or drag treatment (added drag block) – was alternated between subjects to control for an order effect. Behavioural and energetics data were recorded simultaneously during both return trips to Año Nuevo; these measurements are described in detail below.

### Data collection and processing

#### Behaviour

For each seal we recorded coarse-scale dive and transit behaviours during homing under both treatments using TDR and GPS tracking instrumentation (Wildlife Computers, Bellevue, WA, USA: Mk9 archival tag, 1 s sampling rate and Mk10-AFB transmitting fast-GPS tag, ~45 s repetition rate, respectively). Raw GPS tracks were truncated according to departure/arrival times identified using the diving record, and then processed using a speed/turn-angle filter to remove unlikely position estimates. The raw time-series of depth measurements were processed in MATLAB using the IKNOS toolbox (Y. Tremblay, unpublished program). To make behavioural observations between treatments comparable, only data recorded during directed transit across the bay were used in analysis of diving and transiting behaviours (Fig. 1).

For the six seals measured in 2010, flipper strokes were additionally monitored using three-axis accelerometer/magnetometers (Wildlife Computers MK10-style prototype, 16 Hz sampling rate). The raw time-series of accelerometry measurements were truncated according to departure/arrival times identified using the diving record, and flipper strokes isolated using a custom-written program in Igor Pro 6.22A (WaveMetrics, Inc., USA). In brief, side-to-side flipper movements were detected as fluctuations in the transverse axis – 'swaying' acceleration – and the static (positional) component was separated from the dynamic (movement) component using a 1 Hz low-pass filter (Sato et al., 2003; Mitani et al.,



2010). The remaining peaks and troughs in the dynamic swaying acceleration with amplitudes greater than a threshold value were considered to be individual flipper strokes and were used in analyses. Amplitude thresholds differed between seals because of small differences in accelerometer placement during attachment, and perhaps because of inherent differences between seals, but threshold values were held constant between treatments within individuals. Only data recorded during directed transit across the bay were used in analysis of flipper stroking behaviours (Fig. 1).

### Energetics

At-sea metabolic rates of homing seals were measured using the doubly-labelled water method (Nagy and Costa, 1980; Nagy, 1983; Speakman, 1997), which has been validated for use with seals (Costa, 1987; Sparling et al., 2008). Prior to its first release, each seal was given a 5 ml intravenous injection of sterile tritiated water containing 1.0 mCi ml<sup>-1</sup> (2009) or 0.2 mCi ml<sup>-1</sup> (2010) of the heavy hydrogen isotope (H-3), and 71 ml (2009) or 25 ml (2010) of sterile H<sub>2</sub>O<sup>18</sup> containing 24% and 68% enrichment of the heavy oxygen isotope (O-18), respectively. These amounts were determined based on the average mass of juvenile (1–2.5 years old) elephant seals (180 kg), a desired initial enrichment of ~1 g oxygen isotope per 1 kg of animal, the half-life of O-18 (4.97 days), and the rate of water turnover in elephant seals (very slow) relative to the maximum anticipated return date of translocated seals (less than 2 weeks). Seals were not translocated a second time if blood samples were collected more than 11 days after the initial translocation, as blood O-18 levels would have been approaching natural background levels. For this reason, four of the 12 seals involved in this study were considered unsuitable for a second translocation: two returned to Año Nuevo after 11 days, and two hauled out at alternative locations that delayed accessibility to the seals for timely collection of blood samples.

Isotopes were allowed 90 min post-injection to equilibrate with the seals' body water pools (Kelso et al., 2012), and blood samples were taken pre-injection, post-equilibration and as soon as possible upon each seal's two return arrivals at Año Nuevo. Blood samples were kept on ice in a cooler while in the field. Within 6 h of collection, samples were centrifuged for 10 min at 3000 rpm, and the serum was decanted into 5 ml screw-cap vials and placed in -20°C storage until analysis. Specific activity of tritiated water was determined in triplicate by scintillation spectrometry (Beckman LS 6500, Beckman Coulter, Fullerton, CA, USA) of water obtained from serum using the dry ice distillation method (Ortiz et al., 1978). Specific activity of O-18 water was determined by mass ratio spectrometry of water distilled from blood serum (Metabolic Solutions, Nashua, NH, USA).

Initial total body water (TBW) was determined using the initial dilution space of O-18, while final TBW was calculated as the percentage initial body water multiplied by the seal's final mass (Nagy and Costa, 1980; Nagy, 1983; Speakman, 1997). CO<sub>2</sub> production was calculated using Speakman's (Speakman, 1997) two-pool equation because of the seals' large body size and in order to account for isotope fractionation (Sparling et al., 2008).

To determine whether seals were foraging while homing, we assigned behaviours to each dive using a custom-written dive classification program in MATLAB (P. Robinson, unpublished program). Classification was based on dive shape as described previously (e.g. Le Boeuf et al., 1992; Crocker et al., 1997). With only one exception (see Results), dive typing was not suggestive of the complex activities putatively indicative of foraging, but rather of simple transiting and resting behaviours only (Le Boeuf et al., 1992; Crocker et al., 1997; Robinson et al., 2007; Robinson et al., 2010). As such, we assumed homing seals were fasting and exclusively metabolizing fat, and thus used an energy conversion factor of 26.81 kJ l<sup>-1</sup> CO<sub>2</sub> in calculating FMRs (Costa, 1987). As these measurements included variable amounts of onshore FMRs for each seal (range=8–78%, mean=37±21%), FMRs were corrected for any time spent on land during the measurement period in order to estimate at-sea FMRs. FMR was normalized to estimate the at-sea component by plotting total FMR as a function of time at sea and then using least-squares linear regression equations to predict the FMR for each seal for its respective percentage of time at sea (Costa and Gales, 2003).

We determined the CPS for the six seals in this study for which we were able to measure both energetics and flipper stroking dynamics concurrently by dividing total at-sea field costs by the total number of flipper strokes

measured. In addition, we calculated the cost of locomotion ( $C_L$ ) under both treatments as the difference between the total at-sea FMR of each seal and its basal maintenance costs according to the equation:

$$C_L = \text{FMR}_{\text{at-sea}} - (\text{BMR} \times t), \quad (5)$$

where  $C_L$  and  $\text{FMR}_{\text{at-sea}}$  are in kJ kg<sup>-1</sup>, BMR is in kJ kg<sup>-1</sup> d<sup>-1</sup>, and  $t$  is the duration of the measurement period in days [modified from eqn 1 in Williams et al. (Williams et al., 2004b)]. We assumed the BMR of swimming seals to approach Kleiber predictions (Kleiber, 1975), as has been demonstrated in previous experiments on quiescent, submerged pinnipeds (Webb et al., 1998a; Costa and Williams, 1999; Hurley and Costa, 2001; Williams et al., 2004b; Costa, 2009). We examined the evidence for, and the implications of, this assumption in the Discussion.

### Data analysis

Dive duration, inter-dive rest duration, dive depth, descent and ascent rates, relative bottom time, and swimming effort during directed transit across the Monterey Bay were compared between treatments (hereafter referred to collectively as 'dive variables'). For each dive, duration was measured as the total amount of time required for one complete dive cycle (descent, bottom time and ascent); rest duration was expressed as the duration of the surface interval between dives (i.e. time spent resting between dives); depth was expressed as the maximum depth achieved; and bottom time was expressed relative to dive duration. To calculate bottom time, the bottom phase was first determined by changes in the descent and ascent slopes of the seal relative to maximum depth. In brief, the start of the bottom phase was designated by the first point within 70% of the seal's maximum depth where vertical speed fell below 20% of maximum speed during descent. The end of the bottom phase was determined in reverse. Finally, swimming effort was determined by measurements of flipper stroking frequency and amplitude, as described above. As stroking amplitude depends on the placement of the instrumentation on the animal, which varied slightly across individuals, amplitudes between treatments were only compared within individuals, and thus are reported here as relative values only.

Due to the non-linear, nested structure of the data, GAMMs were used to model the effects on the dive variables of the continuous explanatory variables – time of day, elapsed time into trip and mass – and the factor explanatory variables – treatment (control or added drag), deployment number (whether it was the animal's first or second trip) and individual animal (random effect). Separate models were fitted for each of the response dive variables listed above. The intercept of these models was permitted to vary randomly across animals and any within-seal autocorrelation was modelled using a first-order autoregressive autocorrelation structure to account for repeated measurements on the same animal during a trip. A power variance function structure was used to model within-group heteroscedastic error, allowing the variance to increase as a power of the absolute fitted values. Candidate models were of the form:

$$Y_{ij} = \beta_0 + a_i + f_1(\text{Hour}) + f_2(\text{Elapsed time}) + \beta_1 \text{Treatment} + \beta_2 \text{Mass} + \beta_3 \text{Deploy} + \varepsilon_{ij}, \quad (6)$$

where  $Y_{ij}$  is the  $j$ th observation from the  $i$ th animal;  $\beta_0$  is the overall intercept;  $a_i \sim N(0, \sigma_a^2)$  is the random effect (intercept) of the  $i$ th animal;  $f_1$  and  $f_2$  represent penalized, cyclic cubic regression spline functions with  $f_1$  having the same start and end point;  $\beta_1$ ,  $\beta_2$  and  $\beta_3$  are coefficients; and  $\varepsilon_{ij}$  is the residual random error term with specified power variance function and correlation structure. Interactions between the smooth and factor terms were also modelled, where appropriate.

Analyses were performed using the 'gamm' function (with restricted maximum likelihood method) of the 'mgcv' package (Wood, 2006) in R 2.15.1 (R Development Core Team, 2012). All model combinations were fitted with best model fits based on the lowest Akaike information criterion corrected for small sample size (AIC<sub>c</sub>), and AIC<sub>c</sub> differences less than 2.0 were considered substantial evidence for competing models, with preference given to models with fewer terms (Burnham and Anderson, 2002; Zuur, 2009). Residual plots and partial residual plots were examined to assess model fits. The significance of terms included in the final models was examined using approximate  $P$ -values from the 'mgcv' output.

We used OLS models to explore potential predictive relationships between number of flipper strokes, FMR, time spent at sea, cost per stroke and mass. We used data from the entire trip in these comparisons, as the resolution of the metabolic data did not make it possible to parse out FMR during directed transit across the bay from the total FMR of the entire trip. In each pairwise comparison, we tested for a treatment effect by including the interaction between the response variable and treatment (control or added drag) in the model. Pooled data were used where no significant treatment effect was detected, but kept separate otherwise. In the latter case, regression equations are not presented for data under the drag treatment as, representing an artificial situation, they would have no biologically relevant predictive value.

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#### Competing interests

The authors declare no competing financial interests.

#### Author contributions

J.L.M., S.E.S. and D.P.C. conceived the question and design of the experiment. J.L.M. carried out the experiment, analyzed the data and wrote the manuscript. S.E.S. and B.I.M. assisted with data collection and sample processing, and, along with D.E.C., contributed to data analysis and interpretation. T.M.W. contributed to data interpretation, and along with all other authors, contributed to the writing of the manuscript.

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