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DIFFERENCES IN NICHE BREADTH AMONG SOME TEUTHIVOROUS MESOPELAGIC MARINE MAMMALS

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An important issue in ecology is how species which are members of the same ecological guild differ in their use of resources (Emlen 1973, pp. 175–178). Species may use particular resources in different proportions, or, more generally, employ more or fewer resource types, so having relatively wide and narrow niche breadths, respectively. Another way of expressing this variation is from generalists, with wide niche breadths, to specialists, with narrow niches.

One of the great food resources of the Earth is the cephalopod biomass of the mesopelagic and bathypelagic ocean (Clarke 1977). These animals are preyed upon by a number of deep-diving marine mammals, especially sperm whales (*Physeter macrocephalus*), beaked whales (family Ziphiidae), and elephant seals (*Mirounga* spp.). Here, we ask whether the mammalian mesopelagic cephalopod predators (which have sufficient diet information available) differ in their niche breadth. Do some use relatively more squid taxa than others? If so, why might this be?

Diet in these species has been principally determined by examining the cephalopod lower beaks which accumulate in their stomachs. These beaks can be allocated to genus, and sometimes species, and a size of the original animal may be extrapolated (Clarke 1986). Thus squid beaks retrieved from the stomachs of dead or lavaged animals may be used to estimate diet (*e.g.*, Clarke 1980). However this method possesses potential biases. These include the omission of the non-

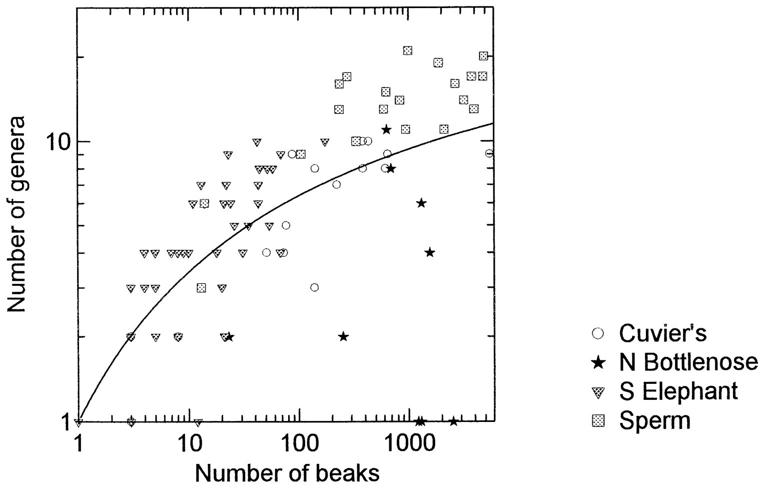

Figure 1. Number of cephalopod genera plotted against number of lower beaks examined for four species of mesopelagic teuthivore with curve fitted to all data (see text).

cephalopod part of the diet, that beaks of certain species may be more or less likely to accumulate in the stomach, and that prey of prey may be inadvertently included in the diet (Clarke 1980, R. Clarke *et al.* 1988). In this paper we consider only cephalopod prey, and acknowledge that niche breadth may in some cases be underestimated if the beaks of commonly used species have low rates of accumulating in the stomach, or overestimated if prey of prey have been included. However, we suspect that these effects will be small (see, for instance, Clarke *et al.* 1993) compared to the magnitude of the range in niche breadth of species that emerged.

In examining niche breadth from the diversity of beak material in stomachs, there is a confounding factor: the number of lower beaks examined, which can vary from one to several thousand in any particular stomach. Thus, we examined the number of cephalopod genera recorded from the stomach of an individual animal, using as a covariate the number of lower beaks examined and for which a genus could be determined. There were four species for which we could gather adequate data (at least nine stomachs of different animals): the sperm whale, two beaked whale species (the northern bottlenose whale, *Hyperoodon ampullatus* and Cuvier's beaked whale, *Ziphius cavirostris*), and the southern elephant seal (*Mirounga leonina*). For these species we have plotted in Figure 1, the number of genera identified from the lower beaks in an animal's stomach against the number of beaks examined.

The number of genera found in a stomach increases, as might be expected, with the number of beaks examined, but one other pattern is very apparent: for a given number of beaks examined, the northern bottlenose whales generally had eaten cephalopods of fewer genera than animals of the other three species.

To quantify the pattern shown in Figure 1, and to test for differences in niche breadth between the species, we fitted a logistic model to the data. The asymptote

Table 1. Summary of data and results on niche breadth in mesopelagic teuthivores: number of stomachs examined, median and range of number of beaks obtained from each stomach, and estimates of niche breadth parameter (k) and its standard error.

	n	Data sources[a]	Median beaks (range)	Niche breadth parameter, k (SE)
Northern bottlenose whale	9	1.	1,220 (23–2,531)	0.208[b]
Cuvier's beaked whale	16	2.	140 (3–5,495)	0.680 (0.064)
Sperm whale	20	3.	890.5 (13–4,886)	1.250 (0.086)
-North Atlantic	7		3,217 (628–4,886)	1.190 (0.109)
-Southern Ocean	7		945 (235–4,772)	1.476 (0.157)
-Pacific	6		191 (13–595)	1.122 (0.165)
Southern elephant seal	45	4.	12.5 (1–174)	0.899 (0.065)
Overall	90			0.786 (0.059)

[a]Data sources:

1. Clarke and Kristensen 1980 (2 animals); Hooker *et al.* 2001 (2); Lick and Piatkowski 1998 (1); Santos *et al.* 2001*a* (4).
2. Blanco *et al.* 1997 (3 animals); Blanco and Raga 2000 (1); Carlini *et al.* 1992 (1); Fiscus 1997. (1); Foster and Hare 1990 (1); Fordyce *et al.* 1979 (1); Lefkaditou and Poulopoulos 1998 (3); Podesta and Meotti 1991 (1); Santos *et al.* 2001b (3); S. C. Smith, personal communication (1).
3. Clarke and MacLeod 1976 (1 animal); Clarke *et al.* 1976 (3); Clarke 1980 (7); Clarke *et al.* 1993 (9).
4. Rodhouse *et al.* 1992 (45 animals).

was the total number of genera found in all the stomachs combined: 45 genera. The model is:

$$g = k \times b/(1 + k \times b/t)$$

where g = Log (number of genera in a stomach) ; b = Log (number of beaks examined in a stomach); t = Log (total number of genera in all stomachs = 45).

In this model, if one beak is examined, only one cephalopod genus is found, and if an infinite number are examined, 45 genera are found. However, the rate at which the genera found increases from one to 45 as more beaks are examined (increasing from one to infinity) is determined by the parameter k. Large k indicates a wide niche breadth, and small k a narrow one. This is not a standard measure of niche breadth (see Krebs 1989), but standard methods do not deal with the wide variation in the amount of information available among animals and species in our data set, and so are inappropriate here (we tried some of them!).

Using the NONLIN routines of SYSTAT (Wilkinson *et al.* 1996), the model was fit to all the data (Fig. 1), as well as to that for each species, and to just the sperm whales in each ocean, with a value of the niche breadth parameter k and (where possible) its standard error being produced for each (see Table 1). The residuals from the best fit of the model to all the data (shown in Fig. 2) were calculated and used to test for differences between groups of animals using the Kruskal-Wallis test: (1) among all species (sperm whale, northern bottlenose whale, Cuvier's beaked whale, and southern elephant seal) $P < 0.0001$; (2) among all species excluding northern bottlenose whale (sperm whale, Cuvier's beaked whale, and southern

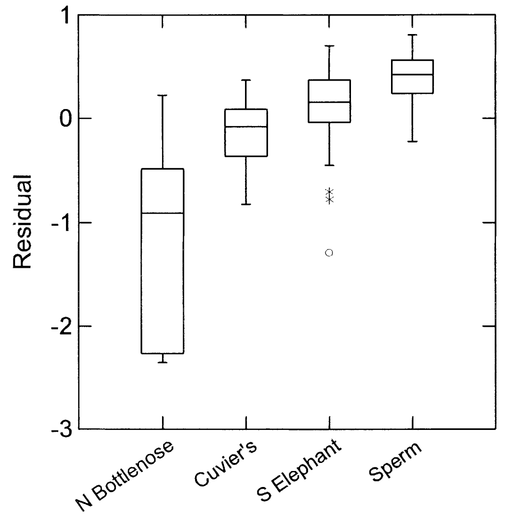

Figure 2. Box plot showing distributions of residual differences between number of genera identified.

elephant seal) $P < 0.0001$; and (3) among sperm whales in different oceans (North Atlantic, Pacific, Southern Oceans) $P = 0.267$.

These results indicate that there are real differences in niche breadth between the species and that this is not just the result of the very low niche breadth of the northern bottlenose whale. However, there is no significant difference in niche breadth between sperm whales in different oceans.

From this analysis we obtain a ranking of the species from generalists to specialists: sperm whale, southern elephant seal, Cuvier's beaked whale, and northern bottlenose whale. The apparent specialization of the northern bottlenose whale, principally on adult members of *Gonatus* species, had been suggested previously (*e.g.*, Lick and Piatkowski 1998; MacLeod *et al.*, in press) but not shown quantitatively. The differences among the other species are less obvious and should be treated more cautiously, as they may be influenced by methodology (for instance biases from variation in rates of accumulation in stomachs among different squid species, inclusion of prey-of-prey, of the form of curve fitted to the data).

There are a range of modes of specialization whereby some animals may have a more restricted diet than others (Emlen 1973, pp. 175–178). Perhaps the most basic of these is when some animals live in simpler environments than others and so have fewer potential prey types. Thus the northern bottlenose whale's particularly narrow niche breadth might be explained by a depauperate cephalopod fauna in the North Atlantic, to which these animals are restricted. However, the diet of the North Atlantic sperm whales is neither substantially nor significantly less broad than that of the sperm whales in other oceans (Table 1), and the North Atlantic sperm whales providing the data for these analyses were caught from areas within the range of the northern bottlenose whale. Thus, interocean differences in cephalopod diversity cannot fully explain the patterns we have found.

Moving to smaller scales may help. All four species dive regularly to several hundred meters beneath the ocean while foraging (Papastavrou *et al.* 1989, Jonker and Bester 1994, Hooker and Baird 1999, Heyning 2002, Watkins *et al.* 2002). However, the limited available evidence indicates that the northern bottlenose, with a median dive depth of about 1,000 m (Hooker and Baird 1999), may generally dive deeper than the other species. Lower cephalopod diversity at such depths might then explain the more specialized diet of this species.

However, movement contrasts are more dramatic in horizontal space. For sperm whales (Clarke 1980), and probably the other species, the cephalopod beaks found in the stomach likely usually represent the results of 24 h of feeding. Over a 24-h interval, a sperm whale has displaced approximately 26 km in a straight line (Whitehead 2001), a southern elephant seal about 31 km (McConnell and Fedak 1996), while the northern bottlenose whales whose movements were studied off Nova Scotia were, on average, only 4 km from their positions 24 h earlier (Hooker *et al.* 2002). We know little of the movements of Cuvier's beaked whales, but they may well be intermediate between those of the wide-ranging sperm whales and southern elephant seals and the much more restricted travels of the northern bottlenose whales. Animals with larger day ranges will generally encounter more types of prey, and so have larger niche breadths.

In conclusion then, differences in niche breadth of the mesopelagic teuthivores may be closely related to their movement patterns. Those that travel most widely, sperm whales and elephant seals, encounter the greatest variety of squid species and have the widest niche breadths, while the northern bottlenose whale with its more localized travels and distribution, centered around the 1,000-m contour in the northern N. Atlantic, specializes on the *Gonatus* that predominate in these waters. We do not know whether prey specialization caused localized movement or *vice versa*, or whether both attributes are results of some other aspect of the biology of the mesopelagic teuthivores.

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