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VOLUMETRIC ANALYSIS OF SENSORY BRAIN AREAS INDICATES ONTOGENETIC SHIFTS IN THE RELATIVE IMPORTANCE OF SENSORY SYSTEMS IN ELASMOBRANCHS

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ABSTRACT. – Studies on the brains of teleost fishes have shown that the relative size of sensory brain areas reflects sensory specialisations and the relative importance of a given sensory system. Moreover, the relative size of these brain areas can change in relation to ontogenetic shifts in habitat and feeding ecology. However, although elasmobranchs (sharks, skates and rays) also exhibit ontogenetic shifts in habitat and diet, little is known about how their sensory systems and brains may adapt to these changes. In this paper, we compare the relative volumes of four sensory brain areas; the olfactory bulbs, optic tectum, anterior lateral line lobes and posterior lateral line lobes (that receive input from the olfactory epithelium, eye, electroreceptors and lateral line, respectively) in juveniles and adults of seven species of elasmobranch (six species of shark and one species of ray). The relative volume of each brain area was expressed as proportion of the total sensory brain, the combined volume of the four brain areas. Significant differences were found in the relative proportions of the sensory brain areas between juveniles and adults. In all species, the optic tectum was relatively larger in juveniles, whereas the size of the olfactory bulbs was relatively greater in adults. This paper provides the first evidence for shifts in the size of sensory brain areas in elasmobranchs and suggests that vision is relatively more important than olfaction in juvenile elasmobranchs and vice versa in adults.

KEY WORDS. – Brain, ecomorphology, ontogeny, ray, sensory system, shark.

INTRODUCTION

An animal's lifestyle is reflected in the organization of its central nervous system (Nieuwenhuys et al., 1998). This relationship has been particularly well-studied in teleost fishes, whose unparalleled diversity among the vertebrates has allowed scientists to study relationships between brain structure and sensory ecology. In particular, the relative size or complexity (i.e. number of sensory cells per unit area) of the peripheral sense organs has been found to scale positively with the input to the related brain centres. Both measures provide an accurate indication of the relative importance of a particular sensory system in any given species (reviewed by Kotrschal et al., 1998).

The life histories of many teleost fishes involve one or more shifts in habitat (Helfman et al., 1997) that are often associated with metamorphosis from larval to juvenile form. This often involves a vertical or horizontal habitat shift and changes in feeding behaviour and diet. These shifts can subject a fish to a range of new biotic and abiotic conditions during its life and are associated with distinct anatomical, physiological, behavioural and ecological adaptations. Such adaptations include the modification of the sensory systems, presumably to increase their efficiency in each new set of conditions (Higgs & Fuiman, 1996, 1998; Beaudet & Hawryshyn, 1999; Shand et al., 2000). Modifications to the peripheral sense organs are in turn reflected centrally as changes in the relative size or structure of sensory brain areas (Cadwallader, 1975;

Brandstätter & Kotrschal, 1989, 1990; Montgomery et al., 1997; Kotrschal et al., 1998; Wagner, 2003).

The elasmobranch fishes (the sharks, skates and rays) exhibit very different life history strategies to those of teleost fishes. They successfully utilise a variety of reproductive modes, all involving internal fertilisation and long gestation times. No larval stage exists and in contrast to teleosts, small numbers of highly-developed young are produced, which in many respects are small replicas of the adults. However, like teleosts, many elasmobranchs also undergo ontogenetic shifts in environment and diet. A number of species utilize nursery areas to increase the chances of survival for their offspring (Springer, 1967; Castro, 1993). These areas tend to be shallow, energy-rich coastal areas where food is abundant and the risk of predation from larger sharks is low. Ontogenetic dietary shifts have also been reported for a large number of sharks (Talent, 1976; Cortés & Gruber, 1990; Lowe et al., 1996; Huepel & Bennett, 1998) and rays (Abdel-Aziz, 1994; Gray et al., 1997; Platell et al., 1998). These dietary shifts are often reflected in changes in the type and size of prey and may be attributed to several factors: 1) larger animals can feed on larger prey; 2) different-sized animals may occupy different habitats and 3) larger animals may be more efficient hunters (due to acquired hunting skills) and more physically able to capture larger and/or faster prey (Lowe et al., 1996).

The analysis of the peripheral sense organs in elasmobranchs has provided some evidence that sensory systems in these fishes can also adapt to ontogenetic shifts. For example, in the lemon shark (*Negaprion brevirostris*), shifts in the chromophore (A_2-based porphyropsin to A_1-based rhodopsin) and the spectral sensitivity (from 522 to 501 nm) of the rod photoreceptor visual pigment have been correlated with ontogenetic shifts in habitat, as juveniles leave the green waters of their shallow lagoon nursery and venture into the deeper, bluer waters frequented by adults (Cohen et al., 1990). Sisneros et al. (1998) and Sisneros & Tricas (2002) have also demonstrated that the response properties of the electrosensory systems of both skates (*Raja eglanteria*) and stingrays (*Dasyatis sabina*) change ontogenetically, reflecting changes in the nature of the bioelectric stimuli these species encounter during their life histories. However, it is not known whether the relative importance of a sensory modality may shift during development in elasmobranchs as has been shown in teleost fishes. As in teleosts, discrete sensory brain areas can be identified in elasmobranchs (Northcutt, 1978; Smeets et al., 1983) and there is evidence that the relative size of these brain areas reflects the relative importance of their corresponding sensory modalities (Northcutt, 1978; Demski & Northcutt, 1996; Nieuwenhuys et al., 1998). Therefore, we investigated gross brain morphology in juveniles and adults of six species of shark and one species of ray. This analysis provides evidence of post-embryonic ontogenetic variation in the relative size of four sensory brain areas and in particular, the olfactory bulbs and the optic tectum, which may reflect ontogenetic shifts in the relative importance of these sensory systems.

MATERIALS AND METHODS

Animals. **–** The brains from juveniles and adults of six species of shark and one species of ray were analysed in this study (Table 1). The sharks consisted of five Carcharhiniformes [the grey reef shark, (*Carcharhinus amblyrhynchos*), the silky shark (*C. falciformis*), the bull shark, (*C. leucas*), the blacktip reef shark (*C. melanopterus*) and the scalloped hammerhead shark (*Sphyrna lewini*)] and one member of Lamniformes, the great white shark (*Carcharodon carcharias*). The one species of ray was represented by the blue-spotted maskray, (*Dasyatis kuhlii*) (Rajiformes). The larger great white shark analysed was classified as a 'sub-adult' since the animal was not considered sexually mature upon examination of its reproductive organs but it was within published size-at-maturity ranges for this species.

All specimens were collected and sacrificed according to the ethical guidelines of the National Health and Medical Research Council of Australia. For each specimen, the brain was removed and was immersion-fixed in either 10% formalin or 4% paraformaldehyde in 0.1 M phosphate buffer. In some cases, the animals were frozen and after partial defrosting, the brain was exposed and the head was further thawed while immersed in fixative. All brains were post-fixed for at least two months before further dissection and analysis. For species where data for more than one individual of a particular level of maturity was available, means were calculated and where three or more individuals were available, standard deviations were also calculated. For information on the number of specimens analysed for each species, see Table 1.

Brain analysis. **–** The meninges, blood vessels, choroid plexa and connective tissue were dissected away from each brain and the cranial and sensory nerves were transected at their base. Four sensory brain areas that receive primary projections from the olfactory epithelium (olfactory bulbs), the eye (optic tectum) and the octavolateralis senses, the electroreceptors [anterior lateral line lobes (ALLLs)] and the acousticolateralis system [posterior lateral line lobes (PLLLs)], were identified in each specimen (using the criteria of Northcutt, 1978 and Smeets et al., 1983). The use of optic tectum size as an indicator of the importance of vision has been questioned since the optic tectum is a multimodal centre and receives input from other modalities, as well as being the primary projection site for primary visual fibres originating from the retinal ganglion cells. (Davis & Northcutt, 1983; Bodznick, 1991). However, the strong correlations between eye-size, the number of axons in the optic nerve and optic tectum size in fishes (Brandstätter & Kotrschal, 1990; Guthrie, 1990; Nieuwenhuys et al., 1998) provide evidence for the optic tectum size being an accurate indicator of visual capabilities.

The sizes of the four sensory brain areas were assessed volumetrically with the assumption that they were perfect half-ellipsoids (Huber et al., 1997; Wagner, 2001a, 2001b). This is with the exception of the scalloped hammerhead shark and the blue-spotted maskray, where the olfactory bulbs were deemed to more closely resemble half-cylinders. Linear

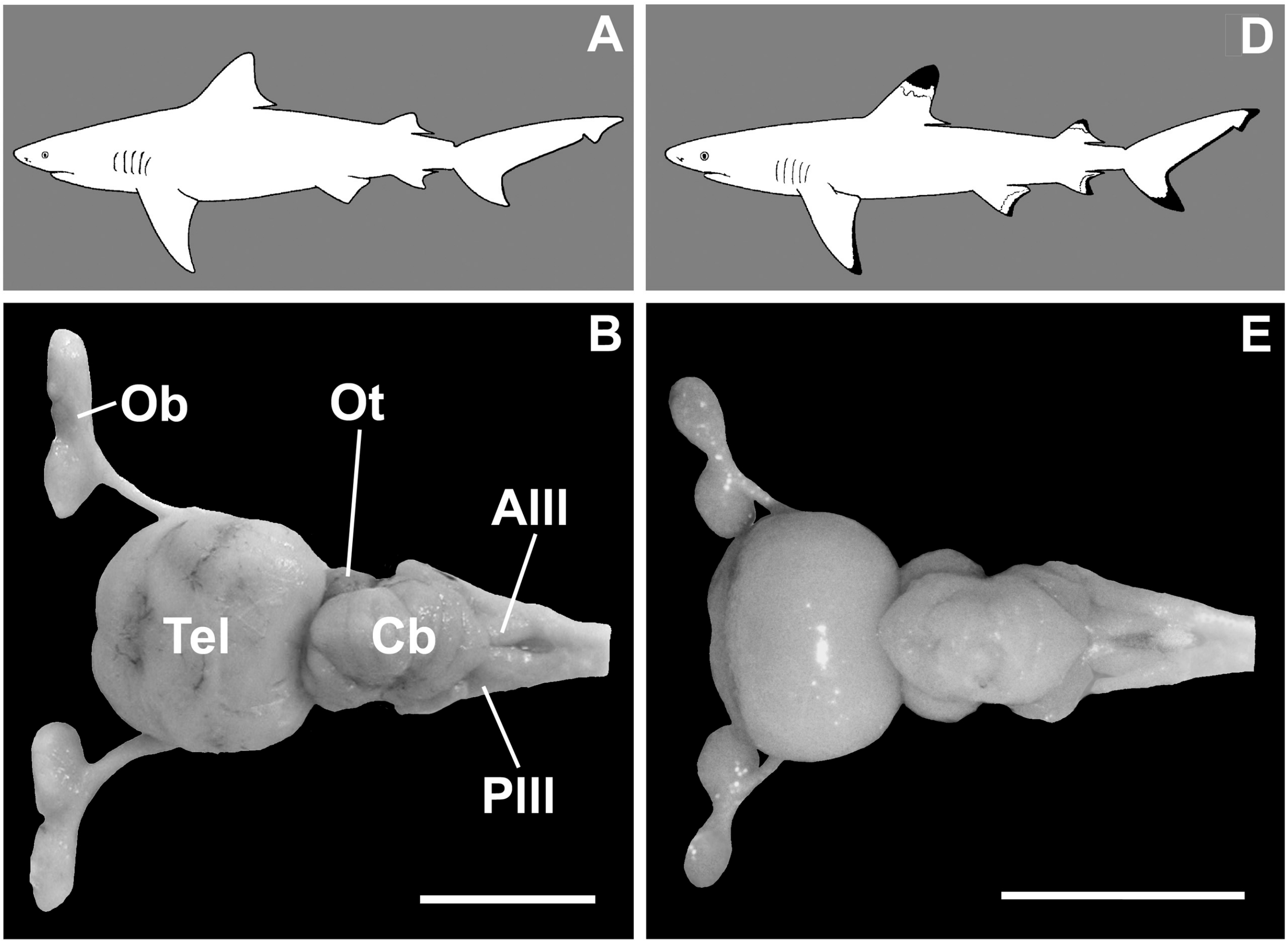

Fig. 1. Habitus diagram (top) and dorsal views of the juvenile (middle) and adult (bottom) brains from two species of shark. A to C) bull shark, *Carcharhinus leucas*, D to F) blacktip reef shark, *C. melanopterus*. Alll = anterior lateral line lobe; Cb = cerebellum; Ob = olfactory bulb; Ot = optic tectum; Plll = posterior lateral line lobe; Tel = telencephalon. Scale bars = 2 cm. Habitus diagrams adapted from Compagno et al. (2005).

Table 1. Maturity class, number of individuals examined and size (body length and body mass) of juveniles and adults of the seven species of elasmobranch studied. Note that for the sharks, body length is expressed as total length, whereas for the ray, disc width is shown. The size ranges are given for species or maturity classes in which more than one specimen were examined.

Order	Species	Maturity Class	n	Length (cm)	Body Mass (kg)
Carcharhiniformes	*Carcharhinus amblyrhynchos* (grey reef shark)	Juvenile	1	90	4.10
		Adult	4	138 - 169	16.50 - 31.00
	Carcharhinus falciformis (silky shark)	Juvenile	1	65.4	1.33
		Adult	1	264	97.96
	Carcharhinus leucas (bull shark)	Juvenile	4	76 - 87	3.10 - 4.00
		Adult	1	210	72.85
	Carcharhinus melanopterus (blacktip reef shark)	Juvenile	1	64.1	1.27
		Adult	1	112	7.65
	Sphyrna lewini (scalloped hammerhead shark)	Juvenile	5	55.0 - 59.7	0.55 - 0.75
		Adult	1	176	25.00
Lamniformes	*Carcharodon carcharias* (great white shark)	Juvenile	1	160	36.29
		Sub-adult	1	427.5	727.27
Rajiformes	*Dasyatis kuhlii* (blue-spotted maskray)	Juvenile	3	23 - 25	0.36 - 0.38
		Adult	3	31 - 47	1.03 - 2.96

measurements of the length (a), width (b) and depth (c) of each brain structure were taken using callipers (accurate to 0.1 mm). In the case of the half-cylinders, the length (l) and radius (r) were taken. The linear measurements were translated into volumetric measures (V) using the formulae $V = 1 / 12 (\pi \times a \times b \times c)$ and $V = (\pi \times r^2 \times l) / 2$ for the half-ellipsoids and the half-cylinders, respectively. No evidence of lateralisation was found and so the left and right volumes of paired structures were combined. Each of the four sensory brain areas was assessed in terms of its proportion to the total 'sensory brain', the combined volume of all four sensory brain areas (Wagner, 2001a, 2001b). No histological analysis was attempted on the brains, as in many cases the animals had been either dead for several hours prior to fixation, or had been frozen and thawed in fixative, rendering the tissue unsuitable for such analysis (Demski & Northcutt, 1996; Ito et al., 1999). All statistical analyses were performed on arcsine transformed data using GraphPad Prism 4.0 software (GraphPad Software, San Diego, CA, USA).

RESULTS

Gross brain morphology. – Photographs of representative juvenile and adult brains from the bull shark and the blacktip reef shark are shown in Figure 1. Qualitatively, the juvenile and adult brains appear very similar, with the major difference being the relative length of the olfactory peduncles, which connect the olfactory bulbs to the telencephalon. These structures were longer in the adults for all species and consequently, the olfactory bulbs are situated further from the telencephalon in adults compared to juveniles. The olfactory bulbs also appeared to be relatively larger in the adults of all species.

Sensory brain areas. – The volume of each of the four sensory brain areas (the olfactory bulbs, optic tectum, ALLLs and PLLLs) was assessed in juveniles and adults from seven species of elasmobranch. The volume of each brain area was expressed in terms of its proportion of the total 'sensory brain', which is the combined volume of all four sensory brain areas (Table 2 & Fig. 2). Although some interspecific

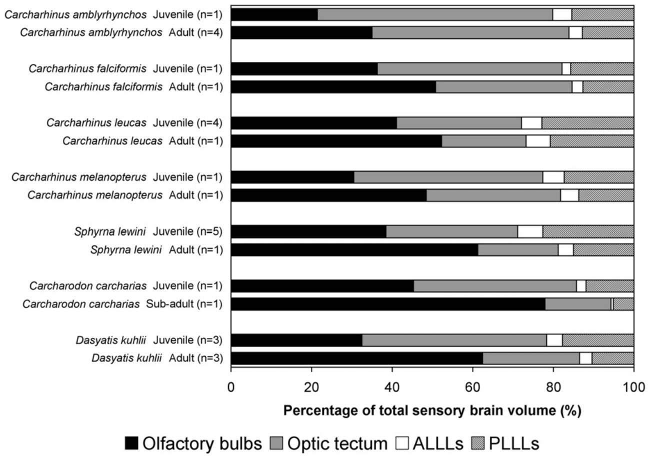

Fig. 2. The relative volumes of four sensory brain areas [the olfactory bulbs, optic tectum, anterior lateral line lobes (ALLLs) and posterior lateral line lobes (PLLLs)] as a proportion of the total sensory brain volume in juveniles and adults of seven species of elasmobranch.

Table 2. Absolute and relative volumes of four sensory brain areas (the olfactory bulbs, optic tectum, anterior lateral line lobes and posterior lateral line lobes) in juveniles and adults of the seven species of elasmobranch studied. Averages are given for species or maturity classes in which more than one specimen was available. Standard deviations are given in species with three or more specimens.

Species	Maturity Class	Olfactory bulbs		Optic tectum		Anterior lateral line lobes		Posterior lateral line lobes	
		Vol (mm^3)	Vol (%)	Vol (mm^3)	Vol (%)	Vol (mm^3)	Vol (%)	Vol (mm^3)	Vol (%)
Carcharhinus amblyrhynchos (grey reef shark)	Juvenile	203.10	21.4	553.37	58.4	45.13	4.8	146.17	15.4
	Adult	639.87 ± 63.35	35.5 ± 1.5	857.08 ± 125.83	47.4 ± 1.6	64.55 ± 13.56	3.6 ± 1.0	242.44 ± 34.24	13.5 ± 1.2
Carcharhinus falciformis (silky shark)	Juvenile	174.36	41.5	188.78	44.9	10.44	2.5	46.87	11.1
	Adult	1652.43	50.8	1102.64	33.9	88.77	2.7	411.89	12.6
Carcharhinus leucas (bull shark)	Juvenile	241.73 ± 42.08	39.2 ± 1.7	192.17 ± 23.58	31.3 ± 1.0	192.17 ± 9.83	5.4 ± 1.9	148.00 ± 27.90	24.0 ± 1.9
	Adult	1294.05	52.3	518.27	20.9	149.33	6.0	514.13	20.8
Carcharhinus melanopterus (blacktip reef shark)	Juvenile	97.54	30.5	150.27	47.0	16.80	5.2	55.52	17.3
	Adult	514.86	48.5	354.18	33.3	47.78	4.5	145.50	13.7
Sphyrna lewini (scalloped hammerhead shark)	Juvenile	300.33 ± 25.53	38.5 ± 4.4	258.62 ± 60.58	32.7 ± 4.8	49.33 ± 9.5	6.2 ± 0.7	177.57 ± 28.63	22.6 ± 2.8
	Adult	2814.10	61.3	914.19	19.9	174.52	3.8	689.91	15.0
Carcharodon carcharias (great white shark)	Juvenile	500.61	45.3	446.24	40.4	26.21	2.4	131.59	11.9
	Sub-adult	6596.67	80.9	1382.74	17.0	40.49	0.5	137.08	1.7
Dasyatis kuhlii (blue-spotted maskray)	Juvenile	128.87 ± 43.73	32.5 ± 1.0	184.06 ± 73.16	45.8 ± 1.2	15.01 ± 2.57	3.9 ± 0.9	71.46 ± 29.17	17.8 ± 0.6
	Adult	426.56 ± 81.42	62.4 ± 3.2	162.08 ± 9.25	24.1 ± 2.7	20.45 ± 2.33	3.1 ± 0.8	71.43 ± 19.81	10.4 ± 1.6

variation in the relative volume of the four sensory brain areas was noted, especially in the olfactory bulbs and the optic tectum, the relative proportions of the four sensory brain areas were generally similar across the seven species.

For example, in both juveniles and adults of all species, the olfactory bulbs or the optic tectum were the largest sensory brain areas, while the ALLLs were the smallest. However, the analysis also revealed differences in the relative volumes of the sensory brain areas between juvenile and adults in all seven species (Fig. 3). In particular, the optic tectum was relatively larger and the olfactory bulbs relatively smaller in juveniles, compared to adults. On average, the olfactory bulbs and the optic tectum accounted for 35.1% and 43.0% of the total sensory brain in juveniles respectively, compared to 55.4% and 28.1% in adults. Differences in the relative sizes of the ALLLs and PLLLs between juveniles and adults were also noted, but they were much smaller. In juveniles, the ALLLs made up 4.3% and the PLLLs 17.7% of the total sensory brain. In adults, the ALLLs and the PLLLs constituted 3.4% and 12.9%, respectively.

Due to the small sample sizes, no statistical analysis was performed on the variation in relative sensory brain area volume in each species. However, by combining the data for all juveniles and all adults, differences in the mean relative size of the sensory brain areas between juveniles and adults was analysed using a two-way ANOVA, using age and sensory brain area as the two variables. A significant interaction between age and sensory brain area ($F = 10.96$, Dfn = 3, Dfd = 48, $P < 0.0001$) indicated that age does not have the same effect on each of the four sensory brain areas, which in turn suggests that there is some ontogenetic variation. Bonferroni post-tests were then used to test for differences between juveniles and adults for each sensory brain area. Differences in relative olfactory bulb size ($t = 4.410$, $P < 0.001$) and relative optic tectum size ($t = 3.358$, $P < 0.01$) between juveniles and adults were significant, but that the differences in the relative size of the ALLLs ($t = 0.511$, $P > 0.05$) and the PLLLs ($t = 1.451$, $P > 0.05$) were not.

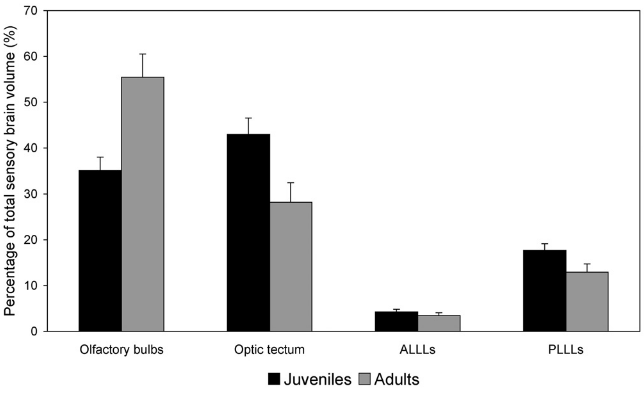

Fig. 3. The mean relative volume of four sensory brain areas [the olfactory bulbs, optic tectum, anterior lateral line lobes (ALLLs) and posterior lateral line lobes (PLLLs)] as a proportion of the total sensory brain volume, in juveniles (black) and adults (grey) of seven species of elasmobranch. In particular, note the differences in the mean size of the olfactory bulbs and the optic tectum between juveniles and adults. Error bars = standard errors.

DISCUSSION

The relative importance of four sensory modalities, olfaction, vision, electroreception and the lateral line was assessed in juvenile and adult elasmobranchs by comparing the relative volume of their corresponding sensory brain areas, the olfactory bulbs, optic tectum, anterior lateral line lobes (ALLLs) and posterior lateral line lobes (PLLLs), using a gross volumetric approach based on external brain morphology (Huber et al., 1997; Wagner, 2001a, 2001b). This technique has been widely used in recent years to assess sensory specialisations and the relative importance of various senses in a range of fishes such as cichlids (Huber et al., 1997), deep-sea fishes (Collin et al., 2000; Wagner 2001a, 2001b, 2002, 2003) and large pelagic sharks and teleosts (Lisney & Collin, 2006). It has been particularly useful in making reasonable inferences about the sensory ecology of little-known or largely-inaccessible species such as deep-sea fishes and sharks. For a critical discussion of this technique, see Wagner (2001a).

In all seven species investigated, the olfactory bulbs were relatively smaller and the optic tectum relatively larger in juveniles as compared to adults, while the relative volumes of the ALLLs and PLLLs were similar. This represents the first evidence of shifts in gross brain morphology in elasmobranchs. The variation in the relative size of the olfactory bulbs and the optic tectum in juvenile and adult elasmobranchs suggest that vision may be relatively more important than olfaction in juveniles and vice versa in adults. Juveniles also have relatively larger eyes than adults (Hueter, 1980; T. J. Lisney, unpublished), which supports the idea that vision may be more important in younger animals.

Ontogenetic changes in the relative size of various sensory brain areas have been found in a number of teleost fishes including New Zealand galaxids (Cadwallader, 1975), European cyprinids (Brandstätter & Kotrschal, 1989, 1990), the Antarctic silverfish, *Pleuragramma antarcticum* (Montgomery et al., 1997) and the deep-sea grenadier, *Corphaenoides armatus* (Wagner, 2003). In most species, these changes appear to be strongly related to ontogenetic shifts in both habitat and diet and feeding strategy. For example, in cyprinids, a relative reduction in the optic tectum during ontogeny from larva to adult coincides with an increase in the size of chemosensory brain areas associated with taste (the facial and vagal lobes). This reflects the shifts from a diurnal, planktonic larval phase towards crepuscular or nocturnal activity and a benthic lifestyle exhibited by many cyprinids (Brandstätter & Kotrschal, 1989, 1990), with the exception of the sabre carp (*Pelecus cultratus*), which develops into a predominantly surface-feeding adult with enlarged octavolateralis brain areas (Brandstätter & Kotrschal, 1990).

Many elasmobranchs use nursery areas (Springer, 1967;

Castro, 1993), where the young animals develop before gradually expanding their home ranges and moving into areas occupied by adults. They experience shifts in environmental conditions throughout their lives that may be related to the apparent changes in the relative importance of olfaction and vision. For example, nursery areas are usually shallow coastal areas where a greater range of wavelengths of light may be available in comparison to deeper waters occupied by adults (McFarland, 1991). Therefore, juveniles may take advantage of this and rely more heavily on visual cues.

In teleost fishes, there are particularly strong relationships between the development of sensory brain areas and feeding strategies (Kotrschal et al., 1998). Ontogenetic shifts in diet have also been reported for a number of elasmobranchs, including four of the species investigated in this study, i.e., the bull shark (Cliff & Dudley, 1991), the great white shark (Tricas & McCosker, 1984; Cliff et al., 1989; Long & Jones, 1996), the grey reef shark (Wetherbee et al., 1997) and the scalloped hammerhead shark (Clarke, 1971; Stevens & Lyle, 1989). This suggests that these animals may employ different foraging and prey detection strategies as juveniles and as adults, which may be related to shifts in the importance or role of different sensory systems. For example, both stomach content analysis (Tricas & McCosker, 1984) and data from pop-up satellite archival tags (Dewar et al., 2004) suggest that small juvenile great white sharks forage for small bottom-dwelling elasmobranchs and bony fish by day. Dewar et al. (2004) proposed that visual cues are important for foraging in these young animals as these sharks have a retina adapted for diurnal vision (Gruber & Cohen, 1985), although electroreception may also play a significant role (Tricas & McCosker, 1984). Larger (> 3 m total length) individuals are a major predator of marine mammals, especially pinnipeds (Le Boeuf et al., 1982; Tricas & McCosker, 1984; Long & Jones, 1996) and also scavengers of larger cetacean carcasses (Long & Jones, 1996). Pinniped colonies and cetacean carcasses create considerable odoriferous material (Strong et al., 1992; Long & Jones, 1996) and the resultant odour trails can be carried long distances by tides and currents. A keen olfactory sense may be of considerable importance for prey location in larger sharks. This may be especially so for cetacean carcasses, although the periodicity and locality of these food sources are unpredictable. This is because the energetic benefits of consuming whale blubber are so great (Carey et al., 1982) that it has been suggested that dead cetaceans may be a primary food source for great white sharks in certain areas or seasons (Carey et al., 1982; Klimley, 1994; Long & Jones, 1996).

Other factors that could drive a shift in the relative importance of sensory systems are predator avoidance and reproductive behaviour. As predator avoidance may be more important to young elasmobranchs in nursery grounds than prey abundance (Heupel & Hueter, 2002), the greater reliance on vision in juveniles could reflect the importance of this sense in predator, rather than prey detection. In contrast, olfaction may be more important in sexually mature adults as pheromones are thought to play an important role in reproductive behaviour (Bass, 1978; Johnson & Nelson, 1978).

The patterns of brain growth described here do not appear to be confined to one particular group of elasmobranchs and so an ontogenetic shift in the relative importance of vision and olfaction may actually be widespread among these fishes. However, it is difficult to do more than speculate on the factors behind this apparent shift in the absence of both detailed life-history data for the majority of species and information on the role of the senses in juvenile and adult elasmobranchs. Whatever the adaptive significance, the apparent shift in the relative importance of each of the sensory modalities with development and knowing what sensory cues are important to juvenile and adult elasmobranchs is important in understanding their ecology and may have management implications, such as the identification of critical habitats and susceptibility to different types of fishing gear.

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