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Individual dietary specialization and dive behaviour in the California sea otter: Using archival time–depth data to detect alternative foraging strategies

M.T. Tinker[a,*], D.P. Costa[a], J.A. Estes[b], N. Wieringa[c]

[a]*Department of Ecology and Evolutionary Biology, Long Marine Laboratory, University of California Santa Cruz,*
100 Shaffer Road, Santa Cruz, CA 95060, USA
[b]*US Geological Survey, Western Ecological Research Center, Long Marine Laboratory,*
100 Shaffer Road, Santa Cruz, CA 95060, USA
[c]*Institute for Biodiversity and Ecosystem Dynamics (IBED), Department of Aquatic Microbiology, University of Amsterdam,*
Nieuwe Achtergracht 127, 1018 WS Amsterdam, The Netherlands

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Abstract

The existence of individual prey specializations has been reported for an ever-growing number of taxa, and has important ramifications for our understanding of predator–prey dynamics. We use the California sea otter population as a case study to validate the use of archival time–depth data to detect and measure differences in foraging behaviour and diet. We collected observational foraging data from radio-tagged sea otters that had been equipped with Mk9 time depth recorders (TDRs, Wildlife Computers, Redmond, WA). After recapturing the study animals and retrieving the TDRs it was possible to compare the two data types, by matching individual dives from the TDR record with observational data and thus examining behavioural correlates of capture success and prey species. Individuals varied with respect to prey selection, aggregating into one of three distinct dietary specializations. A number of TDR-derived parameters, particularly dive depth and post-dive surface interval, differed predictably between specialist types. A combination of six dive parameters was particularly useful for discriminating between specialist types, and when incorporated into a multivariate cluster analysis, these six parameters resulted in classification of 13 adult female sea otters into three clusters that corresponded almost perfectly to the diet-based classification (1 out of 13 animals was misclassified). Thus based solely on quantifiable traits of time–depth data that have been collected over an appropriate period (in this case 1 year per animal), it was possible to assign female sea otters to diet type with >90% accuracy. TDR data can thus be used as a tool to measure the degree of individual specialization in sea otter populations, a conclusion that will likely apply to other diving marine vertebrates as well. Our ultimate goals must be both to understand the causes of individual specialization, and to incorporate such variation into models of population- and community-level food web dynamics.

Keywords: Data loggers; Diets; Diet specialization; Foraging behaviour; Statistical analysis

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[*] Corresponding author. Tel.: +1 831 459 2357; fax: +1 831 459 2249.
E-mail address: tinker@biology.ucsc.edu (M.T. Tinker).

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1. Introduction

Questions about the ecological significance of alternative dietary specializations within wildlife populations have been largely overlooked (Bolnick et al., 2003), primarily because opportunities for detecting such alternative strategies have been limited by the difficulty of collecting longitudinal dietary data from individuals. As more and more studies are designed to monitor individual diets and feeding behaviour, it has become clear that individual specialization is much more common than once suspected (e.g., Heinrich, 1976; West, 1986, 1988; Werner and Sherry, 1987; Bridcut and Giller, 1995; Beauchamp et al., 1997; Estes et al., 2003). Such specialization has important implications for spatial and temporal variation in trophic interactions: if all members of a population of consumers do not have similar diets, it stands to reason that the impact of any sub-set of the consumer population on prey communities may vary considerably. It is also possible that, for many top predators, individual prey specializations represent an adaptive response to reduced food resources and increased intra-specific competition (Glasser, 1982; Schindler et al., 1997). Thus, the relative degree to which individuals specialize may be a useful index of population status with respect to resource abundance; however, the utility of such an index depends on the ability of researchers to detect and measure the relative degree of dietary specialization within a population.

For researchers studying air-breathing marine vertebrates, longitudinal studies of individual diets have, until recently, proven difficult or impossible, resulting in an under-appreciation of the importance or even existence of individual foraging specializations (with a few notable exceptions: see, for example, Smolker et al., 1997; Annett and Pierotti, 1999). This situation has drastically changed with recent developments in bio-logging technology, which offer new and powerful tools for detecting and quantifying the extent of individual foraging specialization within marine bird and mammal populations. Using bio-logging technologies, individually variable foraging behaviour has now been detected in a variety of species including Antarctic fur seals (Lea et al., 2002b; Staniland et al., 2004), grey seals (Austin et al., 2004), narwhals (Laidre et al., 2003), cormorants (Kato et al., 2000), and several species of penguins (Radl and Culik, 1999; Tremblay and Cherel, 2000). In most of these cases the variation between individuals appears to be associated with differences in feeding habitat: this may occur if key prey species are distributed at different depths in different locations (e.g., Tollit et al., 1998). Such spatially-driven variation often can be detected using satellite transmitters or GPS-equipped bio-loggers. More problematic are species that exhibit trophic polymorphisms, because individuals may utilize the same habitat at the same time but feed on different prey species. This type of specialization may not be detected by measuring feeding location or spatial use patterns, and so is harder to study. However, to the extent that dietary differences in marine birds and mammals are accompanied by differences in diving behaviour (e.g., Costa and Gales, 2000), they could potentially be detected through the deployment of time–depth recorders (TDRs).

One difficulty in testing such a hypothesis is that it necessarily requires longitudinal data on individual diets to interpret and validate behavioural differences detected using TDR technology. Such dietary data can be acquired using a variety of techniques including stomach flushing (Radl and Culik, 1999; Tremblay and Cherel, 2003), colon flushing (Staniland et al., 2004), or fatty-acid analysis (Lea et al., 2002a; Iverson et al., 2004). Unfortunately, with all of these methods, it is impossible to link a specific dive or set of dives to a specific prey type, and thus the direct functional link between prey selection and dive behaviour is difficult to describe. Perhaps the best way to study the relationship between diet and feeding behaviour is direct observation of foraging behaviour; while this is logistically difficult for most marine mammal species, it has been achieved for a few species using animal-mounted video cameras, or ‘‘crittercams’’ (Ponganis et al., 2000; Parrish et al., 2005). The critercam technique, while very promising, is still limited in terms of its ability to provide prolonged dietary records for individuals. Alternatively, for species such as sea otters that consume their prey at the surface in fairly close proximity to the shore, prey selection is directly observable with a sufficiently powerful telescope, and is relatively easy to quantify for individuals over periods of months or even years (Ralls et al., 1995).

Southern sea otters (*Enhydra lutris nereis*) are an excellent study species not only because of their tractability for collecting dietary data, but also because research has shown that sea otters along the central coast of California (where population density is highest) tend to be prey specialists rather than generalists (Lyons, 1991; Estes et al., 2003). It also has been found that individual dietary variation tends to aggregate into three types of prey specialization (Tinker, 2004): type 1 specialists prey on large, rare and energy-rich invertebrate species such as cancer crabs (*Cancer* sp.) and abalone (*Haliotis* sp.); type 2 specialists consume small and intermediate-sized species including bivalve molluscs and kelp crabs (*Pugettia producta*); and type 3 specialists feed almost exclusively on kelp-dwelling marine snails (primarily turban snails, *Tegula* sp., and *Calliostoma* sp.). It remains unclear whether or how prey specialists differ with respect to their dive behaviour; however, because the various prey species are often found in different microhabitats and require unique capture and handling techniques, it is conceivable that individual diet specializations could be recognized from dive characteristics measured remotely using archival TDRs. Here we attempt to answer two fairly simple questions: (1) are there behavioural differences associated with the individual diet specializations previously described for sea otters (Estes et al., 2003; Tinker, 2004) that can be measured remotely using archival TDRs; and (2) if there are measurable differences, are they sufficiently distinct and consistent enough to reliably classify individuals by diet type and to measure the extent of individual specialization, thereby providing a tool for gauging the status of populations with respect to food resources?

2. Methods

Between March 2001 and April 2004, we collected longitudinal data on diet and diving behaviour from sea otters along the central coast of California between San Simeon Point and Point Estero (Fig. 1). Here we report on data from 13 adult female study animals that represent a sub-set of a larger sample of otters ($n = 117$) monitored via radio telemetry as part of a comprehensive population study (Tinker et al., 2006) conducted under federal permit MA672624-13 issued by the Fish and Wildlife Service to JAE. All study animals were captured by scuba divers using re-breather equipment and "Wilson Traps" (Ames et al., 1986). Captured animals were transported to a shore-based veterinary mobile laboratory where they were immobilized using standard anaesthetic techniques (Monson et al., 2001), equipped with flipper tags for visual identification at distance, and surgically instrumented (Williams and Siniff, 1983) with abdominally implanted VHF transmitters (ATS Inc., Isanti, MN) and archival TDRs (Mk-9 models constructed by Wildlife Computers, Redmond, WA). Otters were revived post-surgery using a reversal agent (Monson et al., 2001), transported back to their capture location and released, after which their survival, reproductive success and habitat use patterns were monitored for 1–3 years using telemetric methods (Siniff and Ralls, 1991; Ralls et al., 1996). We also systematically collected observational foraging data from study animals using standard protocols (Ralls et al., 1995; Watt et al., 2000; Estes et al., 2003); a full analysis of these observational data is presented elsewhere (Tinker, 2004; Tinker et al., 2006) and we focus here specifically on TDR data on dive behaviour.

We were able to recapture and retrieve TDR instruments from 22 study animals (15 females and 7 males) that survived and remained within the study area for >1 year post-deployment, although three of these instruments had corrupted data files and were unusable. We thus collected TDR dive records from 13 female and 6 male sea otters for which we also had available a large sample of observational dietary data (>500 feeding dives and prey captures recorded for each animal over a minimum of 1 year). We restrict our analyses here to the 13 female study animals, as we were interested primarily in the potential use of TDR dive data for detecting dietary specialization and the female sample included representatives of the three recognized dietary specializations (see Tinker, 2004); we thus avoid the complication of sex-based differences in dive behaviour (males are known to utilize deeper feeding depths than females: Bodkin et al., 2004).

Initial TDR data processing—including correction of electronic drift (zero-offset) and the identification of the start and end of individual dives—was conducted using Wildlife Computers Instrument Helper software (Wildlife Computers, Redmond, WA). A dive was considered to be an immersion to a minimum of 1.5 m (3 times depth resolution of the instruments) for at least 12 s (6 times the sampling interval), and was considered to have ended if the depth reading came within 0.5 m of the offset-corrected "zero" depth. A number of standard parameters were calculated for each dive, including the maximum dive depth, duration of the sub-surface interval (DT), duration of time at spent at the bottom of the dive (BT), duration of the

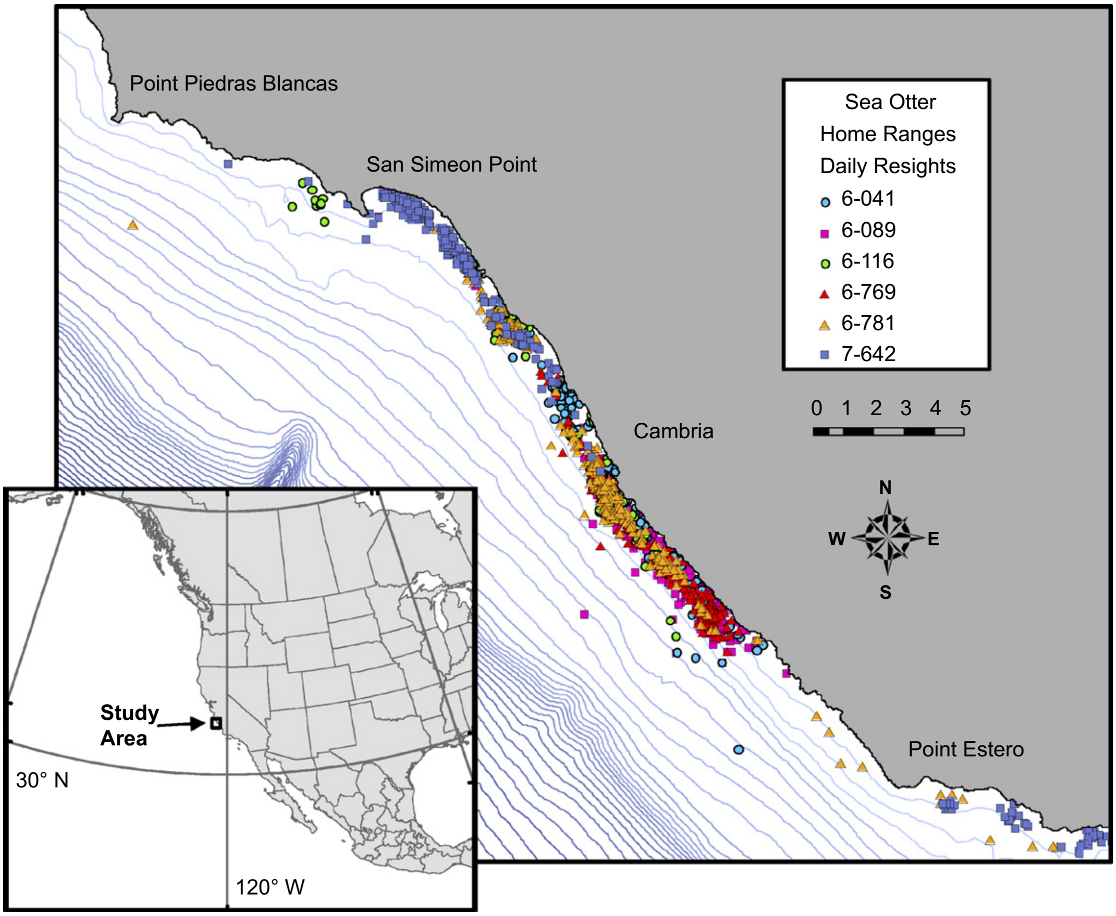

Fig. 1. Map of study area in central California, showing all daily re-sight locations collected between March 2001 and April 2004 for 6 adult female sea otters. Water depth is displayed as 10-m bathymetric contours. As evident from the spatial distribution of these re-sights, all 6 individuals exhibited roughly similar patterns of habitat use and overlapping home ranges; however, their diets varied significantly, with 3 distinct patterns of dietary specialization each represented by 2 of these animals. Type 1 (circular symbols) specialized on large but rare prey species, type 2 (square symbols) specialized on medium-sized, relatively abundant prey, and type 3 (triangle symbols) specialized on small, kelp-dwelling prey, primarily turban snails.

post-dive surface interval (or PDI, the time elapsed until the next dive), descent rate (vertical swim-speed from surface to bottom) and ascent rate (vertical swim-speed from bottom to surface). Time spent at the bottom for each dive was assumed to correspond to time spent at 70% or more of maximum dive depth.

After initial processing, our first step was to distinguish foraging dives from non-foraging dives. Because sea otters are benthic foragers and then conduct all prey handling at the surface, their feeding dives can be distinguished from non-feeding dives based on measurable characteristics of the time–depth profile. Making use of this fact, Bodkin et al. (2004) have developed a method for categorizing dives into feeding and non-feeding dives using the logistic regression equation

$$\log\left(\frac{P}{1-P}\right) = \alpha + \beta_1 k_1 + \beta_2 k_2 \ldots + \beta_i k_i, \qquad (1)$$

where P is the estimated probability that the dive in question is a feeding dive, α is a constant and β_i are the slope parameters associated with the independent variables k_i. The independent variables we utilized were dive duration, the ratio of bottom time to dive duration (BT/DT), ascent rate, descent rate, and two interaction terms: dive duration × ascent rate and BT/DT × descent rate. We applied Eq. (1) to our TDR data set (model parameterisation was identical to Bodkin et al., 2004), and classified all dives with $p > 0.5$ as feeding dives: this resulted in a sample size of 333,247 feeding dives for the 13 female study animals (Table 1).

An almost unique feature of sea otter dive data is the ability to corroborate methods for identification and classification of dives from TDR records by "ground truthing" against observational data. For each of our study animals we matched TDR dive profiles with activity data collected during one or more 12-h focal-animal monitoring sessions. During these observational sessions, activity was classified at 10-min intervals as "feeding", "resting", or "non-feeding activity", resulting in an estimate of the time-activity budget for the 12-h session (reported as percent time feeding, following Ralls and Siniff, 1990). We then calculated equivalent estimates of percent time feeding from TDR data collected over the same set of 12-h periods, by assuming at each 10-min interval that the animal was feeding if it was engaged in a feeding dive or if it had surfaced from a feeding dive within 20 min (i.e. the same criteria used for the observational activity sessions). Our first validation of the accuracy of our TDR data processing methodology was thus a comparison of estimated percent time foraging based on TDR data and by direct observation. We report mean estimates for each method and mean pair-wise differences between estimates, along with 95% confidence intervals. Our second approach to validation, slightly more labour intensive, was dive-by-dive matching of the TDR dataset with detailed observational foraging data collected over a 1-h period for each animal (selected arbitrarily from within a 12-h focal animal monitoring session). By examining the proportions of observed feeding dives that were accurately detected and classified from the TDR data we were able to gauge the reliability of our data processing methods. Dive-by-dive matching also provided us with a way of qualitatively interpreting the likely behavioural causes of any measurable differences in dive parameters found between animals using alternative diet specializations, as the outcome of each recorded feeding dive was known with respect to prey capture success, prey species, number of prey items and handling time at surface (see Tinker, 2004 for details).

Using observational data on diet composition, we initially classified our 13 female study animals into 1 of 3 diet types using multivariate cluster analysis (refer to Tinker, 2004 for details on collection of observational foraging data and diet classification analyses). A total of 16,250 feeding dives were observed and 9865 prey captures recorded for these 13 animals (Table 1): based on these data, 6 of the animals were classified as type-1 specialists (large prey with low encounter rates), 5 animals were identified as type-2 specialists (small to medium-sized prey with intermediate encounter rates), and 2 animals were identified as type-3 specialists (small prey, mostly turban snails, with high encounter rates). To determine whether TDR data could be used to detect individual dietary specialization within a population, it was first necessary to identify the dive parameters most useful for correctly classifying animals by diet type. For this first set of analyses, we sub-sampled our data to achieve a balanced and fully comparable sample for each diet type: specifically, we selected six females (two from each diet type) whose annual home ranges overlapped almost entirely (thus precluding spatially-driven differences; Fig. 1), and for each of these animals we randomly selected 20 feeding bouts from the larger TDR dataset, subject to the criteria that selected bouts were a minimum of 2 h long. Foraging in sea otters occurs in discreet "bouts" of feeding dives (typically lasting 1–4 h), between which they generally rest and/or perform other non-feeding activity such as travelling, interacting and grooming. Although raw data were available for each individual dive, we assumed that measurements made from dives within a feeding bout would be highly auto-correlated, and thus to ensure independence we collapsed all data into per-bout summary statistics, and used these bouts as the fundamental sampling unit for further analysis ($n = 120$).

We identified a priori 11 variables of potential utility for classifying animals by diet type: these were the range of dive depths spanned within a feeding bout (maximum depth–minimum depth), mean and variance of dive depth, mean and variance of DT, mean and variance of PDI, "inter-dive consistency" (IDC, defined as the proportion of feeding dives in a bout whose depth was equal to the depth of the previous feeding dive, or within a range of ±10%; Tremblay and Cherel, 2000), covariance between dive depth and DT, covariance between BT and PDI, and the ratio of non-feeding dives to feeding dives (NF/FD) within a bout. We conducted univariate contrasts for each of the 11 variables, using nested analysis of variance to test the significance of 2 hierarchical effects, diet type and individual variation (individuals were nested within diet types, and bouts were nested within individuals). Significant differences found for

Table 1
Summary of diving and dietary data for the 13 adult female study animals used in this analysis

Otter ID	No. of feeding dives recorded		Prey captures recorded	% Dive success	Mean prey size (cm)	Proportion of diet comprised by main prey functional groups							
	TDR	Observed				Abalone	Cancer crab	Kelp crab	Urchin	Clam	Mussel	Turban snail	All other prey
Diet type 1													
1	18502	1185	695	72.3	6.0	0.02	0.70	0.13	0.11	0.02	0.01	0.00	0.01
2	17126	1342	683	60.5	5.8	0.30	0.48	0.10	0.03	0.02	0.06	0.00	0.01
3	19807	639	459	75.6	5.9	0.01	0.64	0.21	0.02	0.01	0.00	0.00	0.11
4	21024	970	490	65.1	6.4	0.01	0.71	0.17	0.00	0.04	0.00	0.00	0.08
5	49686	1046	699	70.5	5.2	0.01	0.54	0.27	0.01	0.00	0.00	0.15	0.01
6	62691	1526	529	59.4	5.1	0.02	0.59	0.22	0.07	0.01	0.06	0.00	0.03
	Diet type 1 mean:			67.2	5.7	0.06	0.61	0.18	0.04	0.02	0.02	0.03	0.04
	Standard deviation:			6.6	0.5	0.12	0.09	0.07	0.04	0.01	0.03	0.06	0.04
Diet type 2													
7	12686	1821	1133	73.5	4.3	0.00	0.47	0.28	0.15	0.05	0.00	0.00	0.04
8	44277	1624	1120	73.6	3.6	0.00	0.21	0.56	0.02	0.19	0.00	0.00	0.02
9	3484	1813	1216	77.9	4.3	0.00	0.25	0.51	0.04	0.07	0.06	0.00	0.07
10	22692	2045	1260	71.1	4.2	0.00	0.59	0.23	0.00	0.14	0.00	0.00	0.04
11	3783	985	525	87.1	2.5	0.00	0.06	0.01	0.00	0.34	0.47	0.00	0.12
	Diet type 2 mean:			76.6	3.8	0.00	0.32	0.32	0.04	0.16	0.11	0.00	0.06
	Standard deviation:			6.3	0.8	0.00	0.21	0.22	0.06	0.12	0.20	0.00	0.04
Diet type 3													
12	11810	555	450	88.8	2.4	0.00	0.16	0.17	0.00	0.06	0.00	0.52	0.08
13	45679	699	606	87.9	1.9	0.00	0.07	0.21	0.00	0.00	0.00	0.56	0.16
	Diet type 3 mean:			88.4	2.1	0.00	0.12	0.19	0.00	0.03	0.00	0.54	0.12
	Standard deviation:			0.6	0.3	0.00	0.06	0.03	0.00	0.04	0.00	0.02	0.06

Individuals are shown grouped by diet specialization type (see Tinker (2004) for details of diet classification), and numbers in bold-face type indicate animals that were sub-sampled for detailed dive analysis. Sample sizes are shown for numbers of feeding dives recorded (by TDR and by direct observation) as well as number of prey captures observed, percent of observed feeding dives where prey were captured, and mean diameter of all observed prey items. Diet composition (on the basis of wet edible biomass) is shown as the proportion of the diet comprised by eight main prey categories.

specific dive parameters (Table 2) were further examined and interpreted by graphical examination of the TDR records in conjunction with prey capture records (Fig. 2). We next used multiple linear discriminant analysis to determine which combined suite of dive parameters was most useful for classifying animals by diet type (McGarigal et al., 2000). Non-significant or highly correlated variables were removed using step-wise backward iteration, with the threshold for removing a variable set at $F \leqslant 1.50$. Variation in the remaining independent variables was collapsed into 2 discriminant functions, or canonical variables, representing orthogonal linear combinations of the original variables. Wilk's λ was used to test for differences between diet types, and jack-knife re-sampling of the classification matrix was used to estimate the proportion of foraging bouts that would be correctly assigned to diet type using the final discriminant functions (McGarigal et al., 2000). We also reasoned that if diet types are to be reliably distinguished by TDR data, a substantial amount of variance in the dive parameters must be attributable to differences in diet type, as opposed to within-individual variation. Accordingly, we conducted a variance component analysis to estimate the proportion of variance in the canonical variables explained by each of 3 effects: diet type differences, individual differences (nested within diet type) and within-individual variation. Variance components were estimated using standard parametric techniques (Neter et al., 1990) and averaged for the 2 canonical variables.

Having used a sub-set of the data to identify the TDR parameters most useful for classifying otters by diet type, the next step was to test the efficacy of this classification using the full data sets for all 13 animals. We used hierarchical cluster analysis to detect discontinuous groupings of individual otters in the n-dimensional space formed by the standardized dive variables. The standardized Euclidean distance measure was calculated for each pair of individuals, Ward's minimum variance method was used to link similar points, and the number of significant clusters was determined by graphical examination of the resulting dendrogram and scree plot of inter-cluster distance vs. number of clusters (McGarigal et al., 2000). After classifying each otter by cluster membership, we used multiple linear discriminant analysis to evaluate the effectiveness of the classification (i.e. the frequency with which otters would consistently be assigned cluster membership using a jack-knife re-sampling test procedure), and to graphically compare the correspondence between group membership assigned by the cluster analysis of TDR data and

Table 2
Mean values for 11 parameters measured from TDR data sets collected from southern sea otters (associated standard errors are in parentheses)

Parameter	Mean values by diet type						Significant differences for		Used for DA?
	Type 1		Type 2		Type 3		Diet types	Individuals	
Within-bout depth range (m)	9.2	(0.56)	8.3	(0.50)	8.5	(0.60)	n.s.	n.s.	
Mean dive depth (m)	10.8	(0.71)	6.8	(0.43)	11.1	(0.80)	***	***	Yes
Variance in dive depth	6.0	(1.06)	5.1	(0.93)	5.7	(0.97)	n.s.	n.s.	
Mean dive duration (DT) (s)	86.7	(3.00)	72.6	(2.26)	92.3	(3.62)	***	***	Yes
Variance in DT	489	(32.9)	374	(28.6)	493	(47.7)	*	**	
Mean post dive inteval (PDI) (s)	58.3	(3.41)	40.7	(1.89)	100.6	(5.55)	***	**	Yes
Variance in PDI	6,163	(1500)	1694	(302)	5578	(809)	**	n.s.	Yes
Inter-dive consistency (IDC)	0.65	(0.024)	0.59	(0.021)	0.62	(0.028)	n.s.	***	Yes
Dive depth vs. DT	0.51	(0.079)	0.50	(0.011)	0.69	(0.086)	*	*	Yes
BT vs. PDI	0.17	(0.025)	0.13	(0.015)	0.17	(0.019)	n.s.	*	
Non feeding dives/feeding dives	0.33	(0.070)	0.58	(0.101)	0.20	(0.037)	**	**	

All depth-based parameters are in units of meters, while all time-based parameters are in units of seconds. Separate estimates are provided for each of three diet specialist types, as calculated from 120 feeding bouts selected randomly from 6 study animals (two representatives of each diet type). The three columns on the right indicate whether parameters differ significantly between diet types or between individual animals (the number of "*" symbols indicates significant level: $\alpha = 0.05$, $\alpha = 0.01$ and $\alpha = 0.001$, respectively), and whether the parameter was included in subsequent discriminant analyses to classify otters by diet type. See Section 2 for further explanation.

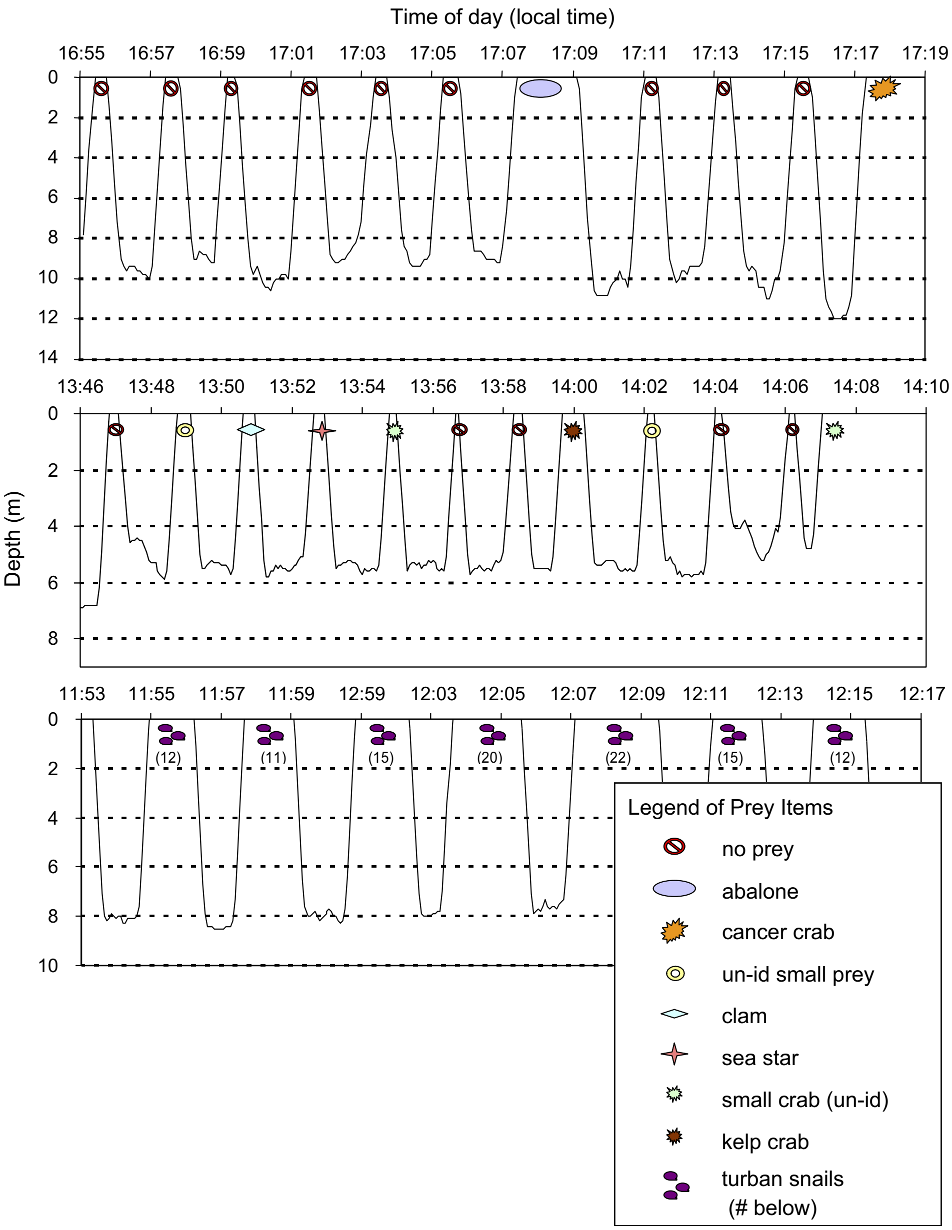

Fig. 2. Sample time–depth profiles taken from three of the TDR records collected from sea otters. Each set of axes shows a typical sequence of day-time feeding dives for approximately 20 min of time: the top axes show TDR data for a type 1 specialist, the middle axes show TDR data for a type 2 specialist, and the bottom axes show TDR data for a type 3 specialist. Note the slightly different depth scales for each graph. Also shown are the prey items captured during each dive and consumed during the post-dive surface interval (PDI), as recorded by a field observer (visual records of dives were matched to the corresponding dives in the TDR record).

the a priori classification based on diet composition. We used a Monte-Carlo randomisation test (Efron and Tibshirani, 1993) to evaluate the relative level of support for non-random correspondence between classifications based on diet and dive behaviour: specifically, we created 100,000 simulated datasets in which 13 individuals were classified into three dietary groups, exactly as observed, but in which group membership based on dive data was randomly assigned (we allowed up to four dive-based groupings). Approximately 1% of the randomised simulations resulted in a relatively high degree of correspondence (dive-based group assignments were identical to diet-based groupings for at least 10 of the 13 individuals) by chance alone; consequently, we conclude that the null hypothesis of no significant correspondence could be safely rejected (at $\alpha = 0.01$) if fewer than 4 of the 13 animals were misclassified.

All data processing and analyses were conducted in the MATLAB programming environment (MathWorks Inc., Natick, MA), with the exception of the initial TDR data processing, which were conducted using Wildlife Computers "Instrument Helper 1.0" software, and the hierarchical cluster analyses and discriminant analyses, which were conducted using SYSTAT 10.0 statistical software (SPSS, Evanston, IL).

3. Results

For 25 activity sessions having matching, independent estimates of percent time foraging, the telemetry-based method resulted in a mean estimate of 35.4% time feeding, while the TDR estimate was 34.6%. These estimates were not significantly different (mean difference = −0.08%, 95% confidence interval = −4.73% to 3.13%), suggesting that the TDR data processing resulted in generally reliable identification of feeding vs. non-feeding activity. A closer examination of TDR dive profiles matched against observational data indicated that, for 12 of the 13 study animals, all successful feeding dives recorded by an observer over a 1-h period were correctly identified and classified in the TDR record (Fig. 2). There were a very small number of "unsuccessful dives" (i.e. dives within a foraging bout that did not result in capture of new prey items) that were classified as non-feeding dives; however, most of these were very short (<20 s DT) and were usually associated with the focal otter retrieving dropped prey items, avoiding prey theft by con-specifics, diving to avoid breaking waves, or other activities that likely did not include attempts at new prey acquisition. For these 12 animals, we found no observed non-feeding dives (e.g., travelling or interacting dives) that were misclassified as feeding dives in the TDR record. In the case of the 13th study animal, a significant number of feeding dives (approximately 30%) recorded during field observation were misclassified as non-feeding dives; this proportion varied greatly when further 1-h periods were examined. This particular animal often engaged in an unusual feeding strategy referred to as "kelp tunnelling", which consisted of very shallow dives just below the surface kelp canopy in order to capture canopy-dwelling invertebrates. During these kelp tunnelling dives, the otter often could be seen as a moving lump beneath the kelp: the TDR data profile reflected such activity as a series of short "V-shaped" dives, rather than as a single long dive, with the result that logistic regression analysis resulted in these being misclassified as non-feeding dives. In spite of this particular issue, the majority of feeding dives were still correctly identified even for this animal and, as with the other 12 study animals, all dives that were identified as feeding dives corresponded to real feeding dives and never to non-feeding dives. We conclude that our approach to classifying feeding dives was both consistent and accurate, and all further results are reported for feeding dives only.

Based on the sub-set of 120 foraging bouts from 6 females (with each diet type represented by 2 individual animals and 40 feeding bouts), it appeared that for several dive parameters there were consistent differences between diet types and between individual animals (nested within diet types); these results are summarized in Table 2. Most striking were the differences in dive depth and PDI: types 1 and 3 specialists tended to have deeper dives than type 2 specialists, a longer PDI on average (particularly for type 3 specialists), and greater variance in the PDI (particularly for type 1 specialists). These trends were visually obvious in the TDR dive profiles, and the likely reasons for these differences became evident when the dives were matched with observational data on dive success (Fig. 2). Type 2 specialists tended to feed on small to medium-size prey located at fairly shallow depths and had fairly consistent dive success rates, and therefore had similar handling times at the surface from dive to dive. Type 1 specialists tended to feed on larger but less abundant prey types at slightly greater depths, and the highly variable PDI was associated with variation in dive success: there were very short surface times when no prey was captured interspersed with long surface times when a single large prey item was captured. In contrast, the longer PDI of type 3 specialists was associated with the cumulative handling time for the many turban snails captured each dive, and PDI variance in this case was due to variable numbers of snails captured, rather than variable success rates.

Of the 11 variables examined, 6 were most useful for classifying individuals by diet type using linear discriminant analysis (Table 2), and diet types were statistically distinguishable along the first 2 canonical axes (Wilk's $\lambda = 0.289$, approximate $F = 16.055$, df. 12/224, $p < 0.001$). Using a Jack-knife resampling analysis, individual feeding bouts were correctly classified to diet type 71% of the time, while individual otters were classified correctly 100% of the time. The misclassification of bouts indicates that there was substantial bout-to-bout variance in dive parameters for individual otters: this was confirmed by variance component analysis (Fig. 3). Approximately 45% of the variance in the canonical variables was explained by within-otter variation, with a similar amount explained by differences between diet types and about 10% attributable to differences between otters within diet types.

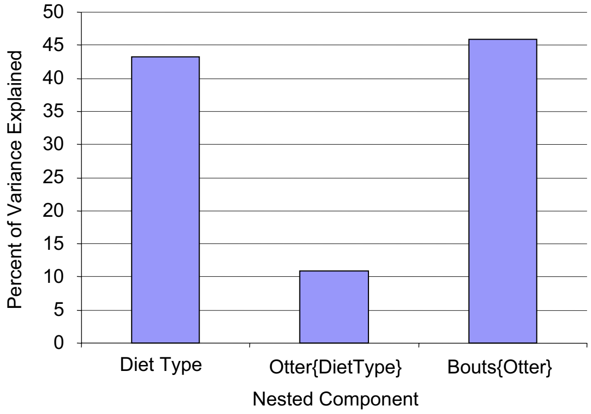

Fig. 3. Results of a variance components analysis conducted following nested analyses of variance of canonical variables that represent orthogonal linear functions of 6 dive parameters measured from TDR records. Bars indicate the proportion of variance explained by 3 hierarchical effects: differences between diet types, differences between individual otters (nested within diet types), and differences between bouts (nested within individual otters), or within-individual variation.

Broadening our analysis to include the full TDR datasets collected for 13 female study animals, a "blind" cluster analysis (based solely on variance in the 6 dive parameters and using no dietary data or a priori information about group membership) revealed 3 distinct aggregations of animals (Fig. 4A). Discriminant analysis of the 3 clusters showed that they were highly distinct (jack-knife classification accuracy of 100%; Fig. 4B) and examination with respect to information on diet composition revealed that 12 of the 13 animals had been "correctly" grouped with animals having the same diet specialization. The probability of this degree of correspondence between independent classifications occurring by chance is approximately 0.0001 (based on 100,000 Monte-Carlo simulations). The only animal that was clustered with otters of a different diet type turned out to be the same animal for which feeding dives were occasionally missed in the initial dive-processing step. These missed feeding dives would tend to inflate the estimated mean PDI for this animal, probably explaining why it was grouped with type 3 specialists rather than other type 2 specialists.

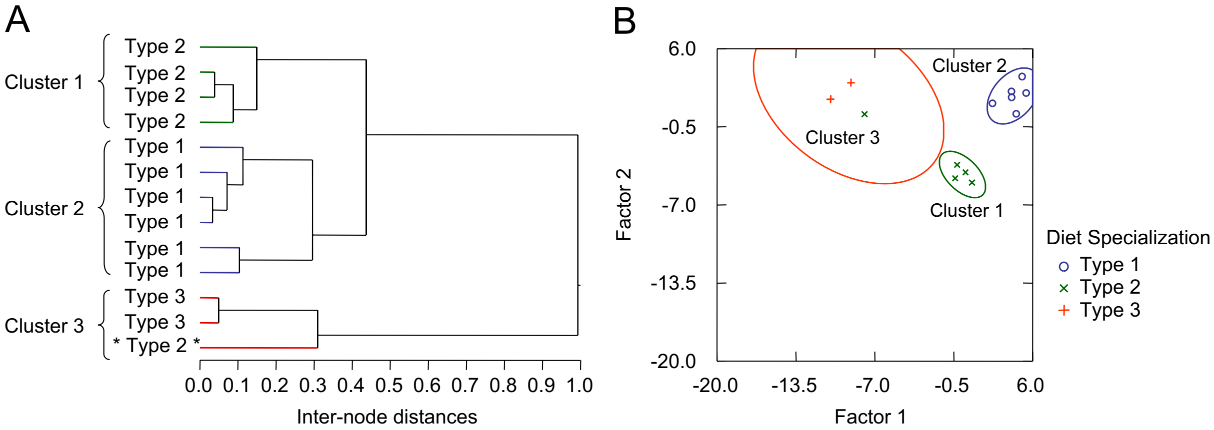

Fig. 4. (A) Results of a multivariate cluster analysis of 13 adult female sea otters, clustered based on variation in 6 dive parameters measured from TDR records. (A) dendrogram of inter-node distances, illustrating the pattern of aggregation into 3 distinct clusters. The diet specialization of each otter is indicated at the left of each node, although this information was not used in the cluster analysis. (B) Ordination of 2 canonical factors resulting from a discriminant analysis of the clusters shown in (A). Circles around the 3 clusters of data points indicate 95% jack-knife confidence ellipses. Note that only 1 of the 13 otters was grouped with animals of a different diet specialization.

4. Discussion

In general it appears that, at least for adult females, measurable and predictable differences in dive behaviour are associated with the previously described dietary specializations in southern sea otters (Lyons, 1991; Estes et al., 2003; Tinker, 2004). More practically, a relatively small suite of parameters measured from TDR archival data can be used to detect the presence of distinct dietary specializations and classify animals by diet type (Fig. 4). If all individuals within a population were generalists, then we would expect that within-individual variance in dive parameters would far exceed between-individual variance, resulting in no distinct clusters. In contrast, the current study suggests that a large proportion of variance is attributable to differences between individuals utilizing alternative prey specializations (Fig. 3). Nonetheless, there remained considerable variation between bouts for individual animals: while not unexpected given the dietary overlap between individuals, it does mean that reliable identification of individual specialization will require a substantial sample of TDR data for each individual animal, collected over a period of time sufficient to avoid spurious results (ideally multiple seasons or years). This is particularly important because seasonal or inter-annual differences in dive behaviour may correspond to temporal variation in environmental factors, rather than individual specialization (Boveng et al., 1996; Croxall et al., 1999).

The success of this approach for sea otters depends primarily on differences between prey species with respect to typical capture depths, relative capture frequency (assumed to correspond to relative abundance), and the time required to handle each prey item (Fig. 2). We must emphasize that the individual diets we report here (Table 1) are in no way an exhaustive representation of sea otter diets everywhere, being biased by our particular study site and sampling design (i.e. adult animals feeding in kelp-dominated habitat over predominantly rocky substrate). Diets will undoubtedly differ in other sea otter populations and in other habitat types (e.g., soft-sediment habitat such as tidal flats), and it remains to be seen whether individual prey specializations occur in such situations and if they will be reflected by differences in dive behaviour. Wider application of this approach to other sea otter populations, let alone other marine mammal or bird populations, will obviously depend on behavioural and dietary traits of the species in question; however, to the extent that alternative prey species utilize different depth ranges or require different capture or handling techniques, our results suggest that individual foraging specializations should be detectable from TDR data alone. Indeed, a similar pattern has been reported for Antarctic fur seals, where variation in dive parameters reflect differences in prey choice (Lea et al., 2002b; Staniland et al., 2004). These differences in prey choice were apparently related to spatial and temporal variability in the availability of prey species (Lea et al., 2002b), whereas in the case of sea otters the differences in prey choice and dive behaviour are seen among individuals with almost identical home ranges (Fig. 2), apparently reflecting a behaviourally mediated trophic polymorphism (Estes et al., 2003).

It has been hypothesized that the high degree of individual specialization in California sea otters reflects increasingly limited prey resources (Tinker, 2004), and data recently collected from an isolated, food-rich environment (San Nicolas Island, CA) support this hypothesis, as no dietary specialization has been found among these animals (Bentall, 2005). To the extent that this pattern is generally applicable to sea otters, TDR data could be a useful tool for assessing the status of other populations where questions exist about the role of food resources in population dynamics, such as southwest Alaskan sea otters (Doroff et al., 2003). Such an approach also may be useful for interpreting population status or impacts on prey communities by other marine vertebrate predators in which individual specialization occurs: prey specializations are already recognized in penguins (Radl and Culik, 1999; Tremblay and Cherel, 2003), killer whales (Ford et al., 1998; Baird et al., 2000), bottlenose dolphins (Smolker et al., 1997; Mann and Sargeant, 2003; Kruetzen et al., 2005), Minke whales (Hoelzel et al., 1989), sea lions and fur seals (Harcourt, 1993; Lea et al., 2002b; Staniland et al., 2004), and likely exist undetected in many other taxa.

Although further validation and testing on other taxa is needed, the current analyses strongly suggest that TDR data can be used as a tool to detect and discriminate between alternative diet specializations. This raises a number of questions that can be addressed by future research: how common are individual foraging specializations among marine birds and mammals? How general is the relationship between increased intra-specific competition and increased individual specialization? Are there any broadly repeated patterns to alternative foraging specialization in marine predators, such as large/rare prey vs. small/abundant prey, or low-value prey at shallow depths vs. high-value prey at great depths? Although it will be some time before such questions can be definitively answered, it seems certain that bio-logging technology will play a principal role in this area of research. Our ultimate goals must be to both understand the causes of individual specialization, and to incorporate such variation into models of population-level and community-level food web dynamics.

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