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Plasticity of trophic interactions among sharks from the oceanic south-western Indian Ocean revealed by stable isotope and mercury analyses

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ABSTRACT

Sharks are a major component of the top predator guild in oceanic ecosystems, but the trophic relationships of many populations remain poorly understood. We examined chemical tracers of diet and habitat ($\delta^{15}N$ and $\delta^{13}C$, respectively) and total mercury (Hg) concentrations in muscle tissue of seven pelagic sharks: blue shark (*Prionace glauca*), short-fin mako shark (*Isurus oxyrinchus*), oceanic whitetip shark (*Carcharhinus longimanus*), scalloped hammerhead shark (*Sphyrna lewini*), pelagic thresher shark (*Alopias pelagicus*), crocodile shark (*Pseudocarcharias kamoharai*) and silky shark (*Carcharhinus falciformis*), from the data poor south-western tropical Indian Ocean. Minimal interspecific variation in mean $\delta^{15}N$ values and a large degree of isotopic niche overlap – driven by high intraspecific variation in $\delta^{15}N$ values – was observed among pelagic sharks. Similarly, $\delta^{13}C$ values of sharks overlapped considerably for all species with the exception of *P. glauca*, which had more ^{13}C-depleted values indicating possibly longer residence times in purely pelagic waters. Geographic variation in $\delta^{13}C$, $\delta^{15}N$ and Hg were observed for *P. glauca* and *I. oxyrinchus*. Mean Hg levels were similar among species with the exception of *P. kamoharai* which had significantly higher Hg concentrations likely related to mesopelagic feeding. Hg concentrations increased with body size in *I. oxyrinchus*, *P. glauca* and *C. longimanus*. Values of $\delta^{15}N$ and $\delta^{13}C$ varied with size only in *P. glauca*, suggesting ontogenetic shifts in diets or habitats. Together, isotopic data indicate that – with few exceptions – variance within species in trophic interactions or foraging habitats is greater than differentiation among pelagic sharks in the south-western Indian Ocean. Therefore, it is possible that this group exhibits some level of trophic redundancy, but further studies of diets and fine-scale habitat use are needed to fully test this hypothesis.

1. Introduction

Sharks are a major component of the top predator guild in open-ocean ecosystems along with tunas, billfish, and cetaceans. These "pelagic sharks" occur from cold temperate to tropical waters, from the surface to 1000 m depth or more (Compagno, 2008) and include some of the most wide-ranging marine predator species (Pitkitch et al., 2008). Their extensive movements and ocean-basin scale migrations are most likely related to oligotrophy and the patchy nature of food resources in open-ocean ecosystems as well as directed movements for social and reproductive purposes. Many pelagic sharks use coastal/continental shelf waters in addition to open oceanic waters throughout ontogeny although certain biological functions, for example, gestation may be restricted to the open ocean (Compagno, 1984; Bonfil, 2008; Nakano and Stevens, 2008). Even though pelagic sharks commonly occur in an environment far from human populations, they commonly overlap and interact with offshore fisheries. Currently, three-quarters of pelagic elasmobranchs are classified as Threatened or near Threatened (IUCN Red List Status), and 11 species are globally threatened with a high risk of extinction (Dulvy et al., 2008). Despite clear evidence for shark population declines, including in oceanic ecosystems (Baum et al., 2003; Myers and Worm, 2003; Ferretti et al., 2010), relatively little is known on the feeding ecology of many species and the ecological importance of this guild is poorly understood (Ferretti et al., 2010; Heithaus et al., 2010; Kitchell et al., 2002).

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Sharks can play important roles in marine ecosystems through diverse mechanisms, but their relative importance may vary significantly among ecosystems, species and contexts (Heithaus et al., 2008, 2010). While the decline of large predatory sharks in some coastal ecosystems may initiate trophic cascades and affect overall community structure (see Heithaus et al., 2008; Ferretti et al., 2010 for reviews), it is still unclear whether the removal of pelagic sharks affects community structure in open-ocean ecosystems (Stillwell and Kohler, 1982; Ward and Myers, 2005). Evidence from ecosystem models from the central Pacific Ocean suggest pelagic shark declines may be mitigated by compensatory increases in populations of large teleosts (Kitchell et al., 2002). However, these models generally categorize pelagic sharks into a single homogenous trophic group when in fact there may be interspecific variation in habitat use and trophic interactions resulting in greater trophic complexity and less trophic redundancy than assumed for pelagic ecosystems. More ecological data on the relative trophic position and trophic interactions of oceanic sharks is required to test such model assumptions. If species are functionally redundant (i.e. they occupy similar trophic niches, hence consume the same prey base and perform the same functional role; Walker, 1992), the loss of one or several may not result in large scale community rearrangements because of compensation by other species (e.g. Kitchell et al., 2002), but rather density compensation effects among the remaining species (Walker, 1992). Recent studies suggest that sympatric shark species show considerable variation in trophic interactions (Hussey et al., 2011; Kinney et al., 2011; Speed et al., 2011). However, patterns of trophic redundancy within a given community are likely to be biologically and environmentally context-dependent (e.g. ocean productivity, intra-guild species richness), and are expected to vary accordingly.

In the tropical Indian Ocean (between 10°N and 10°S), the most commonly caught pelagic sharks are blue (*Prionace glauca*), silky (*Carcharhinus falciformis*), pelagic thresher (*Alopias pelagicus*) and short-fin mako sharks (*Isurus oxyrinchus*). Between 10°S and 25°S, sharks are less abundant and the community is dominated by *P. glauca* and *I. oxyrinchus* (Huang and Liu, 2010). Despite evidence for high bycatch levels of pelagic sharks in the Indian Ocean (Romanov, 2002; Huang and Liu, 2010), there is a paucity of reliable data to facilitate assessing historical changes in shark catch rate trends (Smale, 2008). Similarly, knowledge on the trophic ecology of pelagic sharks is limited in the Indian Ocean (and globally), particularly at the community level (Rabehagasoa et al., 2012).

The use of naturally occurring carbon and nitrogen stable isotopes provide chemical tracers to examine the ecology of organisms in a given ecosystem. Carbon and nitrogen stable isotopic ratios (δ^{13}C and δ^{15}N) can depict the food webs in which consumers are foraging and their relative trophic position, respectively (Hobson, 1999). Stable isotope analyses may provide complementary or, in some cases, an alternative method to traditional diet (e.g. based on analyses of stomach contents) and costly habitat and movement methodologies (e.g. telemetry). They have already been successfully used to understand elasmobranch ecology, including community trophic interactions and ontogenetic variation in trophic position and foraging habitats (Hussey et al., 2011; Kinney et al., 2011; Vaudo and Heithaus, 2011).

Mercury (Hg) is a non-essential metal that is released from natural (e.g. volcanism) and anthropogenic sources (e.g. discharge by hydroelectric industries, mining), reaching the open ocean through runoff, riverine input and atmospheric deposition (Fitzgerald et al., 2007). Mercury provides an indicator of foraging habitats and trophic position of large marine predators because body burden concentrations are highly correlated to size/age, environmental

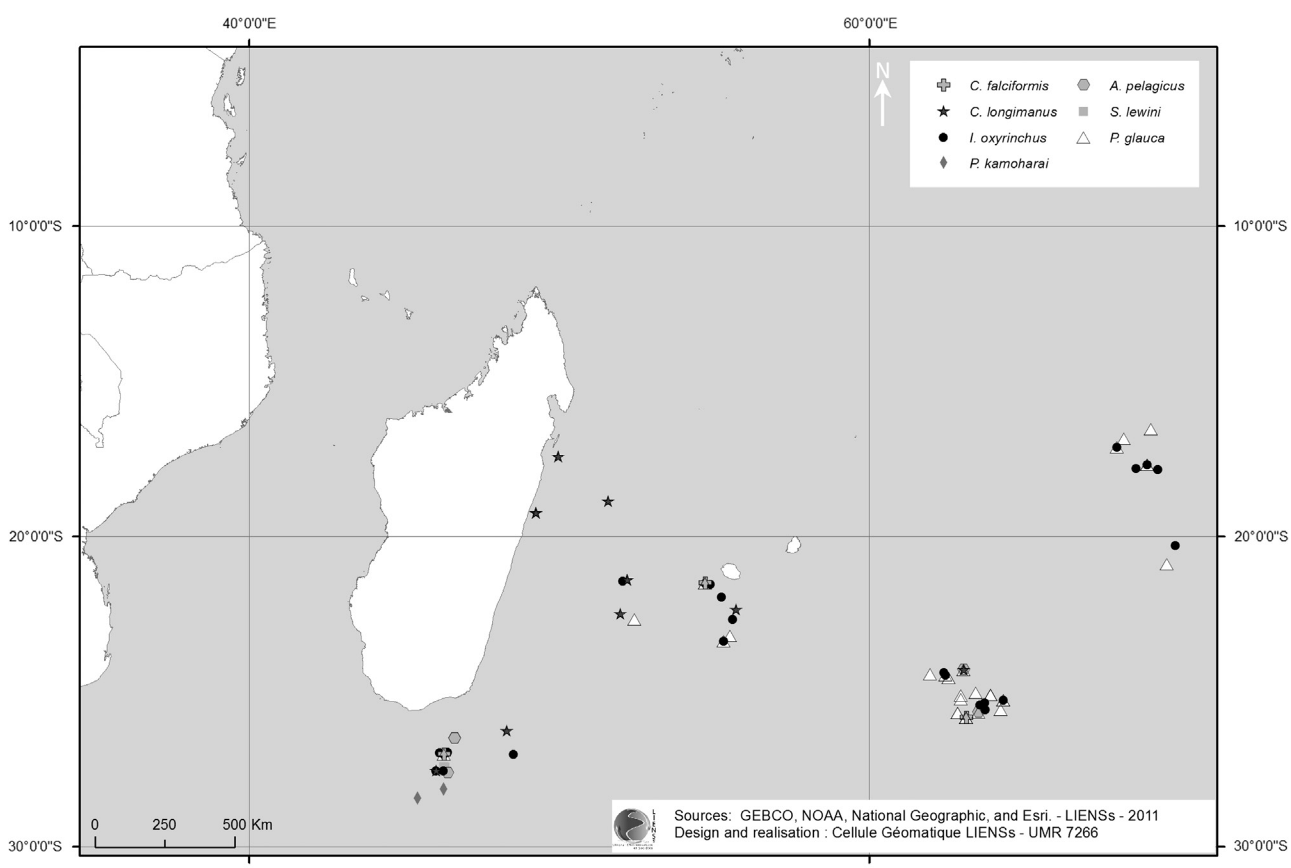

Fig. 1. Distribution of sampled oceanic sharks in the south-western Indian Ocean ($n=92$).