

# Feeding ecology of two high-order predators from south-eastern Australia: the coastal broadnose and the deepwater sharpnose sevengill sharks

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**ABSTRACT:** Quantifying the feeding ecology of marine predators is essential for understanding their trophic interactions and their potential regulatory effects in marine ecosystems. I quantified the feeding ecology of 2 related predators that overlap only in part in spatial distribution: the coastal broadnose *Notorynchus cepedianus* and the deepwater sharpnose *Hepttranchias perlo* sevengill sharks. I found the following: These 2 shark species have different diet specialisation patterns, but show similarities in their prey handling mode. *N. cepedianus* has a generalised diet, whereas *H. perlo* shows high specialisation and lower prey diversity. For both shark species, small, medium and large individuals use different strategies for handling different prey groups. *H. perlo* preys largely on deepwater teleosts, mainly *Lepidorhynchus denticulatus*, with larger individuals (901 to 1365 mm total length, TL) also consuming high proportions of large predatory teleosts of the families Gempylidae and Trichiuridae. *N. cepedianus* has a diverse diet. Small individuals ( $\leq 900$  mm TL) prey largely on teleosts and secondarily on chondrichthyans. Medium individuals (901 to 1520 mm TL) prey primarily on chondrichthyans and secondarily on teleosts. Chondrichthyans (mainly *Mustelus antarcticus*) are also the main prey of large *N. cepedianus* ( $> 1700$  mm TL), but this group also shows a greater preference (than small and medium individuals) for fur seals. Despite the overall differences in dietary composition and the minimal overlap in spatial distribution, the 2 shark species consume prey that migrate from deep to coastal waters (ommastrephid squid and gempylid fish).

**KEY WORDS:** Top predator · Feeding ecology · *Hepttranchias perlo* · *Notorynchus cepedianus* · Shark · Cow sharks · Hexanchidae

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## INTRODUCTION

As a group, sharks are tertiary consumers and many species occupy the upper trophic levels (Cortés 1999). Fieldwork and modelling studies indicate that some shark species may be important in structuring marine communities (Cortés 1999, Stevens et al. 2000, Bascompte et al. 2005, Heithaus 2005, Shepherd & Myers 2005, Myers et al. 2007). However, there is currently little quantitative information on the feeding ecology of sharks (Wetherbee & Cortés 2004), particularly for deepwater and large top-predatory species. For these species less information is available than for their shal-

low-water and smaller counterparts given the logistic constraints of collecting deepwater and large sharks. Hence, quantifying the feeding ecology of these species is essential for modelling their trophic interactions and their potential regulatory effects in the structure and function of marine ecosystems.

Cow sharks (Hexanchidae) are large top-predatory sharks; as a group, cow sharks have a higher trophic level than any other shark group (Cortés 1999). Within the hexanchids, the broadnose sevengill shark *Notorynchus cepedianus* exhibited the highest trophic level among 149 shark species (Cortés 1999) — even higher than the great white shark *Carcharodon carcharias* —

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due to the high contribution of elasmobranchs to its diet. The sharpnose sevengill shark *Heptranchias perlo* is a less studied species that is considered to be a top predator within the marine communities it inhabits (Frentzel-Beyme & Köster 2002).

*Notorynchus cepedianus* and *Heptranchias perlo* have bladelike teeth on the upper jaw and comb-shaped teeth on the lower jaw, as well as comparable body shapes, although *N. cepedianus* attains a larger body size (3 m TL). These shark species have little overlap in spatial distribution. *N. cepedianus* is commonly found in temperate waters no deeper than 200 m, although larger individuals can range into deeper waters offshore (Bass et al. 1975, Compagno 1984, Last & Stevens 1994). *H. perlo* is commonly found in tropical and temperate depths between 27 and 720 m, occasionally down to 1000 m, (Bass et al. 1975, Compagno 1984, Last & Stevens 1994, Frentzel-Beyme & Köster 2002). *N. cepedianus* and *H. perlo* are widely distributed around the world (Last & Stevens 1994), but their feeding ecologies are only known for specific areas. Studies in California, USA (Ebert 1986, 1989), southern Africa (Ebert 1991a) and north Patagonia, Argentina (Lucifora et al. 2005), showed that *N. cepedianus* preys on chondrichthyans, teleosts, marine mammals, molluscs, lampreys and decapod crustaceans, shifting from a teleost-based to a chondrichthyan-based diet with ontogeny (Ebert 2002). At the Great Meteor seamount, eastern Atlantic, *H. perlo* preys mainly on teleosts and cephalopods, and to a lesser extent on chondrichthyans (Frentzel-Beyme & Köster 2002), whereas, off the coast of Tunisia, crustaceans are the second-most consumed prey after teleosts (Capapé 1980). For Australia, there is no information on the feeding ecology of any sevengill shark species and, therefore, no knowledge on the ecological role of these predators or on their interactions with other species. In south-eastern Australia, *N. cepedianus* is the only high-order predatory shark to exhibit an increase in abundance from the 1970s (Walker et al. 2005). As for other deepwater systems, *H. perlo* is likely to be a top predator of the Australian continental slope. It is therefore essential to quantify the feeding ecology of these species to understand their potential regulatory effects across the south-eastern Australia ecosystems.

Australia is currently embracing an ecosystem-based approach to the management of marine resources. For the implementation of such an approach, it is essential to quantify the feeding ecology of marine organisms, as this information is used as a proxy to their trophic interactions in ecosystem models. The feeding ecology information of high-order predators is particularly scarce. Therefore, there is a current need to continue improving our understanding of the feed-

ing ecology of this trophic group, particularly of the feeding ecology of *Notorynchus cepedianus* and *Heptranchias perlo* in Australian waters. Hence, the specific aims of this study were to: (1) determine the feeding periodicity and prey handling strategies of these shark species, (2) quantify their dietary composition and (3) identify their diet breadth and diet specialisation strategies.

## MATERIALS AND METHODS

**Sampling.** Specimens were collected from the bycatch of the Australian Southern and Eastern Scalefish and Shark Fishery. Individuals of *Notorynchus cepedianus* were collected opportunistically between 30 and 146 m depth from shark gillnet and trawl vessels operating in waters of South Australia and Victoria, Australia, on a monthly basis between 2002 and 2004. Individuals of *Heptranchias perlo* were collected opportunistically between 200 and 476 m depth from trawl vessels operating in Victoria, between February and May 2003. Each specimen was sexed and measured (total length [TL]  $\pm$  1 mm).

**Laboratory processing.** Feeding ecology was determined from prey identification and analysis of stomach contents. The stomach of each shark was removed and stored frozen, and the contents were identified in the laboratory to the lowest taxon practical.

**Overall diet.** Diet was assessed by species and size class, based on known ontogenetic shifts in the diet of *Notorynchus cepedianus* in California, southern Africa (Ebert 2002) and north Patagonia (Lucifora et al. 2005), and the sizes at maturation of the 2 species (Ebert 1989, Frentzel-Beyme & Köster 2002, Lucifora et al. 2005). The following size classes were considered for *Heptranchias perlo*, small ( $\leq$ 900 mm TL) and large (901 to 1400 mm TL), and for *N. cepedianus*, small ( $\leq$ 900 mm TL), medium (901 to 1700 mm TL) and large ( $>$ 1700 mm TL).

*Notorynchus cepedianus* can be attracted to gillnets to feed on entangled prey (author's pers. obs.); hence, the degree of digestion of each prey item was recorded as fresh or digested to determine the degree of net-feeding (Bethea et al. 2004). Fresh prey had no sign of digestion. Stomachs containing fresh prey items normally caught by gillnets were excluded from further analyses. Likewise, *Heptranchias perlo* may occasionally feed while caught in the trawl nets (author's pers. obs.), so stomachs containing fresh prey items normally caught by this gear were also excluded from further analyses.

**Prey diversity.** Cumulative prey diversity curves were used to determine the minimum number of stomachs required for a precise description of dietary com-

position (Ferry & Cailliet 1996). Items such as sponges, hydroids and algae were considered incidental, and were excluded from the analysis. The cumulative number of randomly pooled stomachs was plotted against the cumulative diversity of stomach contents. Diversity was calculated using the pooled quadrat method based on the Brillouin index of diversity (HZ; Pielou 1966). To ensure that curves reached an asymptotic value, 100 random orders of stomachs (curves) were calculated and the mean ( $\pm$ SD) was plotted. Diversity curves were considered asymptotic if at least 2 previous values to the total sample diversity were in the range of the asymptotic diversity  $\pm$  0.05 value (Koen Alonso et al. 2002). Diversity curves were calculated for each species and size combination.

**Feeding periodicity and prey handling.** Stomach fullness (SF), and the number and body parts of prey (PBP) found in each stomach were recorded to determine the feeding pattern for each species and size combination. SF was recorded using a quarterly scale (1: 1–25% full; 2: 26–50% full; 3: 51–75% full; 4: 76–100% full; Braccini et al. 2005). PBPs were classified as whole prey, head only and body only. Log-likelihood ratios (Zar 1999) were used to test for differences in the distribution of SF and PBPs of each species/size group. The PBP analysis was done for each of the following taxonomic groups: cephalopods, chondrichthyans, teleosts and fur seals (large *Notorynchus cepedianus* only).

**Prey importance.** For each species and size combination, prey item importance was evaluated using percentage mass (%M), percentage number (%N), percentage frequency of occurrence (%FO) and percentage index of relative importance (%IRI; Pinkas et al. 1971, Cortés 1997). These diet descriptors only provide point estimates of prey importance with no measure of uncertainty around its estimation (Tirasin & Jørgensen 1999). Hence, bootstrap methods (1000 replicates; Haddon 2001) were used to estimate 95% CIs (2.5th and 97.5th percentiles) around estimates of the dietary parameters. From the original data matrix, random samples of the observations (i.e. each individual stomach) with replacement were generated to obtain the probability distribution of prey importance parameters (Braccini et al. 2005).

**Intraspecific diet comparisons.** The effect of the factor size was tested using %IRI data for the main prey items (mean %IRI > 5%). Unidentified teleosts, unidentified molluscs and other unidentified materials were excluded from the comparative analysis as they may contain remnants of >1 dietary category (White et al. 2004). Non-parametric multidimensional scaling (nMDS) on Bray-Curtis similarity measures (Clarke 1993) were used to visualize patterns of variation in dietary composition. A 1-way non-parametric

permutation multivariate analysis of variance (PERMANOVA) using Bray-Curtis distances (Anderson 2001) was used to test for the effect of the factor size class (small or large for *Heptranchias perlo*; small, medium, or large for *Notorynchus cepedianus*) on dietary composition. Size was treated as a fixed factor. Equal sample sizes (n = 100) were used. Samples were randomly selected from the 1000 bootstrapped values of %IRI for each species/size group.

**Diet breadth.** Levin's index  $\beta$  (Krebs 1989) was used to determine the diet breadth of the species/size groups studied. The index was calculated as:

$$\beta = \frac{1}{\sum P_i^2}$$

where  $P_i$  is the proportion (derived from %IRI) of individuals using the  $i$ th resource (prey item). The values ranged from 1 (highly specialised diet) to the total number of prey categories (the broadest diet).

Levin's index was calculated 1000 times using the bootstrapped %IRI values to estimate 95% CIs around a mean diet breadth estimate.

**Diet specialisation.** For the different species/size groups, diet specialisation was identified by plotting the prey-specific abundance ( $P_i$ ) of the main prey groups (crustaceans, cephalopods, chondrichthyans and teleosts) against a point estimate of %FO (Amundsen et al. 1996). Prey-specific abundance refers to the relative abundance among prey species found in the stomachs. This was calculated as the number of prey  $i$  divided by the total number of prey in the stomachs that contained prey  $i$ , expressed as a percentage. In Amundsen's method, any prey located close to 100%  $P_i$  and 100% FO represents population specialisation.

## RESULTS

### Overall diet

The stomach contents and fullness of 116 *Heptranchias perlo* and 181 *Notorynchus cepedianus* were examined. In all, there were 67 small (485 to 900 mm TL) and 49 large (901 to 1365 mm TL) *H. perlo*; and 39 small (550 to 895 mm TL), 129 medium (901 to 1520 mm TL) and 13 large (1740 to 2740 mm TL) *N. cepedianus*.

### Prey diversity

Cumulative prey diversity reached a stable level at ~80 and 100 stomachs for the overall diet of *Heptranchias perlo* and *Notorynchus cepedianus* (Fig. 1). *N. cepedianus* had a more diverse diet than did *H. perlo*, with prey diversity of medium *N. cepedianus*

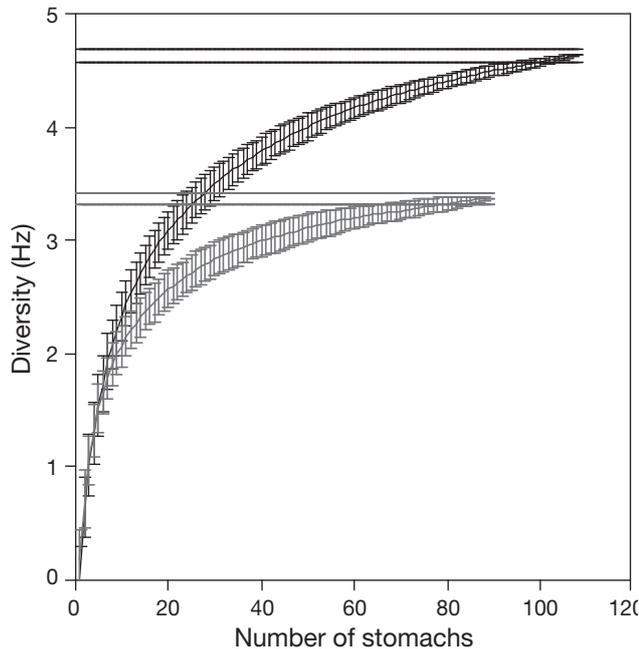


Fig. 1. *Heptranchias perlo* and *Notorynchus cepedianus*. Cumulative diversity of prey items for the overall diet of *H. perlo* (grey) and *N. cepedianus* (black). Straight lines: range of asymptotic diversity  $\pm 0.05$ . Data were mean  $\pm$  SD

being higher than that for the other groups. For small and large *H. perlo* and medium *N. cepedianus*, cumulative prey diversity curves reached stable levels at 50, 30 and 65 stomachs, respectively (Fig. 2). For small and large *N. cepedianus*, however, the curves did not reach an asymptote (Fig. 2), indicating that more stomachs are needed for a more precise description of their diet.

### Feeding periodicity and prey handling

Of the stomachs of *Heptranchias perlo* and *Notorynchus cepedianus* examined, 88 (76%) and 110 (61%), respectively, contained prey. Small (80%) and large (71%) *H. perlo* showed higher percentages of stomachs with prey than small (66%) and medium

Table 1. *Heptranchias perlo*, *Notorynchus cepedianus*. Log-likelihood ratios testing for differences in the distribution of stomach fullness values (df = 3). 1: 1–25% full; 2: 26–50% full; 3: 51–75% full; 4: 76–100% full

Group	Stomach fullness (%)				G	p
	1	2	3	4		
Small <i>H. perlo</i>	29	31	22	18	2.4	0.49
Large <i>H. perlo</i>	14	43	26	17	6.6	0.09
Small <i>N. cepedianus</i>	44	16	12	28	6.1	0.11
Medium <i>N. cepedianus</i>	31	26	14	29	5.2	0.16
Large <i>N. cepedianus</i>	31	15	15	38	2.1	0.55

(55%) *N. cepedianus*. Large *N. cepedianus* always had prey in their stomachs. For stomachs with prey, the distribution of SF was relatively even in each category. There were no significant differences among the frequency of individuals in each SF category for each species/size group (Table 1). A consistent pattern of number of prey per stomach was found across the species/size groups. Stomachs contained mostly 1 or 2 items (Fig. 3), but up to 11 small teleosts were found in 1 stomach of a small *H. perlo*. PBPs found in stomachs of the different shark groups varied with prey type. Cephalopods were mostly found whole (Table 2). Teleosts were mostly found whole in stomachs of small and large *H. perlo* (Table 2). Heads and body portions found in *H. perlo* stomachs corresponded to large-sized predatory teleosts of the family Trichiuridae and Gempylidae. Teleosts were mostly found as body portions in the stomachs of small, medium and large *N. cepedianus* (Table 2). Teleosts found whole corresponded to small-sized species (<0.3 m TL). Chondrichthyans were mostly found whole or as body portions in stomachs of small *N. cepedianus* (Table 2) and mostly as body portions in stomachs of medium and large individuals (Table 2). Chondrichthyans found whole corresponded to small-sized species, whereas those found as body portions corresponded to medium-sized species (<1 m TL). All fur seals were found as body portions.

### Prey importance

The stomachs of small *Heptranchias perlo* contained 23 taxonomic levels of prey items: 2 crustaceans, 5 cephalopods, 1 chondrichthyan and 15 teleosts (Table A1 available in MEPS Electronic Supplementary Material at: [www.int-res.com/articles/suppl/m371p273\\_app.pdf](http://www.int-res.com/articles/suppl/m371p273_app.pdf)). Teleosts were the most important prey group. *Lepidorhynchus denticulatus* was the dominant prey item, contributing the highest values of %M (26.65%), %FO (23.48%) and %IRI (37.63%), and the second highest value of %N (15.96%). The second-most dominant prey by mass (12.52%), occurrence (19.97%) and %IRI (30.65%) was *Apogonops anomalus*, which showed the highest %N (28.28%). Teleosts from the families Trichiuridae and Gempylidae and ommastrephid squids (mainly *Nototodarus gouldi*) were also important. Decapod crustaceans were not important as they contributed <1% of %IRI.

The stomachs of large *Heptranchias perlo* contained 17 taxonomic levels of prey items: 1 crustacean, 3 cephalopods and 13 teleosts (Table A1). Teleosts were the most important prey group. *Lepidorhynchus denticulatus* was the dominant prey item, contributing the highest values of %N (28.01%), %FO (40.15%) and

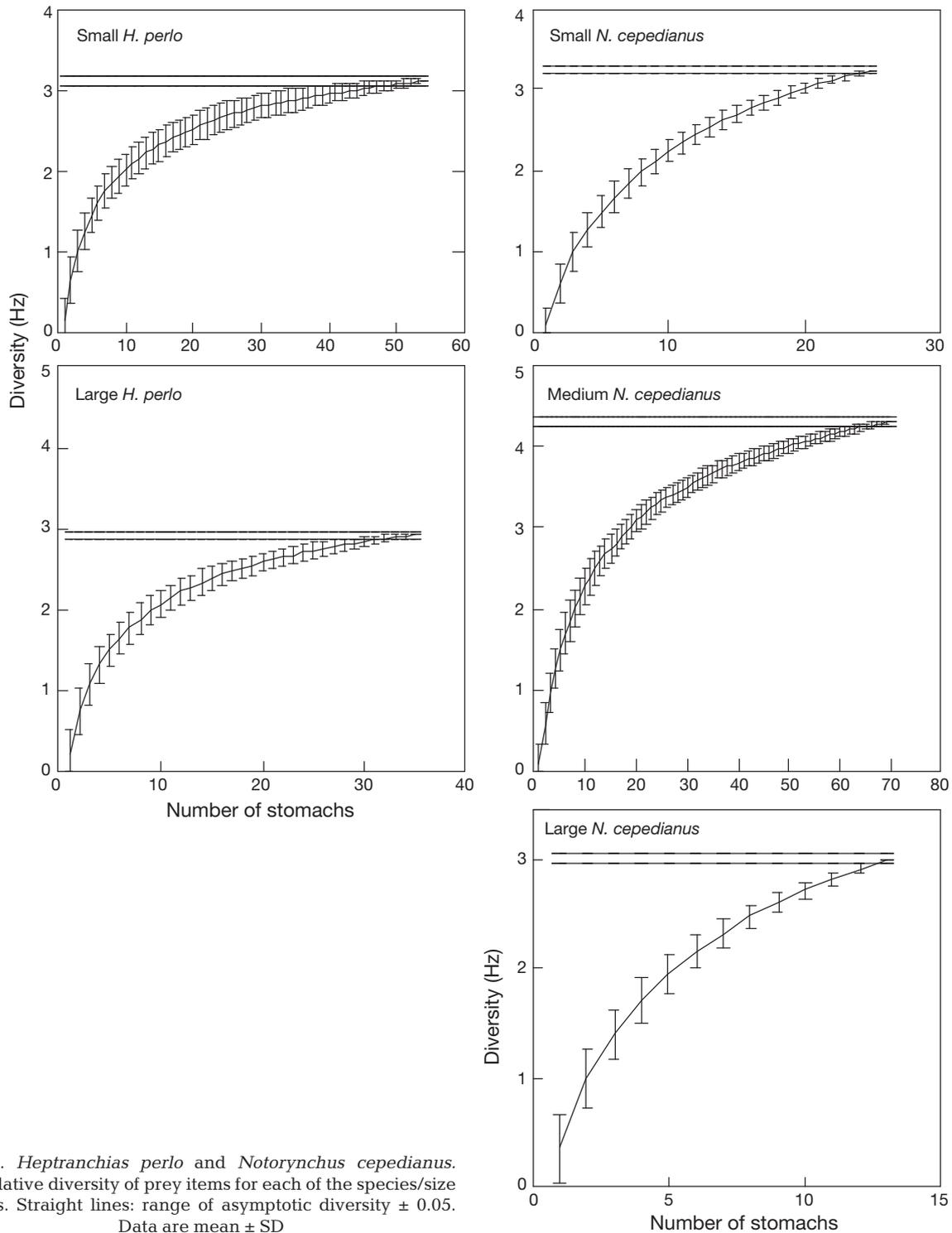


Fig. 2. *Heptranchias perlo* and *Notorynchus cepedianus*. Cumulative diversity of prey items for each of the species/size groups. Straight lines: range of asymptotic diversity  $\pm$  0.05. Data are mean  $\pm$  SD

%IRI (49.44%), and the third highest value of %M (12.49%). Teleosts from the families Gempylidae and Trichiuridae were the second- and third-most dominant prey by %IRI (15.45 and 12.60%, respectively), with Trichiuridae showing the highest %M (18.09%). Other teleost species such as *Paraulopus nigripinnis*

and *Apogonops anomalus* were also important. Cephalopods and decapod crustaceans were not important as they contributed <1% of %IRI.

The stomachs of small *Notorynchus cepedianus* contained 20 taxonomic levels of prey items: 1 crustacean, 4 cephalopods, 8 chondrichthyans, 5 teleosts, 1 fur

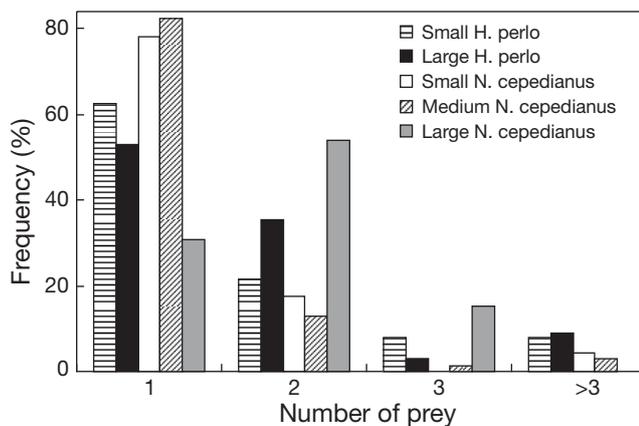


Fig. 3. *Heptranchias perlo* and *Notorynchus cepedianus*. Frequency of different numbers of prey found in stomachs of *H. perlo* and *N. cepedianus*

seal and unidentified animal material (Table A2 available in MEPS Electronic Supplementary Material at: [www.int-res.com/articles/suppl/m371p273\\_app.pdf](http://www.int-res.com/articles/suppl/m371p273_app.pdf)). Unidentified teleosts were the dominant prey item, contributing the highest values of %N (12.56%), %FO (15.99%) and %IRI (23.19%). The second-most dominant prey by number (8.96%) and %IRI (13.35%) was *Mustelus antarcticus*, which showed the highest %M (15.33%). *Myliobatis australis* and ommastrephid squids were the third- and fourth-most dominant prey by %IRI (9.75 and 8.15%, respectively). Other important prey included *Urolophus paucimaculatus* and *U. cruciatus*. Decapod crustaceans and fur seals were less important.

The stomachs of medium *Notorynchus cepedianus* contained 43 taxonomic levels of prey items: 2 crustacean, 6 cephalopods, 14 chondrichthyans, 19 teleosts and 2 fur seals (Table A2). *Myliobatis australis* was the dominant prey item by %M (14.24%) and %IRI (17.17%). The second-most dominant prey by mass (14.21%) and %IRI (13.31%) was *Callorhynchus milii*. Other important prey included unidentified teleosts, ommastrephid squids and unidentified chondrichthyans. Decapod crustaceans and fur seals were less important.

The stomachs of large *Notorynchus cepedianus* contained 19 taxonomic levels of prey items: 1 cephalopod, 10 chondrichthyans, 6 teleosts and 2 fur seals (Table A2). *Mustelus antarcticus* was by far the dominant prey item by all dietary metrics. The second-most dominant prey by number (8.71%), occurrence (15.37%) and %IRI (8.99%) were unidentified teleosts. Other important prey included conspecifics and fur seals (Otariidae). Cephalopods were not important.

There was variability around the estimation of overall mean %IRI when the mean values obtained from bootstrapping were compared with those obtained from point estimates of overall diet (Tables A1 & A2). For important prey, variability ranged up to 4 and 2% for small and large *Heptranchias perlo*, respectively, and to 15, 4 and 17% for small, medium and large *Notorynchus cepedianus*, respectively. Variability was higher for less important prey and ranged up to 16 and 14% for small and large *H. perlo*, respectively, and to 19, 10 and 30% for small, medium and large *N. cepedianus*, respectively.

**Intraspecific diet comparisons**

There was a significant effect of the factor size in the dietary composition of *Heptranchias perlo* (Table 3) and *Notorynchus cepedianus* (Table 3). Small and large *H. perlo* consumed similar prey items, but in different proportions (Table A1), and hence had different diets. This was reflected in their clustering pattern, where small and large *H. perlo* formed 2 separate clus-

Table 3. *Heptranchias perlo* and *Notorynchus cepedianus*. PERMANOVA testing for the effects of the factor size class on dietary composition

Factor	df	F	p
<b><i>H. perlo</i> (n = 100)</b>			
Size	1	260.69	0.0002
Residual	198		
<b><i>N. cepedianus</i> (n = 100)</b>			
Size	2	262.72	0.0002
Residual	297		

Table 2. *Heptranchias perlo* and *Notorynchus cepedianus*. Log-likelihood ratios testing for differences in the distribution of prey body parts found in stomachs (df = 2). ND: no data

Group	Cephalopods (%)			G	p	Teleosts (%)			G	p	Chondrichthyans (%)			G	p
	Whole	Head	Body			Whole	Head	Body			Whole	Head	Body		
Small <i>H. perlo</i>	75	12.5	12.5	18.1	<0.05	67	10	23	403.8	<0.05	ND	ND	ND	ND	ND
Large <i>H. perlo</i>	75	0	25	6.1	<0.05	65	11	24	218.4	<0.05	ND	ND	ND	ND	ND
Small <i>N. cepedianus</i>	75	0	25	6.1	<0.05	25	0	75	20.9	<0.05	43	7	50	39.4	<0.05
Medium <i>N. cepedianus</i>	77	8	15	40.5	<0.05	37	10	53	118.1	<0.05	21	8	71	175.9	<0.05
Large <i>N. cepedianus</i>	ND	ND	ND	ND	ND	25	12	63	15.5	<0.05	33	9	58	31.1	<0.05

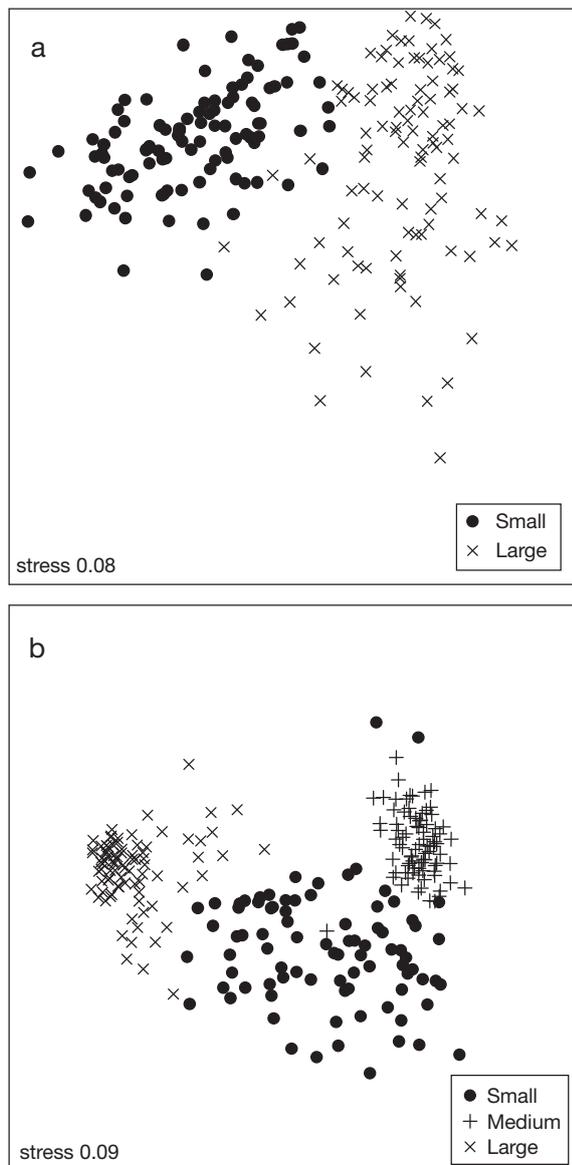


Fig. 4. *Heptranchias perlo* and *Notorynchus cepedianus*. Non-parametric multidimensional scaling ordination of the stomach contents of (a) small and large *H. perlo* and (b) small, medium and large *N. cepedianus*

ters (Fig. 4a). Samples of small, medium and large *N. cepedianus* were also separated into 3 groups (Fig. 4b, pairwise comparisons). Overall, these size classes also preyed on similar items, but, as for *H. perlo*, they consumed them in different proportions (Table A2).

#### Diet breadth

Small and large *Heptranchias perlo* showed a narrow diet breadth and a similar distribution of breadth values (Fig. 5), averaging 3.70 (median: 3.65; 95% CI:

2.61 to 5.00) for small and 3.27 (3.22; 2.09 to 4.76) for large individuals, respectively. These distributions were different in comparison to the diet breadth distributions of small, medium and large *N. cepedianus*, which showed higher dispersion (Fig. 5). Diet breadth averaged 6.12 (5.99; 3.19 to 9.84) for small individuals, 9.24 (9.13; 5.36 to 14.15) for medium individuals and 3.00 (2.61; 1.45 to 6.52) for large individuals.

#### Diet specialisation

Small and large *Heptranchias perlo* showed a similar specialisation pattern (Fig. 6). For both shark groups, the population was specialised on teleost consumption, and only a few individuals specialised on crustaceans. *Notorynchus cepedianus* showed a different specialisation pattern (Fig. 6). Small individuals showed a high between-phenotype contribution (i.e. variation in resource use among individuals; Amundsen et al. 1996) to the diet breadth, with some individuals consuming chondrichthyans, some consuming teleosts, some consuming cephalopods and a few consuming crustaceans. Medium individuals had a similar pattern to small individuals, with a higher degree of specialisation on chondrichthyans and teleosts. Large individuals showed population specialisation on chondrichthyans, but this specialisation pattern was not as distinct as for *H. perlo* given the important contribution of teleosts to the diet of large *N. cepedianus*.

## DISCUSSION

#### Feeding periodicity and prey handling

A high percentage of *Notorynchus cepedianus* (39%) and to a lesser extent of *Heptranchias perlo* (24%) had empty stomachs. In addition, for stomachs with prey, both species showed similar distributions of SF values and a low number of prey per stomach. These findings are consistent with other feeding periodicity studies of sharks (e.g. Simpfendorfer et al. 2001, Braccini et al. 2005), supporting the hypothesis that sharks are intermittent feeders. For intermittent feeders, short periods of active feeding are followed by longer periods of reduced predatory activity (Wetherbee et al. 1990, Wetherbee & Cortés 2004). Predatory activity of intermittent feeders, however, can vary with body size. Given that specific metabolic rate decreases with increasing body size (Schmidt-Nielsen 1984), for a given species, smaller individuals would have higher energetic requirements and consumption rates. Hence, smaller individuals would feed more frequently and show a higher percentage of stomachs with prey (Lucifora et al. 2006). This size-

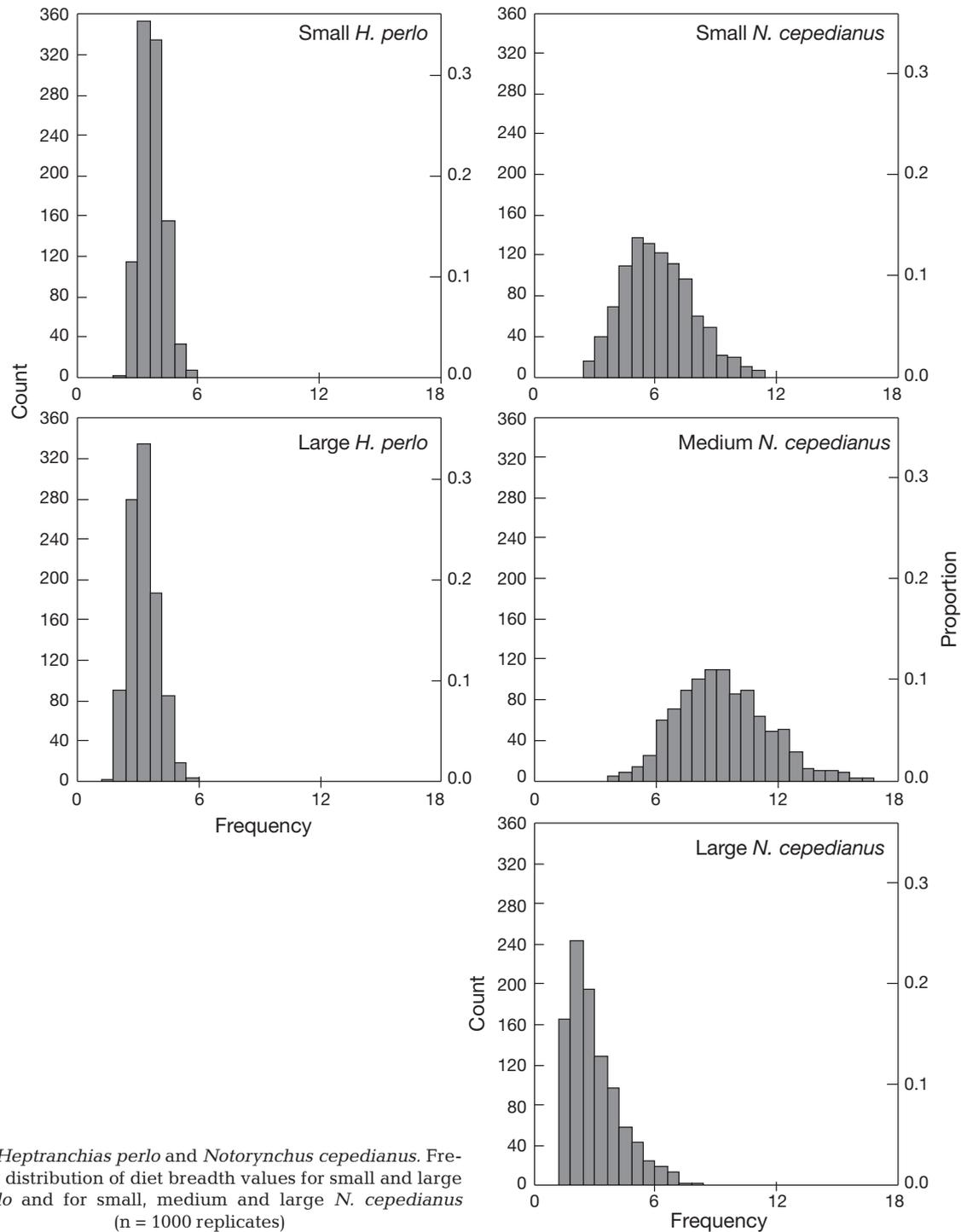


Fig. 5. *Heptranchias perlo* and *Notorynchus cepedianus*. Frequency distribution of diet breadth values for small and large *H. perlo* and for small, medium and large *N. cepedianus* (n = 1000 replicates)

related pattern has been reported for *N. cepedianus* in north Patagonia (Lucifora et al. 2005) and other shark species (e.g. Bethea et al. 2006, Lucifora et al. 2006). Our findings support this hypothesis as small individuals of *H. perlo* and *N. cepedianus* showed a higher percentage of stomachs containing prey than larger individuals. The occurrence of a high percentage of stomachs with prey

for large *N. cepedianus* is considered an artefact of the low sample size (n = 13).

Maximum prey size and prey type is commonly determined by predator gape size, with most piscivorous fish ingesting prey whole (Scharf et al. 1997). However, large predators such as great white *Carcharodon carcharias*, bull *Carcharhinus leucas* and tiger

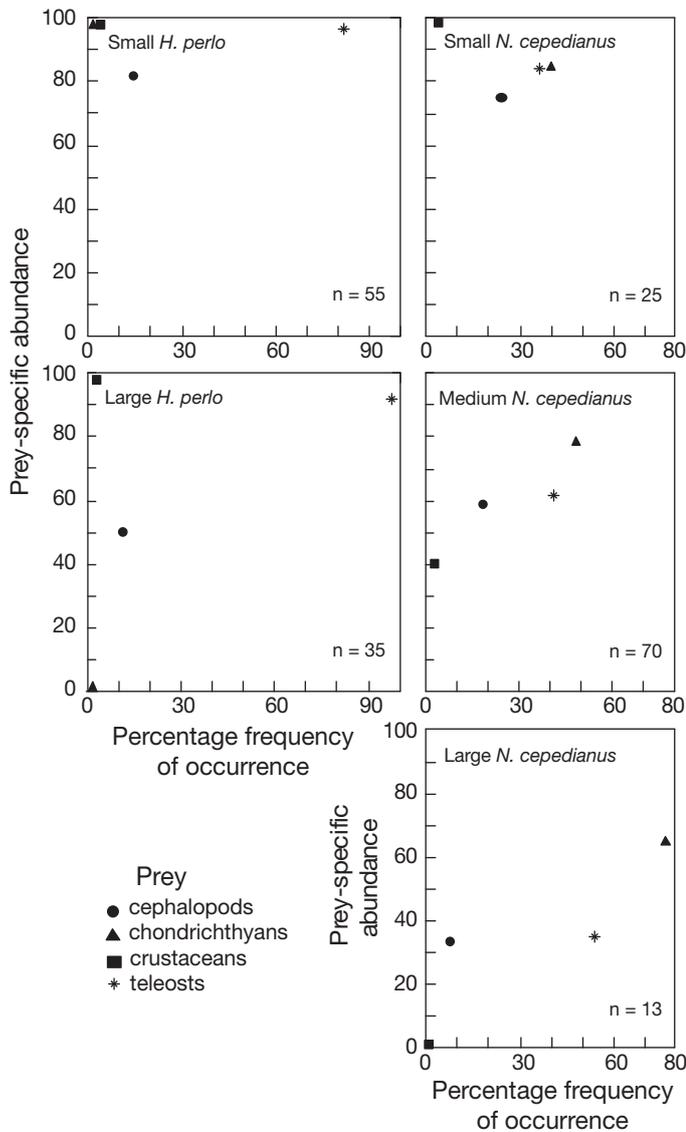


Fig. 6. *Heptranchias perlo* and *Notorynchus cepedianus*. Graphical representation of the diet specialisation of small and large *H. perlo* and of small, medium and large *N. cepedianus*. Prey-specific abundance plotted against percentage frequency of occurrence of the main prey categories given in the key

*Galeocerdo cuvier* sharks exhibit different prey handling strategies that allow them to evade gape limitations (Lucifora et al. 2006). In this way, these species can feed on large prey (marine mammals, sea turtles and chondrichthyans) by cutting pieces off their prey using their large serrated teeth (Frazzetta 1988, Lucifora et al. 2006). *Heptranchias perlo* and *Notorynchus cepedianus* have upper jaw teeth with hooked cusps and small lateral cusplets and, in the lower jaw, wide comb-shaped teeth, each with a main mesial cusp and several large distal cusplets (Last & Stevens 1994). The PBPs found in the stomachs of all sizes of both shark

species varied by prey type, suggesting that small, medium and large individuals use different strategies for handling different prey groups. For both shark species, cephalopods were consumed whole and teleosts were consumed whole when small (<0.3 m TL) or sectioned when larger. For *N. cepedianus*, fur seals were found as sectioned PBPs, and chondrichthyans found whole corresponded to small-sized species and were mostly found in stomachs of small *N. cepedianus*. For larger individuals, chondrichthyans were mostly found as sectioned PBPs and corresponded to medium-sized species (<1 m TL). These findings are consistent with the range of prey handling strategies displayed by *N. cepedianus*, which cut chondrichthyan and marine mammal prey in several pieces after attacking them, except when these prey are small and hence consumed whole (Ebert 1991b, Lucifora et al. 2005). *H. perlo* has the capability to dismember relatively large prey (Frentzel-Beyme & Köster 2002), suggesting that it also has a range of strategies for handling prey of different sizes. The evolved range of strategies for handling prey of different sizes would allow *N. cepedianus* and *H. perlo* to overcome gape size limitations and exploit a wider range of prey.

#### Prey importance and diet comparisons

*Heptranchias perlo* and *Notorynchus cepedianus* showed different degrees of variability around estimates of prey importance. For small and large *H. perlo* and medium *N. cepedianus*, variability was low given that the sample size was large enough to precisely describe their dietary composition. For small and large *N. cepedianus*, on the contrary, larger variability was found as sample sizes were not large enough for a precise description of diet. Large variability in dietary composition of sharks would result from the combination of small sample sizes and a high proportion of empty stomachs (Braccini et al. 2005) due to the opportunistic nature of many shark species (Wetherbee et al. 1990). In these cases, the use of bootstrapping methods is particularly appropriate for generating a measure of uncertainty around prey importance parameters. This, in turn, is mostly relevant for representing predator-prey interactions of sharks and other opportunistic marine predator in foodwebs of ecosystem models. Most of these models use %M data to represent interactions among species; however, when only point estimates of prey importance are used the presence of one very heavy but infrequent prey item can have an unrealistic contribution to diet composition, creating a bias in predator-prey interactions (Braccini et al. 2005). By bootstrapping the diet data matrix, the degree of uncertainty in diet composition can be determined and

then incorporated when representing the relationships among components of the modelled foodwebs.

*Heptranchias perlo* mostly consumed demersal-benthic and demersal-pelagic deepwater teleosts. Off Tunisia, deepwater teleosts were also the main prey item (Capapé 1980). At the Great Meteor seamount, however, *H. perlo* showed a more generalised diet, as demersal-benthic deepwater teleosts and cephalopods were almost equally important in its dietary composition (Frentzel-Beyme & Köster 2002). *Notorynchus cepedianus* consumed a wide range of demersal prey, including crustaceans, cephalopods, teleosts, chondrichthyans and marine mammals. These findings are consistent with the overall diet spectrum reported in California (Ebert 1986, 1989), southern Africa (Ebert 1991a) and north Patagonia (Lucifora et al. 2005). Although cetaceans were not found in the stomachs of *N. cepedianus*, these prey have been commonly observed by commercial shark fishers during the gutting, particularly in stomachs of larger individuals (Gary Robinson pers. comm.). For *N. cepedianus* elsewhere and other large top-predatory shark species, predation of cetaceans and other marine mammals also increases with body size (Lowe et al. 1996, Ebert 2002, Lucifora et al. 2005, Estrada et al. 2006).

*Heptranchias perlo* and *Notorynchus cepedianus* showed ontogenetic changes in dietary composition. These changes were mostly a result of differences in the proportional contribution of prey to the diet of the different size groups rather than differences in the type of prey consumed by small, medium and large individuals. Small *H. perlo* mostly consumed small-sized teleosts, whereas large *H. perlo* considerably increased the consumption of large predatory teleosts (Gempylidae and Trichiuridae). Teleosts were the main prey of small *N. cepedianus*, whereas individuals between 901 and 1520 mm TL preyed mostly on chondrichthyans. The consumption of fur seals also increased with body size for this species. The diet of *N. cepedianus* in southern Africa, California and Patagonia also changes ontogenetically in a similar fashion (Ebert 2002, Lucifora et al. 2005). The ontogenetic changes that became apparent in the diet of the 2 sevengill shark species indicate an increasing capacity to capture and handle larger prey with increasing body size. Gape size would not be a limitation for small *H. perlo* and *N. cepedianus* for handling prey given that they can consume relatively large prey by sectioning them into manageable pieces. Hence, the observed ontogenetic differences may be attributed to a better hunting capacity of larger sharks to subdue different prey, to differences in habitat use, or both. Differences in habitat use seem a less likely explanation, as individuals from all size classes were collected together. This suggests that small, medium and large individuals

would utilize similar habitats; however, information on the movement pattern and habitat use of this species is required to better understand the ontogenetic patterns in diet.

There are 2 caveats to the intraspecific comparative analysis performed. In this study, I described the dietary composition of large *Notorynchus cepedianus* based on only 13 individuals, assuming this was representative of the whole population off southern Australia. Furthermore, I compared samples collected within a very large region (south-eastern Australia), and seasons and sexes were pooled given the small sample sizes collected for some of the Season  $\times$  Sex combinations of *N. cepedianus* and the lack of samples of *Heptranchias perlo* for winter and spring. Hence, analyses were done without considering sex, season, or a smaller spatial resolution as potential sources of variation based on the assumption that size was the factor explaining most of the variation. Increased sampling of different sexes at different spatial and temporal scales would allow testing of my assumptions and hence would contribute to a better intraspecific comparative characterisation of the dietary composition of these 2 shark species.

#### Prey diversity, diet breadth and diet specialisation

*Notorynchus cepedianus* had a more diverse diet than *Heptranchias perlo*, so a larger number of stomachs was needed for the characterisation of its overall dietary composition. Also, the diversity curves of small and large *N. cepedianus* did not reach an asymptote, indicating that higher values of prey diversity may result from an increase in stomach sampling. Stomach contents of generalist elasmobranchs show higher prey diversity, and numerous samples are required for a precise description of dietary composition (e.g. Bethea et al. 2004, Braccini et al. 2005). Stomachs of more specialised elasmobranchs commonly show lower prey diversity values, with diversity curves reaching an asymptote at generally <50 stomachs (e.g. Carrassón et al. 1992, Braccini & Perez 2005). Therefore, the prey diversity values of *N. cepedianus* suggest this species has a more generalist feeding pattern than *H. perlo*.

*Heptranchias perlo* showed smaller diet breadth values and narrower diet breadth distributions than medium *Notorynchus cepedianus*, which showed higher and more dispersed values of diet breadth. Small and large *N. cepedianus* showed similar diet breadth values to small and large *H. perlo* due to the under-representation of their dietary composition (i.e. lack of asymptotic prey diversity curves). This diet under-representation is reflected in the higher dispersion of diet breadth values of small and large *N. cepe-*

*dianus*. These findings support the hypothesis of a specialised diet for *H. perlo* and a more generalised diet for *N. cepedianus*.

The contrasting diet specialisation patterns of *Heptranchias perlo* and *Notorynchus cepedianus* could be related to the diversity of prey these shark species encounter in their primary habitats. Due to the near-universal decrease in species diversity with increasing depth (e.g. Rex et al. 1997, Rex & Etter 1998, Smith & Brown 2002), a versatile predator like *N. cepedianus* would encounter a wider range of prey on the continental shelf than would *H. perlo*. Higher prey diversity would result in a broader range of prey options and, therefore, a more generalised diet should enable *N. cepedianus* to capitalise on this situation. Alternatively (or, most likely, in combination), slight morphological differences in body form and feeding structure, and differences in foraging behaviour, would also contribute to explaining the specialisation patterns of *H. perlo* and *N. cepedianus*.

Morphological specialisation of trophic mechanisms is commonly reported for aquatic animals as a strategy for resource partitioning (e.g. Ross 1986, Dejen et al. 2006). Despite sharing similar tooth structure and body morphology, the more slender body and narrower head with pointed snout of *Heptranchias perlo* would restrict its diet to mainly fish and cephalopod prey, constraining its access to certain food types (e.g. large chondrichthyans, marine mammals). On the contrary, *Notorynchus cepedianus* attains a larger body size and has a broader and more robust head, allowing it access to a wider range of food types. Observations on the predatory behaviour of *N. cepedianus* revealed several foraging strategies, such as social facilitation, stealth, burst of speed and ambush (Ebert 1991b), which might allow this species access to a range of different prey types. There are presently no reported observations on the foraging strategies of *H. perlo*. There is clearly no obvious and straightforward explanation for the foraging patterns of predators, particularly for large predators such as sharks. Ecological (e.g. prey diversity, abundance and availability), biological (e.g. body form, life history) and behavioural (e.g. foraging strategies) attributes are most likely interacting to establish the resulting foraging patterns. Which of these attributes, if any, contributes the most remains unclear and warrants further examination under a more rigorous hypothesis testing framework.

### Conclusions

Many shark species are long-range foragers, and many marine prey undergo vertical and open ocean-coastal migrations. Hence, marine predators with little

overlap in spatial distribution could exploit the same migratory prey species. Overall, *Notorynchus cepedianus* and *Heptranchias perlo* showed different dietary compositions, diet breadth and specialisation patterns. However, they also consumed prey that migrate from deep to coastal waters (ommatrephid squid and gempylid fish), probably due to morphological and behavioural similarities.

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