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Journal of Experimental Marine Biology and Ecology 328 (2006) 228–239

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Diet estimation based on an integrated mixed prey feeding experiment using *Arctocephalus* seals

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Received 20 April 2005; received in revised form 11 July 2005; accepted 22 July 2005

Abstract

Food web models depend on identifying which taxa are eaten and in what proportion they are consumed. *Arctocephalus* seals are generalist foragers and are an ongoing focus of Southern Hemisphere marine ecosystem research. This is the first feeding experiment to use *Arctocephalus* spp. to assess the utility of hard part scat analysis for diet estimation, based on mixed prey diets integrated over several days. Recovery rates of otoliths were extremely low for all taxa (0–9%). Although we could not collect scats produced during a 90 min period each day, during which the seals had access to a large pool, this result could not be attributed to otolith robustness, pinniped species or class, activity level, meal size or frequency, or fat content of the diet. We conclude that the unusually low recovery rates in this study may be due to unaccounted scats produced during 90 min of each day, if they contained otolith numbers an order of magnitude greater than all otoliths retrieved from scats produced during the other 22.5 h of each day, and/or may be related to the digestive processing of a mixed prey diet. Our study demonstrates the inadequacy of using otoliths in field collected scats for diet estimation due to the high level of unexplained variability of otolith occurrence in scats. We also identify two new potential sources of this variability. These are variability in numbers of otoliths per scat depending on activity level when a scat is excreted, and variability in recovery rates of otoliths as a function of the complexity of the diet.

Keywords: *Arctocephalus*; Diet estimation; Feeding experiment; Fur seal; Scats

1. Introduction

Accurate assessment of the diet of predators is essential in defining their role in food webs (Boyd, 2002; Trites, 2003; Iverson et al., 2004). *Arctocephalus* spp. are important predators in Southern Hemisphere marine ecosystems and estimating their diet has been central to many studies investigating

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doi:10.1016/j.jembe.2005.07.009

predator–prey relationships (Daneri and Carlini, 1999; Harcourt et al., 2002; de Bruyn et al., 2003; Beauplet et al., 2004), interactions with fisheries (Green et al., 1989; Crawford et al., 1992; Croll and Tershy, 1998; Boyd, 2002; Lea et al., 2002; Naya et al., 2002) and monitoring the marine environment (Agnew, 1997). As direct observation of marine mammal feeding is uncommon, indirect methods are employed to determine their prey. Identifying undigested prey remains in scats is currently the most widely used method of diet sampling in pinnipeds because scat collection is relatively easy and non-invasive (compared, for example, with stomach lavage, Ferreira and Bester, 1999; lethal sampling, Berg et al., 2002; and fatty acid analysis, Iverson et al., 1997; Lea et al., 2002). Although not the only diagnostic structure, sagittal otoliths are most commonly used to identify fish taxa, numbers and sizes from seal scats, because they are relatively easy to classify and are the most consistently useful structure across fish species. Cephalopod mouth-parts and exoskeleton remains in scats are used to identify cephalopod and crustacean prey, respectively (Cottrell et al., 1996; Bowen, 2000; Tollit et al., 2003).

However, prey hard parts are not excreted in the same numbers and proportions that they were ingested, so that the estimated contribution of different prey species to diet may be significantly biased. The cephalopod portion of diet is often inaccurately represented in scats because large beaks tend to accumulate in pinniped stomachs and are regurgitated (Pierce and Boyle, 1991). The presence of identifiable otoliths in scats depends on their size and how long they are retained in the gastrointestinal tract, with some otoliths being completely digested (Harvey, 1989; Tollit et al., 1997). Retention times of digesta, in turn, are affected by factors such as activity level (Tollit et al., 2003), meal size (Marcus et al., 1998) and the species of pinniped (Harvey and Antonelis, 1994; Cottrell and Trites, 2002).

In an attempt to quantify these inaccuracies, there have been numerous feeding studies carried out on captive pinnipeds, but these have almost exclusively been based on single meal, single prey species experiments (reviewed in Bowen, 2000). However, the output of undigested remains over time is uneven, so that individual scats can contain hard remains of prey consumed over several days and a single scat does not represent a single meal (Richardson and Gales, 1987; Dellinger and Trillmich, 1988; Tollit et al., 2003). The contents of scats are not the product of an experimental meal in isolation. Rather, they are likely to reflect the integrated digestion of meals consumed over a period of time. Also, brief trials allowing little acclimation time to the experimental diet may not provide sufficient time for enzymatic modulation and may be inadequate to detect changes in digestive processes of different diets (Lawson et al., 1997; Hilton et al., 2000).

Further, it is not clear to what extent recovery rates from these studies reflect the digestive processes of wild seals consuming a diverse range of prey (Goodman-Lowe et al., 1999). Meal composition is likely to influence the passage rate of digesta (Prime and Hammond, 1987; Dellinger and Trillmich, 1988; Bowen, 2000; Tollit et al., 2004). The retention times of components of a mixed diet are modified by the remainder of the diet (Warner, 1981) and an animal can optimise retention time to maximise the net rate of energy gain (Sibly and Calow, 1986). Although these digestive interactions are poorly understood (Rosen and Trites, 1997; Goodman-Lowe et al., 1999), one influence appears to be that gastric emptying and intestinal motility decrease as the energy density (lipid content) of food increases (Lawson et al., 1997; Trumble et al., 2003). Diet reconstruction of generalist foragers may therefore be improved when based on experiments where meals comprise a variety of prey species and are fed for a period at least as long as the retention time of digesta.

Fur seals are flexible foragers (McCafferty et al., 1998; Georges et al., 2000; Harcourt et al., 2001). Analyses of scats and stomach contents of free-living *Arctocephalus* spp. confirm their consumption of a wide range of prey (often >20 taxa). Their diet appears dominated by relatively few species, but these change seasonally and inter-annually (Castley et al., 1991; Reid and Arnould, 1996; Green, 1997; Klages and Bester, 1998; Dellinger and Trillmich, 1999; Harcourt et al., 2002; Lea et al., 2002; Naya et al., 2002; Hume et al., 2004). Although high latitude otariid seals may have fewer prey species to choose from than temperate fur seals (Harcourt et al., 2001), and it is likely that fur seals commonly encounter and consume single species assemblages (Daneri, 1996), there is evidence that even in the short term, *Arctocephalus* spp. may forage on a variety of prey. The number of prey groups per scat has