Relative prey size consumption in toothed whales: implications for prey selection and level of specialisation

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ABSTRACT: We investigated whether toothed whales consume prey in relation to their availability in the local environment based on the fact that availability of potential prey is likely to decrease exponentially with increasing size, reflecting the usual size–abundance relationships found in marine communities. We calculated relative prey size frequency spectra for 13 species of toothed whale from the northeast Atlantic. These differed considerably from an exponential distribution, suggesting that toothed whales preferentially consume larger, less abundant organisms over smaller, more abundant ones. The prey size spectra of the various cetacean species could be separated into 3 distinct groups based on the strength of the mode, maximum value and inter-quartile range. Group 1 species, such as the common dolphin, consume a wide range of relatively large organisms. In contrast, Group 2 and 3 species, such as the northern bottlenose whale and the sperm whale respectively, specialise on narrow ranges of relatively small organisms. We hypothesise that these differences are related to the mode of prey capture. Group 1 species can capture prey using pincer-like movement of jaws containing a large number of small, homodont teeth, as well as suction-feeding, allowing them to be relatively generalist in terms of relative prey size. In contrast, Group 2 and 3 species have a greatly reduced dentition and specialise on using suction to capture prey. The morphological adaptations that make suction-feeding more efficient restrict the size of prey that can be ingested, so that suction-feeders are limited to relatively small prey.

KEY WORDS: Prey size · Prey preferences · Diet · Odontocetes · Toothed whales

INTRODUCTION

Variations in diet of toothed whales

Studies on toothed whale diet have traditionally concentrated on examining the taxonomic composition of prey consumed and the sizes of individual prey species (e.g. Sekiguchi et al. 1996, Santos et al. 1999, 2001a,b, 2004, Ohizumi et al. 2000, Walker et al. 2002, Wang et al. 2002). This has provided a great deal of information on cetacean diet and dietary differences between species, but it is not always clear why cetaceans consume different proportions of organisms and/or prey sizes at different locations (e.g. Olsen & Holst 2001, Walker et al. 2002, Santos et al. 2004), at different times (e.g. Ohizumi et al. 2000) or why different cetacean species have different diets (e.g. Wang et al. 2002, Dolar et al. 2003, MacLeod et al. 2003).

Are toothed whales dietary specialists or generalists?

One aspect that may relate to these differences is the level of dietary specialisation. Predators may selectively consume specific types or classes of prey regardless of their local abundance, making them dietary specialists, or they may feed indiscriminately on the most abundant prey in their surroundings, switching

from one prey type to another as prey change in abundance, making them dietary generalists (Scharf et al. 2000, McDonald et al. 2003). The identification of species as dietary specialists or generalists based on how species select prey in comparison to the range available to them is a common factor in many ecological studies (Town 1980, Churchill 1994, Kutt et al. 1998, Yamada & Boulding 1998, McDonald et al. 2003, Bearhop et al. 2004) and is the basis for measures of a species' dietary niche width (e.g. Feinsinger et al. 1981, Bearhop et al. 2004).

In terms of toothed whales, it may be intuitively expected that they are, to a greater or lesser extent, dietary specialists that preferentially consume specific classes of organisms based on some preferred quality (e.g. size, ease of capture, or energy content). Therefore, dietary differences between toothed whales could relate to differences in dietary specialisation between areas, times and species. However, it is also possible that cetaceans are simply generalist foragers that take different classes of organisms in proportion to their availability in the local environment, switching between prey types as local prey abundance changes over time. As a result, differences in diet may simply reflect differences in the local availability of potential prey organisms rather than differences in prey selection. Determining which of these is correct is important for interpreting how toothed whale species will interact with both the local ecosystem and with each other. In particular, if toothed whale species are dietary specialists, identifying the extent of their specialisation, and the reasons behind it, will provide a greater understanding of their role as predators in the marine environment.

Investigating whether toothed whales are dietary generalists or specialists in terms of how they select prey relative to prey availability in the local environment is difficult for at least 2, closely related, reasons. (1) Diet is primarily studied by analysing stomach contents and such data provide only a snapshot of the most recently consumed organisms for any one individual (Pierce & Boyle 1991); the foraging location where these organisms were consumed is rarely known, and stranded animals may not strand in close proximity to their last foraging location. (2) Even if the foraging location represented by individual stomach contents data is known, it is unlikely that there will be contemporaneous data on the local relative abundances of different prey species, sizes or types. Without this information, it is impossible to know the exact structure of the community on which a cetacean was foraging and, therefore, whether an individual cetacean was simply consuming different prey types in relation to their local availability or preferentially selecting specific classes of organisms from those available.

Using prey size to investigate the level of dietary specialisation in toothed whales

While the species composition of available prey at the location of foraging is unlikely to be known, the highly size-structured nature of many marine food chains may allow some inferences to be made on prey consumption preferences. In general, smaller animals will be more abundant than larger ones in marine food webs, due to size-based food chains and trophodynamic transfer efficiencies (Sheldon et al. 1972, Rice & Gilason 1996, Scharf et al. 2000, Jennings et al. 2002). As a result, at any location and time, the relative size frequency spectra of potential prey for an individual toothed whale, regardless of spatial and temporal variations in the exact values, is likely to have an approximately exponential distribution. Therefore, if a cetacean species is a dietary generalist that simply consumes organisms in relation to their abundance in the local environment, it would be expected that in stomach contents summed across all individuals the smallest size class of prey would be the most abundant (Scharf et al. 2000) and the size frequency distribution of prey items would be approximately exponential (e.g. similar to idealised generalist prey size frequency spectra shown in Fig. 1 with smaller prey being more common than larger prey). Exponential generalist prey size frequency spectra could be achieved if either all individuals within the species are dietary generalists (Type A generalist population) or if different individuals within the species specialise on different specific sizes of prey (Type B generalist population; Bearhop et al. 2004). These 2 types of generalist species can be separated by comparing the size frequency spectra of a
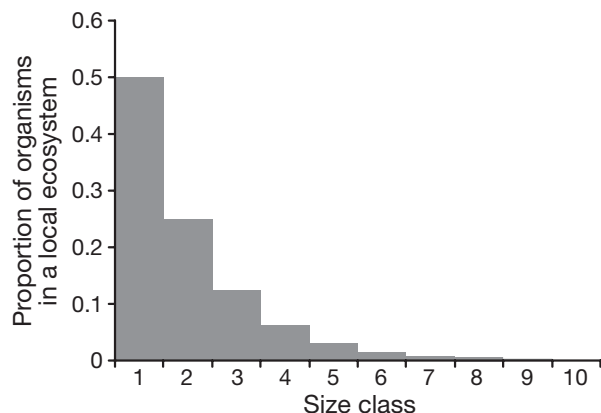

Fig. 1. Idealised size frequency spectra of a generalist predator foraging in a size-structured marine food chain. Size class 1 represents the smallest size of prey consumed while size class 10 represents the largest. As small prey are more common than large prey, due to trophodynamic transfer efficiency (Sheldon et al. 1972, Rice & Gilson 1996, Scharf et al. 2000, Jennings et al. 2002), a generalist consumer consumes a higher number of the more abundant smaller prey

number of different individuals within the population. In contrast, if a predator specialises on organisms of a specific size class, this size class would be expected to be over-represented in its diet, particularly in comparison to smaller size classes. As a result, the size frequency spectra of a specialist species would have a distribution that is clearly not exponential (i.e. one that differs greatly from the idealised size frequency spectra in Fig. 1). This type of size frequency spectra approach to examining predator–prey relationships has previously been applied to marine predatory fish (Scharf et al. 2000); however, this is the first time that it has been applied to toothed whales.

Any prey specialisation based on prey size in toothed whales could result from a number of different factors. In particular, prey specialisation could result from a 'sampling' bias, i.e. when animals cannot capture certain sizes of available organisms due to mechanistic constraints (e.g. predators may have problems capturing or swallowing prey of certain sizes; Scharf et al. 2000, Domenici 2001, MacLeod et al. in press), or from a 'behavioural' bias, i.e. when a predator chooses to select a organism based on some sort of behavioural trade-off

(e.g. cost of prey handling vs. energy obtained; Yamada & Boulding 1998), or a combination of the two. While 'behavioural' biases may be flexible for a given individual, specialisation due to 'sampling' biases that result from mechanistic constraints are not. However, within a species, mechanistic constraints can be altered over time if the appropriate selection pressure and individual variation are present. Therefore, 'sampling biases' due to mechanistic constraints are important ecological characteristics of a species and will be closely linked to the niche it occupies (e.g. Grant 1968, Grant & Grant 1996, Yamada & Boulding 1998, Nilsson & Bronmark 2000, Scharf et al. 2000, Mascitti & Kravetz 2002).

The present study examined the prey size consumption of toothed whale species from stomach contents collected over an extended period of time from the northeast Atlantic in order to investigate whether, at the species level, toothed whales are dietary generalists or specialists, at least in terms of prey size. In addition, the prey size consumption of different toothed whale species was compared to investigate whether there are interspecific variations in prey size preferences.

Table 1. Species of toothed whales analysed in this study along with number of stomachs analysed, total number of prey items, number of prey items with estimated lengths, average cetacean body size and details of the predator–prey size ratios (PPSRs) of each species

Species	Origins of samples	No. of stomachs analysed per region	Total no. of stomachs analysed	Average cetacean body length (cm)	Total no. prey recovered from stomachs	Total no. prey items with estimated length	Predator–prey size ratio				Group
							Modal class	% of prey in class	Inter-quartile range	Max.	
White-sided dolphin *Lagenorhynchus acutus*	Scotland	17	17	201	3949	819	0.01–0.02	16.8	0.037	0.174	1
White-beaked dolphin *Lagenorhynchus albirostris*	Scotland	17	17	225	2415	981	0.04–0.05	11.4	0.055	0.230	1
Common dolphin *Delphinus delphis*	Scotland Galicia	9 300	309	183	90392	16702	0.03–0.04	11.1	0.058	0.283	1
Striped dolphin *Stenella coerueolalba*	Scotland Galicia	18 18	36	185	8711	1585	0.04–0.05	17.1	0.033	0.230	1
Bottlenose dolphin *Tursiops truncatus*	Scotland Galicia	10 44	54	273	10268	2694	0.06–0.07	14.4	0.045	0.331	1
Harbour porpoise *Phocoena phocoena*	Scotland Galicia	171 16	187	131	33178	5959	0.05–0.06	13.9	0.045	0.389	1
Sowerby's beaked whale *Mesoplodon bidens*	Scotland	4	4	471	1573	157	0.02–0.03	36.9	0.013	0.062	2
Northern bottlenose whale *Hyperoodon ampullatus*	Scotland Ireland	2 1	3	607	3569	2828	0.02–0.03	34.1	0.019	0.062	2
Cuvier's beaked whale *Ziphius cavirostris*	Scotland Galicia	1 3	4	525	6400	4091	0.02–0.03	25.7	0.023	0.106	2
Risso's dolphin *Grampus griseus*	Scotland Galicia	9 6	15	272	868	455	0.02–0.03	26.6	0.022	0.156	2
Pygmy sperm whale *Kogia breviceps*	Scotland Galicia	2 5	7	252	2386	1043	0.01–0.02	64.1	0.011	0.188	3
Sperm whale *Physeter macrocephalus*	Scotland	12	12	1302	15023	6624	0.01–0.02	94.1	0.002	0.039	3
Long-finned pilot whale *Globicephala melas*	Scotland Galicia	2 18	20	525	1282	392	0.02–0.03	58.2	0.009	0.133	3

MATERIALS AND METHODS

Data sources. Species-specific size frequency spectra were constructed using data from the stomachs of stranded toothed whales primarily collected from Scotland and Galicia in northwest Spain between 1990 and 2004 (Table 1); data were thus provided across the range of each species in the northeast Atlantic and over a wide range of time periods (Table 2). The stomachs were routinely collected as part of stranding reporting schemes in these areas and were collected to allow investigation of diet and feeding ecology. While much of the data used in this study have previously been published (e.g. Santos et al. 1999, 2001a,b, 2004, Santos & Pierce 2005), species-specific size frequency spectra have not previously been calculated and compared. Inevitably, due to differences in the frequency of occurrence of different species in records of strandings, sample sizes for individual species will vary when using such a data set. The data set used for this analysis is one of the largest available on cetacean stomach contents and this will minimise the under-representation of rarer species as much as possible. However, the potential effects of a limited sample size for some species on interspecific comparisons must be borne in mind, and this is considered further below.

Data processing. Prey items found in stomachs were identified to the lowest possible taxonomic level based on their morphology. Where possible, size was estimated following the standard protocol using published regression equations (e.g. Clarke 1986, Härkönen 1986) to calculate total length (fish) or mantle length (cephalopods) that relate morphometric characteristics of the prey remains (fish otoliths or cephalopod beaks, respectively) to body length. While no correction for prey digestion was undertaken, the level of bias introduced by this is likely to be similar across different cetacean species, particularly when similar taxa of prey

are considered, and can only result in an under-estimation of prey size rather than an over-estimation. When >30 otoliths or cephalopod beaks of similar size were recorded for a single species of prey in a single stomach, only a random sample ≥30 was measured. Again, while this may introduce a bias into the construction of the size frequency spectra, the same rule was used for all species and all prey items, meaning that the bias will be similar for all cetacean species. To assess the likely impact of this bias, the size distribution of all prey items (rather than just those measured) was estimated using the size distribution of the measured prey items and the total number of remains of each prey species.

Data from all individuals of the same toothed whale species were pooled to provide a species-specific dataset of prey sizes consumed. While individuals that contain more prey items will make a greater contribution to the overall species size frequency spectra, using only a sample of prey species with large numbers of similar-sized prey remains within individual stomachs will reduce the differential contribution and reduce the likelihood that size frequency spectra reflect the dietary preferences of only a small number of individuals rather than the whole species. Therefore, the combined size frequency spectra are likely to represent the dietary preferences of the species as a whole, particularly when data from a large number of individuals are combined.

In order to allow a direct comparison of the size frequency spectra of different cetacean species, it was preferable to use comparable size class divisions for each species. However, the cetaceans examined ranged in size from <1.5 m in harbour porpoises *Phocoena phocoena* to >15 m for sperm whales *Physeter macrocephalus*, meaning that classes based on absolute prey sizes were unlikely to be directly comparable, being too large for the smallest cetacean species and too small for the largest. Therefore, the size classes were defined in relation to a predator–prey size ratio

Table 2. Temporal spread of stomach contents data used in analysis. ?: unknown month of stranding for one individual of a species. NB: individual of *Hyperoodon ampullatus* from Ireland not included

Species		Scotland			Galicia	
	N	Years	Months	N	Years	Months
Delphinus delphis	9	1992, 1994, 1999, 2001, 2003	1, 2, 4–6, 9, 12	300	1991	1–12
Globicephala melaena	2	1996, 2001	4	18	1991–1994, 1997–1999	2–6, 11, 12
Grampus griseus	9	1992–2002	2, 4, 5, 8, 10	6	1991–1994, 1997	24, 12
Hyperoodon ampullatus	2	1895, 2001	?, 9	0	–	–
Kogia breviceps	2	1999	10	5	1995, 1997, 1999, 2002	1, 10, 12
Lagenorhynchus acutus	17	1992, 1994–1998, 2000–2002	1, 3–7, 10–12	0	–	–
Lagenorhynchus albirostris	17	1992–1996, 1998–2003	1–4, 6–9, 12	0	–	–
Mesoplodon bidens	4	1992, 1994, 1996, 2001	4, 8, 10	0	–	–
Phocoena phocoena	171	1992–2003	1–12	16	1991, 1993–1995, 1997–1999, 2003	1, 2, 4–8, 10–12
Physeter macrocephalus	12	1994–1996, 1998, 2002	1, 3, 8, 12	0	–	–
Stenella coeruleoalba	18	1992–1995, 1998–2003	1–4, 7–12	18	1994–1996, 1998–1999, 2002–2003	2–5, 9–12
Tursiops truncatus	10	1990, 1993–1996, 1998–1999	1, 3–7, 12	44	1990–1999, 2001–2002	1–12
Ziphius cavirostris	1	1999	2	3	1990, 1995, 2000	2, 11

(PPSR). For this study PPSRs were calculated by dividing the estimated length of each prey item by the total body length of the cetacean from which it was recovered. For example, a prey item with an estimated length of 10 cm recovered from a 500 cm long cetacean would have a PPSR of 0.02.

Using a PPSR. Removed the effect of differences in body size between species and allowed direct comparisons to be made between prey size frequency spectra. This approach will not alter the type of size distribution that is found in a species and, therefore, any inferences about prey selection. Scharf et al. (2000) used a similar relative size frequency spectra approach when comparing prey size preferences of marine fish species.

Interspecific comparisons of PPSR frequency spectra. The PPSR frequency spectra were compared to the approximately exponential distribution expected if prey were taken in proportion to local availability of all organisms and to each other to assess whether there were differences between individual species. The PPSR frequency spectra of different cetacean species were compared by identifying 3 basic measures of the spectra distribution: (1) the proportion of prey items in the modal PPSR class, (2) the inter-quartile range of the PPSR values and (3) the maximum PPSR. These measures were used, rather than more commonly used measures of a distribution such as mean ± SD, due to the non-normal distribution of the data across the PPSR size classes. While the 3 measures may be correlated in certain potential frequency spectra, this is not true for all possible frequency spectra. Therefore, these 3 measurements are independent variables that describe different aspects of the shape of a species PPSR frequency distribution. Principal component analysis (PCA) was then used to assess the variation between species based on these 3 measures of the PPSR frequency spectra and to investigate whether species could be separated into distinct groupings. Discriminant analysis (DA) was used to check the true distinctiveness of any identified groupings.

To assess how the diet of individual cetaceans related to the PPSR frequency spectra of the species as a whole, a second PCA was conducted using the strength of the mode, the maximum PPSR and the inter-quartile range of each individual from each species with >30 prey items measured from the stomach contents. A biplot of the first 2 PC axes was then used to assess variation in each species and to compare this variation between species, particularly of different PPSR frequency groupings. In addition, this allowed an assessment of whether sample size contributed to apparent differences between species by showing whether individual PPSR frequency spectra from species with small sample sizes were simply a random subset of PPSR frequency spectra of all individuals from species with larger sample sizes.

Effect of sample size on PPSR frequency spectra. In order to assess the effect of sample size on species PPSR frequency spectra, data for the species with the most individuals and the most variation between individuals (the common dolphin *Delphinus delphis*) were examined in detail. PPSR frequency spectra were calculated for sets of randomly selected individuals to generate simulated PPSR frequency spectra for common dolphins based on sample sizes of 5, 10, 15 and 20. This was repeated 1000 times for each sample size to examine the range of possible PPSR frequency spectra that could have been obtained for a given sample size. Each individual simulated PPSR frequency spectrum was compared to the actual overall PPSR frequency spectrum for common dolphins and the absolute difference in the proportion of samples in each PPSR frequency class calculated. These proportions were then summed to give a single score expressing the difference between the simulated spectrum and the actual common dolphin spectrum. For each sample size, the 1000 simulated spectra were sorted according to the difference score and the 5% of spectra most dissimilar from the original common dolphin spectrum were then discarded. The remaining 95% of simulated spectra were plotted to allow visualisation of the 95% confidence interval for a PPSR frequency spectrum for common dolphins calculated from that number of individuals.

RESULTS

PPSRs were calculated for a total of 44 653 prey items from 685 individuals of 13 species of toothed whale (Table 1). However, for individual species, sample sizes ranged from 3 (northern bottlenose whale) to 309 individuals (common dolphin) and from 157 (Sowerby's beaked whale) to 16 702 prey items (common dolphin). The PPSR frequency spectra of all species (Figs. 2 to 4) differed considerably from the idealised prey size frequency spectra expected if a species was a dietary generalist (Fig. 1). In general, the smallest PPSR classes (generally those <1% of cetacean body length and especially those <0.5%) were greatly under-represented. This suggests that all species do not simply consume organisms based on their availability in the local environment; instead it suggests that toothed whales consume larger, less abundant organisms in preference to smaller, more abundant ones. PCA suggested that the 13 cetacean species could be divided into 3 distinct groups (Fig. 5). The distinctiveness of these 3 groups was confirmed by DA, which correctly assigned each species to its putative group in every case. A similar result was obtained regardless of whether the PPSR frequency spectra were created from the sampled data or the estimated
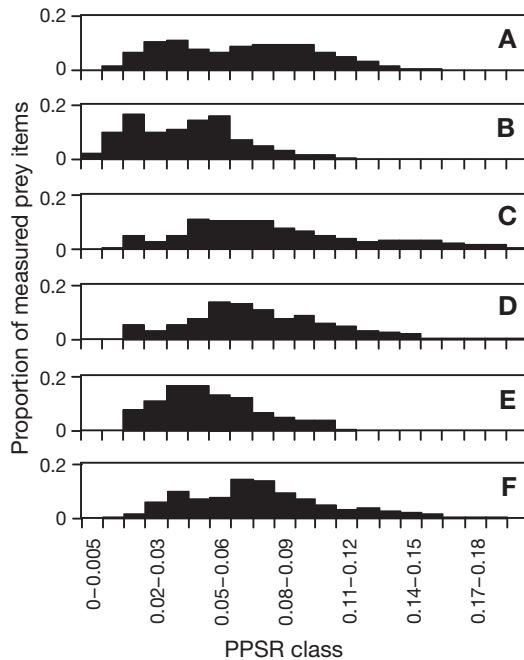
Fig. 2. Predator-prey size ratio (PPSR) frequency spectra for Group 1 species of toothed whales from the north-east Atlantic. (A) Common dolphin; (B) Atlantic white-sided dolphin; (C) white-beaked dolphin; (D) harbour porpoise; (E) striped dolphin; (F) bottlenose dolphin
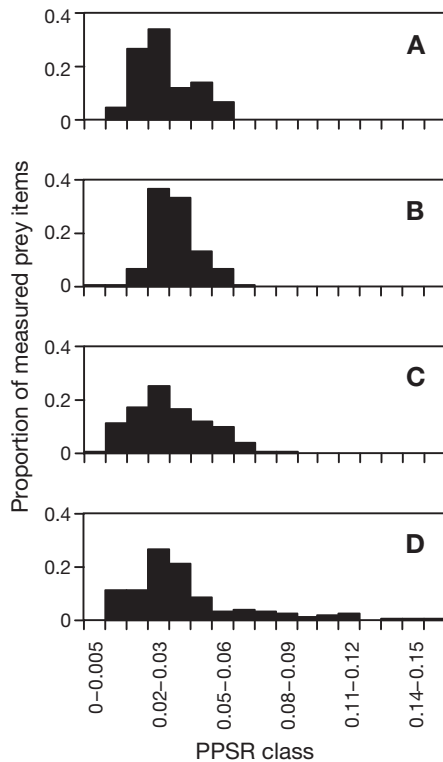
total prey size distribution; however, only the results from the sampled data are presented here.

Group 1 consisted of species that have only a weak modal class (<20% of all prey items), relatively large inter-quartile range and a relatively large maximum PPSR (Fig. 2). This means these species consume a wide range of prey sizes, including both relatively small and large prey, and are not reliant on a single narrow range of prey sizes. Therefore, Group 1 species are the most generalist group of toothed whales in terms of the relative sizes of prey consumed. However, relatively large prey (>5% of body length) are particularly over-represented in the diet in comparison to an approximately exponential distribution. In contrast, all the remaining species have strong modal PPSR at a relatively small prey size, much narrower inter-quartile ranges and smaller maximum PPSRs (Figs. 3 & 4). This means that these species rely on a narrow size range of relatively small organisms. These species can be separated into 2 further groups. Group 2 consists of species in which there is a single, clear mode at a relatively small PPSR (2 to 3% of body length in all species), but where the mode is only moderately strong (between 25 and 50% of all prey items; Fig. 3). In contrast, Group 3

Fig. 3. Predator-prey size ratio (PPSR) frequency spectra for Group 2 species of toothed whales from the north-east Atlantic. (A) Northern bottlenose whale; (B) Sowerby's beaked whale; (C) Cuvier's beaked whale; (D) Risso's dolphin
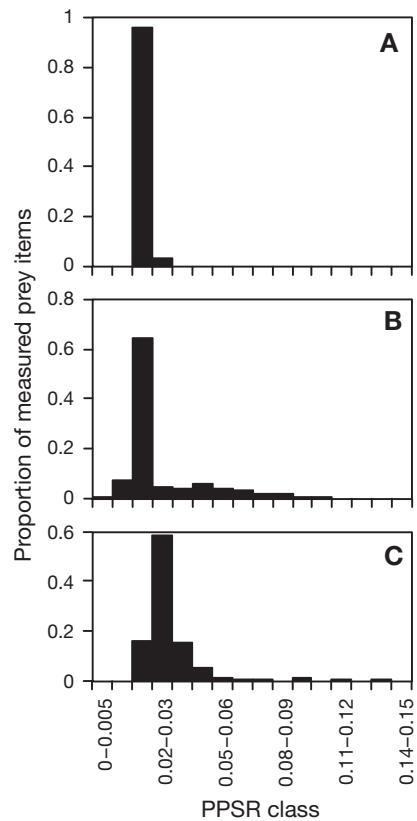

Fig. 4. Predator-prey size ratio (PPSR) frequency spectra for Group 3 species of toothed whales from the north-east Atlantic. (A) Sperm whale; (B) pygmy sperm whale; (C) long-finned pilot whale
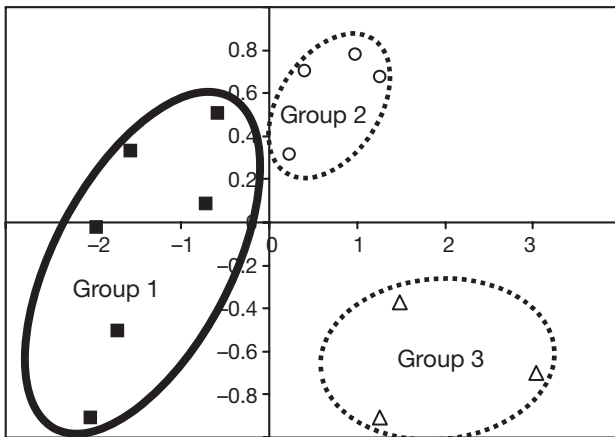
Fig. 5. Biplot of first and second axes of PCA using strength of the mode, maximum predator-prey size ratio (PPSR) and interquartile range of PPSRs. Group 1 species (■); Group 2 species (○); Group 3 species (△). The most important variable for the first PC is the interquartile range (–0.608). Group 1 species are therefore separated from Groups 2 and 3 along this first axis because they have a greater interquartile range, which indicates a greater variation in PPSR

consists of species in which there is a single, very strong mode (>50% of all prey items) at a PPSR <0.03 (Fig. 4). Therefore, the majority of prey consumed by Group 3 species are very small (<3% of whale body length) and fall within a very narrow range (1% of whale body length), indicating a greater level of specialisation on organisms of a specific relative size in Group 3 than Group 2 species.

Inter-individual variation within species

There was noticeable inter-individual variation in the PPSR frequency spectra within each species (Fig. 6). However, even at the individual level there were differences between the 3 PPSR frequency spectra groupings that were consistent with the species

Table 3. Results of the principal component analysis (PCA) analysis conducted using all tooth whales with >30 prey items measured from the stomach. Three variables were used: strength of the mode, the maximum predator-prey size ratio (PPSR) and the interquartile range. Together, the first and second PC axes accounted for 86.2% of the variation in the data

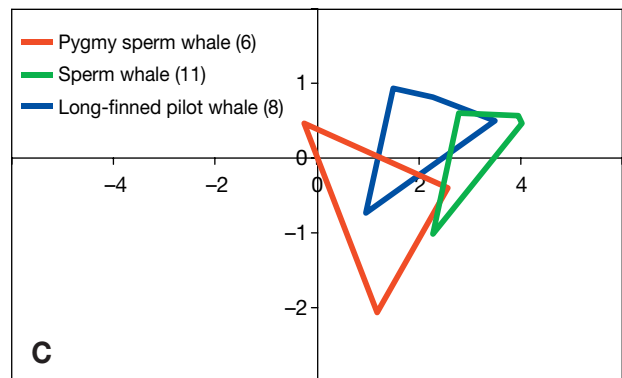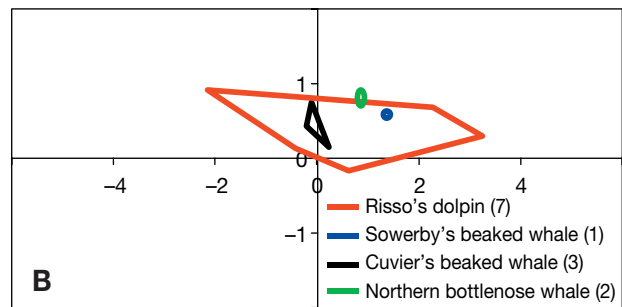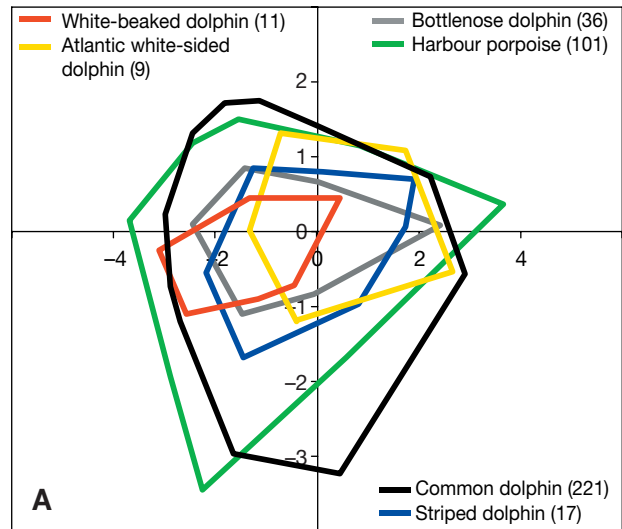|	PC1	PC2	PC3
Eigenvalue	1.9704	0.6153	0.4143
Proportion	0.657	0.205	0.138
Cumulative proportion	0.657	0.862	1.000
Eigenvectors			
Strength of mode	0.611	–0.164	0.755
Maximum PPSR	–0.542	–0.800	0.258
Interquartile range	–0.577	0.577	0.578

Fig. 6. Biplot of the first and second axes of the PCA of individual tooth whales for each of species using the strength of the mode, the maximum predator–prey size ratio (PPSR) and the interquartile range of the PPSR. (A) Group 1 species; (B) Group 2 species; (C) Group 3 species. Polygons represent the spread of data for each species. These were added by hand and connected the outermost points of the distribution (e.g. minimum convex polygons). Axes are the same scale. The number of individuals with >30 measured prey items in the stomach is shown in brackets

level differences. Group 1 species had the highest levels of variation, and individuals ranged from having a restricted range of prey sizes in their stomachs to having an almost even distribution of different prey sizes. This is consistent with Group 1 species being more

generalist, consuming a wide variety of prey sizes and that these species are a mix of Type A and Type B individuals (Bearhop et al. 2004). However, there was a tendency for the spread of Group 1 species to be centred to the left and below the origin on the biplot. Strength of the mode was the most important variable on Axis 1 (eigenvector: 0.611) and maximum PPSR for Axis 2 (eigenvector: –0.800; see Table 3). Therefore, across all individuals, Group 1 species tended to have relatively weak modes and high maximum PPSRs.

In contrast, Group 2 and 3 species had less variation between individual animals in terms of the 3 variables and the spread of individuals on the biplot tended to be centred on the right-hand side of the biplot (Fig. 6). This is consistent with these species having stronger

modes (i.e. higher eigen scores on PC1) and, therefore, specialising on a narrower range of prey sizes. Differences between Group 2 and Group 3 species were primarily on the PC2 axis, with Group 3 species tending to have lower values. This suggests that Group 3 species tend to consume prey with a higher maximum PPSR and this is consistent with the differences in the species level PPSR frequency spectra.

Effect of sample size on PPSR frequency spectra

In terms of the effect of sample size on the calculated PPSR frequency spectra, increasing the sample size decreased the variation around the actual species
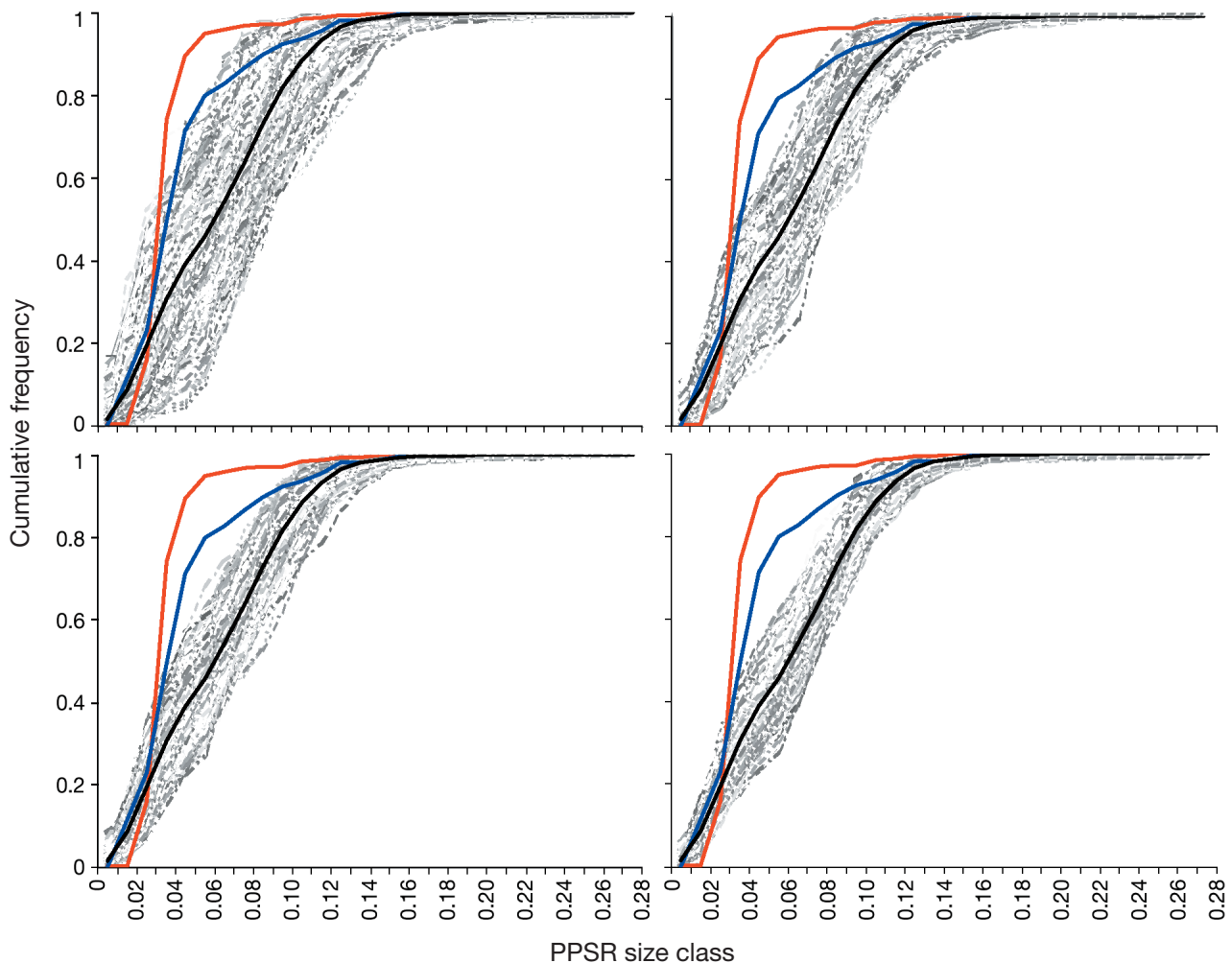

Fig. 7. Effect of sample size on predator-prey size ratio (PPSR) frequency distribution in the common dolphin *Delphinus delphis*. Variation in cumulative frequency distribution when based on sample sizes of (A) 5, (B) , (C) 15 and (D) 20 individuals. Solid black line: cumulative frequency distribution for common dolphin from all samples (n = 309); grey lines: 95% of 1000 sampling events with the lowest difference from the species cumulative frequency distribution; blue lines: typical cumulative frequency distribution for Group 2 species (Risso's dolphin *Grampus griseus*); red line: typical cumulative frequency distribution for Group 3 species (long-finned pilot whale *Globicephala melaena*)

PPSR frequency spectra generated from all common dolphin data. However, even when only 5 individuals were sampled, in 95% of all cases PPSR frequency spectra were distinct from those of Group 2 and 3 species in that they did not have the strong mode at a low PPSR class typical of these groups. Therefore, Group 1 species are unlikely to generate PPSR frequency spectra typical of a Group 2 or 3 species by chance alone even with as few as 5 individuals. When 10 or more individuals were sampled, the variation around the actual species PPSR frequency spectra was relatively low, suggesting that such sample sizes are sufficient to get a reliable picture of the PPSR frequency spectra of a species (Fig. 7). For Group 2 and 3 species, with much less variation between individuals than in Group 1 species (Fig. 6), even the small sample sizes available are likely to represent the PPSR frequency spectra of the species. For example, in sperm whales, all but one individual had a very strong mode at 1 to 2% of length, suggesting little variation between individuals and the species PPSR frequency spectra based on a small sample size are likely to represent the actual species spectra.

DISCUSSION

Relative prey size consumption in toothed whales

The results of this study suggest that toothed whales are not generalist predators that consume organisms in proportion to their availability in the local environment, at least in terms of prey size. In all 13 species examined here, the smallest relative sizes of prey were under-represented in comparison to an approximately exponential distribution of organism sizes expected to be available in the local environment.

Possible biases in analysis

However, these results could also be explained by biases in the assumptions and methods used in this study. (1) For some reason the smallest organisms could be under-represented within stomach contents due to increased likelihood of digestion of smaller hard remains. However, if this were the case, it is unlikely that such a similar lower relative size limit (very few prey <0.5% of cetacean body length) would be found in all species ranging from the harbour porpoise to the sperm whale. Across this size range 0.5% of body length would indicate a prey size varying from around 0.75 to 7.5 cm respectively. In addition, a similar lower size limit was found regardless of whether prey remains were otoliths from fish or beaks from cephalo-

pods that are known to have very different digestion rates (Pierce & Boyle 1991).

(2) Similarly, if smaller organisms were for some reason less abundant in the local environments than expected, it would not explain why cetacean species of different sizes feeding on the same organisms in similar general areas have similar modal PPSRs but different absolute prey sizes. For example, in the northeast Atlantic both northern bottlenose and sperm whales primarily feed on squid of the genus *Gonatus*. However, while both species consume similar modal prey sizes, they differ in their absolute prey sizes (Santos & Pierce 2005), indicating that differences in availability of absolute organism sizes are unlikely to explain the under-representation of relatively small organisms.

It is also possible that these results are an artefact of only measuring a sample of prey remains from an individual cetacean when the numbers of specific species of prey were large. However, PPSR frequency spectra of estimated size distribution of all prey remains were very similar to the ones calculated using the sub-sampled data.

Comparison with relative prey size preferences of fish

Therefore, it seems that prey size is an important component of prey selection in toothed whales and that toothed whales preferentially consume larger, less abundant organisms. A similar link between predator size and prey size selection has previously been found in marine fish (Scharf et al. 2000). However, in the toothed whale species examined here, the majority of prey (77 to 100% of all prey items, depending on species) had a PPSR <0.1. In contrast, most fish species examined by Scharf et al. (2000) concentrated on prey ranging from 10 to 20% of predator length to >50% of predator length. Therefore, most fish species appear to consume relatively larger prey than toothed whales. This may relate to the morphology of toothed whales, where the larynx penetrates through the oesophagus, limiting the largest size of prey that can be consumed (MacLeod et al. in press). Fish are not limited in the same way, allowing them to swallow prey of a much larger relative size. As a result, there may be a relatively high overlap in terms of actual prey sizes consumed between toothed whales and fish of very different sizes. In addition, it appears that the minimum prey size consumed by toothed whales is also affected by predator size, with all species having a similar lower limit to relative prey size regularly consumed (around PPSR 0.005). This may reflect hydrodynamic limitations on the ability of pursuit predators to catch relatively small prey (Domenici 2001).

Comparison between toothed whale species

While all toothed whale species examined here showed evidence of being dietary specialists, at least in terms of prey size, it appears they differ in the extent of this specialisation, ranging from the most generalist species in Group 1 to the most specialised species in Group 3.

Possible biases in analysis

(1) It is possible that these differences are an artefact of using a PPSR to construct the size frequency spectra rather than the actual prey size. For example, for species with larger body sizes, each PPSR frequency class will contain a wider range of actual prey sizes than for smaller species. This could result in larger species having a narrower PPSR frequency spectrum simply due to body size differences even if they are consuming organisms of the same range of actual sizes. However, pygmy sperm whales *Kogia breviceps*, Risso's dolphins *Grampus griseus* and bottlenose dolphins *Tursiops truncatus* all have very different PPSR frequency spectra (Figs. 2F, 3D, & 4B) despite having similar average body sizes (252, 272 and 273 cm respectively; Table 1). Similarly, sperm whales and pygmy sperm whales have almost identical PPSR frequency spectra (Fig. 4A,B) despite a more than 5-fold difference in average size (Table 1). This suggests that the difference between species are real and not simply an artefact of using PPSR frequency spectra rather than size spectra.

(2) Similarly, the sample sizes used to construct the species PPSR frequency spectra differed greatly between species. In general, the sample sizes for Group 2 and 3 species were smaller than those for Group 1 species, and it could be that the apparent greater specialisation in members of the first 2 groups is actually an artefact of an incomplete sampling of the full range of variation in these species. This variation in the number of individuals reflects the relative availability of samples from stranded animals within this region; in cetacean research a lack of data for certain species is a widespread problem for comparative studies such as this one. This lack of data for species which strand more rarely (e.g. beaked whales) is unlikely to be overcome in the near future and waiting until comparable sample sizes are available for all species would effectively result in little comparative research being conducted on cetaceans. Therefore, the results of this comparison should be considered preliminary and may require amending when more data become available. However, the fact that species with similar numbers of sampled individuals fall into different PPSR frequency spectra groups (e.g. white-beaked and Atlantic white-sided dolphins into Group 1,

Risso's dolphins into Group 2 and long-finned pilot whales into Group 3) suggests that the segregation of toothed whale species into groups with different relative prey size preferences is not simply due to insufficient sampling of certain species' actual prey size preferences. In addition, if the apparent division into 3 separate groups was due to incomplete sampling of the variation in prey size consumed by species with smaller sample sizes, it would be expected that the samples from individuals of Group 2 and 3 species would be a random subset of samples from Group 1 species. However, the PCA based on data from individual animals suggests that this is not the case since the distribution of Group 2 and Group 3 individuals are consistent with each other and are not a random subset of the individuals of Group 1 species (Fig. 6). Finally, detailed investigation of the effect of sample size on PPSR frequency spectra in the common dolphin suggests that even with as few as 5 individuals sampled, it is unlikely that a Group 1 species would generate a spectrum typical of a Group 2 or 3 species with a strong mode at a low PPSR. Therefore, it seems unlikely that the differences between the groups are a result of small sample sizes. The effect of sample size on common dolphin PPSR frequency spectra suggests that once sample sizes reach 10, the PPSR frequency spectra obtained is likely to be similar to that generated from much larger sample sizes (Fig. 7). While adding more samples affects the exact form of the PPSR frequency spectra, it will have little effect the outcome of the type of interspecific comparison conducted in this study.

What drives interspecific differences?

There are a number of possible explanations for the suggested differences between species. (1) It may be related to phylogeny, with each distinct PPSR frequency spectra group consisting of closely related species. However, none of the 3 PPSR frequency spectra groups are monophyletic. Group 1 consists of dolphin species (family Delphinidae) and the harbour porpoise *Phocoena phocoena* (family Phocoenidae), while Group 2 consists of beaked whales (family Ziphiidae) and Risso's dolphin *Grampus griseus* (family Delphinidae) and Group 3 consists of sperm whales (families Physeteridae and Kogiidae) and the long-finned pilot whale, *Globicephala melas* (family Delphinidae).

(2) On average, Group 1 species have the smallest body size, while Group 3 species have the largest body size. However, as noted above, all groups contain species of similar body sizes (e.g. bottlenose dolphin, Risso's dolphin and pygmy sperm whale) and wide variation in body sizes (Group 1: 131 to 273 cm; Group 2: 272 to 607 cm; Group 3: 252 to 1302 cm;

see Table 1). Therefore, while body size may contribute to differences in size-based prey selection, with species larger species being more specialist than smaller species, this does not account for all differences between the groups.

(3) The difference between groups could relate to other aspects of prey preferences. For example, many species in Groups 2 and 3 are thought to primarily forage on cephalopods and it could be that a preference for cephalopods over a more generalist diet, or one primarily consisting of fish, is responsible for differences in prey size preferences. However, at least one of the Group 2 species, Sowerby's beaked whale, primarily consumes fish in the northeast Atlantic (MacLeod et al. 2003), suggesting that this is also not a complete explanation.

(4) All members of Group 1 are relatively shallow-diving species, primarily foraging in the top 200 m of the water column (Schreer & Kovacs 1997; Otani et al. 1998), while most members of Groups 2 and 3 are thought to primarily forage at depths >500 m (e.g. northern bottlenose whale: Hooker & Baird 1999; long-finned pilot whale: Heide-Jorgensen et al. 2002, Baird et al. 2002; sperm whale: Lockyer 1997). Therefore, the specialisation on a narrow range of relatively small organisms could relate to deep-diving. Deep-diving undoubtedly places constraints on air-breathing animals, which could lead to very tight constraints on energy budgets and foraging requirements. This, in turn, could result in deep-diving species concentrating on a narrow range of prey sizes. However, it might be expected that larger organisms would provide better energetic returns per unit effort and that deep-divers would specialise on proportionately larger rather than proportionately smaller prey than shallow-diving species. In addition, Risso's dolphin, a Group 2 species, frequently occurs in relatively shallow coastal waters in the northeast Atlantic (e.g. The Minch in northwest Scotland; Gill et al. 1997), where diving to depth >200 m is not possible. This suggests that deep-diving does not, in itself, result in the specialisation on a narrow range of relatively small organisms.

Relative prey size preferences and prey capture

In contrast to the above explanations, a link with the primary prey capture technique used by the different groups may provide a more complete explanation for differences between groups. Group 1 species primarily capture prey using a pincer movement of the jaws, which contain a large numbers of relatively small, simple, peg-like teeth that are well adapted for piercing, gripping and handling prey (Heyning &Mead 1996,

MacLeod 1998). Such a prey capture technique can be used with equal efficiency to capture both relatively small and relatively large prey. In addition, species with this morphology can also use alternative methods of prey capture, such as suction-feeding, when required, further enhancing the range of prey sizes than can be captured and consumed. The only limitation to the largest size of prey that these species can consume is whether it will fit down the oesophagus either whole or in pieces (MacLeod et al. in press). In contrast, Group 2 and 3 species have a reduced dentition, and in most species those teeth that remain are adapted to function as weapons rather than for foraging (Heyning & Mead 1996, MacLeod 1998). This reduced dentition is primarily thought to be an adaptation for foraging on cephalopods, since small, peg-like teeth are poorly adapted for gripping the rubbery flesh, and prey capture is primarily by suction (Heyning & Mead 1996). However, specialising in suction-feeding places a number of pressures on cetacean morphology. In particular, suction-feeding is more efficient when the entrance to the mouth is smaller, as the pressure difference produced by movements of structures in the mouth and buccal cavity is concentrated in a smaller area. Toothed whales that specialise in using suction to capture prey have adaptations that reduce the size of the entrance of the mouth. These include a reduced gape in beaked whales, a relatively narrow mouth in sperm whales and the ability to use their lips to narrow the opening of the mouth in delphinids (Heyning & Mead 1996). As a result, species that specialise in using suction to capture prey are limited in the upper size of prey that they can ingest, potentially explaining why they preferentially consume a narrow range of relatively small organisms. Under these circumstances, the specialisation on a narrow range of prey sizes is not a 'choice' but a 'sampling' bias imposed by morphological adaptations. Therefore, it seems likely that while a specialisation in prey capture by suction may have evolved as a method for effectively capturing cephalopods, it is not the consumption of cephalopods per se but the specialisation in prey capture by suction that results in a specialisation on a narrow range of relatively small organisms. Similarly, larger species and deeper divers tend to be specialist suction-feeders (but not necessarily vice versa) and this may explain why there is a partial link between these characteristics and prey size specialisation.

Possible reasons for differences in relative prey size preferences between suction feeding specialists

Reasons for the division of suction-feeding species into Groups 2 and 3 currently remain unclear. It may

be related to the fact that the use of suction as the primary mode of prey capture has evolved independently in a number of different lineages (e.g. families Ziphiidae, Physeteridae, Kogiidae and Delphiniidae). As a result, specific adaptations for suction-feeding, such as the way in which the entrance to the mouth is limited to increase the suction power, vary between species. These variations may limit prey ingestion to different extents and in different ways. However, this would not explain why species that have independently evolved suction-feeding have similar relative prey size preferences (e.g. Ziphiidae and Risso's dolphin) or why 2 delphinid species fall into separate groups. As yet unknown ecological characteristics may explain this convergence between some suction-feeding species in terms of their PPSR frequency spectra and the divergence between others.

Implications of suction feeding for other aspects of foraging ecology

The limitations that suction-feeding places on toothed whale species have implications for other aspects of their ecology. In particular, by limiting the size of prey that can be consumed, suction-feeding may affect the proportion of time an animal needs to spend foraging to meet its daily energy requirements. For example, a 15 m long sperm whale primarily consuming *Gonatus* spp. of 2% of its body length may need to ingest more than 100 squid h^{-1} in order to achieve its estimated daily energy requirements of 3.25% of body weight (Lockyer 1991, Santos et al. 1999). Therefore, while suction-feeding may have evolved as an aid in the capture and consumption of cephalopods, it places additional pressures on toothed whales in terms of meeting their daily energy budgets by requiring specialisation on relatively small organisms.

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