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## An overview on the role of Hexanchiformes in marine ecosystems: biology, ecology and conservation status of a primitive order of modern sharks

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The large size, high trophic level and wide distribution of Hexanchiformes (cow and frilled sharks) should position this order as important apex predators in coastal and deep-water ecosystems. This review synthesizes available information on Hexanchiformes, including information not yet published, with the purpose of evaluating their conservation status and assessing their ecological roles in the dynamics of marine ecosystems. Comprising six species, this group has a wide global distribution, with members occurring from shallow coastal areas to depths of c. 2500 m. The limited information available on their reproductive biology suggests that they could be vulnerable to over-exploitation (e.g. small litter sizes for most species and suspected long gestation periods). Most of the fishing pressure exerted on Hexanchiformes is in the form of commercial by-catch or recreational fishing. Comprehensive stock and impact assessments are unavailable for most species in most regions due to limited information on life history and catch and abundance time series. When hexanchiform species have been commercially harvested, however, they have been unable to sustain targeted fisheries for long periods. The potentially high vulnerability to intense fishing pressure warrants a conservative exploitation of this order until thorough quantitative assessments are conducted. At least some species have been shown to be significant apex predators in the systems they inhabit. Should Hexanchiformes be removed from coastal and deep-water systems, the lack of sympatric shark species that share the same resources suggests no other species would be capable of fulfilling their apex predator role in the short term. This has potential ecosystem consequences such as meso-predator release or trophic cascades. This review proposes some hypotheses on the ecology of Hexanchiformes and their role in ecosystem dynamics, highlighting the areas where critical information is required to stimulate research directions.

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## INTRODUCTION

Apex predators can play key roles in retaining ecosystem health, diversity and stability (Estes *et al.*, 1998; Heithaus *et al.*, 2008; Baum & Worm, 2009). For the vast majority of apex predators, however, very little is known about their biology, ecology or behaviour. The paucity of such information makes it difficult to determine their role in ecosystems, hindering understanding of ecosystem structure and function. Limited information also makes the assessment of conservation priorities difficult for apex predators, their prey and the systems in which they are integral components.

Hexanchiformes (cow and frilled sharks) have the potential for playing important ecological roles as apex predators; however, this order has been little studied. Comprising six species, this order has a wide global distribution, with members occurring from shallow coastal areas to depths of *c.* 2500 m (Ebert, 1990, 2003), suggesting they are components of a number of ecosystems. The relatively large size of some Hexanchiformes and their high trophic levels rival those of other large shark species considered important apex predators such as tiger shark *Galeocerdo cuvier* (Péron & Lesueur 1822) and white shark *Carcharodon carcharias* (L. 1758) (Cortés, 1999). Unlike these species, considerably less information is available on hexanchiform species. The first detailed studies on the life history and biogeography of Hexanchiformes were conducted in the 1980s (Ebert, 1984, 1990). Since then, research has focused mostly on the bluntnose sixgill shark *Hexanchus griseus* (Bonnaterre 1788) and the broadnose sevengill shark *Notorynchus cepedianus* (Péron 1807). The work on *H. griseus* and *N. cepedianus* has contributed to a greater extent to understanding their roles in ecosystem dynamics. For the other hexanchiform species, however, there is very little information available on their basic biology, ecology or ecosystem roles. Therefore, the aim of this review is to synthesize the available biological and ecological information on hexanchiform species, present previously unpublished information and review the information in an ecosystem context to propose hypotheses on resource use, competition and the role of Hexanchiformes in ecosystem dynamics. The conservation concerns for each species are also discussed. The information and hypotheses highlight research priorities and hopefully stimulate much needed work on this shark group.

## CLASSIFICATIONS

Current taxonomy recognizes eight orders of sharks, with 34 families, 106 genera and *c.* 500 species (Ebert & Winton, 2010). On the basis of their numbers and relatively high species diversity, four shark orders are considered to be major orders, while four are minor orders due to their low diversity. The Hexanchiformes are a minor order, containing two families, four genera and six species (Appendix). These are usually considered to be one of the more primitive groups of modern day sharks, with the most distinctive features being that they possess six or seven paired gill openings, a single dorsal fin and an anal fin (Ebert & Winton, 2010) (Appendix). Besides the Hexanchiformes, only the sixgill sawshark *Pliotrema warreni* Regan 1906 (order Pristiophoriformes) has more than the customary five paired gill openings.

The frilled sharks (family Chlamydoselachidae) are a small group represented by a single genus and two species, the frilled shark *Chlamydoselachus anguineus* Garman 1884 and the African frilled shark *Chlamydoselachus africana* Ebert & Compagno

2009. Chlamydoselachidae are distinctive in having a slender, eel-like body, with prominent keels on the abdomen. The head has six paired gill openings, with the lower ends of the first gill extending across the throat. The snout is extremely short and truncated, the mouth being terminal. The teeth are alike in the upper and lower jaws, with three strong cusps and a pair of intermediate cusplets. The anal fin is larger than the dorsal fin and the caudal fin lacks a sub-terminal notch. These are moderately large sharks, with adults up to 196 cm in total length ( $L_T$ ) (Table I). The family and genus had long been considered to be monotypic with a single wide-ranging species, *C. anguineus*. Ebert (1990) in comparing Chlamydoselachidae from different geographical regions found, however, consistent differences in morphometrics, size at maturity, chondrocranial morphology, vertebrae counts, vertebrae morphology and calcification patterns, pectoral fin skeletal morphology and radial counts, and intestinal valve counts that lead to the separation of *C. africana* into a separate species (Ebert & Compagno, 2009).

The cow sharks (family Hexanchidae) are a little known but wide-ranging group of predominately deep-water sharks, and they include the genera *Hexanchus* (Rafinesque 1810), *Heptranchias* (Rafinesque 1810) and *Notorynchus* (Ayres 1855). The genus *Hexanchus* as currently recognized has two species, *H. griseus* and the bigeyed sixgill shark, *Hexanchus nakamurai* Teng 1962. The presence of six paired gill openings, a subterminal mouth, comb-like lower anterolateral teeth and a subterminal notch on the caudal fin can easily distinguish both species. *Hexanchus griseus* can be separated from its congener by a relatively short blunt snout, broad mouth, smaller eye diameter and a relatively smaller dorsal-caudal space (Bass *et al.*, 1975). *Hexanchus griseus* has six rows of large lower anterolateral teeth as compared to five for *H. nakamurai*. *Hexanchus griseus* is the largest member of the family Hexanchidae with a maximum confirmed  $L_T$  of 482 cm (Table I) (Bolivar, 1907), but with an unconfirmed report of 550 cm  $L_T$  (Ebert & Compagno, 2012), while *H. nakamurai* is a moderate-sized species that grows to 178 cm  $L_T$  (Table I) (Springer & Waller, 1969).

The two sevengill shark species are each in a monotypic genus, *Heptranchias* and *Notorynchus*. *Heptranchias perlo* (Bonnaterre 1788), commonly referred to as the perlon or sharpnose sevengill shark, can be distinguished by its narrow snout, seven paired gill openings and a mouth that is sub-terminal and longer than wide. This is the smallest hexanchoid, attaining a maximum  $L_T$  of 137 cm (Table I) (Garrick & Paul, 1971). The genus *Notorynchus* consists of a single species, *N. cepedianus*. The presence of seven paired gill openings, a broad head, large anal fin and spots covering the dorsal surface of the body easily distinguish *N. cepedianus*. The lower jaw has six rows of large anterolateral teeth as compared to five in *H. perlo*. *Notorynchus cepedianus* is a large species reaching 296 cm  $L_T$  (Table I) (Ebert, 1989). Several nominal species of *Notorynchus* have been described, including the type species for the genus, *Notorynchus maculatus* (synonym of *N. cepedianus*) Ayres 1855. More recent work has tended to synonymize this genus into a single wide-ranging species (Ebert, 1990; Ebert & Compagno, 2012).

## BIOGEOGRAPHY

Hexanchiformes are wide-ranging in all seas. In temperate zones, they occur in shallow and deep-water areas, whereas in the tropics, they only occur in deep water.

TABLE I. Summary of reproductive variables for Hexanchiformes

Species name	Sex	Maximum $L_T$ (cm)	$L_T$ at maturity (cm)	Maximum follicular diameter (mm)	Gonadal cycle	Gestation cycle	Litter size	Parturition	$L_T$ at birth (cm)	Mating	Source
<i>Chlamydoselachus africana</i>	F	117	n.d.	n.d.	n.d.	n.d.	At least 3	n.d.	n.d.	n.d.	Ebert & Compagno (2009)
<i>Chlamydoselachus anguineus</i>	M	99	92	n.d.	n.d.	1–2 years, at least 3–5 years	2–12	n.d.	40–60	Spring (off Japan)	Gudger (1940); Tanaka <i>et al.</i> (1990); Nakaya & Bass (1978)
<i>Hexanchus nakamurai</i>	F	178	142–178	$\geq 50$	Viable sperm all year round; no seasonal $I_G$	n.d.	13–26	n.d.	40–43	n.d.	Springer & Waller (1969); Compagno <i>et al.</i> (2005); Ebert (1990)
<i>Hexanchus griseus</i>	M	155	123–157	n.d.	n.d.	n.d.	22–108	Spring-summer	61–93	n.d.	Springer & Waller (1969); Ebert (1986a, b, 2002); Last & Stevens (2009)
<i>Heptranchias perlo</i>	F	348	315	n.d.	Viable sperm all year round; no seasonal $I_G$	n.d.	6–20	n.d.	n.d.	n.d.	Garrick & Paul (1971), Ebert (1990)
<i>Notorynchus cepedianus</i>	M	107	75–85	n.d.	n.d.	12 months	60–107	Spring-summer	45	n.d.	Ebert (1989, 1996); Lucifora <i>et al.</i> (2005)

F, female;  $I_G$ , gonado-somatic index;  $L_T$ , total length; M, male; n.d., no data.

All species are considered demersal and occur in a wide range of marine habitats, from intertidal, *e.g.* shallow bays and estuaries, to the continental shelves, continental and insular slopes and seamounts and submarine ridges to at least 2500 m.

*Chlamydoselachus anguineus* is found in the North Atlantic and the Pacific Oceans, including Australia and New Zealand; however, its distribution throughout this range is patchy (Last & Stevens, 2009). Thus far, *C. africana* has only been reported for the southern Africa region (Ebert & Compagno, 2009). *Chlamydoselachus* species are usually caught on or near the bottom in deep water between 120 and 1450 m depth, although they readily make excursions into the midwater column (Shiobara *et al.*, 1987; Ebert, 2003).

Both *Hexanchus* species occur along the outer shelves and upper slopes, but also occasionally come close inshore (Bass *et al.*, 1975; Ebert, 2003; Compagno *et al.*, 2005). *Hexanchus nakamurai* is patchily distributed in tropical and warm-temperate waters of the western Pacific, Atlantic and Indian Oceans, but appears to be absent from the entire eastern Pacific Ocean (Last & Stevens, 2009). Their depth range has been reported as 60–620 m (Compagno *et al.*, 1989; Last & Stevens, 2009), but with occasional excursions into midwater and inshore; one individual was caught in the protective shark nets along the KwaZulu-Natal coast at *c.* 10 m depth (Bass *et al.*, 1975). Regarding global distribution, *H. griseus* has one of the most extensive geographical ranges among vertebrates (Ebert, 2003; Compagno *et al.*, 2005; Last & Stevens, 2009), and has the deepest recorded depth range among the Hexanchiformes, at 2500 m (Ebert, 2003).

*Heptranchias perlo* is a moderately deep-water species occurring on or near the bottom of the continental and insular shelves and upper slopes between 27 and 720 m depth, but has been recorded both close inshore and down to 1000 m (Compagno *et al.*, 1989; Last & Stevens, 2009). It has a fairly wide distribution, being found in most oceans, but particularly in tropical and temperate parts of the Atlantic (including the Mediterranean Sea) and Indian Oceans, and also around Australia and Asia. The eastern North Pacific Ocean is a notable place where *H. perlo* is not present (Last & Stevens, 2009).

*Notorynchus cepedianus* is the only common nearshore coastal hexanchoid species and is widely distributed in temperate coastal regions around the world, with the exception of the North Atlantic Ocean. They occur from close inshore, in bays and estuaries, to at least 200 m on continental shelves (Ebert, 2003; Last & Stevens, 2009; Barnett *et al.*, 2010a; Ebert & Compagno, 2010; A. Barnett, unpubl. data).

## REPRODUCTIVE BIOLOGY

Knowledge on the reproductive biology of the Hexanchiformes is very limited, due to a combination of opportunistic sampling and incomplete information for all stages of the reproductive cycle. A summary of the reproductive information shows a significant paucity of data for the variables required to accurately explain the reproductive strategies of the species within the order (Table I).

Within the Chlamydoselachidae family, more extensive work has been done on *C. anguineus* (Gudger, 1940; Nakaya & Bass, 1978; Bass, 1979; Tanaka *et al.*, 1990; Compagno *et al.*, 2005), with some information on *C. africana* recently reported (Ebert & Compagno, 2009). Chlamydoselachids display a viviparous reproductive

mode (Tanaka *et al.*, 1990; Ebert & Compagno, 2009). Musick & Ellis (2005) categorized the entire Chlamydoselachidae family as lecithotrophic, in which embryos rely solely on yolk stores (yolk sac) derived from the maternal liver for the entire gestation period, displaying an overall dry mass loss from egg to embryos of *c.* 20% (Wourms, 1981; Hamlett *et al.*, 2005). Tanaka *et al.* (1990) suggested, however, a matrotrophic reproductive mode for *C. anguineus*. In this reproductive strategy, the maternal organism supplements yolk from other sources (uterine secretions, ova, siblings or placental transfers) for at least a portion of the gestation with a dry mass loss from egg to embryo >20% (Wourms, 1981; Hamlett *et al.*, 2005). In *C. anguineus*, fertilized eggs and embryos <6 cm  $L_T$  with an external yolk sac are enclosed in an egg capsule, while 8 cm  $L_T$  embryos, with no external yolk sac, are free inside the maternal uterus. Tanaka *et al.* (1990) proposed that egg capsules are sloughed off and discharged when embryos reach 6–8 cm  $L_T$ , and once free inside the maternal uterus, embryos are probably nourished by the mother as organic mass loss between ovarian eggs and fully developed embryos was *c.* 13%. The authors could not identify the source of embryo nutrition but taking into consideration that no ova, sibling or placental structures were distinguished within the uterus as a source of nutrients, it is likely that embryo nutrition comes from uterine secretions (histotrophy) (Wourms, 1981; Wourms *et al.*, 1988; Hamlett *et al.*, 2005).

*Chlamydoselachus africana* males reach sexual maturity at 92 cm  $L_T$ , while no information on size at maturity for *C. africana* females has been reported (Ebert & Compagno, 2009). Males have two functional testes capable of producing viable sperm throughout the year, reaching sexual maturity at smaller sizes than females (Tanaka *et al.*, 1990) (Table I). Females display two functional ovaries with only one distinct size-class of ovarian follicles developing at a time. They are able to ovulate from at least summer to autumn and maintain the embryos only in the right uterus (Tanaka *et al.*, 1990). Tanaka *et al.* (1990) found females with near-term embryos but not large follicles within the ovaries, concluding that the ovarian cycle does not run in parallel with the gestation cycle. On the basis of observations of embryo monthly growth in captive *C. anguineus*, Tanaka *et al.* (1990) suggested a 3.5 year gestation period. This hypothesis is based on small sample size ( $n = 4$ ) of fully encapsulated yolk sac embryos. Given that the rate at which the embryo develops depends on various factors, *e.g.* water temperature and maternal nutrient input (Wourms, 1977; Hamlett *et al.*, 2005), changes in growth rates of non-encapsulated embryos within the uterus are expected. This was previously reported for other shark species such as spiny dogfish *Squalus acanthias* L. 1758 (Jones & Ugland, 2001). In contrast, Gudger (1940) and Compagno *et al.* (2005) proposed a 1 to 2 year gestation period for *C. anguineus*. Similar litter sizes per reproductive cycle were reported for both *C. anguineus* and *C. africana* (Tanaka *et al.*, 1990; Ebert & Compagno, 2009) (Table I).

Within the Hexanchidae family, reproductive data on *H. nakamurai*, *H. griseus* and *H. perlo* are sourced from rather sporadic observations (Springer & Waller, 1969; Ebert, 1986*a, b*, 2002*a*), while *N. cepedianus* has been studied in more detail (Ebert, 1989, 1996; Lucifora *et al.*, 2005) (Table I). No precise information is available on the reproductive mode of the hexanchid species, apart from the general classification for the entire family as viviparous lecithotrophic (Musick & Ellis, 2005). The sole and very limited information comes from captive *N. cepedianus* (in two different aquariums). In this species, empty egg capsules have been observed both

inside the maternal uterus of a dead specimen or discharged at the bottom of water tanks (J. Janez & V. Hodges, pers. comm.). These findings are in accordance with what was previously reported for *C. anguineus* (Tanaka *et al.*, 1990), suggesting that *N. cepedianus* may display a similar reproductive mode.

All male hexanchids reach sexual maturity at smaller sizes than females (Ebert, 1990, 1996, 2002a; Lucifora *et al.*, 2005) (Table I). Males of *H. griseus* were found to produce sperm all year round (Ebert, 2002a), while Ebert (1996) and Lucifora *et al.* (2005) reported possible seasonal fluctuations in the gonado-somatic index ( $I_G$ ) of male *N. cepedianus*. Hexanchid females have two functional ovaries and uterus, and two distinct size-class ovarian follicles are distinguished in mature females, with only one group of follicles developing at a time (Ebert, 1996). For both *N. cepedianus* and *H. griseus*, however, the ovulation cycle length and timing have not been determined because females were not sampled throughout the year. Preliminary results on reproductive hormone levels (testosterone, progesterone and  $17\beta$ -O-estradiol) on *N. cepedianus* suggest an asynchronous mode of reproduction as females of all reproductive stages were distinguished between spring to early autumn (C. A. Awruch, unpubl. data). Nevertheless, Ebert (1986b, 1989) hypothesized a 6–12 month ovarian cycle, with ovulation occurring in late spring-summer, based on the sampling of females with large follicles, no embryos and mating scars. Females carrying near-term embryos and no large follicles in the ovaries suggest that the ovarian cycle does not run in parallel with the 1 year gestation cycle (Ebert 1986b, 1989, 1996). On the basis of the ovarian and gestation cycles, the length of the reproductive cycle for *N. cepedianus* would be 18–24 months (Ebert, 1989). Parturition was reported to occur in late spring-summer for both *H. griseus* and *N. cepedianus* with up to 108 embryos per litter (Ebert, 1986b, 1996, 2002a). While no information on parturition is available for the smaller hexanchid species (*H. nakamurai* and *H. perlo*), litter size ranges from 2 to 26 embryos per litter (Ebert, 1990; Compagno *et al.*, 2005) (Table I).

## ECOLOGY AND ROLE IN COASTAL AND DEEP-WATER ECOSYSTEMS

Detailed diet information for each hexanchiform species is essential for establishing the position in the food webs of which they form part. In addition to feeding ecology knowledge, information on distribution, movement behaviour, habitat use and abundance is also needed for understanding the ecological roles of this order. Furthermore, an understanding of what other species overlap in distribution and share resources is required to evaluate the role of Hexanchiformes in ecosystem dynamics.

## FEEDING ECOLOGY

Very little is known about the feeding ecology of *Chlamydoselachus* species. Their unique body shape, long mouth, highly distensible jaws and buccal cavity and inwardly projecting needle-sharp teeth suggest *Chlamydoselachus* species have optimal morphology for grasping and engulfing large prey, possibly at least half their own body length (Ebert & Compagno, 2009). Individuals examined thus far have preyed on teleosts, squid and deep-water sharks, in particular catsharks from the family Scyliorhinidae (Kubota *et al.*, 1991; Ebert & Compagno, 2009).

There are currently no representative dietary studies on *H. nakamurai*. The few stomachs opportunistically examined contained teleosts and in one case a crustacean

TABLE II. Diet of *Hexanchus nakamurai* and *Hepranchias perlo* presented as % $I_{RI}$  for broad taxonomic groups: % $F$ (% $N$  + % $W$ ), where % $N$ , % $W$  and % $F$  are the per cent contributions of a prey species in terms of number, mass and frequency of occurrence in the stomachs examined. The  $I_{RI}$  values were converted to a percentage following Cortés (1997). Specimens of *H. nakamurai* collected in Taiwan ( $n = 10$ ), Caribbean ( $n = 1$ ), Gulf of Mexico, Florida ( $n = 2$ ) and South Africa ( $n = 1$ ) are pooled. *Hepranchias perlo* samples presented separately from Taiwan and South Africa

Species	Location	Teleost	Cephalopod	Crustacean	Elasmobranch
<i>H. perlo</i> ( $n = 36$ )	Taiwan	95	1	4	0
<i>H. perlo</i> ( $n = 12$ )	South Africa	48	52	0	0
<i>H. nakamurai</i> ( $n = 14$ )	Various	98.5	0.5	0.3	0.7

(Forster *et al.*, 1969; Last & Stevens, 2009). Teleosts occurred in all 14 individuals presented in this review (Table II). Most teleosts were unidentifiable, but two were shallow-water coastal-associated largehead hairtail *Trichiurus lepturus* L. 1758, and the other was a benthopelagic Japanese jack mackerel *Trachurus japonicus* (Temminck & Schlegel 1844). An unidentified octopus, an elasmobranch and a crustacean were also consumed.

The only dietary study with a reasonable sample size for *H. griseus* ( $n = 137$  stomachs inspected, 97 containing prey) was done in southern Africa (Ebert, 1994). Apart from this study, there are few general diet observations (Ebert, 1986a, 1994). The available information indicates that *H. griseus* consumes a variety of prey including cephalopods, chondrichthyans, teleosts and marine mammals, including scavenging on whale carrion (Ebert, 1986a, 1994; Crow *et al.*, 1996). Ontogenetic changes in diet were observed, with juveniles (<120 cm  $L_T$ ) feeding almost exclusively on cephalopods and teleosts, and as they grow, the diet changes to chondrichthyans and marine mammals (Ebert, 1994). Larger teleosts also increased in importance with increasing shark size (Ebert, 1994). This may reflect the habitat in which the different size classes forage (Ebert, 1994). For instance, juveniles appear to forage in shallower waters and therefore diet may be influenced by the prey species occurring at these depths and habitats (Ebert, 1994). Although *H. griseus* is considered benthic associated (Carey & Clark, 1995), its diet suggests it also forages in the water column and in shallower coastal areas and, despite appearing sluggish, its diet consists of fast-moving prey such as swordfishes and dolphins (Ebert, 1994, 2003).

*Hepranchias perlo* shows a greater degree of dietary specialization than *N. cepedianus* and *H. griseus*. This species preys largely on deep-water teleosts, with cephalopods and crustaceans being secondary prey in most regions where dietary data are available (Capapé, 1980; Frentzel-Beyme & Köster, 2002; Braccini, 2008; Table II). Slight differences in prey composition are evident in some regions. At the Great Meteor Seamount, eastern Atlantic Ocean and off southern Africa, teleosts and cephalopods were almost equally important in the dietary composition (Frentzel-Beyme & Köster, 2002; Table II). In southern Australia, chondrichthyans also featured in the diet (Braccini, 2008). Ontogenetic changes were evident in southern Australia, with smaller *H. perlo* mostly consuming small-sized teleosts, whereas large *H. perlo* considerably increased the consumption of large predatory teleosts (Braccini, 2008). From the limited data available, *H. nakamurai* appear to have a similar feeding ecology to *H. perlo*, *i.e.* a mostly teleost-based diet (Table II).



*Notorynchus cepedianus* showed similar dietary patterns at a global spatial scale. In California, southern Africa, Patagonia and southern Australia, chondrichthyans, marine mammals and teleosts were the main prey; trophic roles discussed below provide further information on regional diets (Ebert, 1989, 1991a, 2002a; Lucifora *et al.*, 2005; Braccini, 2008; Barnett *et al.*, 2010b, c). Ontogenetic dietary shifts from teleosts to elasmobranchs and mammals were also evident (Ebert, 2002b; Lucifora *et al.*, 2005; Braccini, 2008). Direct observations of foraging behaviour and fine-scale acoustic tracking suggest a number of different tactics used in hunting and subduing prey: directed burst speed attacks at a predetermined prey, ambush tactics in conditions of poor light (*e.g.* night-time, overcast days or when visibility is poor) or stealth tactics to sneak up on prey (Ebert, 1991b; Barnett *et al.*, 2010d). Given that the diet of *N. cepedianus* regularly consists of very large prey, pack hunting or group feeding has been proposed (Ebert, 1991b). Further research is needed to determine if this order is capable of such co-ordinated social behaviour. Furthermore, as for *H. griseus*, *N. cepedianus* will readily consume carrion (Ebert, 1991b; A. Barnett, pers. obs.).

#### SPATIAL ECOLOGY: DISTRIBUTION, MOVEMENT AND HABITAT USE

No detailed movement, habitat use or population structure studies are available for *Chlamydoselachus* species, *H. nakamurai* or *H. perlo*, so any information on distribution and habitat use has been derived from fishery and scientific survey catches or from stomach contents. All these species are classified as deep-water demersals, but are believed to at least occasionally forage in mid to shallower waters (Forster *et al.*, 1969; Braccini, 2008; Ebert & Compagno, 2009; Last & Stevens, 2009).

Similar to the other deep-water *Hexanchiforme* species, *H. griseus* has been reported to enter relatively shallow waters, normally in areas adjacent to deep-water trenches or shelves, *e.g.* the Strait of Georgia (British Columbia, Canada) and Puget Sound (Washington State, U.S.A.) (Dunbrack & Zielinski, 2003, 2005; Dunbrack, 2008; Andrews *et al.*, 2009). *Hexanchus griseus* also occurs seasonally in San Francisco Bay, U.S.A., which has been attributed to its comparatively deep (120 m) entrance (Ebert, 1986a). Mainly large juveniles and sub-adults (110–353 cm  $L_T$ ) occur in all these locations (Ebert, 1986a, 2003; Dunbrack & Zielinski, 2005; Andrews *et al.*, 2010; Williams *et al.*, 2010). In contrast to these deep-water coastal areas, a single *H. griseus* (340 cm  $L_T$ ) was caught *c.* 30 km up the Derwent River, Tasmania, over 100 km from the deeper waters of the continental shelf (Barnett *et al.*, 2010e).

In the first movement study on *H. griseus*, two immature females tracked in Bermuda moved up and down the continental slope between 600 and 1500 m (Carey & Clark, 1995). Three more detailed studies were done in Puget Sound (Andrews *et al.*, 2007, 2009, 2010), a highly urbanized inland estuary with an average depth of 150 m and a maximum depth of nearly 300 m (Williams *et al.*, 2010). In this estuary, juveniles reside for long periods (up to 4 years), during which they show site fidelity, moving between core areas, and seasonal north-south movements. Consistent diel vertical migrations also occur, with juveniles using deeper waters during the day and shallower waters at night (Andrews *et al.*, 2009, 2010). These habitat use patterns suggest that, as active predators and passive scavengers, juvenile *H.*

*griseus* are capable of foraging across the food web of Puget Sound (Andrews *et al.*, 2009, 2010). Dietary information from other areas also suggests foraging from deep to shallow habitats (Ebert, 1994).

After residing in Puget Sound for up to 4 years post-tagging, *H. griseus* generally migrate out of the estuary to the outer coast (Williams *et al.*, 2010). These data agree with an earlier prediction that *H. griseus* juveniles inhabit shallower water and move down the continental slope as they grow (Ebert, 1990, 1994). The focus of spatial studies on juvenile *H. griseus* only is probably due to their regular occurrence in some coastal areas, making them easier to catch and acoustically track. Despite the logistical difficulties of working with acoustic equipment in deep waters, further work on larger size classes is needed to improve understanding of the spatial ecology of this species.

Regarding *N. cepedianus*, the population structure has been investigated in the coastal areas of California, Patagonia, Tasmania and Washington State, U.S.A. (Ebert, 1989; Lucifora *et al.*, 2005; Barnett *et al.*, 2010a; Williams *et al.*, 2012). In addition, movement patterns have been studied using electronic tagging technology in Tasmania (Barnett *et al.*, 2010d, 2011; Barnett & Semmens, in press) and Washington State (Williams *et al.*, in press). The common pattern is the seasonal increase in occurrence of *N. cepedianus* during spring to autumn and their near absence in winter. While Anegada Bay (Patagonia) and California are pupping areas (Ebert, 1989, 1996, 2002a; Lucifora *et al.*, 2005), no neonates and very few small juveniles (<120 cm  $L_T$ ) occur in Tasmania and Washington State (Barnett *et al.*, 2010a; Williams *et al.*, 2011). In Tasmania, foraging appears to be the main reason for the seasonal occurrence of *N. cepedianus*, as they seasonally follow prey into and out of the coastal areas (Barnett *et al.*, 2010b; Barnett & Semmens, in press). In California, however, foraging and pupping purposes may be playing simultaneously. When *N. cepedianus* main prey (*e.g.* triakid sharks and myliobatid rays) enter northern Californian bays to give birth, female *N. cepedianus* give birth in the same area. Newborn *N. cepedianus* have a relatively large mouth and readily consume neonates of other elasmobranchs (Ebert, 1986c, 1989, 2002a).

In Tasmania and Washington State, two locations where *N. cepedianus* has similar population structure, similar movement patterns are also evident. In both locations, site fidelity is prominent, with a high percentage of sharks returning to the same areas after winter (Barnett *et al.*, 2010a, 2011; Williams *et al.*, 2012). In addition, different groups of sharks showed fine spatial scale differences in habitat use and temporal segregation, with females arriving in coastal areas prior to males (Barnett *et al.*, 2010b, 2011, Williams *et al.*, 2012). Furthermore, in both locations, individuals undergo long-distance migrations after departing coastal areas in winter (Barnett *et al.*, 2011; Williams *et al.*, 2012). In Tasmania, males make northerly migrations of *c.* 1000 km to southern New South Wales (NSW), Australia, returning to Tasmania the following summer (Barnett *et al.*, 2011). In Washington State, sharks move to open coastal areas and out to the continental shelf, with some individuals dispersing as far as 1800 km south to California (Williams *et al.*, 2012).

Movement and catch rates data also suggest the possible segregation of different life stages of *N. cepedianus* along the west coast of the U.S.A. For instance, only sub-adults and adults occur in Washington State, whereas those caught in California are predominately smaller (neonates and juveniles) or adults, and sub-adults are not common (Ebert, 1989, 2002a). This suggests that the southern limits of their range

may be more beneficial for juvenile survival. Furthermore, given that *N. cepedianus* can be cannibalistic, a behaviour mainly associated with sub-adults, fewer sub-adults in an area may reduce predation pressure on neonates and limit competition for available resources (Ebert, 1991a, 2002a; Barnett *et al.*, 2010b). In contrast to the west coast of the U.S.A., it is unknown whether juveniles in Tasmania or southern Australia use specific locations or habitats (Barnett *et al.*, 2010a). On the basis of the patterns reported for the west coast of the U.S.A., neonates and small juveniles in Australia should be found towards the northern limit of the species distribution, *i.e.* in the warmest area. Catch rates of *N. cepedianus* between 1972 and 2009 from the shark control (beach meshing) programme in NSW (northerly limit for *N. cepedianus*) only captured one neonate or juvenile (75 cm  $L_T$ ), however. In addition, 80% of the catch were males, and with only two females at a mature size (>220 cm  $L_T$ ) caught, pupping in NSW appears unlikely (Krogh, 1994; Reid *et al.*, 2011; V. Peddemors, unpubl. data).

In Tasmania, some females remain in close proximity to coastal areas over winter (Barnett *et al.*, 2010a, 2011), while others leave the study area, but where they move to is yet to be determined (Barnett *et al.*, 2011). Stable isotope data show that some females have higher  $\delta^{13}\text{C}$  values than others, which could result from these females spending longer periods of time in coastal areas (Abrantes & Barnett, 2011). The females with lower  $\delta^{13}\text{C}$  could have similar movement patterns to the sharks in Washington State (Williams *et al.*, 2012), where individuals move to open coast and continental shelf habitats over winter. The separation of females may be related to pregnant individuals moving elsewhere to pup. In general, there is very little information available on the habitat use of pregnant females in all regions. There is a considerable gap in understanding the population ecology of *N. cepedianus*.

## RESOURCE OVERLAP AND HABITAT PARTITIONING

Few species share resources with Hexanchiformes. In the habitats they occupy, equivalent-sized sympatric squaloids, lamnoids and carcharhinoids generally feed at lower trophic levels. In deep-water systems, large squaloids such as the sleeper shark *Somniosus pacificus* Bigelow & Schroeder 1944 are potential competitors of *H. griseus*. These species share characteristics with *H. griseus*, including large body size (>7 m  $L_T$ ), similar movement patterns (*e.g.* vertical migrations) and depth use (from surface to >2000 m) and feeding on high trophic level prey such as marine mammals and teleosts (Hulbert *et al.*, 2006; Sigler *et al.*, 2006; Yano *et al.*, 2007). Resource overlap, however, may be limited to certain areas and certain prey, as *H. griseus* has a wider distribution and *Somniosus* spp. have relatively smaller mouths. Of the deep-water lamnoids (Cetorhinidae, Megachasmidae, Mitsukurinidae and Odontaspidae), none has a large body size, large mouth or powerful jaws. *Hexanchus griseus* is also an active predator on other chondrichthyans, whereas the lamnoid species tend to feed exclusively on teleosts and invertebrates (Ebert & Compagno, 2012). *Hexanchus nakamurai*, *H. perlo* and frilled sharks are comparable in size to many of the sympatric gulper sharks (*Centrophorus* spp.), but the jaw and teeth morphology of the Hexanchiformes is stronger and better equipped for obtaining larger prey (Ebert & Compagno, 2012). In coastal systems, the only comparable species that overlaps in resource use with *N. cepedianus* is *C. carcharias*. Sympatric requiem sharks (*Carcharhinus* spp.) would only be sharing a small proportion of resources, as they tend to feed mainly on teleosts (Ebert & Compagno, 2012).

The available information on diet and distribution suggests that there is potential for resource sharing among hexanchiform species in areas where their distribution overlaps. Although this is more likely to occur among deep-water Hexanchiformes, there is also the chance of resource overlap between *N. cepedianus* and deep-water Hexanchiformes in areas where deep-water species move into shallow water or when *N. cepedianus* move out of coastal areas onto the continental shelf, e.g. to depths c. 200 m. Possible resource overlap has only been considered between *N. cepedianus* and *H. perlo* in southern Australia (Braccini, 2008). Differences in dietary composition, diet breadth and limited spatial overlap suggest only limited resource overlap (Braccini, 2008).

*Notorynchus cepedianus* and *H. griseus* are both large sluggish looking predators with similarities in movement behaviour, body form, morphology and diets, suggesting the two species could share resources in areas where they overlap in distribution. On the west coast of North America, the areas where *H. griseus* is consistently found in coastal waters are towards the northern limit of *N. cepedianus* distribution. The use of these coastal areas by juvenile *H. griseus*, where *N. cepedianus* appear to be less abundant, may reduce competition for resources, and avoid predation by large *N. cepedianus* in coastal areas. Conversely, the general use of shallow coastal habitats by *N. cepedianus* may be to avoid predation from larger *H. griseus*. As adult *H. griseus* can be cannibalistic, the use of coastal habitats by juvenile *H. griseus* may also avoid predation and competition with adults (Carey & Clark, 1995). In southern Africa, *H. griseus* juveniles (<120 cm) are mainly caught on the outer continental shelf and slopes, an area deep enough to avoid large coastal predators such as *N. cepedianus*, but shallow enough to also avoid adult *H. griseus*. Overall, these two species are largely separated in habitat use, and this could partition resources between predators that play similar roles in ecosystem dynamics.

The distribution patterns of the deep-water hexanchiform species show regions of high overlap such as in south-east Asia, Australia, the Mediterranean and north-west Africa and possibly sections of east Africa (Last & Stevens, 2009). For example, samples collected from Indonesian fisheries and scientific surveys off east Africa consisted of *H. perlo*, *H. nakamurai* and *H. griseus* (Forster *et al.*, 1969; White & Dharmadi, 2010). Off east Africa, almost all individuals were caught within the same depth range of 200–600 m (Forster *et al.*, 1969). Similarities in depth range, diets, body size and morphology between *H. perlo* and *H. nakamurai* suggest that resource sharing in areas of overlap could be possible. Resource overlap between *H. griseus* and the other deep-water hexanchiform species is less marked, as *H. griseus* has a much more varied diet.

## TROPHIC ROLES

Current understanding of the deep-water Hexanchiformes diets, abundance and movement is still inadequate to assess the importance of each species in deep-water systems. As a group, Hexanchiformes predominately consume meso-predator species (defined as predators that occupy trophic positions directly below apex predators) such as smaller sharks, batoids, large teleosts and many marine mammals. Therefore, Hexanchiformes potentially play important roles in regulating meso-predator populations and having a spill-over effect on those meso-predators' prey. In general, understanding of how elasmobranch predation impacts prey populations is limited

by the scarcity of information on prey availability and abundance, and the complexity of the temporal and spatial patterns of prey consumption (Braccini *et al.*, 2005; Heithaus *et al.*, 2010). Further trophic studies are clearly needed, and as Hexanchiformes have wide distributions, studies in multiple regions that incorporate a number of spatial ranges are encouraged (Barnett *et al.*, 2010b).

Of the deep-water Hexanchiformes, *H. perlo* is the only species for which there are diet studies in multiple regions (Capapé, 1980; Frentzel-Beyme & Köster, 2002; Braccini, 2008; Table II). The prominence of teleosts and cephalopods at all locations suggests that they fill a similar trophic role in all regions. *Hexanchus nakamurai* probably fills the same role as *H. perlo*, while the morphology of *Chlamydoselachus* species suggests that they would be a significant predator in deep-water systems (Ebert & Compagno, 2009). *Hexanchus griseus* seems to be a larger version of *N. cepedianus*, so information on the role of *N. cepedianus* in multiple coastal systems can be used as a proxy to determine the importance of *H. griseus* in deep-water systems. Thus, *H. griseus* is likely to be an important apex predator and regulator of multiple prey species in deep-water systems.

As there are several detailed diet studies for *N. cepedianus*, a multiregion comparison of their trophic ecology gives further insight into their role in coastal ecosystems. There are consistent global-scale predator–prey links between *N. cepedianus* and triakid sharks, myliobatid rays and marine mammals (Barnett *et al.*, 2010b). In particular, sharks from the genus *Mustelus* (family Triakidae) are the most common prey in all regions, and other triakid species are also important in areas where they occur (Barnett *et al.*, 2010b). In coastal areas where *N. cepedianus* is abundant, triakids appear to be under high predation pressure, so *N. cepedianus* may restrict the influence of triakids in coastal communities. For example, in Tasmanian coastal systems, gummy shark *Mustelus antarcticus* Günther 1870 feed mainly on crustaceans, but also on cephalopods, teleosts, sipunculids and polychaete worms (Stevens & West, 1997; J. Yick, unpubl. data), so *N. cepedianus* may regulate the effects of *M. antarcticus* on the benthic, and to a lesser extent, mid-water communities in coastal areas of Tasmania.

Prey availability and intraspecific behavioural variations (*e.g.* foraging behaviours) at multiple spatial scales also need consideration when evaluating the importance and role of a predator such as *N. cepedianus*. For example, chondrichthyans are the most important prey in three of four regions sampled in southern Africa (Ebert, 1991a), while marine mammals are consumed more in the fourth location. This fourth region has the highest concentration of seal rookeries in southern Africa, suggesting prey availability influences diet (Ebert, 1991a). Moreover, for a given habitat, abundance estimates of available prey and habitat use information of *N. cepedianus* are needed to determine dietary preferences. For instance, in Tasmania, dietary differences were detected between *N. cepedianus* sampled in two coastal areas only separated by *c.* 30 km, and prey availability influenced dietary composition to some extent (Barnett *et al.*, 2010b). Foraging behaviour could also play a role, as sharks from the two locations rarely overlapped in habitat use (Barnett *et al.*, 2011). This suggests that individual sharks have preferential foraging areas over relatively fine spatial scales. Stable isotope data also suggest interpopulation differences in habitat use and foraging behaviour (Abrantes & Barnett, 2011). Overall, the available information on habitat use in all regions (*e.g.* seasonal high abundance in coastal areas) complements dietary data (*e.g.* similarities in meso-predator prey such as triakids on a global scale).

in predicting that *N. cepedianus* are important predators of meso-predators in the coastal temperate systems in which they occur. The consistent predator–prey links over large spatial scales and the differences over the finer scales show the importance of incorporating spatial variability in dietary analysis to explore the trophic ecology of wide-ranging predators such as Hexanchiformes.

## FISHERIES

Although environmental stressors such as pollution and habitat degradation can negatively affect Hexanchiformes [*e.g.* *H. griseus* use urbanized polluted waters and accumulate toxins (Levin *et al.*, 2012) and the inshore bays used by *N. cepedianus* as pupping areas may be exposed to pollution (Compagno, 2005)], this shark order is most threatened by fishing exploitation. Hexanchiformes are not generally targeted by commercial fisheries; instead, they comprise a small but regular by-catch component of multispecies commercial fisheries operating in temperate and tropical waters using a range of different gears. In addition, some species are taken in recreational fisheries (Compagno, 1984). Hexanchiformes have been recorded in the catches of several different fisheries worldwide.

*Chlamydoselachus anguineus* is a small by-catch component of many bottom and midwater trawl, deep-set longline and gillnet fisheries (Paul & Fowler, 2003a). Tanaka *et al.* (1990) reported this species as commonly taken in bottom gillnets and midwater trawls in Suruga Bay, Japan. This species is also occasionally taken in the Australian Southern and Eastern Scalefish and Shark Fishery (SESSF) (Walker *et al.*, 2008). *Chlamydoselachus africana* is a recently described species (Ebert & Compagno, 2009) and no fishery information is available. It is expected, however, that within its geographical distribution, *C. africana* is vulnerable to the same fishing gears as *C. anguineus*.

*Hexanchus nakamurai* is uncommonly taken in trawl and longline fisheries (Compagno, 1984). Small numbers have been recorded in the catches of the Mexican shark fishery of Yucatán, as by-catch of snapper fisheries in the Cayman Islands, trawl fisheries off Taiwan (Ebert, 1990) in the SESSF (Walker *et al.*, 2008) and in the catches of artisanal fisheries of Indonesia (White & Dharmadi, 2010). This species has also been reported in the catches of longline fisheries in the Mediterranean Sea (Megalofonou *et al.*, 2005).

*Hexanchus griseus* is mostly caught as by-catch of longline, handline, gillnet, traps, trammel net and pelagic and bottom trawls (Cook & Compagno, 2005). In Puget Sound, a targeted commercial fishery during the 1940s and 1950s ended due to the development of synthetic products in *c.* 1946 and hence a drastic drop in market demand for shark livers (Andrews *et al.*, 2007; D. A. Ebert, unpubl. data). Also in Puget Sound, a small fishery targeted at *H. griseus* operated during the 1980s (D. A. Ebert, pers. obs.). In British Columbia, *H. griseus* has been the focus of at least three targeted pulse commercial fisheries: the first during the early 1920s, the second between 1937 and 1946 and finally an experimental fishery between the late 1980s and early 1990s, which terminated due to conservation concerns (McFarlane *et al.*, 2002; COSEWIC, 2007). This species has also been recorded in the catches of the Venezuelan longline fishery (Arocha *et al.*, 2002), the bottom trawl, purse seine, pelagic longline and gillnet fisheries off Turkey (Kabasakal, 2006), the

deep-sea fishery off Bermuda (Carey & Clark, 1995), the deep-water longline fisheries off Ireland (Clarke *et al.*, 2005), the pelagic longline fisheries in the Mediterranean Sea (di Natale, 1998), the bottom longline fisheries off Taiwan and the Maldives (Fowler *et al.*, 1997), the artisanal fisheries of Indonesia (White & Dharmadi, 2010), the SESSF (Walker *et al.*, 2008) and the U. K., French and Portuguese fisheries in the north-east Atlantic Ocean (ICES, 2010).

*Heptranchias perlo* is mostly taken as by-catch of bottom trawl and deep-water longline fisheries (Paul & Fowler, 2003b). This species has been reported in the catches of pelagic drift net, longline (di Natale, 1998; Megalofonou *et al.*, 2005) and trawl (Scacco *et al.*, 2002) fisheries of the Mediterranean Sea, the bottom trawl fisheries off Taiwan (Fowler *et al.*, 1997; D. A. Ebert, pers. obs.), the catches of artisanal fisheries of Indonesia (White & Dharmadi, 2010), in the SESSF (Walker *et al.*, 2008) and the longline fisheries off northern Spain (López Losa, 2001).

*Notorynchus cepedianus* is mostly restricted to coastal temperate waters (Ebert, 1990; Ebert & Compagno, 2012). The coastal zone is generally more heavily fished than the deep water where other Hexanchiformes occur, exposing *N. cepedianus* to potentially higher fishing exploitation rates from a range of fishing gears such as bottom trawl, longline and gillnet. This might have been the case for the central California stock in San Francisco Bay, subjected to intense targeted recreational fishing and a component of the mixed shark commercial fishery during the late 1970s and 1980s (Ebert, 2003). Similar fishing pressure is expected for most of the species distribution, particularly off China, Argentina, California, Namibia, south-eastern Australia and South Africa (Compagno, 2005). During 1990 in Luderitz Lagoon, southern Namibia, *N. cepedianus* were fished down to the point where the fishery closed due to the extremely low abundance within the first 9 months of fishing (D. A. Ebert, pers. obs). *Notorynchus cepedianus* is commonly taken as by-catch of mostly gummy and school shark fisheries in the trawl, gillnet and longline catches of the SESSF (Walker *et al.*, 2005; Walker & Gason, 2009) and the demersal shark longline and commercial line fishery of South Africa (Da Silva & Bürgener, 2007; C. Da Silva, per. comm.). In South Africa, recreational fishers may take up to 10 individuals per day per person, and recently there have been reports of *N. cepedianus* livers being used as chum in the *C. carcharias* tourism industry (A. Kock, pers. comm.). The species is also targeted by recreational fisheries in a major pupping area in north Patagonia, Argentina (Lucifora *et al.*, 2005).

Time series of fisheries catch landings have been poorly recorded for Hexanchiformes due to the incidental nature of catches and the low economic value of this order. For *C. anguineus*, *C. africana*, *H. nakamurai* and *H. perlo*, there are no time series either at a regional or global level.

For *H. griseus*, regional time series of catch landings are available for British Columbia (COSEWIC, 2007). Between 1942 and 1946, a total of 276 t of liver were marketed, equating to c. 3810 individuals based on a 10–20% liver to round mass ratio. Between 1985 and 2005, a total of 75 t were reported with a peak at 14.6 t in 1985. Recent catches (1996 onwards) comprise exclusively by-catch in the longline and to a lesser extent trawl fisheries targeted at halibut *Hippoglossus hippoglossus* (L. 1758) and scyliorhinids. Global time series of catch landings are available from the United Nations Food and Agricultural Organisation (FAO) for 2001–2009. During this period, annual landings increased from just over 1 t in 2001 to 30 t in 2004, they then declined to c. 2 t in 2008 and increased again to c. 30 t in 2009.

For *N. cepedianus*, regional time series of catch landings are available for U.S.A. and Australia. In the west coast of the U.S.A., mostly in San Francisco Bay, during the 1980s, annual landings peaked to 1.5 t in 1981 and declined to <0.1 t in 1986 (Compagno, 2005). The decline in catches was mostly due to a loss of interest in the species rather than a drastic decline in abundance. For south-eastern Australia, annual catch landings remained at zero between 1986 and 2000, and rapidly increased to 50–60 t year<sup>-1</sup> during 2001 and 2006 (Walker & Gason, 2009). At a global level, time series are available from FAO for 1988–2009. During this period, landings increased from almost 2 t in 1988 to c. 5 t in 2001 and 2003, they then declined to 2 t during 2004–2006 and peaked at 27 t in 2009. The fluctuations in the landing time series would reflect the sporadic nature of the catches of these species and the lack of enforcement and incentives of fisheries management agencies for keeping accurate fishing records. It is also worthwhile pointing out the inconsistencies between regional and FAO global landing records. For example, for all years between 2000 and 2005, >50 t were reported for *N. cepedianus* in the SESSF, whereas global landings reported by FAO remained well below 50 t, suggesting that global statistics are uncertain.

Finally, it must be stressed that a large proportion of the effect of fishing on Hexanchiformes would be through the by-catch component of fishing mortality. Unfortunately, the only available time series of by-catch levels are for *H. griseus* in British Columbia (COSEWIC, 2007) and for *N. cepedianus* in south-eastern Australia (Walker & Gason, 2009). Being by-catch species, a large proportion of captured individuals would be discarded but there are no estimates of the post-discarding mortality for any hexanchiform species.

## CONSERVATION STATUS AND FISHERIES MANAGEMENT

The conservation status of exploited species results from the interaction of the species demographic capacity to withstand the exploitation and the level of such exploitation (Dulvy *et al.*, 2008). The impact of fishing exploitation is estimated or inferred through a range of approaches, from complex quantitative assessments to less data-demanding methods. The minimum requirement for quantitative fisheries assessments is information on removals due to harvesting (*i.e.* time series of catches) and an index of relative abundance (Hilborn & Walters, 1992). Unfortunately, the poorly recorded time series of conventional fisheries data, and particularly the lack of reliable abundance time series, impede the application of these methods for the assessment of Hexanchiformes conservation status. In addition, research resources for stock assessment are generally allocated to species with higher economic value. Therefore, conventional strategies used in fisheries management for promoting sustainability and conservation (*e.g.* reduction of fishing effort and establishment of total allowable catches) have generally not been adopted for this order (but see the few exceptions for *H. griseus* and *N. cepedianus* below). Rather, assessment of conservation status for this order has largely been based on expert opinion, and qualitative and semi-quantitative information through the application of the IUCN-World Conservation Union Red List Categories and Criteria (IUCN, 2004), at a global scale, and risk assessments (Walker *et al.*, 2008), at a regional scale. These assessments are based on the available information on ecology, life history, distribution, habitat, threats, population trends, catch susceptibility and conservation measures, used



to determine relative threats of extinction (IUCN, 2001, 2004) and ecological risks (Walker *et al.*, 2008).

At a global level, based on the IUCN criteria, two hexanchiform species were assessed as data deficient (*i.e.* the risk of extinction cannot be assessed with the current available data; IUCN, 2006), three species were assessed as near threatened and one species, *C. africana*, was not evaluated. None of the species were assessed based on population size and trends as this information is not available. Furthermore, biological productivity cannot be determined for any species due to incomplete life-history data (Walker *et al.*, 2008).

*Chlamydoselachus anguineus* was assessed as near threatened according to the IUCN criteria on the assumption that even incidental catches may have a very large effect on the population (Paul & Fowler, 2003a). This species has a global distribution in deep water, although it is considered rare to uncommon in general. Although very little is known on the life history of *C. anguineus* (*e.g.* no age and growth variables), the species was considered to have very low resilience to fishing exploitation due its possibly very low reproductive rate [females mature at 126–150 cm  $L_T$ , produce only 2–12 pups per reproductive cycle and possibly have a long gestation period, Paul & Fowler (2003a)]. In south-eastern Australia, *C. anguineus* is considered rare based on reported commercial catches, and to have moderate to low catch susceptibility to trawl, gillnet and hook fishing gears, classing this species as in high ecological risk in terms of abundance and moderate risk in terms of catch susceptibility.

*Hexanchus nakamurai* was assessed as data deficient according to the IUCN criteria due to insufficient information on life-history and population trends (Ebert *et al.*, 2008). With an almost worldwide but patchy distribution in tropical and warm-temperate deep waters, *H. nakamurai* is considered an uncommon to rare species (Ebert, 1990). Females mature at 123–157 cm  $L_T$  and produce 13–26 pups per reproductive cycle, although the duration of the cycle is unknown (Table I). In south-eastern Australia, *H. nakamurai* is considered rare based on reported catches, and to have moderate to low catch susceptibility to trawl, gillnet and hook fishing gears, categorizing this species as at high ecological risk in terms of abundance and moderate risk in terms of catch susceptibility.

*Hexanchus griseus* was assessed as near threatened according to the IUCN criteria on the assumption that the species was not capable of sustaining either sport or commercial fisheries efforts (Fowler *et al.*, 2005). Females mature at >400 cm  $L_T$  and produce 47–108 pups per reproductive cycle, although the duration of the cycle is unknown (Table I). In British Columbia, an underwater video survey and scuba diver encounters showed consistent and gradual declines in sightings from 1999 to 2005, although this index may not record abundance but behavioural patterns at the sites (COSEWIC, 2007). Genetic studies in Puget Sound suggest the local population is fairly large (Larson *et al.*, 2010), but there is apparent cohort-specific, broad variation in abundance (Williams *et al.*, 2010). In Puget Sound and British Columbia, management actions are based on a conservative application due to sparse data (D. Low, pers. comm.). Canada considers *H. griseus* as a species of special concern and currently has a specific management plan under review (Fisheries & Oceans Canada, unpubl. data), whereas in Puget Sound the catch of *H. griseus* has been banned since 2001 (Andrews *et al.*, 2007). In south-eastern Australia, *H. griseus* is considered rare based on reported catches, and to have moderate to low catch susceptibility to trawl,

gillnet and hook fishing gears, classing this species as in high ecological risk in terms of abundance and moderate risk in terms of catch susceptibility.

*Hepranchias perlo* was assessed as near threatened according to the IUCN criteria based on the assumption that the species had low intrinsic rate of population increase and hence poor resilience to fishing exploitation (Paul & Fowler, 2003b). This wide-ranging species in tropical and temperate seas has a higher occurrence on the outer shelf, slope and seamounts, where commercial fishing effort has been rapidly increasing (Paul & Fowler, 2003b). Females mature at 90–105 cm  $L_T$  and produce six to 20 pups per reproductive cycle, although the length of the cycle is unknown (Table I). In the Tyrrhenian Sea, *H. perlo* disappeared from the catches of coastal and deep waters (Ferretti *et al.*, 2005). Population declines may have occurred in other regions (*e.g.* southern Mozambique) where demersal trawl effort has been operating over the past few decades (Paul & Fowler, 2003b). In south-eastern Australia, *H. perlo* have a sparse abundance based on reported catches, and a moderate to low catch susceptibility to trawl, gillnet fishing gears, but high catch susceptibility to hook fishing gears (automatic longline), classing this species as in moderate ecological risk in terms of abundance and high risk in terms of catch susceptibility.

*Notorynchus cepedianus* was assessed as data deficient according to the IUCN criteria due to insufficient information on life-history and population trends (Compagno, 2005). Females mature at 220 cm  $L_T$ , produce 82 pups on average, have a slow growth rate, a predicted life span of 32 years and an unknown reproductive cycle length (Table I) (Braccini *et al.*, 2010). In south-eastern Australia, *N. cepedianus* is considered common based on reported catches, and to have moderate to low catch susceptibility to trawl and hook fishing gears but high vulnerability to gillnet gear, categorizing this species as at high ecological risk in terms of abundance and high risk in terms of catch susceptibility (Walker *et al.*, 2007). A rapid quantitative sustainability assessment for fishing effects (SAFE) also ranked the species as at high risk in the gillnet sector of the SESSF due to the estimated fishing mortality rate being larger than the maximum sustainability fishing mortality (Zhou *et al.*, 2007). In the gillnet sector, mesh size is restricted to 152–165 mm (6–6.5 inches) limiting the size classes taken due to strong gear size-selective effects (Walker, 1999). In addition, there are upper (used to indicate an increase in targeted fishing) and lower (used to indicate stock decline) reference points in place for *N. cepedianus*. In 2009, none of the reported catches resulted in a breach of the upper or lower reference points, although *N. cepedianus* catches were close to the lower limits (S. Weekes, pers. comm.).

## GENERAL DISCUSSION

Although in recent times there has been a small number of studies on *H. griseus* and *N. cepedianus*, overall knowledge on almost all aspects of the biology, ecology and fisheries impacts on Hexanchiformes is still rudimentary. In general, there are no reliable quantitative indicators of the conservation status of Hexanchiformes with the exception of *N. cepedianus* in south-eastern Australia. Assessments are hindered by a scarcity of time series of catch and abundance information and key life-history data such as the length of the reproductive cycle and growth variable estimates (see Braccini *et al.*, 2010 for *N. cepedianus* growth analysis). By-catch estimates are largely unknown, as is the proportion of discarded individuals killed during the fishing process. Current species assessments are largely based on expert judgement

and the application of the precautionary approach where *C. anguineus*, *H. griseus* and *H. perlo* were classed as near threatened on the assumption that their life-history traits, though incompletely known, do not allow for almost any fishing exploitation, despite the level of such exploitation being largely unknown. Furthermore, Hexanchiformes remain a low priority for fishery management agencies, further jeopardizing the collection of time series of fisheries and abundance data. If stocks were actually overexploited, this could go unnoticed given that Hexanchiformes are mostly taken as by-catch of multispecies fisheries where yields can be sustained by more productive species (Graham *et al.*, 2001). The worldwide expansion of deep-water fisheries over the last decades is likely to further increase the risk of stock overexploitation and overfishing.

To improve the conservation status assessment of Hexanchiformes and to establish the management measures required for sustainable exploitation, there is a clear need to initiate the regular collection of fisheries data and to improve understanding of key life-history information. In particular, there is a paucity of basic information for *H. perlo*, *H. nakamurai* and *Chlamydoselachus* species. Using the information available for *N. cepedianus* and *H. griseus* as indicators for Hexanchiformes, it can be argued that sharks of the order Hexanchiformes, although lacking the diversity of the major shark orders, play an integral role in the marine environment, particularly as there are very few or no other species that consume such high trophic level prey in the habitats where Hexanchiformes occur. The distribution, movement and diets of Hexanchiformes suggest they could move between different habitat types (on both a daily and a seasonal basis), and therefore link coastal and deep-water habitats. Although more work is needed to clarify the ecological role of the different species from this order in most systems, Hexanchiformes have the potential to play important roles in regulating coastal and deep-water systems. For most of the deep-water species, the sparse biological and ecological information available prevents any prediction of the effects of their removal through fishing exploitation. There is arguably enough information, however, for *N. cepedianus* to predict that their removal from coastal systems could have considerable ecosystem dynamics consequences.

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#### APPENDIX. KEY TO HEXANCHIFORMES (MODIFIED AFTER EBERT & COMPAGNO, 2012)

- 1a. Head snake-like, with short snout and terminal mouth. Teeth tricuspidate in both jaws. Body elongated and eel-like. Family Chlamydoselachidae. 2.
- 1b. Head not snake-like, with moderate snout and subterminal mouth. Teeth cuspidate in upper jaw and compressed and comb-like in lower jaw. Body moderately stout and not eel-like. Family Hexanchidae. 3.
- 2a. Total vertebral centra 147, MP-DP transition at 18th vertebral segment just behind the posterior end of the pectoral fins. Spiral intestinal valve counts 26–28. Head length ( $L_H$ ) 17.3–17.9%. *Chlamydoselachus africana*.
- 2b. Total vertebral centra 160–171, MP-DP transition between the 72nd and 75th vertebral segment and occurs about over the pelvic fins. Spiral intestinal valve counts 35–49.  $L_H$  13.1–16.2% of total length ( $L_T$ ). *Chlamydoselachus anguineus*.
- 3a. Six pairs of gill openings. 4.
- 3b. Seven pairs of gill openings. 5.
- 4a. Snout shorter, blunt and broad; lower jaw usually with six rows of large, comb-like anterolateral teeth on each side; dorsal fin base separated from upper caudal fin origin by a distance about equal to or slightly greater than its length; size very large, up to 4.7 m  $L_T$ . *Hexanchus griseus*.
- 4b. Snout longer, more pointed and narrow; lower jaw usually with five rows of large, comb-like anterolateral teeth on each side; dorsal fin base separated from upper caudal fin origin by a distance much greater than its length; size smaller, up to 1.8 m  $L_T$ . *Hexanchus nakamurai*.
- 5a. Eyes very large, head extremely narrow and pointed. Body plain without spots; size small, to c. 1.4 m  $L_T$ . *Heptranchias perlo*.
- 5b. Eyes small, head broad and rounded. Body usually with scattered small black spots and sometimes white spots. Size larger, to c. 3.0 m  $L_T$ . *Notorynchus cepedianus*.