Depletion of deep marine food patches forces divers to give up early

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Summary

1. Many optimal foraging models for diving animals examine strategies that maximize time spent in the foraging zone, assuming that prey acquisition increases linearly with search time. Other models have considered the effect of patch quality and predict a net energetic benefit if dives where no prey is encountered early in the dive are abandoned. For deep divers, however, the energetic benefit of giving up is reduced owing to the elevated energy costs associated with descending to physiologically hostile depths, so patch residence time should be invariant. Others consider an asymptotic gain function where the decision to leave a patch is driven by patch-depletion effects – the marginal value theorem. As predator behaviour is increasingly being used as an index of marine resource density and distribution, it is important to understand the nature of this gain function.

2. We investigated the dive behaviour of the world's deepest-diving seal, the southern elephant seal *Mirounga leonina*, in response to patch quality. Testing these models has largely been limited to controlled experiments on captive animals. By integrating *in situ* measurements of the seal's relative lipid content obtained from drift rate data (a measure of foraging success) with area-restricted search behaviour identified from first-passage time analysis, we identified regions of high- and low-quality patches.

3. Dive durations and bottom times were not invariant and did not increase in regions of high quality; rather, both were longer when patches were of relatively low quality. This is consistent with the predictions of the marginal value theorem and provides support for a nonlinear relationship between search time and prey acquisition.

4. We also found higher descent and ascent rates in high-quality patches suggesting that seals minimized travel time to the foraging patch when quality was high; however, this was not achieved by increasing speed or dive angle. Relative body lipid content was an important predictor of dive behaviour.

5. Seals did not schedule their diving to maximize time spent in the foraging zone in higher-quality patches, challenging the widely held view that maximizing time in the foraging zone translates to greater foraging success.

Key-words: aerobic dive limit, buoyancy, functional response, patch model, rate maximizing

Introduction

Optimal foraging theory is a widely used conceptual framework for understanding the mechanisms driving the behaviours of animals in their quest for food. It has been influential in behavioural ecology for over four decades because it confers apparent rigour and generates testable

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Table 1. Ranked linear mixed-effects models of each of the dive variables as the response variable explained by patch quality (PQ), relative lipid content (Fat) and habitat type (Hab). Shown are the three top-ranked models and the intercept-only model. Full results are shown in Table S1. Also shown are the number of estimable model parameters (k), maximum log-likelihood (LL), Akaike's information criterion corrected for small samples (AIC_c), the difference in AIC_c for each model from the top-ranked model (ΔAIC) and the model weight ($wAIC_c$)

Model	k	LL	AIC_c	ΔAIC_c	$wAIC_c$
Max depth ~ Hab + PQ + Fat + Fat × PQ	7	−5710·81	11437·71	0·00	0·40
Max depth ~ Hab + PQ + Fat + Fat × Hab	7	−5711·14	11438·36	0·65	0·29
Max depth ~ PQ + Hab + PQ × Hab	6	−5712·53	11439·11	1·40	0·20
Max depth ~ 1	3	−5726·32	11460·65	22·94	<0·01
Duration ~ Hab + PQ + Fat + Fat × Hab	8	−3164·05	6346·16	0·00	0·99
Duration ~ Hab + PQ + Fat	7	−3174·21	6364·46	18·30	<0·01
Duration ~ Hab + PQ + Fat + Fat × PQ	8	−3173·28	6364·62	18·46	<0·01
Duration ~ 1	4	−3464·73	6939·47	593·31	<0·01
Bottom time ~ Fat + PQ + Fat × PQ	7	−2899·02	5814·07	0·00	0·41
Bottom time ~ Fat + PQ	6	−2900·45	5814·93	0·86	0·26
Bottom time ~ Hab + PQ + Fat + Fat × PQ	8	−2898·66	5815·39	1·32	0·21
Bottom time ~ 1	4	−3147·55	6305·11	491·04	<0·01
% Bottom time ~ Fat + PQ	6	1212·70	−2411·38	0·00	0·97
% Bottom time ~ Hab + PQ + Fat + Fat × Hab	8	1210·66	−2403·27	8·11	0·02
% Bottom time ~ Hab + PQ + Fat	7	1208·93	−2401·81	9·57	0·01
% Bottom time ~1	4	1176·17	−2342·35	69·03	<0·01
Bottom speed ~ Hab + PQ + Fat + Fat × PQ	7	75·67	−135·26	0·00	0·84
Bottom speed ~ Fat + PQ + Fat × PQ	6	72·93	−131·80	3·46	0·15
Bottom speed ~ Fat + Hab	5	68·76	−125·49	9·77	0·01
Bottom speed ~ 1	3	54·17	−100·33	34·93	<0·01
Descent speed ~ Hab	4	198·91	−387·79	0·00	0·57
Descent speed ~ 1	3	196·50	−384·98	2·81	0·14
Descent speed ~ Fat + Hab	5	198·49	−384·95	2·84	0·14
Ascent speed ~ Fat	4	340·10	−670·17	0·00	0·88
Ascent speed ~ Fat + PQ	5	338·05	−664·06	6·10	0·04
Ascent speed ~ Fat + Hab	5	338·02	−664·01	6·16	0·04
Ascent speed ~ 1	3	311·92	−615·82	54·35	<0·01
Descent rate ~ PQ	4	971·81	−1933·59	0·00	0·77
Descent rate ~ Fat + PQ	5	971·10	−1930·17	3·42	0·14
Descent rate ~ 1	3	968·18	−1928·35	5·23	0·06
Ascent rate ~ Fat + PQ	5	811·15	−1610·26	0·00	0·79
Ascent rate ~ Hab + PQ + Fat + Fat × Hab	7	811·21	−1606·33	3·92	0·11
Ascent rate ~ Fat + PQ + Hab	6	809·53	−1605·00	5·26	0·06
Ascent rate ~1	3	784·69	−1561·36	48·89	<0·01
Descent angle ~ Fat + Hab	5	−2273·53	4559·11	0·00	0·33
Descent angle ~ Fat + PQ + Hab	6	−2272·77	4559·59	0·48	0·26
Descent angle ~ Hab + PQ + Fat + Fat × PQ	7	−2271·91	4559·91	0·80	0·22
Descent angle ~ 1	3	−2282·99	4574·00	14·89	<0·01
Ascent angle ~ Hab + PQ	5	−2173·93	4359·89	0·00	0·41
Ascent angle ~ PQ + Hab + PQ × Hab	6	−2173·07	4360·21	0·31	0·36
Ascent angle ~ Fat + PQ + Hab	6	−2174·50	4363·06	3·17	0·09
Ascent angle~ 1	3	−2181·81	4371·62	11·73	<0·01

predictions (Perry & Pianka 1997). Optimal foraging models predict the decisions that foraging animals should make, such as which prey items to consume or when to abandon foraging in a particular area (Stephens & Krebs 1986). The currencies commonly used to evaluate these decisions are the maximization of energy intake rate and minimization of time spent obtaining food (Schoener 1971). The ability to test the validity of these models in free-living animals is hampered by the difficulty of quantifying available food resources in combination with the animal's behavioural responses. The decisions made in spatially and temporally heterogeneous environments underpin an animal's ability to cope with both anticipated

and unexpected fluctuations in food availability, and adjust its behaviour to maximize the opportunities presented under a current set of particular environmental conditions.

The marginal value theorem is one of the most familiar models analysing and predicting how long a forager should stay in a patch. A patch type has associated with it a particular gain function which is assumed to increase asymptotically to a maximum value (Stephens & Krebs 1986). To maximize its rate of gain of resources from such patches, a predator's residence time should be related to the cost of travel to the patch. The model asserts that when travel time increases, so too should patch residence
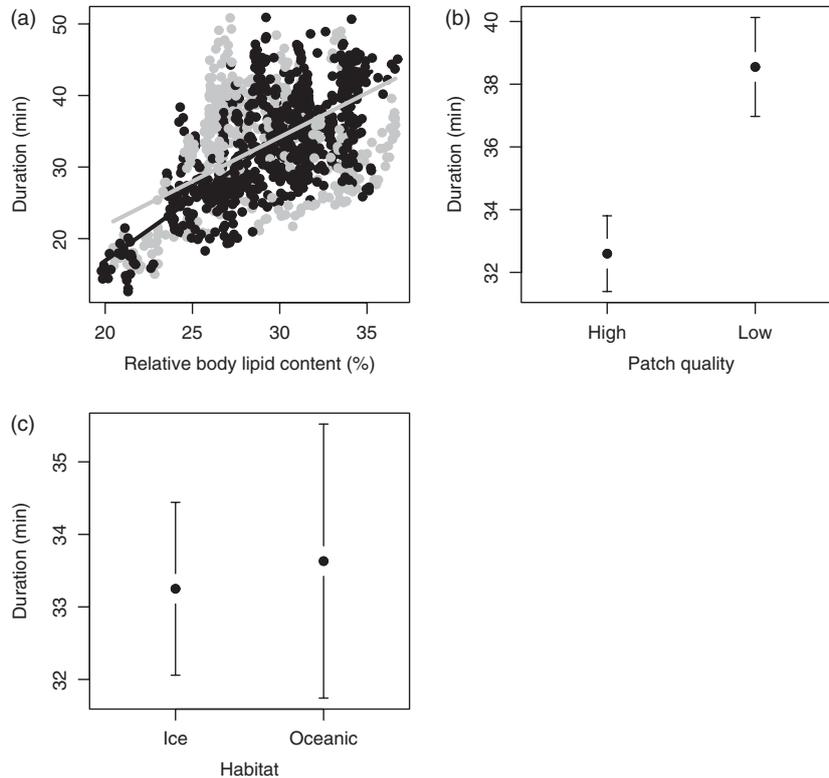
Fig. 1. Relationship between dive duration to the predictors in the top-ranked model from the suite of models tested to explain dive duration. (a) Dive duration vs. relative lipid content for ice- (black) and oceanic (grey) habitat. Shown are fitted lines among seals for high-quality patches (low quality was similar) from the top-ranked model for each habitat category. (b) Fitted values from the top-ranked model showing dive duration relative to patch quality and (c), dive duration relative to habitat type.
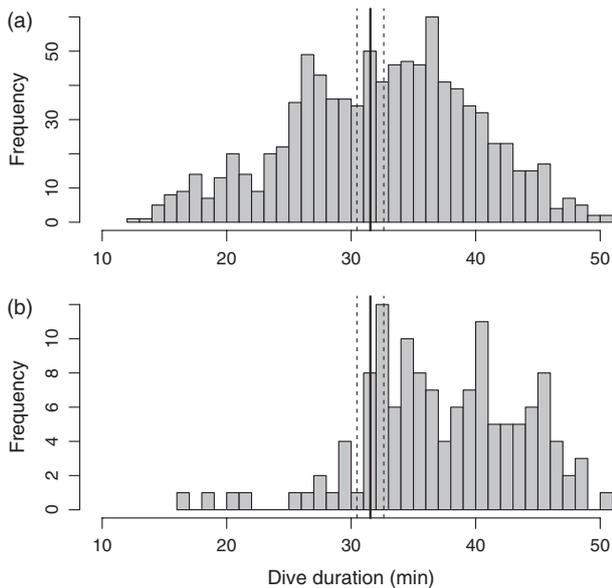
Fig. 2. Frequency distributions of dive durations in high- (a) and low-quality (b) patches in relation to the theoretical aerobic dive limit (ADL). Vertical lines show mean and standard deviation of the theoretical ADL.

time. If patches vary in quality, a predator should leave a patch when the marginal capture rate falls to the average rate for the habitat (Charnov 1976). The model therefore predicts that animals foraging in a patch with better-than-average resources should spend relatively less time there (compared with a lower-quality patch) owing to depletion of prey resources or evasion by prey.

Air-breathing aquatic predators are a special case for optimal foraging models because their prey is found in deep waters, imposing the consideration of oxygen limitation into optimality models (Dunstone & O'Connor 1979). Without (the typically rare) data describing patch quality, an assumption of most optimal foraging models for diving air breathers is that the relationship between prey acquisition and time spent searching is linear. Theoretical studies have therefore examined strategies that maximize time spent in the foraging zone (Kramer 1988; Houston & Carbone 1992; Carbone & Houston 1994). To achieve this, predators are predicted to minimize their transit time to the foraging zone and their subsequent surface time to recover from oxygen depletion and/or the accumulation of toxic by-products produced during facultative anaerobic respiration (Ydenberg & Clark 1989). Many models have considered the need to re-oxygenate as the prime reason for terminating a dive, and thus, most dive durations should be at or approach the aerobic dive limit (ADL) (Thompson & Fedak 2001) – that is, the maximum time of submergence allowed by the body's total oxygen reserves without accumulating blood lactate from anaerobic respiration (Hindell *et al.* 1992). The

Table 2. Mean descent speed, bottom speed (bottom of dive), ascent speed and dive duration calculated for high- and low-quality patches. The last two columns show the minimum cost transport (C_t) speed and the theoretic aerobic dive limit (ADL_t) calculated using measurements made just after seals came ashore for parturition

Seal ID	Descent speed		Bottom speed		Ascent speed		Dive duration		C_t	ADL_t
	High	Low	High	Low	High	Low	High	Low		
b34704	1.68 ± 0.42	1.73 ± 0.2	1.49 ± 0.48	1.95 ± 0.27	1.89 ± 0.32	2.12 ± 0.1	30.39 ± 8.42	35.55 ± 3.35	2.76	32.66
b90004	2.22 ± 0.2	NA	1.78 ± 0.32	NA	2.63 ± 0.24	NA	30.76 ± 7.41	NA	2.77	32.19
c16104	1.31 ± 0.3	NA	1.15 ± 0.38	NA	2.14 ± 0.21	NA	29.65 ± 6.02	NA	2.68	32.18
c16202	1.47 ± 0.16	NA	0.97 ± 0.15	NA	1.58 ± 0.19	NA	32.16 ± 4.63	NA	2.63	30.36
c16204	2.11 ± 0.28	NA	1.48 ± 0.33	NA	2.34 ± 0.25	NA	34.94 ± 5.34	NA	2.61	30.29
c16302	1.96 ± 0.52	1.8 ± 0.96	1.53 ± 0.82	1.55 ± 1.17	2.44 ± 0.44	2.42 ± 0.56	26.27 ± 6.63	28.82 ± 6.75	2.63	NA
c16305	1.53 ± 0.24	1.15 ± 0.1	0.97 ± 0.29	0.59 ± 0.13	2.18 ± 0.32	1.98 ± 0.11	30.28 ± 6.22	36.64 ± 0.97	2.78	31.69
c31002	1.51 ± 0.35	1.3 ± 0.06	1.11 ± 0.41	1.23 ± 0.12	1.73 ± 0.23	1.44 ± 0.07	25.89 ± 7.47	32.01 ± 2.05	2.62	30.22
c31202	1.22 ± 0.23	1.26	0.88 ± 0.35	0.81	1.7 ± 0.12	1.78	37.77 ± 4.79	39.92	2.62	30.61
c69902	2.51 ± 0.4	1.88 ± 0.37	2.17 ± 0.26	1.43 ± 0.6	2.69 ± 0.23	2.58 ± 0.28	28.86 ± 9.17	42.49 ± 4.25	2.95	33.64
f99305	1.31 ± 0.18	1.22 ± 0.06	0.72 ± 0.24	0.55 ± 0.11	1.74 ± 0.35	1.43 ± 0.17	35.65 ± 7.63	40.73 ± 3.40	2.75	31.19
h28504	2.14 ± 0.4	1.66 ± 0.25	1.68 ± 0.59	1.01 ± 0.17	2.82 ± 0.26	2.66 ± 0.21	32.76 ± 9.64	41.91 ± 2.28	2.67	31.13
h83304	1.77 ± 0.26	1.86	0.71 ± 0.13	0.77 0.13	1.97 ± 0.25	1.86	40.47 ± 4.94	48.44	2.79	32.30
Mean ± sd	1.75 ± 0.41	1.54 ± 0.30	1.28 ± 0.45	1.10 ± 0.48	2.14 ± 0.41	2.03 ± 0.46	31.99 ± 4.28	38.50 ± 5.93	2.71 ± 0.10	31.54 ± 1.08

observation that the dive durations of many species do not fit this prediction has prompted the consideration of other factors affecting the decision to leave a patch, namely, aspects of patch quality (Mori 1998; Thompson & Fedak 2001; Mori *et al.* 2002). For example, Thompson & Fedak (2001) developed a model that examined the effects of variation in dive duration in response to changes in patch quality, whilst taking into consideration the constraints of limited oxygen stores. They predicted that divers could increase their average rate of energy gain by using simple rules of thumb to assess patch quality by giving up on dives where no or few prey items are encountered before some threshold time. However, the benefit of adopting such a strategy was reduced for deep divers owing to the high energetic costs associated with obtaining deep depths. This model is conceptually different from the marginal value theorem in that it assumes a linear gain rate and the decision to leave is not driven by patch-depletion effects.

While diving is ultimately constrained by physiology in air breathers, the costs associated with travelling to deep water and remaining there for sufficient time to forage can be minimized by behavioural mechanisms that reduce oxygen consumption, such as adjustments of swim speed during transit and foraging (Thompson, Hiby & Fedak 1993). Thompson, Hiby & Fedak (1993) developed an optimality model that examined how swim speeds affected the energy/ time budgets of a dive and how variation in swimming speed, prey movements and prey density affect the rate of energy acquisition. To reduce oxygen consumption for a given distance travelled, their model predicts that divers should swim at minimum cost of transport during the ascent and descent phases, and then forage at the speed which maximizes energy gain per unit of energy expended (Thompson, Hiby & Fedak 1993). Increases in body angle relative to the horizontal during descent and ascent can also reduce travel time (Thompson & Fedak 2001).

Although behavioural mechanisms to reduce oxygen consumption can be important, diving animals will also be largely affected by buoyancy, which is in turn determined by individual body composition (i.e. relative quantities of lipid and nonlipid tissues) (Crocker, Le Boeuf & Costa 1997). Buoyancy affects rates of ascent and descent (Webb *et al.* 1998; Beck, Bowen & Iverson 2000; Sato *et al.* 2003), with higher buoyancy impeding descent and shortening bottom times (Beck, Bowen & Iverson 2000). Non-neutral buoyancy can also aid in descent or ascent (relative to water density) by permitting gliding during which active swimming can be temporarily interrupted (Sato *et al.* 2003), For example, Weddell seals can reduce energetic cost by employing gliding for up to 60% of diving time (Williams *et al.* 2000).

To test the predictions of foraging models in seals, it is therefore important, where possible, to incorporate measures of buoyancy with information describing the available prey field. Measuring the prey field is difficult for many species, especially for wide-ranging predators that
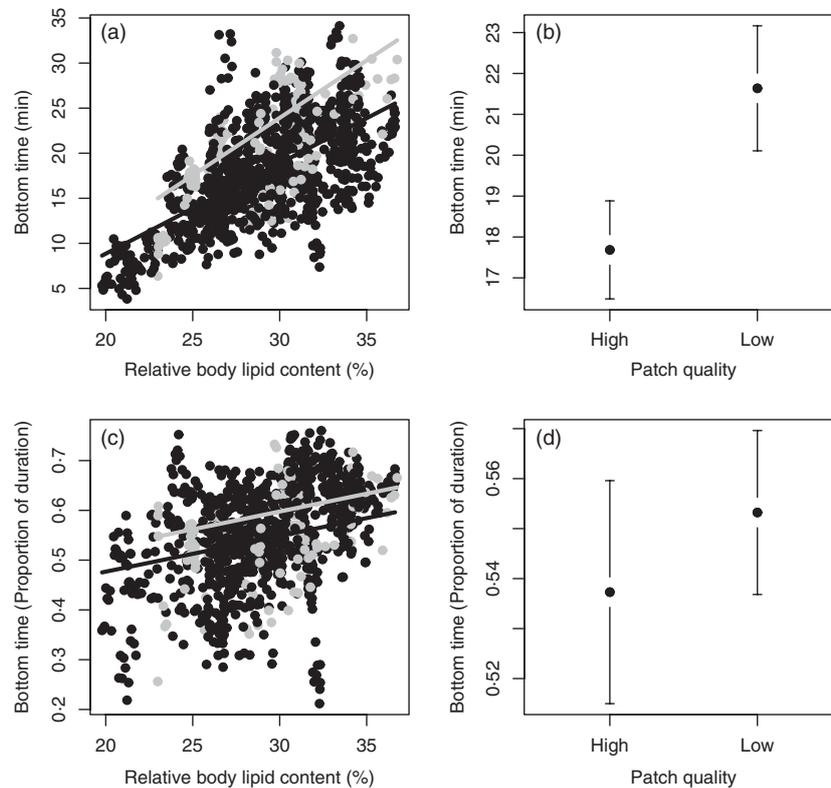
Fig. 3. Bottom time and proportional bottom time relative to the predictors in the top-ranked model from the suite of models tested to explain bottom time and proportional bottom time. (a) Bottom time vs. relative lipid content for high- (black) and low-quality (grey) patches. Shown are fitted lines among seals for ice habitat (oceanic was similar) from the top-ranked model for each patch quality category. (b) Fitted values from the top-ranked model showing bottom time vs. patch quality, (c) Proportional bottom time vs. relative lipid content for high- (black) and low-quality (grey) patches (fitted lines among seals for ice habitat for each patch quality category) and (d) Fitted values from the top-ranked model showing proportional bottom time vs. patch quality.

traverse millions of square kilometres of open ocean (Hindell 2008); therefore, proxies of prey encounter and ingestion are often used to provide indirect information. Various indices of patch quality have been developed from remotely sensed dive data such as the time spent at or the number of speed accelerations occurring during the bottom of dives (Mori *et al.* 2002; Horsburgh *et al.* 2008). While these can provide an index of foraging behaviour and prey encounter, they still do not necessary indicate when and where successful foraging occurs. To bridge this gap, we previously developed a model to estimate the relative lipid content of seals at sea from passive drift rates (Thums, Bradshaw & Hindell 2008a). This method allows for the tracking of changes in daily relative lipid content and thus for inferring foraging success and buoyancy. By integrating such data with animal movement behaviour (e.g. slow and sinuous vs. rapid and directed paths), it is possible to identify high- (high sinuosity combined with increasing relative lipid change) and low- (low sinuosity combined with reduced relative lipid change) quality patches. This explicitly tested the assumptions and predictions of optimal foraging models for a free-ranging diver, making it one of the few studies to do so.

Elephant seals (*Mirounga* spp.) are ideal candidates for investigating foraging decision processes owing to their

continuous, prolonged and deep dives (Le Boeuf *et al.* 1988; Hindell *et al.* 1992). As the time-energy trade-off becomes more constrained in deep divers, we hypothesize that diving behaviour will be more influenced by oxygen stores than changes in behaviour mediated by patch quality. Elephant seals lay down large lipid stores during their winter migration, so switching from neutral to positive buoyancy during the 8- to 9-month winter foraging trip will have a large effect on dive behaviour. Given that elephant seal use distinct oceanic habitats (presumably containing different prey species) in which foraging success differs (Thums, Bradshaw & Hindell 2011), we further hypothesize that dive behaviour is habitat-dependent. Here we regard elephant seals as central-place foragers, with the surface being the central place, the ascent and descent being the travel, and the time spent on the bottom of the dive the patch residence time (Houston & McNamara 1985). We used this scale of foraging, combined with our daily measure of patch quality to test two opposing predictions derived from the optimal foraging models for breath-hold divers: (i) deep divers should stay in the patch up to their ADL regardless of patch quality owing to the elevated energy costs associated with deep diving and (ii) deep divers foraging in a relatively high-quality prey patch should stay longer in that patch. We
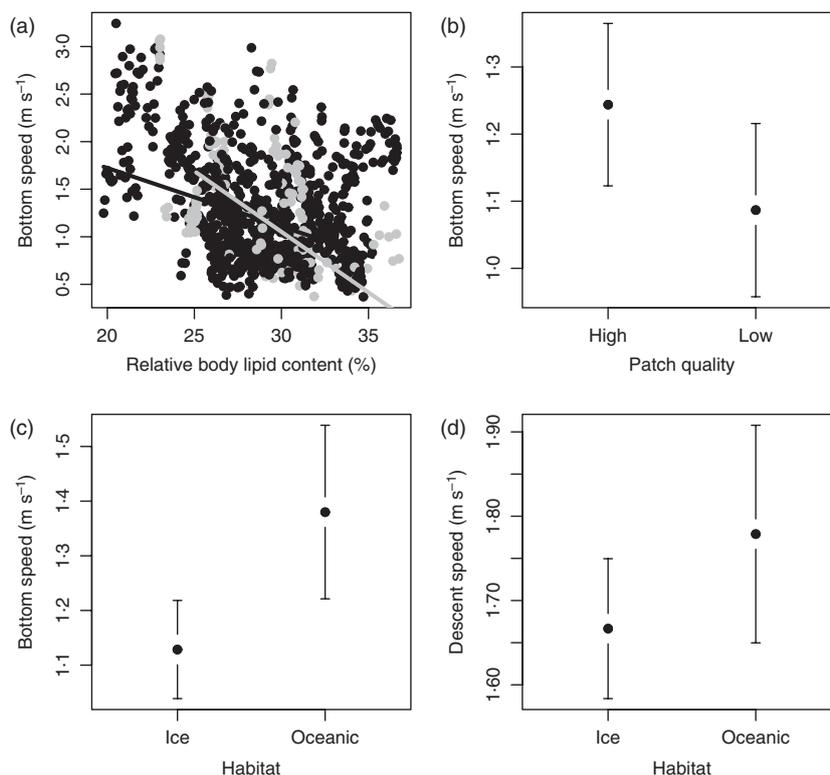
Fig. 4. Bottom and descent speed relative to the predictors in the top-ranked model from the suite of models tested to explain bottom and descent speed. (a) Bottom speed vs. relative lipid content for high- (black) and low-quality (grey) patches. Shown are fitted lines among seals for ice habitat (oceanic was similar) from the top-ranked model for each patch quality category. (b) Bottom speed vs. patch quality and c) habitat type. (d) Descent speed vs. habitat type.

explicitly test whether dive duration and bottom time in elephant seals is affected by patch quality and examine how the various diving variables affect the time and energy budget of the dive cycle in relation to patch quality. We construct a suite of models to examine the relationship between dive variables and buoyancy, habitat and patch quality, thereby testing predictions of optimal foraging models for breath-hold divers, and elucidating the nature of the gain function.

Materials and methods

DATA

We instrumented known-age (born in 1993 and 1994) adult female southern elephant seals *Mirounga leonina* at Macquarie Island (54°35′S, 158°58′E) with velocity-time-depth recorders (Wildlife Computers MK8, Redmond, WA, USA) prior to the 2002 (*n* = 14), 2004 (*n* = 16) and 2005 (*n* = 4) postmoult foraging trips. We captured and sedated seals following the procedures outlined in Field *et al*. (2002) and attached time-depth recorders to the pelage above the shoulders following the procedures described in Hindell & Slip (1997). The time-depth recorders sampled time, depth, light level, revolutions of a flow-driven turbine and temperature every 30 s for the total duration of the foraging trips. We extracted raw data from the recorders using Wildlife Computers software and derived at-sea positions twice daily from the logged light intensities with the R (R Development

Core Team 2011) library `tripEstimation` (Sumner & Wotherspoon 2007) which uses a Bayesian Markov Chain-Monte Carlo approach. This method determines location estimates with measures of uncertainty (Sumner, Wotherspoon & Hindell 2009). We applied a single-twilight solar model incorporating a topographic mask and likely log-normal speed (mean = 1·5 km h^{-1}, SD = 1·6) between fixes to derive a probability distribution for each twilight position (Sumner, Wotherspoon & Hindell 2009), using the spatial mean of each distribution for point estimates.

MOVEMENT BEHAVIOUR

We identified intensive and extensive search modes along each seal's foraging pathway. Intensive search modes had a sinuous path thought to correspond to intra-patch movements, whereas an extensive search mode was a relatively straight path corresponding to inter-patch movements. We measured path sinuosity using the methods outlined in Thums, Bradshaw & Hindell (2011) based on the first-passage time method (Fauchald & Tveraa 2003) implanted via an R package (source code developed by D. Pinaud, CNRS, France). The rationale of first-passage time is that points of a pathway are associated within a circle of a given radius and measuring the time between the first passage of the circle backward and forward along the path measures path sinuosity at each point. First-passage time is scale-dependent and the method also allows for identification of the spatial scale at which the animal concentrates its search effort (Fauchald & Tveraa 2003). For the seals in our study, the mean spatial scale was 250 km (Thums, Bradshaw & Hindell 2011); we thus measured
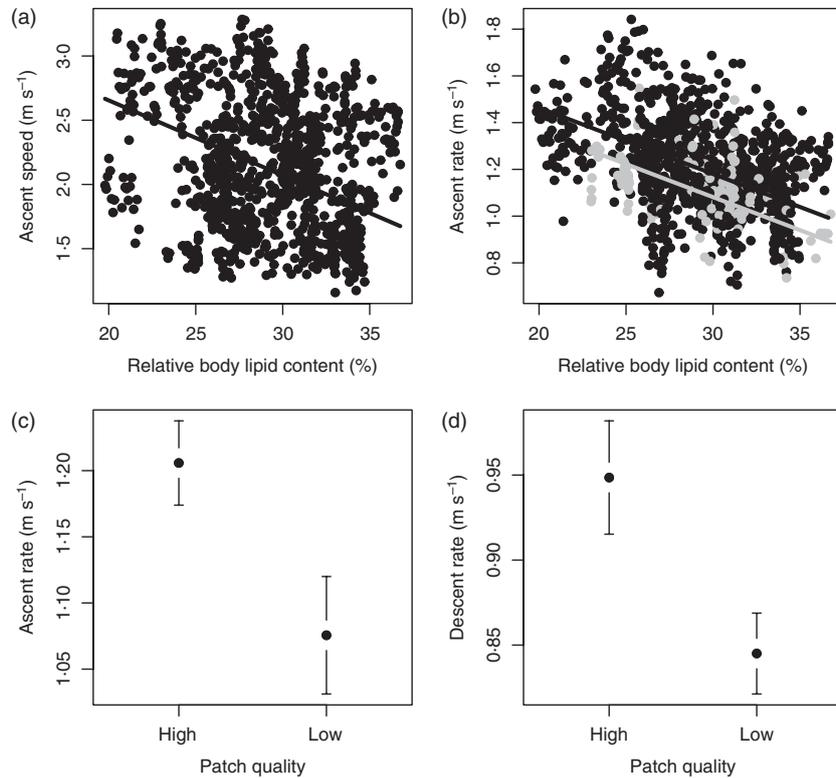
Fig. 5. Ascent speed, ascent rate and descent rate relative to the predictors in the top-ranked model from the suite of models tested to explain these response variables. (a) Shown is the fitted line among seals for ascent speed vs. relative lipid content. (b) Ascent rate vs. relative lipid content for high- (black) and low-quality (grey) patches. Shown are fitted lines among seals for ice habitat (oceanic was similar) from the top-ranked model for each patch quality category. (c) Ascent and (d) descent rate relative to patch quality.
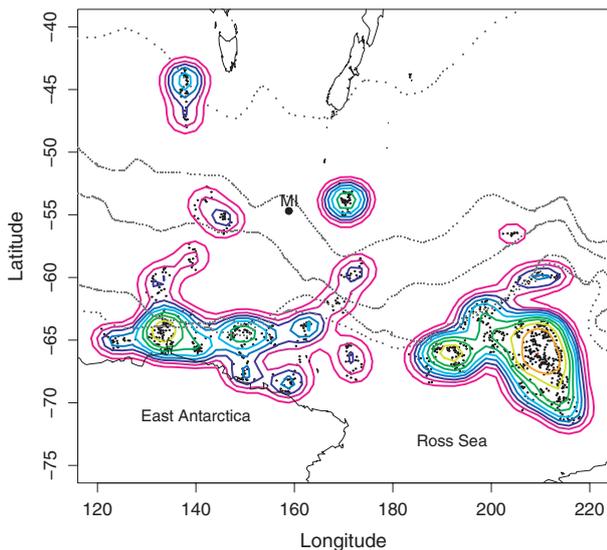
Fig. 6. Kernel density plot of high-quality patch locations. Warmer colours correspond to more points. Individual locations are shown in black dots. Maps show the bottom of Tasmania and New Zealand and the coast of East Antarctica. Major Antarctic circumpolar current fronts are shown from north to south: Subtropical Front, Sub-Antarctic Front, Antarctic Polar Front and Southern Boundary of Antarctic Circumpolar Current Front.

the first-passage time at that spatial scale. A density plot of the resulting first-passage times for each seal revealed bi-modal distributions allowing for a simple identification of search modes

(Pinaud & Weimerskirch 2007; Thums, Bradshaw & Hindell 2011). A short first-passage time indicates fast, often straighter movement between patches ('extensive' movement), and a long first-passage time indicates slower, more sinuous paths ('intensive' movements).

RELATIVE LIPID CONTENT ESTIMATION

We extracted periods of passive drifting during individual dives and used these to predict relative lipid content following the method described in Thums, Bradshaw & Hindell (2008a). Briefly, we defined drift components as periods when the turbine was stalled, thus giving a swim speed reading of 0 m s^{-1}. We then used generalized linear models to examine the relationship between relative lipid content measured on land and drift rate and several other diving variables collected quasi-simultaneously (i.e. within a week). The highest information-theoretic-ranked model explained 90% of the deviance in relative lipid content. Using this model we predicted relative lipid content for each day of the foraging trips for each individual.

We used a constrained quadratic regression B-spline from the COBS library in R to fit a function to the pattern of change in relative lipid content over the course of each seal's foraging trip (Thums, Bradshaw & Hindell 2008a). This summarizes the trend in relative lipid content as a function of day as leaving the island and interpolates values for days when no drift dives occurred. The fitted values provided daily estimates of relative lipid content and based on the direction of change in relative lipid content from day i to $i + 1$, we could determine when

seals were either increasing relative lipid or not (Thums, Bradshaw & Hindell 2008a). We could not unequivocally determine a decrease in relative lipid *per se* because drifting rates do not necessarily reflect absolute changes in lipid composition, even though they can provide good estimates of relative lipid content (Biuw *et al.* 2003). Other determinants of reduced relative lipid composition include (i) recovery of lean tissue losses from breeding early in the trip, and (ii) exponential growth of the lean tissue foetus late in the trip (Thums, Bradshaw & Hindell 2008a). We therefore focus only on increases in relative lipid content.

PATCH QUALITY

We developed a proxy for the quality of the environment encountered per day which we consider to be a relative measure of daily patch quality. We estimated patch quality from the relationship between daily animal search mode (intensive or extensive) and daily foraging success (change in relative lipid content). We considered increasing relative lipid in intensive movement mode to indicate high-quality patches because seals in these areas exhibited highly sinuous movements combined with relative lipid gain. We designated areas as low quality when seals were in the extensive movement mode and not gaining relative lipid. We excluded the outward and inward transit phases from Macquarie Island and further restricted the data to putative foraging dives only, with dive classification done using the methods described in Thums, Bradshaw & Hindell (2008b).

DIVE STATISTICS

We calculated summary parameters for each dive using 'DIVE', a custom dive-analysis program (Stuart Greenhill, Murdoch University, Perth, WA, USA). We selected diving variables used in the analysis *a priori* based on those variables hypothesized to contribute to energy and time management during diving: maximum depth (m), duration (min), total mean speed (m s^{-1}), mean descent speed (m s^{-1}), mean ascent speed (m s^{-1}), mean bottom (of the dive) speed (m s^{-1}), descent rate (m s^{-1}), ascent rate (m s^{-1}), time spent at the bottom of a dive (min), time spent in descent (min), time spent in ascent (min) and the angles of descent and ascent. We defined bottom time as the time of the dive between the end of the descent phase and the beginning of the ascent phase. The end of descent and start of ascent were detected as spikes in the first differential of depth and time.

HABITAT EFFECTS

We included habitat type as a predictor in the models because the magnitude of foraging success depends on general habitat type (Thums, Bradshaw & Hindell 2011). We identified these habitats by applying a hierarchical cluster analysis to all at-sea locations using the hclust function in R. The variables we included to define habitats were as follows: distance to ice edge (calculated from daily SMMR-SSM/I passive microwave estimates of sea ice concentration) (Cavalieri *et al.* 1996; updated 2006) and water depth using the ETOPO2v2 data set (U.S. Department of Commerce 2006). Seals used the ice habitat most commonly in intensive movement mode, with 50% of search locations occurring there, followed by the oceanic habitat (42%) and lastly, the shelf habitat (8%) (Thums, Bradshaw & Hindell 2011).

TESTS OF FORAGING MODELS

We explicitly tested whether patch quality affects dive duration and bottom time. We also examined whether seals adjusted their rates of travel, speed and angles on the different phases of the dive (descent, bottom and ascent) in response to patch quality. We predicted that: (i) dive durations should approach the theoretical ADL and be independent of patch quality (Thompson & Fedak 2001); or (ii) dive duration should increase with patch quality (Thompson & Fedak 2001), (iii) bottom time (absolute and expressed as a proportion of total dive duration) should increase with patch quality if seals are maximizing the time spent in the foraging zone (Fedak 1986); (iv) bottom swimming speed should provide the most efficient energy gain per unit expended; thus, bottom speed should increase with patch quality (Thompson, Hiby & Fedak 1993). Bottom speed could also vary as a function of the type of prey hunted (Thompson, Hiby & Fedak 1993), so differences might also be habitat-dependent; (v) speed on ascent and descent should be close to the minimum cost of transport in both high- and low-quality patches if seals are maximizing the amount of oxygen available in the foraging area (Thompson, Hiby & Fedak 1993); (vi) ascent and descent rates and speeds should increase with patch quality if seals are reducing transit time, (Thompson & Fedak 2001); and (vii) ascent and descent angles should increase with patch quality if seals are reducing transit time, (Thompson & Fedak 2001).

We estimated the minimum cost of transport (C_t) using the generalized multi-species equation of Videler & Nolet (1990):

$$C_t = 0.5M^{0.27} \, (\text{m s}^{-1})$$

where M = mass in kg. We estimated the theoretical aerobic dive limit (ADL$_t$) using the method of Kooyman (1989):

$$\text{ADL}_t = M_l \cdot TO_2/\text{DMR}$$

where M_l = lean mass in kg, TO_2 = total available oxygen store per unit mass in l O$_2$ kg^{-1} and DMR = diving metabolic rate in l O$_2$ min^{-1}. We estimated M_l for each seal using the truncated cones method (Field *et al.* 2002), we took TO_2 as 0.079 l O$_2$ kg^{-1} (Kooyman 1989; Hindell *et al.* 1992); DMR has not been measured in elephant seals, so we used an estimate of the resting metabolic rate ($0.0113M_l^{0.75}$ l O$_2$ min^{-1}) (Hindell *et al.* 1992; Schmidt-Nielsen 1997).

We constructed a suite of linear mixed-effects models using the nlme library in R including all combinations of the individual variables and the two-way interactions. The daily mean of each of the dive variables (listed previously) were the response variables and patch quality (high or low), relative lipid content and habitat were predictor variables, and seal identity was a random variable. For the models for dive duration, bottom time and proportional bottom time we added day of trip into the random effects structure because dive duration and bottom time increase as a function of time at sea (Slip, Hindell & Burton 1994; Le Boeuf *et al.* 1996; Hassrick *et al.* 2007; Zeno *et al.* 2007). There were not enough data in the low-quality patches in shelf habitat; thus, we removed data falling within shelf habitat from analysis. We compared and ranked models using weights of Akaike's information criterion corrected for small sample size (*w*AIC$_c$). AIC$_c$ weight varies from 0 (no

support to 1 (complete support) (Burnham & Anderson 2002) relative to all models in the set. We used the `corCAR1` function to account for the within-group correlation structure. Difference in diving variables (particularly dive duration) between patch qualities could also arise from differences in dive depth, so we also examined the relationship between dive depth and patch quality, relative lipid content and habitat.

Results

FORAGING STRATEGIES

For mean maximum dive depth as the response, there was no clearly superior model. The three top-ranked models had similar information-theoretic weights (Tables 1 and S1). The partial residual plot from the top-ranked model shows a weak relationship between depth and relative lipid content (Fig. S1a) and the data show slightly deeper dives in areas of low quality and a weak effect of habitat type (Fig. S1b,c).

For our first two predictions (i.e. 1. dive duration approaches the theoretical ADL and is independent of patch quality and 2. duration increases with patch quality), the model including relative lipid content, patch quality, habitat and the interaction between relative lipid content and habitat had majority support ($w\mathrm{AIC_c} = 0.99$) (Table 1). There was a positive relationship between dive duration and relative lipid content and a difference in this relationship with habitat (Fig. 1a). Dive duration was longer in low-quality patches (Fig. 1b), and even though habitat was included in the top model, there was not a strong effect of habitat (Fig. 1c). There was a difference in the distribution of dive duration between the two quality categories, with the distribution in high-quality patches relatively symmetrical (Fig. 2a), and the distribution in low-quality patches showing that most dives (86%) were longer than $\mathrm{ADL_t}$ (Fig. 2b). We found strong evidence for a difference in dive duration in low-quality patches and the theoretical ADL with the slope model having 100% support ($w\mathrm{AIC_c} = 1$) over the intercept-only model ($w\mathrm{AIC_c} = 0$). The mean dive duration in high-quality patches (31.99 ± 4.28 min) did not exceed the mean theoretical ADL (31.54 ± 1.08 min), but it did in low-quality patches (38.50 ± 5.94 min) (Table 2, Fig. 1b). In summary, neither prediction was supported.

Neither was the next prediction (3. bottom time is greater in high-quality patches) supported. The model including relative lipid content, patch quality and the interaction between the two had majority support ($w\mathrm{AIC_c} = 0.41$) (Table 1). There was a positive relationship between absolute bottom time and relative lipid content, and a difference in this relationship with patch quality (Fig. 3a). Bottom time was longer in low-quality patches (Fig. 3b) (Table 1).

For proportional bottom time, the model including relative lipid content and patch quality had majority support ($w\mathrm{AIC_c} = 0.97$) (Table 1). Proportional bottom time increased as a function of relative lipid content (Fig. 3c) and proportional bottom time was longer in low-quality patches (Fig. 3d). Therefore, the prediction was not supported for absolute or proportional bottom time. The next predictions (4. bottom swim speed increases with patch quality and differs between habitats; bottom swim speed should be at minimum cost transport) were supported. The model including lipid content, patch quality, habitat and the interaction between patch quality and lipid content had majority support ($w\mathrm{AIC_c} = 0.84$) (Table 1). There was a negative relationship between bottom speed and relative lipid content, and this strengthened in low-quality patches (Fig. 4a). Bottom speed was slightly higher in high-quality patches (14%) (Fig. 4b) and in oceanic habitats (22%) (Fig. 4c). Bottom speed in high- and low-quality patches was below the minimum cost of transport (Table 2).

For the predictions that ascent and descent speeds are at minimum cost of transport and faster in high-quality patches (5), we found support only for the former. The top-ranked model describing descent speed included habitat alone ($w\mathrm{AIC_c} = 0.57$) (Table 1), but seals in the ice habitat had only marginally lower (7%) descent speeds than those in oceanic habitat (Fig. 4d). The top-ranked model for ascent speed included relative lipid content alone and had majority support ($w\mathrm{AIC_c} = 0.88$; Table 1). Mean ascent speed declined as relative lipid content increased (Fig. 5a). The mean descent and ascent speeds in high- and low-quality patches were also well below calculated minimum cost of transport (55% and 76% lower, respectively) (Table 2). The prediction that ascent and descent rates increase with patch quality (6) was upheld. The top-ranked model for ascent rate contained relative lipid content and patch quality and had majority support ($w\mathrm{AIC_c} = 0.79$) (Table 1). There was a negative relationship between ascent rate and relative lipid content and a difference in this relationship with patch quality (Fig. 5b). Ascent rate was greater in high-quality patches (Fig. 5c). The top-ranked model for descent rate contained patch quality alone and had majority support ($w\mathrm{AIC_c} = 0.77$) (Table 1) with greater descent rate in high patch quality (Fig. 5d).

For prediction 7, that ascent and descent angles increase with patch quality, we found little support. There was no single model accounting for most support; rather, the three top-ranked models for descent rate and top two for ascent rate roughly shared equal $\mathrm{AIC_c}$ weights (Table 1). There was only a weak relationship between relative lipid content and descent angle (Fig. S2a), strengthening only slightly in low-quality patches (2% increase) and in ice habitat (5% increase) (Fig. S2b,c). Ascent angles were only slightly steeper in high-quality patches (4%) and in ice habitat (2%) (Fig. S2d,e).

SPATIAL ALLOCATION OF PATCH QUALITY

High-quality patches were predominantly below the Polar Front, mostly occurring in the Antarctic zone in the north

of the Ross Sea, off the coast of East Antarctica on the shelf break and at the ice edge and on the Campbell Island Plateau (Fig. 6).

Discussion

Our results did not conform to either of the predictions of the model developed by Thompson & Fedak (2001) which states that shallow divers should increase dive duration as patch quality improves, but deep divers should have largely invariant durations because the energetic costs of descending are greater. Dive durations and bottom times varied with patch quality but seals did not schedule their diving to maximize time spent in the foraging zone in patches of relatively higher quality. This result is consistent with the predictions of the marginal value theorem (Charnov 1976) which states that animals foraging in a patch with better-than-average resources should spend relatively less time there. This can arise from depletion of prey resources, evasion by prey or the requirements of food processing (Charnov 1976; Stephens & Krebs 1986). Antarctic fur seals also increased time in patches as apparent food availability declined (Mori & Boyd 2004). Neither did deep-diving pilot whales reduce dive duration in dives where no prey were encountered (Soto *et al.* 2008). There was qualitative support for the marginal value theorem in northern elephant seals during nonEl Niño years (seals ceased to behave optimally in El Niño years) with a positive relationship between travel time and patch residence time at the level of dive bouts (Crocker *et al.* 2006). Importantly, our results provide support for a nonlinear relationship between prey acquisition and time spent searching. Most optimal foraging models for diving animals assume a linear relationship (including the Thompson & Fedak 2001 model); however, in practice, the expected gain is likely to be nonlinear and represented by a power (Mori *et al.* 2002) or an asymptotic function as in the marginal value theorem. As predator behaviour is increasingly being used as an index of marine resource density and distribution, it is important to understand this relationship. For example, an increase in foraging success or prey density is commonly inferred from an increase in bottom time (Tremblay & Cherel 2000; Robinson *et al.* 2007, 2010), whereas our results support the opposite.

The lack of support for the prediction that deep divers should have largely invariant dive durations is partly confounded by our inability to measure ADL, either directly or indirectly. ADL is not a constant parameter and is negatively related to DMR (Kooyman 1989; Costa 1991; Hurley & Costa 2001). During an average dive in high-quality patches, elephant seals successfully caught prey; thus, prey pursuits at the bottom of dives or the heat increment of feeding from successful foraging might have reduced ADL through an increase in DMR. On the other hand, the average dive in low-quality patches was not successful. If this was a result of poor resource availability

rather than unsuccessful prey pursuits, then seals might have been able dive for longer as a result of lowered DMR.

Relative lipid content (which directly affects buoyancy) was an influential driver of diving behaviour. Ascent rate, ascent speed, bottom speed, bottom time, % bottom time and duration all varied in response to changes in relative lipid. This is consistent with existing evidence that buoyancy is a strong modifier of dive behaviour (Webb *et al.* 1998; Beck, Bowen & Iverson 2000; Nowacek *et al.* 2001; Miller *et al.* 2004). Diving animals are assisted by negative buoyancy during descent, but then need to expend more energy in ascent owing to the downward force, with the converse true for positive buoyancy. Surprisingly, we found that descent rate and speed were invariant to relative lipid content, suggesting that something else is driving the majority of the variation in this component of diving such as body geometry or heading. Paradoxically though, both ascent speed and rate were negatively correlated with lipid content (cf. Beck, Bowen & Iverson 2000) – fatter seals should theoretically ascend faster owing to the additional lift provided by being positively buoyant. Such results indicate a change in body posture increasing the drag force such as flippers acting as brakes or trim tabs. Bottom speed also declined as relative lipid content increased, possibly due to a reduction in gliding efficiency as the animal endeavours to reach greater depths and thus has to modify swim speed to maintain bottom time. As with the elephant seals we measured, grey seals had longer bottom times and dive durations when they were most buoyant (Beck, Bowen & Iverson 2000).

Consistent with some of the broad predictions for breath-hold divers, ascent and descent rates were higher in high-quality patches. This suggests that seals reduced their travel time; however, the mechanisms that could allow for a reduction in travel time such as swimming faster or increasing dive angles did not differ with patch quality. Again, this suggests a complex interplay between body position and buoyancy; for example, pitch angle affected the power requirements in whale sharks in a manner similar to travel speed (Gleiss, Norman & Wilson 2011). Our result might also indicate a difference in heading, with a more consistent heading used on descent and ascent in high-quality patches; accelerometer data would help to elucidate this process.

Some diving parameters varied between the ice and oceanic habitats: principally, swimming speed during the bottom phases of dives. Seals in the ice tended to swim more slowly on both of these phases than those in open (oceanic) habitats. Indeed, acceleration bursts (associated with prey capture on the bottom of dives) were rarer in seals foraging in ice habitat than in oceanic habitat, thought to be in response to foraging on larger, rarer prey of higher nutritive value (Thums, Bradshaw & Hindell 2011) – an hypothesis consistent with the observation that larger species (Nototheniidae and Moridae) are typical components of within-ice habitat diets (Bradshaw *et al.* (2003).

The disagreement between our results and the Thompson & Fedak (2001) model predictions requires clarification: we did not and cannot assess patch quality per dive; rather, we have expressed it as a daily aggregate. Owing to hierarchical patch dynamics, individual patches of varying prey density still need to be located, such that daily means might incorporate a range of 'qualities'. Our results also suggest that prey size and distribution differ between habitats so that 'optimal' solutions will vary (Costa 1991; Thompson & Fedak 2001). For example, feeding on schooling fish would likely require a different feeding strategy compared with that employed for randomly dispersed, large and dispersed, pelagic or benthic prey. In other words, maximizing the time at maximum depth is unlikely always to provide the most efficient hunting strategy. In a high-quality patch, a seal is therefore likely to obtain a single large prey item sooner than a seal in a low-quality patch. Indeed, there is a relationship with the number of prey taken and dive depth (Costa 1991). Deep divers spend relatively more time in transit to the foraging zone, so they reduce the time available to search for and capture prey thus targeting larger, higher-energy prey as the most economical strategy (Costa 1991). Given the investment made in diving deeply, elephant seals are unlikely to give up early and should stay as long as their oxygen stores allow (Thompson & Fedak 2001).

The role of vertebrates in structuring prey communities depends on the spatial and temporal pattern of predation and in turn, these patterns depend on foraging profitability relative to food density (Lovvorn & Gillingham 1996). However, measuring food availability at scales relevant to the foraging energetics of highly mobile marine vertebrates is currently not feasible. A critical challenge then is to develop useful indices of resource distribution and density. Our results adds to the growing body of empirical evidence relating observed animal behaviour and prey availability (Mori *et al.* 2005; Austin *et al.* 2006; Biuw *et al.* 2007; Horsburgh *et al.* 2008; Soto *et al.* 2008) such that models of oceanic community dynamics can be built. Our approach is also highly attractive because it provides a spatial dimension to the determination of higher predator foraging success, thereby highlighting resource-rich areas important for many other Southern Ocean predator species. Such knowledge of core foraging habitat is needed to manage potential interactions with fisheries and for predicting future population responses to environmental change.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Relationship between dive depth to the predictors in the top-ranked model from the suite of models tested to explain dive duration.

Fig. S2. Descent and ascent angle relative to the predictors in the top-ranked model from the suite of models tested to explain these response variables.

Table S1. Ranked linear mixed-effects models of each of the dive variables as the response variable explained by patch quality (PQ), relative lipid content (fat) and habitat type (Hab).

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