Estimating Diet Composition in Sea Lions: Which Technique to Choose?

Dominic Tollit and Susan Heaslip
University of British Columbia, Marine Mammal Research Unit, Fisheries Centre, Vancouver, British Columbia, Canada

Bruce Deagle
University of Tasmania, Zoology Department, Hobart, Australia

Sara Iverson
Dalhousie University, Biology Department, Halifax, Nova Scotia, Canada

Ruth Joy, David Rosen, and Andrew Trites
University of British Columbia, Marine Mammal Research Unit, Fisheries Centre, Vancouver, British Columbia, Canada

Abstract

Reliable estimates of diets are vital to monitor impacts of sea lion populations on their ecosystems and their interactions with fisheries, and to understand the role of food to animal nutrition and health. Approaches include using (1) prey remnants in stomach contents, spews and scats; (2) prey DNA in scats; (3) fatty acid signatures in blubber; and (4) stable isotope ratios in predator's tissue. Each methodology has particular advantages and limitations, many of which can be assessed and improved through controlled captive feeding trials. Analysis of prey remnants from captive sea lion scats have shown significant variability in digestion between and within prey species, which, coupled with preferential regurgitation and enumeration biases, can confound accurate diet quantification, but does not prevent spatial or temporal comparisons. Correction for partial digestion and use of additional structures besides otoliths can provide reliable prey size estimates. Prey DNA can be consistently isolated from soft remains in scats from captive sea lions, and with further development this approach may allow quantification of diet. Genetic methods can be expensive and representative of only one to two

days foraging (like prey remnant analysis), but may be less affected by differential digestion and can identify prey in scats that could not be identified through structural remnants. Validation of fatty acid signature analysis to quantify diet at longer temporal scales in sea lions is ongoing. This new technique promises to be particularly useful to assess biases in traditional methods, identify the onset of weaning, and highlight the prey that most contribute to lipid reserves. Stable isotope analysis of predator tissues gives only trophic level data, but can provide data on diet changes on many temporal scales. Remote video monitoring of foraging events and lavage/enema techniques can provide valuable diet information, but, like many newer techniques, animal capture is required. Ideally a suite of techniques should be used to study diet. While methods and correction factors developed for Steller sea lions can likely be applied to the other five sea lion species, they should be verified experimentally.

Introduction

Reliable estimates of diets are vital to monitor impacts of sea lion populations on their ecosystems and their interactions with fisheries, and to understand the role of food to animal nutrition and health. The traditional approach was to examine stomach contents. More recent methods include using hard remains in scats and spews, isolating prey DNA from scats, fatty acid signatures in blubber, stable isotope ratios in predators' tissues, and direct video observation. All methods of estimating diet have pros and cons (Table 1), many of which can be assessed and improved through controlled captive feeding trials.

Methods

Captive feeding studies with 2-5 year old female Steller sea lions at the Vancouver Aquarium Marine Science Centre have assessed three different methods to quantify diet. In this review, we summarize the findings of these studies, complement them with results from additional captive studies with sea lions, and discuss the benefits and drawbacks of alternate techniques presently being used to study sea lion diet (Table 1).

1. Prey remains found in scats

The analysis of prey skeletal structures found in scats (feces) is now the most widely used technique for estimating the diet of pinnipeds, with sagittal otoliths being the most commonly used identifying structure (Frost and Lowry 1980, Olesiuk et al. 1990, Bowen et al. 1993, Tollit and Thompson 1996). However, there remain a number of well recognized problems related to identifying prey without hard remains, differential rates of digestion (hence, recovery), and choice of skeletal structures used to identify prey (see reviews by Pierce and Boyle 1991, Bowen 2000).

Table 1. Pros and cons of different methods used to estimate diet in otariids.

Method to estimate diet	Impact on individual	Impact on group	Dietary time period	Prey size estimate	Additional limitations
Scats, hard remains	No	Moderate	Short	Yes	Differential prey digestion and retention. Requires presence of prey hard parts. Special identification skills often required.
Spews, hard remains	No	Moderate	Short	Yes	Differential prey digestion and retention. Requires presence of prey hard parts. Special identification skills often required.
Scats, DNA remains	No	Moderate	Short	No	New technique, relatively untested. Lack of genetic data for many prey.
Lavage (enema)	Moderate (low)	Low-moderate	Short	Yes	Capture and sample size issues. Empty stomachs (colons) reduce sample size.
Stomach samples	Extreme	Moderate-high	Short	Yes	Differential prey digestion and retention. Empty stomachs reduce sample size.
Stable isotopes	Moderate	Low-moderate	Moderate-long	No	Capture and sample size issues. Only trophic level quantification.
Fatty acid signatures	Moderate	Low-moderate	Moderate-long	No	Capture and sample size issues. New technique, relatively untested. Current prey library required.
Head camera	Moderate	Low-moderate	Short	Possible	Capture and sample size issues. High cost and unit recovery required. Low number of feeding events captured.
Direct observation	No	Low	Immediate	Possible	Limited to prey brought to surface. Limited mainly to nearshore interactions.

Recent captive studies (e.g., Gales and Cheal 1992, Orr and Harvey 2001, Cottrell and Trites 2002, Staniland 2002, Tollit et al. 2003) were designed to provide numerical and size correction factors to account for the effects of digestion, and to assess the use of different structures and diet indices in describing diet. More recently, multiple bones in addition to otoliths have been used for prey identification from scat, a technique that requires highly specialized identification skills and a complete reference collection. Nevertheless, the technique was believed to significantly reduce the problems associated with differential digestion (Olesiuk et al. 1990). Our captive studies have therefore concentrated on assessing this new approach by feeding both individual single species meals (see Tollit et al. 2003 for methods) as well as replicated meals of mixed and varying species composition.

A total of three replicated meal feeding trials were undertaken at the Vancouver Aquarium Marine Science Centre in the summer of 2003. As in the single species meal feeding trials, experimental meals were preceded and followed by 3 days of herring fillets. Each trial fed for 15 days the same four species (herring, walleye pollock, coho salmon, and capelin) at the same time (~10:15 and ~15:15), in the same quantity (7.5% body mass per day), but in three different prey ratios (scenario 1, 67.5%, 22.5, 7.5%, 2.5% respectively; scenario 2, 22.5%, 67.5%, 2.5%, 7.5% respectively, and scenario 3, 25% of each species). Other than during tank drains for scat collections, animals had full access to water. The number of fish represented by all recovered structures was estimated using a "minimum number of individuals" technique (Tollit et al. 2003) for each drain and scat recovered over days 2-16. Diet fed (proportion by mass) was compared with diet estimated using both the split sample frequency of occurrence (SSFO) method (Olesiuk et al. 1990) and a simple biomass reconstruction (BR) method, in which it was assumed prey size egested was identical to that ingested and each drain/scat contributed a variable quantity of prey biomass (Laake et al. 2002). Reconstructed biomass estimates were compared when using the "all structure" technique and when using only otoliths.

2. Prey soft remains identified in scats using genetic techniques

Using molecular genetic scatology to study diet is a relatively new and involved technique (Jarman et al. 2004), but it has been successfully utilized to classify morphologically unidentifiable hard parts of salmon from harbor seal scats (Purcell et al. 2004). Many of the biases associated with hard remnant analysis could potentially be investigated using DNA techniques to identify prey from soft material, making this approach very appealing. Our recent collaborative captive study (Deagle et al. 2005) aimed to assess whether prey DNA could reliably be detected from soft remains in scats and whether DNA in scats might be useful in quantifying

diet. In this study, we collected scats from two female Steller sea lions. The first animal (#F97HA, mean mass 146 kg, 6 years old) was in the feeding trial for 48 days; and the second animal (#F00NU, mean mass 131 kg, 3 years old) for 24 days. Four species of prey were fed consistently in the trial: Pacific herring (*Clupea pallasii*), surf smelt (*Hypomesus pretiosus*), sockeye salmon (*Oncorhynchus nerka*), and Californian market squid (*Loligo opalescence*). The basic daily diet (7-8 kg per day, ~5.5% of body mass) was fed in two meals (at ~9:30 and 14:30) and consisted of herring (47% by mass), smelt (34%), sockeye (13%), and squid (6%). This diet was initiated at least 4 days before the first scats were collected. Small subsamples were taken from each scat and the remaining material blended and then also sampled. DNA was extracted and identified to species using polymerase chain reaction (PCR) and denaturing gradient gel electrophoresis. In a preliminary investigation into quantifying diet, proportions of fish DNA present in six scats were evaluated through the screening of PCR clone libraries. See Deagle et al. (2005) for full details of DNA detection and cloning methodology.

3. Fatty acid signature analysis

Fatty acid signatures have been shown to be useful in documenting qualitative variations in diet across species, age, and sex class (e.g., Beck et al. 2005) as well as space and time (e.g., Iverson et al. 1997, Walton and Pomeroy 2003). Quantified fatty acid signature analysis (QFASA) is based on an optimization model that has been developed to estimate the species composition of marine mammal diets by matching the fatty acid (FA) signatures of their blubber with those of their potential prey (Iverson et al. 2004). We conducted captive feeding studies (1-9 months each) on seven juvenile female Steller sea lions to evaluate QFASA's ability to identify known mixed-prey diets and to provide information on FA turnover time and deposition rates down the core of the biopsy. For each animal, 2-9 sequential full-depth blubber biopsies were collected mid-flank, following various periods of controlled diet, including 1-4 week pulses of salmon, capelin, eulachon, walleye pollock, or Atka mackerel. Changes in mass and body composition (using D_2O) were also measured (Tollit et al. 2003). A key prerequisite of QFASA are the FA calibration coefficients (FA-CCs), which aim to account for the differential deposition and synthesis of fatty acids during lipid metabolism. These are typically calculated by using FA signatures in blubber after feeding a long-term diet of pure herring. FA-CCs are available for two species of phocid (Iverson et al. 2004), but none are available for otariids. To assess possible differences in fatty acid metabolism across pinnipeds, blubber biopsies were taken from five Steller sea lions after they were fed pure herring diets for 7-9 months. After lipid extraction, flame ionization detector (FID) gas chromatography was used to assess contributions of 68 fatty acid signatures (see Iverson et al. 2004 for a full methodology).

Results

1. Prey hard remains found in scats

Use of multiple bones (versus only otoliths) increased percent prey recovery (Fig. 1), particularly for salmon. Despite the use of the "all structure" technique, significant differences across prey species in percent recovery (more than tenfold) and passage time (twofold) was documented. Bones in scats were found to consist of a composite of meals eaten 2-148 hours earlier (longer than many phocids) and a single day feeding event was distributed across 1-6 scats (Tollit et al. 2003).

Beaks from the small (~40 g) squid fed were typically found in scats 1-2 days following ingestion, but were also sometimes recovered more than 3 weeks later. A number of meals were subsequently regurgitated, which dramatically reduced the overall recovery of bones in scats, most notably for pollock and salmon. Use of other cranial bones (in addition to otoliths), grading the degree of observed digestion, and the application of experimentally derived grade-specific digestion correction factors (Fig. 2) are fundamental to correctly estimating prey size eaten by Steller sea lions (see also Tollit et al. 2004a,b; Zeppelin et al. 2004).

Regurgitations in scenario 3 of the replicated mixed meal study resulted in fed diets being ~12% pollock and ~29% for the remaining species, not 25% for each species as planned. Analysis of the repeated mixed meal study showed that, despite low contributions of capelin and salmon in scenarios 1 and 2, their presence in subsequent scats was almost always detected when using the "all structure" technique. Consequently, the frequency of occurrence model could not discern the different mixed diet scenarios actually fed. In this particular set of scenarios, the biomass reconstruction (BR) models provided better predictions of the actual amount fed of each species. The BR model using "all structures" did, however, exhibit consistent biases, with capelin consistently underestimated, and salmon and pollock consistently overestimated (Fig. 3). The use of only otoliths to estimate diet resulted in a number of improvements (e.g., salmon) over the "all structure" technique, but also resulted in some poorer predictions (e.g., herring). Capelin, the smallest prey consumed, remained consistently underestimated (Fig. 3).

2. Prey soft remains identified in scats using genetic techniques

Our results show prey DNA can be successfully isolated from soft remains, even in cases when the scats were left out in the sun for a number of days. Detection rates (i.e., frequencies of prey DNA occurrence) were extremely high (98%) when scats were blended together and sampled. When scats were simply subsampled, the detection rates were significantly lower (but still relatively high—89%). Different prey species were generally detected equally despite the large differences in the amount
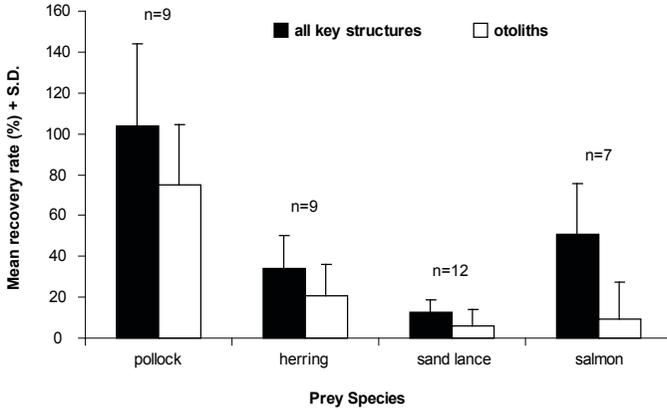
Figure 1. Between-species comparison of mean prey recovery (%), when using multiple bones (all key structures) versus otoliths only. Data represent multiple feeding trials (n) with two female captive Steller sea lions in which meals containing regurgitated material have been excluded. Adapted from Tollit et al. (2003).
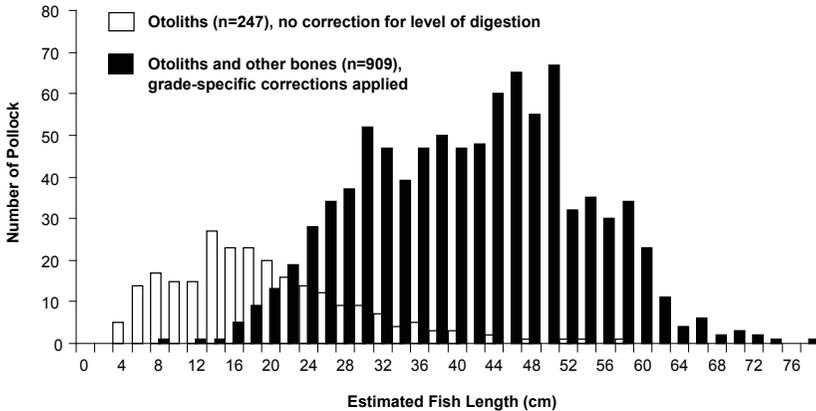

Figure 2. Comparison of two methods to estimate the size of walleye pollock recovered in Steller sea lion scats collected in the field (Southeast Alaska 1993-1999). Fish length predicted from all otoliths regardless of digestive state (mean FL = 20.2 cm) are compared with estimates using six additional cranial structures besides otoliths, of which all are in good or fair condition and to which experimentally derived grade-specific correction factors have been applied to account for level of digestion (mean FL = 42.4 cm).
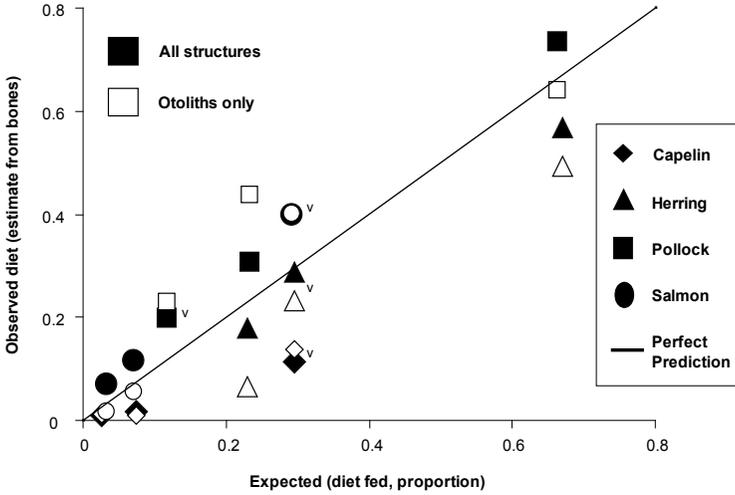
Figure 3. Comparison of using the "all structure" technique versus only otoliths in estimating diet using a biomass reconstruction method (observed diet). Captive Steller sea lions were fed meals of mixed and variable prey composition consistently for 15 days (diet fed). V denotes data points that include evidence of regurgitated hard remains in 36% of scats/tank drains.
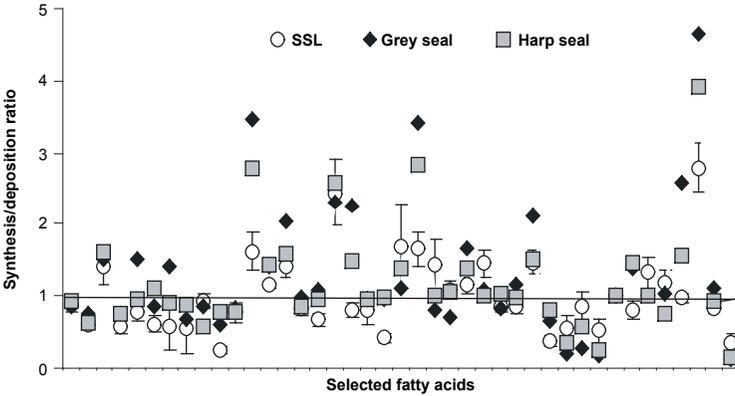

Figure 4. Fatty acid calibration coefficients shown for three pinniped species, including Steller sea lions (SSL). Fatty acids (n = 41) ranging from C12.0 to C24.1w9 are shown, with the line at 1 indicating the proportion found in the diet was identical to that found in the blubber sample (no synthesis or deposition). Data for grey and harp seals are taken from Iverson et al. (2004).

of each fed. Proportions of fish DNA present in six scat samples were roughly proportional to the mass of prey consumed, but directional biases were apparent. For example, herring (fed at 50% of the total fish component) and salmon (fed at 14%) were both slightly overestimated (clone predictions: herring, 56-72%; salmon, 16-28%), while smelt (fed at 36%) was underestimated somewhat, with predictions from clones ranging from 12% to 32%.

3. Fatty acid signature analysis

Optimization of the QFASA model using data from captive animal studies is still ongoing. To date QFASA results were promising, but did result in false identifications of prey, and were dependent on which modeling parameters were used (FA-CCs, number of FAs included, etc.). Preliminary results also showed Steller sea lion FA-CCs were comparable to but not interchangeable with those previously obtained from phocid seals (Fig. 4). Overall, where differences were apparent, Steller sea lion FA-CCs were lower than for those observed for gray and harp seals for fatty acids: C14.1w5, C15.1w8, C16.1w11, C17.0, C17.1, C16.4w1, C18.1w11, C18.1w9, C18.3w3, C18.4w3, C20.5w3, C22.2w6 and C22.5w3; and higher for fatty acids: C14.1w7, C15.1w6, C20.0, C22.1w7, C22.1w9, C22.1w11, C22.4w6, C24.1w9.

Discussion

Scat collections may disturb animals resting on land, but they are otherwise noninvasive. Importantly, they typically provide definitive prey species identification and can often be collected in large numbers. Analysis of prey remnants in scats presently remains the best method for assessing prey size, provided levels of digestion are taken into account (Jobling and Breiby 1986). Low recovery of otoliths in sea lion scats has been shown in a number of species (e.g., Dellinger and Trillmich 1988, Gales and Cheal 1992, Tollit et al. 2003), therefore other techniques are needed to supplement dietary data. For example, the use of alternate bones (as well as accounting for the amount of digestion) was demonstrated to be crucial in assessing the extent of overlap between sizes of pollock taken by Steller sea lions compared to that taken by the commercial fishery (Fig. 2, Tollit et al. 2004a). However, while the use of multiple bones increases species recovery rates, species differences (hence potential biases) are not eliminated and enumeration becomes problematic (see Tollit et al. 2003). This is mainly a result of fish bones from single feeding events being spread over multiple (1-6) scats and consequently resulting in the double counting of the same fish. Counting the most numerous paired bone available or the development of new bone-counting techniques to estimate prey numbers eaten may circumvent this particular problem. However, it is important to note that captive feeding studies often report

information by collapsing data for all scats collected after a meal. A more logical (realistic?) approach would be to provide information at the level of individual scats. For example, while pollock recovery per feeding event was relatively high overall (Fig. 1), it was also distributed across a large number of scats. Nevertheless, the extended scat output we observed in Steller sea lions, and seen also in southern sea lions (D. Rodriguez, CONI-CET, Mar del Plata, Argentina, pers. comm.), does challenge the assumption that scats necessarily represent just nearshore or recent foraging.

Provided sample sizes are sufficient (estimated for biomass reconstruction to be around 100 samples by Hammond and Rothery [1996]), it is reasonable to assume inherent biases are consistent, permitting comparisons of the relative importance of prey species across time periods or geographical areas. Use of correction factors can negate some biases associated with differential digestion, but regurgitation and crushing by gastroliths or stomach rocks of larger bones confound their easy application. Clearly, given the high intraspecific variability observed, multiple experiments are required to produce useful correction factors and the experiment must be designed to be as realistic as possible. Gastroliths in the Australian sea lion may have been a factor in the low otolith recovery observed in captive feeding studies (Gales and Cheal 1992), as well as from scats collected in the wild. In species that are known to regularly regurgitate material (e.g., California sea lion, Steller sea lion, northern fur seal, Galapagos fur seal), it is important to analyze regurgitate material (either from lavage or from land-based regurgitates) to assess possible biases in size and species consumed, compared to assessments solely from scats (Fea and Harcourt 1997, Kiyota 1999). Apparent biases in exclusively using scat data include underestimating large cephalopods and large fish such as gadoids. Data on at-sea feeding episodes and regurgitation rates (using head-mounted cameras) would be useful in this assessment (see Bowen et al. 2002).

Frequency of occurrence indexes can quickly provide useful dietary information, particularly with large sample sizes (Olesiuk 1990, Sinclair and Zeppelin 2002). Our replicated mixed meal study highlighted the reliability of the "all structure" technique in identifying the presence of four prey fed regularly in widely varying proportions (2.5%-67.5%), leading to the split sample frequency of occurrence index (SSFO) to predict all prey were eaten in approximately equal quantities. Olesiuk et al. (1990) recognized SSFO captures the occurrence component of diet and suggested a volume-weighted version. Our results concur that a prey biomass/volume approach is required if fine level diet estimates are required at small scales and within narrow time frames, especially when sample sizes are limited. Thus, while biomass reconstruction generally gave improved predictions of the actual amount fed of each species, systematic biases were observed (Fig. 3), that confirm previous studies (e.g., Harvey 1989; Tollit et al. 1997, 2003) that highlight the need for species-specific numerical

correction factors. The drawbacks of reconstructing prey biomass include the need for prey remains to be enumerated and measured and the need for bone size to fish size regressions. In addition to captive studies, the use of Monte Carlo diet simulations can provide useful information on the biases of each method and to assess the success of possible solutions (Hammond and Rothery 1996, Arim and Naya 2003), such as the use of numerical correction factors to account for species variability in bone recovery rates.

Analysis of prey hard remains clearly can provide useful dietary information that is difficult to obtain using alternate methods. Time permitting, and if suitable regression equations and digestion correction factors exist, then biomass/volume reconstructions are recommended. Further captive studies are required to assess if prey in individual scats should be considered a random and therefore variable subsample of diet or if the contribution of each scat should be fixed to a predetermined constant (e.g., daily mass consumption or calorific requirement)(Laake et al. 2002). For the sake of comparison, it is important to present results using a variety of indices, including percent numbers, frequency of occurrence, and some measure of contribution by mass. Potentially, an index of relative importance (Harvey 1987) can be calculated combining these indices, whereby species are merely ranked, as opposed to supplying a point estimate that may be potentially biased (see discussion by Laake et al 2002).

While isolating prey DNA from scats and using PCR techniques to identify species is clearly involved and presently more expensive than traditional analysis of prey remnants in scats, it does not require prey hard parts and therefore is likely to be less affected by differential bone retention and digestion. The captive feeding study described (see Deagle et al. 2005 for full details) clearly highlights that further investment is warranted; particularly in determining new genetic markers for prey species of interest, trialing the technique on field collected scat samples, and assessing alternate techniques for quantifying DNA in scats (such as Real Time PCR). Like prey remnant analysis, this approach only reflects short-term dietary history. Nevertheless, the technique may prove very useful in studies where prey have fragile bones (such as salmonids), where prey have hard parts that are regurgitated (e.g., large cephalopods), where prey have few or no hard parts, or in species such as Australian sea lions in which bones are poorly represented in scats (Gales and Cheal 1992). We note that DNA methods can also provide information on the predator, including animal sex, species (e.g., Reed et al 1997), and theoretically individual identification information.

Animal capture (if possible) clearly provides useful demographic information and dietary data at the individual level, that can be collected on many temporal scales (long term—vibrissae stable isotope analysis; medium term—QFASA muscle and skin stable isotope analysis, short

term—lavage, enema, cameras). Stable isotope ratio analysis of predator tissues presently provides only trophic level data, but the technique allows one to follow diet changes through time and at different temporal scales (Kurle 2002). Fatty acid signatures have also been useful in documenting both species, as well as spatial and temporal variations in diet (Iverson et al. 1997). While the validation of the QFASA model to quantify diet in Steller sea lions is continuing, preliminary results of this new technique are promising and worth pursuing, particularly to assess biases in traditional methods, the onset of weaning, and the prey that most contribute to lipid reserves. QFASA ideally requires a current and full prey base as well as fatty acid calibration coefficients (FA-CCs). Preliminary results of our study showed Steller sea lion FA-CCs were comparable to but not interchangeable with those previously obtained from phocid seals (Iverson et al. 2004, Fig. 4). Thus it appears either otariid or species-specific FA-CCs are needed or alternatively the comparatively shorter time period herring was fed in the two phocid studies did not result in the full turnover of lipid reserves (i.e., some trace of previous diet remained). Collections of blubber from animals difficult to capture can be obtained remotely using various dart projectors (Barrett-Lennard et al. 1996), but further information is needed to assess if signatures vary around the body and along the length of the blubber core (if only partial samples are collected). Animal capture also allows the ability to deploy cameras. Cameras need to be recovered and are presently somewhat limited by memory capacity, but they can provide useful foraging information, including profitability rates (Bowen et al. 2002), prey types, and search patterns (e.g., benthic, pelagic). Foraging success (intensity) can also be addressed using stomach temperature sensors and, more recently, magnet-based mandibular sensors (Wilson et al. 2002). Overall, while the analysis of prey remnants remains the obvious first step, ideally a suite of techniques should be used to study diet to ensure important components are not missed. Methods and correction factors developed for Steller sea lions can likely be applied to the other four sea lion species, but they should be verified experimentally.

Acknowledgments

References

Arim, M., and D.E. Naya. 2003. Pinniped diets inferred from scats: Analysis of biases in prey occurrence. Can. J. Zool. 81(1):67-73.

Barrett-Lennard, L.G., T.G. Smith, and G.M. Ellis. 1996. A cetacean biopsy system using lightweight pneumatic darts, and its effect on the behavior of killer whales. Mar. Mamm. Sci. 12:14-27.

Beck, C.A., S.J. Iverson, and W.D. Bowen. 2005. Blubber fatty acids of gray seals reveal sex differences in the diet of a size-dimorphic marine carnivore. Can. J. Zool. 83(3):377-388.

Bowen, W.D. 2000. Reconstruction of pinniped diets: Accounting for complete digestion of otoliths and cephalopod beaks. Can. J. Fish. Aquat. Sci. 57:898-905.

Bowen, W.D., J.W. Lawson, and B. Beck. 1993. Seasonal and geographic variation in the species composition and size of prey consumed by grey seals (*Halichoerus grypus*) on the Scotian shelf. Can. J. Fish. Aquat. Sci. 50:1768-1778.

Bowen W.D., D. Tully, D.J. Boness, D. Bulheier, and G. Marshal. 2002. Prey dependent foraging tactics and prey profitability in a marine mammal. Mar. Ecol. Prog. Ser. 244:235-245.

Cottrell, P.E., and A.W. Trites. 2002. Classifying prey hard part structures recovered from fecal remains of captive Steller sea lions (*Eumetopias jubatus*). Mar. Mamm. Sci. 18:525-539.

Deagle, B.E., D.J. Tollit, S.N. Jarman, M.A. Hindell, A.W. Trites, and N.J. Gales. 2005. Molecular scatology as a tool to study diet: Analysis of prey DNA in scats from captive Steller sea lions. Mol. Ecol. 14:1831-1842.

Dellinger, T., and F. Trillmich. 1988. Estimating diet composition from scat analysis in otariid seals (Otariidae): Is it reliable? Can. J. Zool. 66:1865-1870.

Fea, N., and R. Harcourt. 1997. Assessing the use of faecal and regurgitate analysis as a means of determining the diet of New Zealand fur seals. In: M. Hindell and C. Kemper (eds.), Marine mammal research in the Southern Hemisphere: Status, ecology and medicine. Surrey Beatty and Sons Ltd., Chipping Norton, pp. 143-150.

Frost, K.J., and L.F. Lowry. 1980. Feeding of ribbon seal (*Phoca fasciata*) in the Bering Sea in spring. Can. J. Zool. 58:1601-1607.

Gales, N.J., and A.J. Cheal. 1992 Estimating the diet composition of the Australian sea lion (*Neophoca cinerea*) from scat analysis: An unreliable technique. Wildl. Res. 19:447-455.

Hammond, P.S., and P. Rothery. 1996. Application of computer sampling in the estimation of seal diet. J. Appl. Stat. 23:525-533.

Harvey, J.T. 1987. Population dynamics, annual food consumption, dive behaviors, and movements of harbor seals, *Phoca vitulina richardsi*, in Oregon. Ph.D. thesis, Oregon State University, Corvallis. 168 pp.

Harvey, J.T. 1989. Assessment of errors associated with harbor seal (*Phoca vitulina*) fecal sampling. J. Zool. (Lond.) 219:101-111.

Iverson, S.J., K.J. Frost, and L.F. Lowry. 1997. Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. Mar. Ecol. Prog. Ser 151:255-271.

Iverson, S.J., C. Field, W.D. Bowen, and W. Blanchard. 2004. Quantitative fatty acid signature analysis: A new method of estimating predator diets. Ecol. Monogr. 74:211-235.

Jarman, S.N., B.E. Deagle, and N.J. Gales. 2004. Group-specific polymerase chain reaction for DNA-based analysis of species diversity and identity in dietary samples. Mol. Ecol. 13:1313-1322.

Jobling, M., and A. Breiby. 1986. The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. Sarsia 71:265-274.

Kiyota, M., C. Kawai, and N. Baba. 1999. Estimation of diet of male northern fur seals (*Callorhinus ursinus*) based on the analysis of fecal and regurgitated materials. Bull. Nat. Res. Inst. Far Seas Fish 36:1-7.

Kurle, C.M. 2002. Stable-isotope ratios of blood components from captive northern fur seals (*Callorhinus ursinus*) and their diet: Applications for studying the foraging ecology of wild otariids. Can. J. Zool. 80:902-909.

Laake, J.L., P. Browne, R.L. DeLong, and H.R. Huber. 2002. Pinniped diet composition: A comparison of estimation models. Fish. Bull. U.S. 100:434-477.

Olesiuk, P.F., M.A. Bigg, G.M. Ellis, S.J. Crockford, and R.J. Wigen. 1990. An assessment of the feeding habits of harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia, based on scat analysis. Can. Tech. Rep. Fish. Aquat. Sci. 1730. 135 pp.

Orr, A.J., and J.T. Harvey. 2001. Quantifying errors associated with using fecal samples to determine the diet of the California sea lion (*Zalophus californianus*). Can. J. Zool. 79:1080-1087.

Pierce, G.J., and P.R. Boyle. 1991. A review of methods for diet analysis in piscivorous marine mammals. Oceanogr. Mar. Biol. Ann. Rev. 29:409-486.

Purcell, M., G. Mackey, E. LaHood, H. Huber, and L. Park. 2004. Molecular methods for genetic identification of salmonid prey from Pacific harbor seal (*Phoca vitulina richardsi*) scat. Fish. Bull. U.S. 102:213-220.

Reed, Z., D.J. Tollit, P.M. Thompson, and W. Amos. 1997. Molecular scatology: The use of molecular genetic analysis to assign species, sex and individual identity to seal faeces. Mol. Ecol. 6:225-234.

Sinclair, E.H., and T.K. Zeppelin. 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). J. Mammal. 83(4):973-990.

Staniland, I.J. 2002. Investigating the biases in the use of hard prey remains to identify diet composition using Antarctic fur seals (*Arctocephalus gazella*) in captive feeding trials. Mar. Mamm. Sci. 18:223-243.

Tollit, D.J., and P.M. Thompson. 1996. Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. Can. J. Zool. 74:1110-1121.

Tollit, D.J., S.G. Heaslip, and A.W. Trites. 2004a. Sizes of walleye pollock consumed by the eastern stock of Steller sea lions *(Eumetopias jubatus)* in Southeast Alaska from 1994-1999. Fish. Bull. U.S. 102:522-532.

Tollit, D.J., S.J. Iverson, S.G. Heaslip, D.A.S. Rosen, and A.W. Trites. 2003. Validation studies of blubber quantitative fatty acid signature analysis (QFASA) with captive Steller sea lions (*Eumetopias jubatus*). 15th Biennial Conference on the Biology of Marine Mammals, Greensboro, NC, 14-19 December 2003, Abstract book. Society for Marine Mammalogy.

Tollit, D.J., M. Wong, A.J. Winship, D.A.S. Rosen, and A.W. Trites. 2003. Quantifying errors associated with using prey skeletal structures from fecal samples to determine the diet of the Steller sea lion (*Eumetopias jubatus*). Mar. Mamm. Sci. 19:724-744.

Tollit, D.J., S.G. Heaslip, T.K. Zeppelin, R. Joy, K.A. Call, and A.W. Trites. 2004b. Improving size estimates of walleye pollock and Atka mackerel consumed by Steller sea lions using digestion correction factors and bones recovered in scats. Fish. Bull. U.S. 102:498-508.

Tollit, D.J., M. Steward, P.M. Thompson, G.J. Pierce, M.B. Santos, and S. Hughes. 1997. Species and size differences in the digestion of otoliths and beaks: Implications for estimates of pinniped diet composition. Can. J. Fish. Aquat. Sci. 54:105-119.

Walton, M.J., and P. Pomeroy. 2003. Blubber fatty acid profiles detect inter-annual variation in the diet of grey seals (*Halichoerus grypus*). Mar. Ecol. Prog. Ser. 248:257-266.

Wilson, R.P., A. Steinfurth, Y. Ropert-Coudert, A. Kato, and M. Kurita. 2002. Lip-reading in remote subjects: An attempt to quantify and separate ingestion, breathing and vocalization in free-living animals using penguins as a model. Mar. Biol. 140:17-27.

Zeppelin, T.K., D.J. Tollit, K.A. Call, T.J. Orchard, and C.J. Gudmundson. 2004. Sizes of walleye pollock and Atka mackerel consumed by the western stock of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1999-2001. Fish. Bull. U.S. 102:509-521.

Sea Lions in Drag, Fur Seals Incognito: Insights from the Otariid Deviants

J.P.Y. Arnould
Deakin University, School of Biological and Chemical Sciences, Burwood, Victoria, Australia

D.P. Costa
University of California, Department of Ecology and Evolutionary Biology, Santa Cruz, California

Sea lions and fur seals have two broadly divergent foraging patterns. Lactating sea lions generally undertake short trips (1-2 days) foraging mostly on the benthos of continental shelf areas. In contrast, lactating fur seals generally undertake longer trips (4-23 days) foraging mostly on vertically migrating prey in oceanic frontal structures or continental shelf-edges with upwelling regions. Associated with the observed divergent trends of epipelagic and benthic foraging appear to be differences in the population dynamics of sea lions and fur seals. Populations of the various sea lion species have experienced little recovery since the sealing era, whereas fur seals have generally experienced rapid population recovery rates. The divergent patterns of foraging between the two otariid groups were originally thought to be due to the mode of insulation and diving ability. Subsequent studies, however, have shown that some fur seal species regularly forage at pelagic depths deeper and longer than some sea lions. Alternatively, the larger body size of sea lions may make foraging on small pelagic prey energy-inefficient and, hence, may explain why throughout most of their distribution sea lions have adopted the benthic foraging mode. Indeed, exceptions to the general fur seal and sea lion foraging patterns have been documented, which may be related to the productivity of their local marine habitat. California sea lions display epipelagic foraging behavior in the rich California Current, while Australian fur seals have been shown to forage exclusively over the shallow continental shelf of Bass Strait (southeast Australia), a region recognized as being an area of low oceanic productivity. Interestingly,

these uncharacteristic foraging modes are associated with population dynamics uncharacteristic for the respective phylogenetic groups: California sea lions have been steadily increasing, while the Australian fur seal has exhibited a very slow recovery in comparison to the conspecific cape fur seal which feeds epipelagically in the rich Benguela current and is now the most numerous otariid.

Introduction

Since the development in the mid-1970s of electronic time-depth recorders (TDRs) for measuring diving activity and satellite-telemetry methods for monitoring the at-sea movements of animals, there have been numerous studies investigating the foraging behavior of lactating otariid seals (e.g., Gentry and Kooyman 1986; Francis et al. 1998; Thompson et al. 1998; Costa and Gales 2000, 2003). There are nine species of fur seals (plus one subspecies) and five species of sea lions (plus one subspecies) (Reijnders et al. 1993) and these studies have revealed two broadly divergent patterns for the two groups. Lactating sea lions generally undertake short trips (1-2 days) during which they have a continuous dive pattern with no diel variation, foraging mostly on benthic or demersal prey in continental shelf areas (Costa and Gales 2000, 2003). This mode of foraging is, hereafter, referred to as "*benthic*" foraging. In contrast, lactating fur seals generally undertake longer trips (3-23 days), during which diving is mostly nocturnal (Boyd et al. 1991, Francis et al. 1998, Harcourt et al. 2001, Beauplet et al. 2004). The dives occur in bouts to the deep scattering layer, with a pronounced diel variation in depth that reflects the vertical migration of their prey (Boyd et al. 1994, Harcourt et al. 1995, Georges et al. 2000a), and foraging occurs mostly in oceanic frontal structures or continental shelf-edges with upwelling regions (Gentry and Kooyman 1986). This mode of foraging is hereafter referred to as "*epipelagic*" foraging.

Associated with the observed divergent trends of *epipelagic* and *benthic* foraging in otariid seals appear to be differences in the population dynamics of sea lions and fur seals. All species of otariid seals throughout the world were subject to extensive and, in most cases, excessive hunting pressure during the eighteenth and nineteenth centuries (Wickens and York 1997). By the late 1800s, however, most species had acquired total legislative protection or were subject to only regulated managed harvests. Despite this protection, populations of the various sea lion species have experienced very little recovery and in some cases are declining, whereas fur seal species have generally experienced rapid population recovery rates (Wickens and York 1997, Costa et al. 2006). A question these observations pose is whether there may be life-history consequences associated with the different foraging modes that might influence population
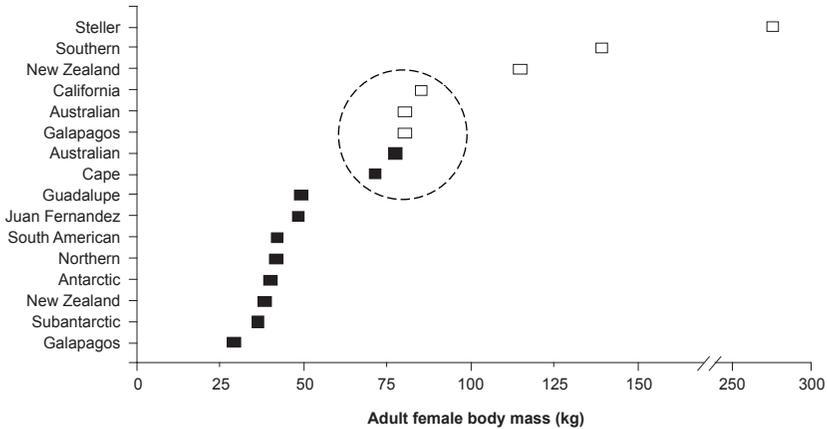
Figure 1. Mean body masses of adult female otariid seals (□ sea lions, ■ fur seals). Circled species represent the narrow range of body masses encompassing both fur seals and sea lions that provide an opportunity for investigating the mechanisms determining foraging mode and its potential impact on life-history parameters. See review in Wickens and York (1997), Warneke and Shaughnessy (1985), Gentry and Kooyman (1986), and Costa and Gales (2000, 2003) for data sources.

dynamics (i.e., is a particular foraging mode more efficient?). However, addressing this question is problematical for several reasons.

First, life-history parameters such as litter size or reproductive rate may be phylogenetically constrained, reflecting selective pressures that may no longer apply (Calder 1984) and that may be independent of foraging mode. Second, the different insulation qualities of the integument in fur seals and sea lions may have significant physiological implications. For example, it has been suggested that the insulating feature of fur seal integument (trapped layer of air) would be inefficient at great depths preventing them from foraging as deep as sea lions (Gentry et al. 1986, Costa 1991). Third, the difference in body size between fur seals and sea lions (Fig. 1), which would have implications for metabolism and reproductive output (Heusner 1991, Blanckenhorn 2000), could also mask any effect of foraging mode on life-history parameters. For example, it has been suggested that the generally larger body size of sea lions (80-273 kg) compared to fur seals (27-76 kg) results in greater oxygen storage capabilities, enabling them to dive aerobically for longer periods and, hence, deeper (Costa 1991, Costa et al. 1998).

Fortuitously, despite the great breadth of body size within the Otariidae, there is a narrow range of adult female body masses that encompasses several fur seal and sea lion species (Fig. 1). This group of species includes the cape fur seal (*Arctocephalus pusillus pusillus*) and its subspecies the Australian fur seal (*A. p. doriferus*), and the California sea lion (*Zalophus californianus*) and its subspecies the Galapagos sea lion (*Z. c. wollebaeki*). It provides a unique opportunity to investigate the potential relationships between foraging mode and life-history parameters within the Otariidae while controlling for differences in integument and body size. The Australian sea lion (*Neophoca cinerea*) also has a similar adult female body mass to the above species, but its unique 17.5 month breeding cycle (Gales and Costa 1997) makes direct comparisons regarding life-history traits problematic.

The aims of this study, therefore, were to (1) compare and contrast the foraging behaviors of adult female cape and Australian fur seals with California and Galapagos sea lions; (2) assess whether there are any relationships between foraging mode and life-history parameters; and (3) place these findings within the context of otariids in general. An additional aim of this study was to highlight deficiencies in the information necessary for better understanding the mechanisms that determine foraging mode in otariid seals and its potential impacts on life-history parameters.

Methods

Information for the comparisons between the four focal species (cape and Australian fur seals, and California and Galapagos sea lions) and with other otariids, were obtained from published reports and unpublished sources. Due to a paucity of information on some species, data were not available for each parameter in each species.

Summary data on diving behavior and foraging mode were collated for the cape fur seal (Kooyman and Gentry 1986), Australian fur seal (Arnould and Hindell 2001), California sea lion (Costa et al. 2004), and Galapagos sea lion (Kooyman and Trillmich 1986). As a means of comparing diving performance between species, published data (Costa et al. 2004) on the ratio of mean dive duration to calculated aerobic dive limit (cADL) for individual Australian fur seals and California sea lions were compared. No comparable data are available for the cape fur seal or Galapagos sea lion, but comparisons were made with other *benthic* (Australian sea lion and New Zealand sea lion, *Phocarctos hookeri*) and *epipelagic* (Antarctic fur seal, *A. gazella*) feeding otariids (Costa et al. 2004).

The proportion of time at sea spent diving was used an index of foraging effort to compare between the four focal species (Gentry et al. 1986, Kooyman and Gentry 1986, Kooyman and Trillmich 1986, Feldkamp et al. 1989, Arnould and Hindell 2001, Costa et al. 2004) and with other

otariids (Gentry et al. 1986; Thompson et al. 1998; Costa and Gales 2000, 2003; Georges et al. 2000b; Costa et al. 2001).

Numerous studies have investigated the diet of fur seals and sea lions and how it relates to foraging activity, focusing on the relative proportions of various prey species in relation to changes in food availability and diving behavior (e.g., Feldkamp et al. 1991, Boyd et al. 1994, Harcourt et al. 2002, Lea et al. 2002). There is little information, however, on how the mode of foraging relates to prey size, an important factor that will influence foraging efficiency. In the present study, information on the size of common prey item size were obtained for the Australian fur seal (Gales et al. 1993, Gales and Pemberton 1994, Hume et al. 2004), California sea lion (Antonelis et al. 1984, Weise 2000), and cape fur seal (Punt et al. 1995; de Bruyn et al. 2003; W.H. Oosthuizen, Marine and Coastal Management, South Africa, unpubl. data). Size data were collated only for the four most numerically abundant prey species identified in each diet study. Similar data were obtained for *epipelagic* Antarctic fur seals (Reid and Arnould 1996, Goldsworthy et al. 1997) and New Zealand fur seals (*A. forsteri*) (Fea et al. 1999); and *benthic* feeding Australian sea lions (Gales and Cheal 1992; R. Campbell, Dept. of Fisheries, Western Australia, unpubl. data) and New Zealand sea lions (Lalas 1997). Where necessary, fish prey mass was calculated from published length estimates using mass-length relationships available on www.fishbase.org.

There are few life-history parameters available for comparison between fur seals and sea lions. Probably the most relevant for assessing the potential influence of foraging mode on population dynamics is adult female reproductive rate as it is likely to be influenced heavily by female foraging success and have a significant impact population dynamics (Boyd 2000). Information on late gestation pregnancy rates and birth rates were obtained for the Australian fur seal (Arnould et al. 2003), cape fur seal (Guinet et al. 1998, Odendaal et al. 2002), and California sea lion (Melin 2002). Similar data are not available for the Galapagos sea lion but are available for the *benthic* foraging New Zealand sea lion (I.S. Wilkinson, Dept. of Conservation, Wellington, New Zealand, unpubl. data) and Steller sea lion (Pitcher et al. 1998); and the *epipelagic* foraging South American fur seal (*A. australis*) (Majluf 1992), subantarctic fur seal (*A. tropicalis*), and Antarctic fur seal (Wickens and York 1997).

Results

Summary information on foraging behavior for Australian and cape fur seals and California and Galapagos sea lions is presented in Table 1. Within the small mass range of the four species (71-85 kg), mean dive depth varied substantially (37-64 m) though this was not related to foraging mode. Interestingly, despite the similar body masses between the four species, differences in foraging mode were apparent within the con-

Table 1.   Adult female foraging behavior of four otariid species (two sea lions and two fur seals) with similar body masses. Means ± SE are presented where indicated in the original studies.

Species	Body mass (kg)	Dive depth (m)	Dive duration (min)	Foraging mode
Australian fur seal[a]	78	63.4 ± 4.0	3.2 ± 0.4	Benthic
Cape fur seal[b,c]	71	45.0 ± 4.0	2.1 ± 0.4	Epipelagic
California sea lion[d]	85	42.2 ± 12.9	1.9 ± 0.2	Epipelagic
Galapagos sea lion[e,f]	80	37.3 ± 0.3	<2	Benthic

[a]Arnould and Hindell (2001); [b]Kooyman and Gentry (1986); [c]Warneke and Shaughnessy (1985); [d]Costa et al. (2004); [e]Gentry et al. (1986); [f]Kooyman and Trillmich (1986).

specific fur seals and sea lions. Australian fur seals are *benthic* foragers, whereas cape fur seals are *epipelagic* foragers; and California sea lions are *epipelagic* foragers, whereas Galapagos sea lions are *benthic* foragers. Hence, Australian fur seals and California sea lions appear to forage in modes not consistent with the trends observed in their respective phylogenetic groups.

The dive performance, measured as the ratio of mean dive duration to calculated aerobic dive limit (cADL), for individual Australian fur seals ($n = 9$) and California sea lions ($n = 6$) is given in Fig. 2. A ratio of 1 would indicate that animals are undertaking dive durations equivalent to their cADL. While mean dive depth did not differ significantly between the two species ($t_6 = 0.2$, $P > 0.1$), the ratio of individual mean dive depth to cADL was significantly greater in Australian fur seals (1.90 ± 0.03) than California sea lions (0.66 ± 0.01; $t_6 = 9.66$, $P < 0.001$). There are no comparable data for the cape fur seal or Galapagos sea lion but these results are consistent with data for the Australian sea lion, New Zealand sea lion, and Antarctic fur seal. This suggests that *benthic* foraging species regularly undertake dive durations exceeding their cADL, whereas the *epipelagic* foraging species rarely dive longer than their cADL.

The most common fish and cephalopod prey of *benthic* foraging Australian fur seals (50-5,000 g) are 10-60 times heavier than those consumed by *epipelagic* foraging, conspecific cape fur seals (4-85 g), but are similar to those consumed by *benthic* foraging sea lions (150-2,500 g) (Table 2). Conversely, the *epipelagic* foraging California sea lion consumes fish and cephalopod prey of similar size (17-150 g) to *epipelagic* foraging fur seals (2-195 g). Information on prey size in the Galapagos sea lion is limited to only a single fish species (anchovy, *Sardinops sagax*) of estimated mean mass 56 g, despite the diet of this species comprising numerous other fish and cephalopods species (Dellinger and Trillmich 1999). Con-
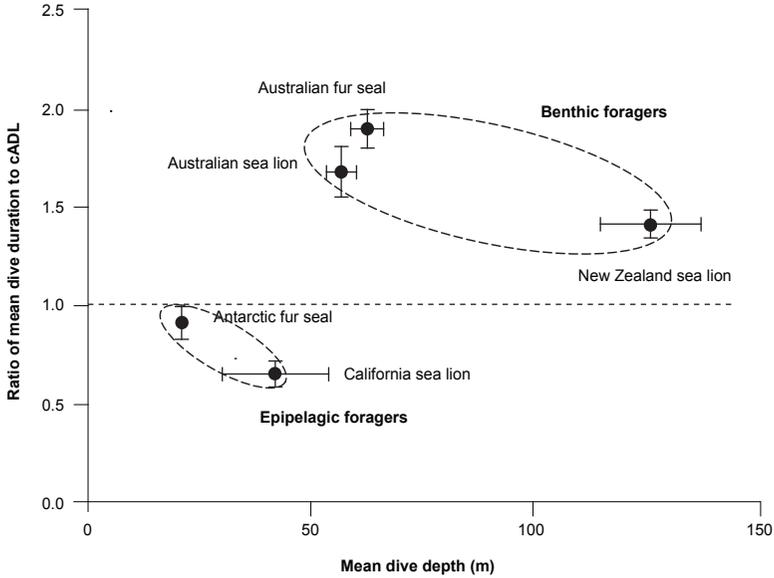
Figure 2. Ratio of mean dive duration to calculated aerobic dive limit (cADL) in adult females of five otariid seal species (3 sea lion, 2 fur seal) in relation to mean dive depth. Data presented as means ± SE. Adapted from Costa et al. (2004).

sequently, adequate comparisons of common prey size between this and other otariid species are not possible.

Foraging effort, measured as the amount of time at sea spent diving, is substantially higher in *benthic* foraging Australian fur seals (41%) than the conspecific cape fur seals (8%) and other *epipelagic* foraging fur seals (15-24%; Fig. 3). Conversely, the time at sea spent diving by *epipelagic* foraging California sea lions (32%) is substantially less than by conspecific Galapagos sea lions (64%) and other benthic foraging sea lions (44-58%). Overall, the proportion of time at sea spent diving is significantly greater (t_8 = 5.68, $P < 0.001$) in *benthic* (51.7 ± 4.3%) than *epipelagic* (20.7 ± 3.4%) foragers. The results suggest that foraging effort is greater in *benthic* foraging otariid species irrespective of phylogenetic grouping or body size.

The reproductive rate of the *benthic* foraging Australian fur seal (55%) is substantially lower than in the conspecific cape fur seal (77-79%) and other *epipelagic* foraging fur seals (77-84%) but is similar to benthic foraging sea lions (Table 3). Conversely, the reproductive rate of the *epipelagic* foraging California sea lion (77%) is similar to *epipelagic* fur seals but greater than in *benthic* foraging sea lions (55-69%).

Table 2.   **Mass of most common prey items consumed by fur seals and sea lions in relation to foraging mode. Range of means given for the four most numerically abundant species recorded in diet analyses.**

Species	Mean mass (g)			Foraging mode
	Fish	Cephalopods	Crustacea	
Australian fur seal[a,b,c]	50-2,000	580-5,000		Benthic
Australian sea lion[m]	?	?	750-1,500	Benthic
New Zealand sea lion[d]	400-2,500	150-1,500		Benthic
California sea lion[e,f]	17-150	23-47		Epipelagic
Cape fur seal[g,h,i]	4-60	14-85		Epipelagic
Antarctic fur seal[j,k]	7-20		<5	Epipelagic
New Zealand fur seal[l]	2-11	195		Epipelagic

[a]Gales et al. (1993); [b]Gales and Pemberton (1994); [c]Hume et al. (2004); [d]Lalas (1997); [e]Antonelis et al. (1984); [f]Weise (2000); [g]Punt et al. (1995; [h]de Bruyn et al. (2003); [i]W.H. Oosthuizen (Marine and Coastal Management, South Africa, unpubl. data); [j]Reid and Arnould (1996); [k]Goldsworthy et al. (1997); [l]Fea et al. (1999). [m]Because of the clearly demonstrated biases resulting from scat analysis in this species (Gales and Cheal 1992), there are no reliable estimates of fish or cephalopod prey size. Direct observations of prey consumption, however, indicate this species regularly consumes large crayfish (R. Campbell, Dept. of Fisheries, Western Australia, unpubl. data).

Discussion

It was originally suggested that the observed differences in foraging mode between sea lions (*benthic*) and fur seals (*epipelagic*) were due to differences in their integument (single- versus double-fur layer) and/or body size (Gentry et al. 1986, Costa 1991, Costa et al. 1998). The results of the present study indicate that within the narrow range where sea lion and fur seal body masses overlap there is a fur seal that adopts the *benthic* foraging mode typical of sea lions (Australian fur seal) and a sea lion that adopts the epipelagic mode typical of fur seals (California sea lion), while the conspecifics of these two species follow the normal trends for their respective phylogenetic groups. This suggests that integument characteristics do not account for the observed differences in foraging mode between sea lions and fur seals. Likewise, the fact that these species are of similar mass suggests body size may not be the sole factor determining foraging mode.

A potential influence on foraging mode in otariid seals may be local marine productivity and its effect on prey availability for these species. The *epipelagic* foraging cape fur seal is mostly distributed along the southwest coast of South Africa and feeds in the nutrient-rich waters of the Benguela Current, whereas the *benthic* foraging Australian fur seal
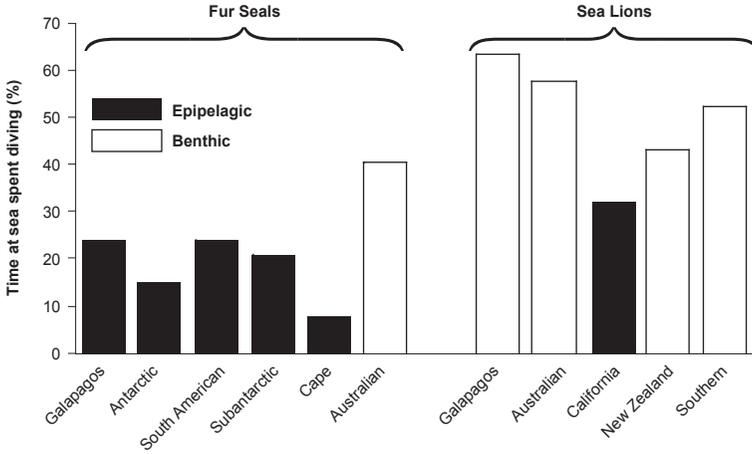
Figure 3. **Proportion of time at sea spent diving by adult females in 11 otariid sea species (5 sea lion, 6 fur seal). References: Galapagos fur seal (Gentry et al. 1986); Antarctic fur seal (Costa et al. 2001); South American fur seal (Gentry et al. 1986); subantarctic fur seal (Georges et al. 2000b); cape fur seal (Kooyman and Gentry 1986); Australian fur seal (Arnould and Hindell 2001); Galapagos sea lion (Gentry et al. 1986); Australian sea lion (Costa and Gales 2003); California sea lion (Feldkamp et al. 1989); New Zealand sea lion (Costa and Gales 2000); Southern sea lion (Thompson et al. 1998).**

feeds exclusively within Bass Strait between the Australian mainland and Tasmania, an area considered nutrient-poor with low marine productivity (Warneke and Shaughnessy 1985). Similarly, California sea lions on the California coast are *epipelagic* foragers in the cold productive waters of the California Current (Feldkamp et al. 1989, 1991), whereas the continental shelf habitat of the *benthic* foraging Galapagos sea lion is of generally lower productivity (Farina et al. 2003, Okey et al. 2004). It may be that, except in very productive regions, large size precludes foraging on a highly patchy but dense prey resource near the surface (zooplankton, small fish or squid) compared to a more evenly distributed but less dense prey resource on the benthos (larger fish, squid, octopus, and crayfish).

The high ratio of mean dive duration to cADL in the Australian fur seal and *benthic* foraging sea lions suggests this mode of foraging incurs a greater physiological cost than *epipelagic* feeding. Optimal foraging theory would predict, therefore, that *benthic* foraging species should consume larger or more rewarding prey than *epipelagic* foraging seals (Stephens and Krebs 1986, Bowen et al. 2002). The differences observed

**Table 3.   The reproductive rates of otariid seals in relation
                to their foraging mode.**

Species	Birth rate (%)	Foraging mode
Australian fur seal[a]	55[i]	Benthic
New Zealand sea lion[b]	69	Benthic
Steller sea lion[c]	55-67[i]	Benthic
California sea lion[d]	77	Epipelagic
Cape fur seal[e,f]	77-79	Epipelagic
Antarctic fur seal[g]	77[i]	Epipelagic
South American fur seal[h]	82	Epipelagic
Subantarctic fur seal[g]	79-84	Epipelagic

[a]Arnould et al. (2003); [b]I.S. Wilkinson (Dept. of Conservation, Wellington, New Zealand, unpubl. data); [c]Pitcher et al. (1998); [d]Melin (2002); [e]Guinet et al. (1998); [f]Odendaal et al. (2002); [g]Wickens and York (1997); [h]Majluf (1992). [i]Late gestation pregnancy rate.

in the present study in the size of common prey items consumed by *benthic* and *epipelagic* foraging otariids of similar body size are consistent with this prediction. However, despite the apparent greater mass of prey items consumed by *benthic* foraging otariid species, they appear to spend a greater proportion of time at sea diving than *epipelagic* feeders (Fig. 3).

A potential consequence of this might be a reduced scope by *benthic* species for increasing foraging effort in times of nutritional stress in comparison to *epipelagic* species which, in turn, could impact reproductive output, offspring growth, or survival. A lower reproductive rate was observed in the Australian fur seal (and *benthic* feeding sea lions) than in the *epipelagic* conspecific cape fur seal and California sea lion, which suggests a relationship between foraging mode and life history in otariid seals. Indeed, the difference between the mean birth rate of all *benthic* (61.7 ± 4.0%) and *epipelagic* (79.1 ± 1.1%) foragers approached significance ($t_2 = 4.15$, $P = 0.053$). The low reproductive rate of Australian fur seals may explain their very slow recovery since the cessation of the commercial sealing era in comparison to the rapid recovery of the conspecific cape fur seal, which is now the most numerous otariid (Table 4). Similarly, the relatively high reproductive rate of the California sea lion is likely to have contributed to its population increase being rapid in comparison to that in *benthic* foraging sea lions.

Table 4.   Population status and trends for benthic and epipelagic foraging otariid seal species.

Species	Foraging mode	Population size	Trend
Australian fur seal	Benthic	60,000	Very slow increase
Australian sea lion	Benthic	<11,700	Stable
New Zealand sea lion	Benthic	13,000	Stable
Southern sea lion	Benthic	275,000	Decreasing
Steller sea lion	Benthic	<75,000	Decreasing
California sea lion	Epipelagic	>237,000	Rapid increase
Antarctic fur seal	Epipelagic	1,600,000	Rapid increase
Cape fur seal	Epipelagic	1,700,000	Rapid increase
Subantarctic fur seal	Epipelagic	>310,000	Rapid increase

Adapted from Costa et al. (2006).

Acknowledgments

References

Antonelis Jr., G.A., C.H. Fiscus, and R.L. DeLong. 1984. Spring and summer prey of California sea lions, *Zalophus californianus*, at San Miguel Island, California, 1978-79. Fish. Bull. U.S. 82:67-76.

Arnould, J.P.Y., and M.A. Hindell. 2001. Dive behaviour, foraging locations, and maternal-attendance patterns of Australian fur seals (*Arctocephalus pusillus doriferus*). Can. J. Zool. 79:35-48.

Arnould, J.P.Y., I.L. Boyd, and R.M. Warneke. 2003. Historical dynamics of the Australian fur seal population: Evidence of regulation by man? Can. J. Zool. 81:1428-1436.

Beauplet, G., L. Dubroca, C. Guinet, Y. Cherel, W. Dabin, C. Gagne, and M.A. Hindell. 2004. Foraging ecology of subantarctic fur seals *Arctocephalus tropicalis* breeding on Amsterdam Island: Seasonal changes in relation to maternal characteristics and pup growth. Mar. Ecol. Prog. Ser. 273:211-225.

Blanckenhorn, W.U. 2000. The evolution of body size: What keeps organisms small? Quart. Rev. Biol. 75:385-407.

Bowen, W.D., D. Tully, D.J. Boness, B.M. Bulheier, and G.J. Marshall. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. Mar. Ecol. Prog. Ser. 244:235-245.

Boyd, I.L. 2000. State-dependent fertility in pinnipeds: Contrasting capital and income breeders. Funct. Ecol. 14:623-630.

Boyd, I.L., N.J Lunn, and T. Barton. 1991. Time budgets and foraging characteristics of lactating Antarctic fur seals. J. Anim. Ecol. 60:577-592.

Boyd, I.L., J.P.Y. Arnould, T. Barton, and J.P. Croxall. 1994. Foraging behavior of Antarctic fur seals during periods of contrasting prey abundance. J. Anim. Ecol. 63:703-713.

Calder, W.A. 1984. Size, function and life history. Harvard University Press, Cambridge.

Costa, D.P. 1991. Reproductive and foraging energetics of pinnipeds: Implications for life history patterns. In: Behaviour of pinnipeds. Chapman and Hall, New York, pp. 300-344.

Costa, D.P., and N.J. Gales. 2000. Foraging energetics and diving behavior of lactating New Zealand sea lions, *Phocarctos hookeri*. J. Exp. Biol. 203:3655-3665.

Costa, D.P., and N.J. Gales. 2003. Energetics of a benthic diver: Seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. Ecol. Monogr. 73:27-43.

Costa, D.P., N.J. Gales, and D.E. Crocker. 1998. Blood volume and diving ability of the New Zealand sea lion, *Phocarctos hookeri*. Physiol. Zool. 71:208-213.

Costa, D.P., N.J Gales, and M.E. Goebel. 2001. Aerobic dive limit: How often does it occur in nature? Comp. Biochem. Phys. A 129:771-783.

Costa, D.P., M.J. Weise, and J.P.Y. Arnould. 2006. Worldwide pinniped population status and trends. In: Whales, whaling and ocean ecosystems. University of California Press, Berkeley.

Costa, D.P., C.E. Kuhn, M.J. Weise, S.A. Shaffer, and J.P.Y. Arnould. 2004. When does physiology limit the foraging behaviour of freely diving mammals? Internat. Congr. Ser. 1275:359-366.

de Bruyn, P.J.N., M.N. Bester, S. Mecenero, S.P. Kirkman, J.P. Roux, and N.T.W. Klages. 2003. Temporal variation of cephalopods in the diet of cape fur seals in Namibia. S. Afr. J. Wildl. Res. 33:85-96.

Dellinger, T., and F. Trillmich. 1999. Fish prey of the sympatric Galapagos fur seals and sea lions: Seasonal variation and niche separation. Can. J. Zool. 77:1204-1216.

Farina, J.M., S. Salazar, K.P. Wallem, J.D. Witman, and J.C. Ellis. 2003. Nutrient exchanges between marine and terrestrial ecosystems: The case of the Galapagos sea lion *Zalophus wollebaecki*. J. Anim. Ecol. 72:873-887.

Fea, N.I., R.G. Harcourt, and C. Lalas. 1999. Seasonal variation in the diet of the New Zealand fur seal (*Arctocephalus forsteri*) at Otago Peninsula, New Zealand. Wildl. Res. 26:147-160.

Feldkamp, S.D., R.L. DeLong, and G.A. Antonelis. 1989. Diving patterns of California sea lions, *Zalophus californianus*. Can. J. Zool. 67:872-883.

Feldkamp, S.D., R.L. DeLong, and G.A. Antonelis. 1991. Effects of El Niño 1983 on the foraging patterns of California sea lions (*Zalophus californianus*) near San Miguel Island, California. In: Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag, Berlin, pp. 146-155.

Francis, J., D. Boness, and H. Ochoa-Acuna. 1998. A protracted foraging and attendance cycle in female Juan Fernandez fur seals. Mar. Mamm. Sci. 14:552-574.

Gales, N.J., and A.J. Cheal. 1992. Estimating diet composition of the Australian sea lion (*Neophoca cinerea*) from scat analysis: An unreliable technique. Wildl. Res. 19:447-456.

Gales, N.J., and D.P. Costa. 1997. The Australian sea lion: A review of an unusual life history. In: Marine mammal research in the Southern Hemisphere. Vol. 1: Status, ecology and medicine. Surrey Beatty and Sons, Chipping Norton, pp. 78-87.

Gales, R., and D. Pemberton. 1994. Diet of the Australian fur seal in Tasmania. Aust. J. Mar. Freshw. Res. 45:653-664.

Gales, R., D. Pemberton, C.C. Lu, and M.R. Clarke. 1993. Cephalopod diet of the Australian fur seal: Variation due to location, season and sample type. Aust. J. Mar. Freshw. Res. 44:657-671.

Gentry, R.L., and G.L. Kooyman. 1986. Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton.

Gentry, R.L., D.P. Costa, J.P. Croxall, J.H.M. David, R.W. Davis, G.L. Kooyman, P. Majluf, T.S. McCann, and F. Trillmich. 1986. Synthesis and conclusions. In: Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, pp. 220-264.

Georges, J.Y., F. Bonadonna, and C. Guinet. 2000a. Foraging habitat and diving activity of lactating subantarctic fur seals in relation to sea-surface temperatures at Amsterdam Island. Mar. Ecol. Prog. Ser. 196:291-304.

Georges, J.Y., Y. Tremblay, and C. Guinet. 2000b. Seasonal diving behaviour in lactating subantarctic fur seals an Amsterdam Island. Polar Biol. 23:59-69.

Goldsworthy, S.D., M.A. Hindell, and H.M. Crowley. 1997. Diet and diving behaviour of sympatric fur seals *Arctocephalus gazella* and *A. tropicalis* at Macquarie Island. In: Marine mammal research in the Southern Hemisphere. Vol. 1: Status, ecology and medicine. Surrey Beatty, Chipping Norton, pp. 151-163.

Guinet, C., J.P. Roux, M. Bonnet, and V. Mison. 1998. Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. Can. J. Zool. 76:1418-1424.

Harcourt, R.G., C.J.A. Bradshaw, and L.S. Davis. 2001. Summer foraging behaviour of a generalist predator, the New Zealand fur seal (*Arctocephalus forsteri*). Wildl. Res. 28:599-606.

Harcourt, R.G., C.J.A. Bradshaw, K. Dickson, and L.S. Davis. 2002. Foraging ecology of a generalist predator, the female New Zealand fur seal. Mar. Ecol. Prog. Ser. 227:11-24.

Harcourt, R.G., A.M. Schulman, L.S. Davis, and F. Trillmich. 1995. Summer foraging by lactating female New Zealand fur seals (*Arctocephalus forsteri*) off Otago Peninsula, New Zealand. Can. J. Zool. 73:678-690.

Heusner, A.A. 1991. Size and power in mammals. J. Exp. Biol. 160:25-54.

Hume, F., M.A. Hindell, D. Pemberton, and R. Gales. 2004. Spatial and temporal variation in the diet of a high trophic level predator, the Australian fur seal (*Arctocephalus pusillus doriferus*). Mar. Biol. 144:407-415.

Kooyman, G.L., and R.L. Gentry. 1986. Diving behavior of South African fur seals. In: Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, pp. 142-152.

Kooyman, G.L., and F. Trillmich. 1986. Diving behavior of Galapagos sea lions. In: Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, pp. 209-219.

Lalas, C. 1997. Prey of Hooker's sea lions *Phocarctos hookeri* based at Otago Peninsula New Zealand. In: Marine mammal research in the Southern Hemisphere. Vol. 1: Status, ecology and medicine. Surrey Beatty, Chipping Norton, pp. 130-136.

Lea, M.A., Y. Cherel, C. Guinet, and P.D. Nichols. 2002. Antarctic fur seals foraging in the Polar Frontal Zone: Inter-annual shifts in diet as shown from faecal and fatty acid analyses. Mar. Ecol. Prog. Ser. 245:281-297.

Majluf, P. 1992. Timing of births and juvenile mortality in the South American fur seal in Peru. J. Zool. (Lond.) 227:367-383.

Melin, S.R. 2002. The foraging ecology and reproduction of the California sea lion (*Zalophus californianus californianus*). Ph.D. thesis, University of Minnesota.

Odendaal, P.N., M.N. Bester, M. van der Merwe, and W.H. Oosthuizen. 2002. Seasonal changes in the ovarian structure of the cape fur seal, *Arctocephalus pusillus pusillus*. Aust. J. Zool. 50:491-506.

Okey, T.A., S. Banks, A.R. Born, R.H. Bustamante, M. Calvopina, G.J. Edgar, E. Espinoza, J.M. Farina, L.E. Garske, G.K. Reck, S. Salazar, S. Shepherd, V. Toral-Granda, and P. Wallem. 2004. A trophic model of a Galapagos subtidal rocky reef for evaluating fisheries and conservation strategies. Ecol. Model. 172:383-401.

Pitcher, K.W., D.G. Calkins, and G.W. Pendleton. 1998. Reproductive performance of female Steller sea lions: An energetics-based reproductive strategy? Can. J. Zool. 76:2075-2083.

Punt, A.E., J.H.M. David, and R.W. Leslie. 1995. The effects of future consumption by the cape fur seal on catches and catch rates of the cape hakes. 2. Feeding and diet of the cape fur seal *Arctocephalus pusillus pusillus*. S. Afr. J. Mar. Sci. 16:85-99.

Reid, K., and J.P.Y. Arnould. 1996. Diet of Antarctic fur seals during the summer breeding period at South Georgia. Polar Biol. 16:105-114.

Reijnders, P., S. Brasseur, J. Van der Toorn, O. Van der Wolf, I.L. Boyd, J. Harwood, D. Lavigne, and L. Lowry. 1993. Seals, fur seals, sea lions, and walrus. Status survey and conservation plan. IUCN/SSC Seal Specialist Group, Gland, Switzerland.

Stephens, D.W., and J.R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton.

Thompson, D., C.D. Duck, B.J. McConnell, and J. Garrett. 1998. Foraging behaviour and diet of lactating female southern sea lions (*Otaria flavescens*) in the Falkland Islands. J. Zool. (Lond.) 246:135-146.

Warneke, R.M., and P.D. Shaughnessy. 1985. *Arctocephalus pusillus*, the South African and Australian fur seal: Taxonomy, evolution, biogeography, and life history. In*:* Studies of sea mammals in south latitudes. South Australian Museum, Adelaide, pp. 153-177.

Weise, M.J. 2000. Abundance, food habits, and annual fish consumption of California sea lions (*Zalophus californianus*) and its impact on salmonid fisheries in Monterey Bay, California. M.S. thesis, San Jose State University, San Jose, California.

Wickens, P., and A.E. York. 1997. Comparative population dynamics of fur seals. Mar. Mamm. Sci. 13:241-292.

Because sea lions consume almost exclusively commercially important prey species, we hypothesized that the potential for competition for specific prey resources would vary with environmental conditions. We evaluated seasonal and annual variation in sea lion diet in Monterey Bay during the strong 1997-98 El Niño and subsequent 1999 La Niña through the exami-nation and identification of prey hard parts found in fecal samples. To identify environmental variables that best explain temporal variation in sea lion diet composition, the relationships between seasonal percentage biomass of prey species and environmental variables were ana-lyzed using the BIOENV procedure in Primer-E v6.0 (Clarke & Warwick 1994). Estimating diet composition in sea lions: Which technique to choose? Save to Library. Download. by D. Tollit. and +1. Andrew Trites. • 5. Assessment of Competition between Fisheries and Steller Sea Lions in Alaska Based on Estimated Prey Biomass, Fisheries Removals and Predator Foraging Behaviour. Save to Library. Download. by Edward Gregr. and +2. Andrew Trites. Tabitha Hui. Intraspecific variation in feeding strategies of Galapagos sea lions: A case of trophic specialization. PLOS ONE, Vol. 12, Issue. 10, p. e0185165. Tollit, D.J., Heaslip, S.G., Deagle, B.E., Iverson, S.J., Joy, R., Rosen, D.A. and Trites, A.W. (2006) Estimating diet composition in sea lions: which technique to choose? In Trites, A.W., Atkinson, S., DeMaster, D.P., Fritz, L.W., Gelatt, T.S., Rea, L.D. and Wynne, K. (eds) Sea lions of the world. Fairbanks, AK: University of Alaska. Trillmich, F. and Ono, K. (1991) The effects of El Niño on pinniped populations in the eastern Pacific.