Trophic ecology of sharks around Baja California Sur, Mexico : resource partitioning, ontogenetic shifts and conservation perspectives

Lucien Besnard

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DOCTORAT SCIENCES BRETAGNE DE LA MER LOIRE ET DU LITTORAL

UBO
Université de Bretagne Occidentale

THESE DE DOCTORAT DE

L'UNIVERSITE
DE BRETAGNE OCCIDENTALE

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Sciences de la Mer et du littoral
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Par
Lucien BESNARD

Trophic ecology of sharks around Baja California Sur, Mexico: resource partitioning, ontogenetic shifts and conservation perspectives.

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LUCIEN BESNARD

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There’s always a bigger fish.

- Qui-Gon Jinn

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Au fil de l'élaboration de cette thèse, la question de l'origine de ma passion pour les requins, ainsi que le monde marin, est souvent revenue. Bien que cela reste encore en partie un mystère, le souvenir de ces après-midis chez mes grands-parents où, assis devant les films du commandant Cousteau, je me livrais à ma première exploration de ce qui deviendrai une passion au-delà du champ professionnel, reste profondément gravé. Je me revois découvrir la plongée sous-marine en compagnie de ma sœur à Marseille, de ces moments suspendus où la gravité est perdue, une « plongée » dans un nouvel univers où l'enfant refait surface, apprenant à se déplacer et à communiquer dans un monde dont on ne possède pas les codes. Pour un si grand fan de science-fiction, le but ultime n'est-il pas de comprendre cet univers parallèle, à la fois si proche, si accessible, mais hors de notre portée ?

Force est de constater qu'au moment de terminer ce chapitre important de ma vie, cet amour du voyage, de la découverte, de l'échange et du partage apparaissent comme une composante majeure de l'éducation qui m'a été inculquée. Je remercie ainsi naturellement mes parents et plus largement ma famille pour la soif de curiosité qu'ils m'ont transmis et qui les anime. Ils m'ont laissé entrevoir la multitude de possibilités que le monde pouvait offrir et, aujourd'hui, je prends pleinement conscience de l'incroyable chance que représente le fait de pouvoir choisir.

Je remercie ma sœur et meilleure amie, Juliette, qui partage cette même curiosité et dont le soutien indéfectible et l'amour qu'elle me porte ont su me redonner force et courage dans les épreuves difficiles. Je ne serai pas allé aussi loin sans sa présence et sa gentillesse. Mes pensées vont aussi vers Alice, ma petite sœur, dont le sourire et la joie de vivre m'ont accompagné tout au long de ces quatre années.

Ma passion, tout ce que j'ai pu accomplir et tout ce que je suis devenu je le dois entièrement à mes parents, à mes sœurs et à ma famille.

J'ai aussi la chance d'avoir une seconde famille dont les membres forment un étrange mélange de personnalités singulières toutes aussi attachantes les unes que les autres. Je remercie fortement ces compagnons d'aventure. Mon parcours de ces dernières années m'a emmené loin de vous et pourtant j'ai constamment la chance, chaque fois que je vous revoie, de ressentir qu'il ne s'était pas passé une semaine depuis mon départ. J'ai une pensée toute particulière pour Nicolas, à qui je souhaite de trouver l'écosystème dans lequel il s'épanouira. Je remercie Raphaël, ce brillant autodidacte que rien ne semble vraiment pouvoir arrêter, pour son soutien et ces nombreuses conversations qui m'ont permis de m'échapper des pressions de la thèse quand elles devenaient trop fortes. Il y aurait trop d'anecdotes à raconter sur Simon, qui m'accompagne depuis l'enfance, ainsi que dans mes nombreux voyages, et qui témoignera de la naissance du premier article scientifique entièrement rédigé sur une table de ping-pong sous le soleil de Provence. J'ai une pensée particulière pour Charles avec qui je partage un nombre incalculable de fous rires et pour Thomas, notre futur parigot Pulitzer dont la persévérance le mènera loin.

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Plusieurs personnes ont revêtu pour moi des capes de super-héros au cours de ces quatre dernières années, les premières que je souhaite remercier sont Gaël et Gauthier. Au-delà de nos passionnantes conversations scientifiques, votre bienveillance, votre appui ainsi que votre positivité ont été les piliers de la réussite de cette thèse. J'espère que l'avenir nous permettra de continuer à travailler ensemble et fera naître de nouveaux projets. Après tout Gauthier, des estrans rocheux aux grands requins blancs, il n'y a qu'un pas ! J'ai aussi une reconnaissance particulière pour Doudou qui a su donner sa chance au petit étudiant de M2 qui, naïvement, voulait travailler sur les requins. Ce projet n'aurait pas pu être construit sans toi.

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CHAPTER 1

GENERAL INTRODUCTION

On the needs and the means to study shark trophic ecology: the case of Baja California Sur, Mexico.

1. Underlying ecological concepts

a. Darwin and the ecological niche

In the revolutionary book “On the Origin of Species by means of Natural Selection, or Preservation of Favoured Races in the Struggle for Life.” published in 1859, Charles Darwin paved the way to the emerging field of evolutionary biology. Beyond the concept of common ancestry within the “great tree” of life and the way species originate from variation and selection, he was also the first to observe that species occupy a “space”, a certain “role” in their habitat (later to be named “ecological niche”), and that this “space” was subject to competition. The fact that species limit each other's growth is incidentally one of the basic findings that led Darwin to formulate his theory (Darwin, 1859). In the middle of the 19th century, Charles Darwin therefore presented, without naming them, the premises of what will be two fundamental concepts in ecology: the ecological niche concept and the competitive exclusion principle.

The first mention of the word “niche” to define the factors, abiotic or biotic, that condition the existence of one population in a given space can probably be attributed to Joseph Grinnel (Grinnell, 1917; Grinnell and Swarth, 1913). The word “niche” was later found in a food-web related approach in Charles S. Elton works where it is associated to the position of a given species in its food chain (Elton, 1927). While Grinnel’s and early conceptions of the niche referred to environmental attributes, the concept took a new dimension in 1957 when George E. Hutchinson proposed that the niche could be seen as an attribute of the population rather than of the environment (Hutchinson, 1957). He thus defined the niche as it is generally accepted today: the “space” a population occupies in an ecosystem given its “fitness” (or “performance”) toward abiotic factor variations, available resource fluctuations (i.e., both food and habitat) and biotic interactions (Hutchinson, 1957). This “space” can be seen as an *n* dimension hypervolume with *n* the number of factors and their associated variations a population can thrive in (and eventually growth and reproduce depending on the definition).

Hutchinson further differentiated two different niches: the “fundamental” and the “realized”. The fundamental niche is the nearly mathematical sum of all factor variations a species can cope with, and can be seen as its possible “maximum” expansion range in the environment. However, field observations generally reveal that the fundamental niche of a species is not met in natural conditions, and that

populations occupy a narrower niche, the realized niche (Figure 1-1). As theorized by Hutchinson, inter-specific interactions, among which competition, play a key role in explaining the gap between fundamental and realized niches (Hutchinson, 1957).

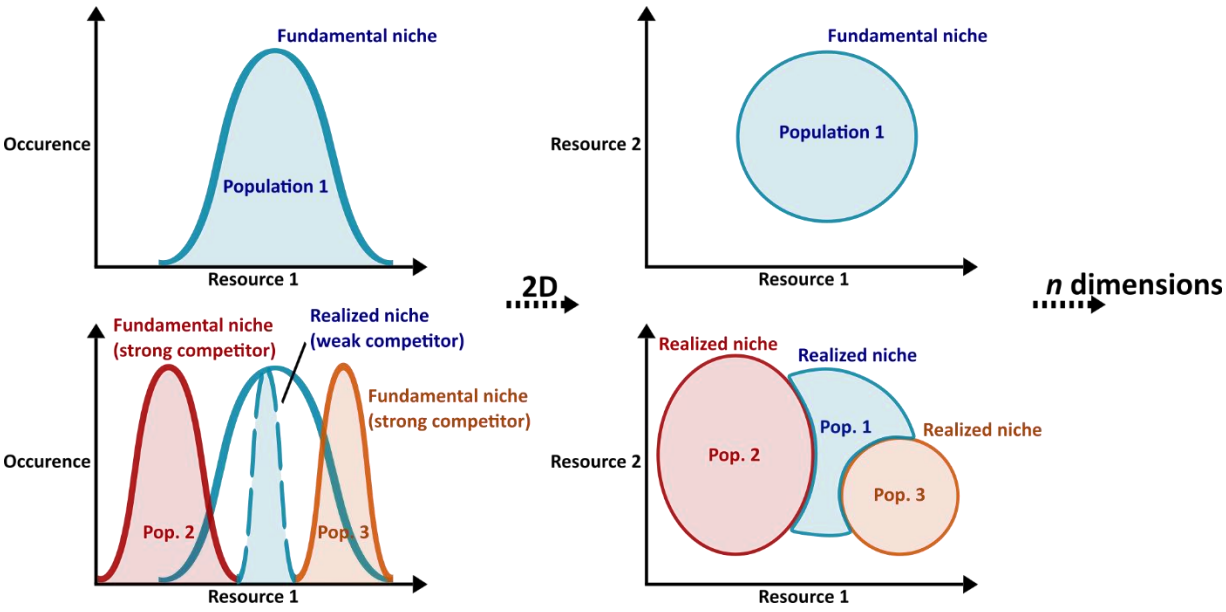


Figure 1-1 – Hutchinson's fundamental and realized niche concepts (Hutchinson, 1957). Population 1 can live in a large range of resource 1 and resource 2 variations (fundamental niche) but narrows its niche due to the occurrence of stronger competitors in natural conditions (realized niche).

b. The competitive exclusion principle

Since Darwin and Grinnel works, the niche concept has been closely related to the competitive exclusion principle (Pocheville, 2015). Generally attributed to Georgy F. Gause and based on Volterra's mathematical approach (Volterra, 1926), the competitive exclusion principle (i.e., also called the "Gause principle") implies that two species occupying, in the same homogenous environment, equivalent niches cannot coexist, resulting in the fittest one (i.e., the more competitive) excluding the other one (Gause, 1934). Therefore, analogous species, rather than competing for limited resources, need to divide the resource pie to survive, a mechanism called "resource partitioning".

Resource partitioning is a common characteristic of co-existing species in shared ecosystems and can be found in both animals and plants (Kahmen et al., 2006; Schoener, 1974). It implies the separation of habitats but also food resources between

analogous species (Schoener, 1974). The most striking studies depicting resource partitioning phenomenon dates from 1958 when five different warblers species in coniferous forest were shown to use different resources and space inside trees to reduce food and habitat competition between them (MacArthur, 1958). From a pure habitat partitioning perspective, a commonly cited example explores the competition between barnacles, *Semibalanus balanoides* and *Chthamalus stellatus*, in the inter-tidal zone. Even if both species present equivalent fundamental niches, the first one, by its higher density of population and growth rate, induces an important mortality on the second one when co-existing, reducing the realized niche of *C. stellatus* much higher in the shore compared to the area inhabited by *S. balanoides* (Connell, 1961). Finally, a key example for food partitioning (e.g., access to nutrients and/or prey) is the description of bumblebee species foraging behaviors. In Colorado, seven bumblebee species feed on different flowers according to their proboscis lengths and the flower corolla lengths displaying efficient food resource partitioning (Pyke, 1982). Of particular interest, competition avoidance has led to character displacement through evolution like the one observed in Darwin's finches. Within 22 years after the arrival of a strongest competitor in remote islands, medium ground finch (*Geospiza fortis*) beak morphology changed, resulting in a specialization on a different resource, thereby reducing inter-specific competition (Grant and Grant, 2006).

The competitive exclusion principle is therefore a key ecological driver shaping ecological niches in all ecosystems. The resulting partitioning of the resource is nowadays recognized as an important mechanism for species coexistence and, as a result, is of particular importance in maintaining species diversity globally (Chesson, 2000). It allows an optimization of the resource exploitation in animal communities and is essential to maintain ecosystems balance and services (Finke and Snyder, 2008; Griffin et al., 2008).

c. Trophic niches and cascading effects

Trophic ecology studies the implications of feeding, which includes food acquisition and its consequences for individuals, populations, communities and the functioning of ecosystems (Majdi et al., 2018). By extension of the above-described concepts, trophic ecology focuses on trophic niches, which can be seen as a list of potential/consumed preys, a dynamics of nutrient intakes or a description of foraging areas and behaviors.

Trophic interactions have tremendous impacts on populations and ecosystem structure, as illustrated by the famous “Green World Hypothesis”, assuming that plants dominate terrestrial ecosystems due to the odd number of trophic levels they generally host, resulting in a regulation of herbivores by predators (Hairston et al., 1960).

At the base of marine or freshwater food webs, primary producers mostly rely on nutrient availability (Morel, 1987; Tilman et al., 1982). Their biomass, composition and temporal/spatial dynamics are fundamental for the establishment of complex food webs. The structural organization of some ecosystems depends almost exclusively on nutrients or basal species biomass variations via “bottom-up” control (e.g., Matsuzaki et al., 2018). At the other end of food webs, predators can influence their entire ecosystems trough consumption of mesopredators via “top-down” effects. A clear illustration of the top-down control under semi-controlled conditions was published by Carpenter et al. in 1987. Manipulating biomasses of predators in Canadian lakes, authors showed that lakes whole-conditions depend equally on both nutrient and predator biomasses due to their trophic regulation of the entire food web. Finally, ecosystem structure can also be controlled by intermediate consumers. Such “wasp-waist” ecosystems can be found in upwelling systems where small pelagic species (e.g., small fish schools or cephalopods) by their larger biomass play a pivotal role in the control of their predators (by bottom-up linkages) and of their planktonic food (by top-down linkages) (Cury et al., 2000). Trophic niches and dietary interactions within food webs are therefore crucial to understand the dynamics of the whole ecosystem (Figure 1-2).

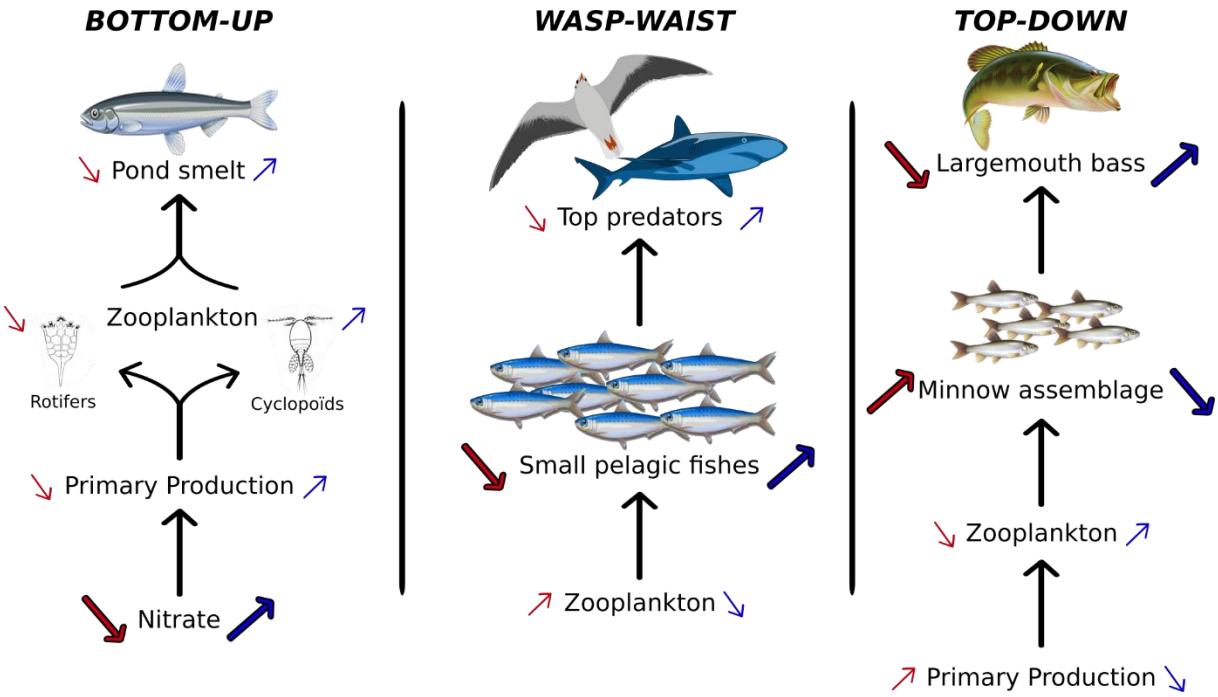


Figure 1-2 – Three different trophic controls of community structure. Bold arrows represent the initiation of the trophic cascades. Bottom-up mechanisms are presented with the case study of Lake Kasumigana (Japan) and the effect of nitrate inputs on the whole system including the pond smelt, Hypomesus nipponensis (Matsuzaki et al., 2018). Wasp-waist control is illustrated by the case of productive upwelling systems where small plankton-feeding pelagic fishes, by their dominant biomass, are affecting zooplankton and top predator biomass (Cury et al., 2000). Top-down control is illustrated by the experiments in Tuesday Lake and Peter Lake (Canada). Studied species were largemouth bass (Micropterus salmoides) and minnow assemblages (redbelly dace, Phoximus eos; finescale dace, P. neograeus; central mudminnows, Umbra limi) (Carpenter et al., 1987). Food webs presented here are a simplification based on the cited published studies.

Obviously, such controls can coexist and vary in intensity trough time and uncertainty on which mechanism is dominant remains in a vast majority of ecosystems (Cury et al., 2000; Hunter and Price, 1992; Ritchie and Johnson, 2009; Roff et al., 2016). An example of such complexity is the top-down control exercised by sea otters (*Enhydra lutris nereis*) on purple sea urchins (*Strongylocentrotus purpuratus*) and kelp forests in the Aleutian archipelago (Estes and Palmisano, 1974; Reisewitz et al., 2006). Relative high otter abundance on the islands supports the development of healthy kelp forests by their predation on sea urchins, a major kelp grazer. Sites with few otters are characterized by an important biomass of sea urchins and few kelps at the sea bottom due to a top-down trophic cascade. However, recent developments showed a higher level of complexity driven by fine-scale sea otter foraging strategies in response to prey dynamics, reducing the overall strength of the top-down forcing previously described

and revealing feedbacks between bottom-up and top-down processes (Smith et al., 2021). This highlights the complexity of the dynamics between top-down and bottom-up regulation, which can vary in importance trough time and space with high impact on ecosystem functioning and characteristics.

Nowadays, a global decrease in predator populations is observed worldwide, limiting the influence of top-down mechanisms with cascading consequences nearly impossible to anticipate (Estes et al., 2011; McCauley et al., 2015). Of particular interest in marine systems, the decline of shark populations in the world ocean has raised concerns in the scientific community (Myers and Worm, 2003; Pacoureau et al., 2021; Roff et al., 2018). Overfishing bears the main responsibility in the decrease of these populations (Figure 1-3), sharks being extensively caught both as by-catch and as targeted species, principally for their fins and meat (Dulvy et al., 2021; Ferretti et al., 2010; Food and Agriculture Organization of the United Nations (FAO), 2015; Pacoureau et al., 2021). While coastal sharks are affected by both industrial and artisanal fisheries, it appears there are no available refuges in the high sea for pelagic species whose movements extensively overlap with fishing efforts at a global scale (Queiroz et al., 2019). Due to some peculiar ecological (i.e., slow growth, low reproduction rate, late maturity), behavioral (i.e., schooling, use of multiple habitats, important movements) and physiological (i.e., low post-release survival rates) traits, shark populations may be significantly affected even when being targeted by small local fisheries (Ferretti et al., 2010; Gallagher et al., 2014a). In the meantime, habitat loss and degradation (especially regarding coastal nursery sites such as mangroves and seagrass beds), as well as climate change, also contribute to the current decline of shark populations worldwide (Figure 1-3). In 2014, 24% of chondricthyans (i.e., sharks, rays and chimaeras) were considered threatened with extinction, increasing to 32.6% in 2021 (Dulvy et al., 2021, 2014).

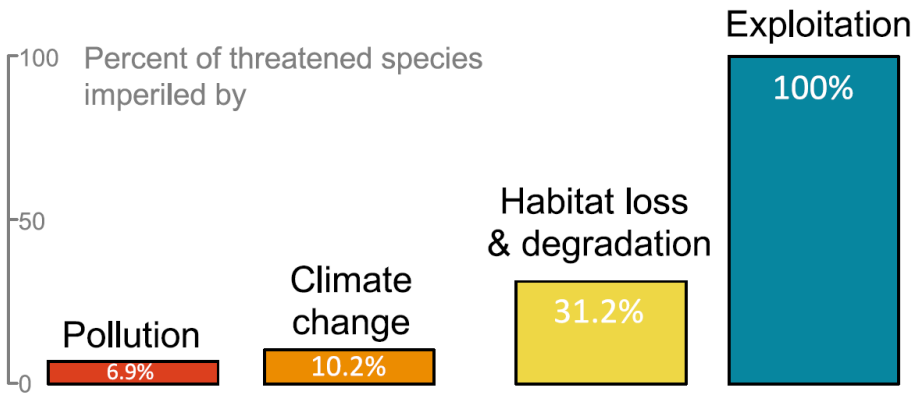


Figure 1-3 – Risks associated to threatened chondrichthyans species worldwide (according to the IUCN Red List). Bar chart corresponds to the percentage of species for which each threat was reported (Dulvy et al., 2021).

The decline of large top predator shark species might induce trophic cascades resulting in mesopredators being released from top-down control, with potential changes in their distribution and behavior. This is due both to the direct consumption effect and to the indirect fear effect sharks have on their prey (Hammerschlag et al., 2015; Heithaus et al., 2008; Suraci et al., 2016). Overall, the strength of potential trophic cascades induced by the decline of shark populations could depend on the ecosystem biological diversity and on the diet and foraging behavior of sympatric species of equivalent trophic guilds. Putative top-down cascading effects have been observed in coastal environment but can be difficult to detect as they are often masked or inversed by fishery or environmental pressures affecting mesopredators release. Moreover, undescribed predator-prey interactions or lack of knowledge on ecosystems functioning make the analysis of trophic cascades difficult in marine environments (e.g., Ferretti et al., 2010; Roff et al., 2016). Understanding the trophic ecology of top predator species is therefore fundamental, particularly in regions where sharks are critically overfished to gain information on the possible effects of their decline. This objective is however difficult to achieve given the complexity and diversity of large shark trophic niches.

2. Sharks in marine ecosystems

a. Habitats

Inhabiting the ocean since approximately 400 million years (Long, 1995), chondrichthyan fishes, characterized by their cartilaginous skeletons, count more than 1200 species including chimeras, skates, rays and sharks. Throughout evolution,

sharks have colonized nearly all marine habitats from coastal shallow to pelagic deep waters, from warm tropical to polar Artic regions, some of them even known for inhabiting freshwater riverbeds (Compagno, 2001). Nowadays, with more than 500 species of sharks described and some still regularly discovered (e.g., Cordova and Ebert, 2021), they display an incredible range of reproduction modes, ecological traits and adaptations to many different habitats.

The large majority of what is known about the ecology of sharks is derived from studies carried out in coastal areas. Coastal ecosystems are key habitats for many shark species, encompassing a broad diversity of dynamics, shaping their distributions and movements worldwide. Due to their high productivity, coastal environments first represent an important source of food like in mangroves (Heithaus et al., 2011) or coral reefs (Roff et al., 2016). These ecosystems also cover a broad range of functionalities, such as reproduction, resting (e.g., to avoid intra-guild aggressive behaviors) or thermoregulation areas to maintain/restore energy needed to support metabolic rate, growth and/or embryonic development (Knip et al., 2010).

Of particular interest, nearshore habitats can be used as nursery areas hosting important densities of neonates, young-of-the-year and juveniles seeking protection against predators, and higher food availability, allowing lower mortality and faster growth rate (Heupel et al., 2018, 2007; Knip et al., 2010; Lyons et al., 2020; McMillan et al., 2021). Coastal nurseries are particularly used by large-bodied shark species of low productivity to enhance recruitment in adult populations (Heupel et al., 2018). Compared to other habitats occupied by early life stages, nurseries are classically identified following three criteria: 1) the area hosts an higher abundance of newborn and young-of-the-year individuals where 2) they spend an important amount of time and 3) this area is used repeatedly across years (Heupel et al., 2007). Nurseries can be found in bays (Duncan and Holland, 2006; García-Rodríguez et al., 2021) or estuaries (Matich and Heithaus, 2014; Murchie et al., 2010; Rosende-Pereiro et al., 2018). Most of the time, these nurseries are shared among juveniles from several species, which coexist in the absence of adult specimens (Heupel et al., 2018). In many shark species, juveniles leave their coastal nursery grounds to avoid food competition between young and adults (Hussey et al., 2011; Shiffman et al., 2014). A single species or population will use several nursery areas and may show philopatric patterns (i.e.,

return of gravid females to their nursery ground/region for parturition) (Chapman et al., 2015; Heupel et al., 2018; Knip et al., 2010).

After leaving their nursery grounds, sharks generally inhabit pelagic environments and some species are recognized as nearly exclusive pelagic such as blue sharks, *Prionace glauca* (Clarke, 1996; Vandeperre et al., 2014), or oceanic whitetip sharks, *Carcharhinus longimanus* (Musyl et al., 2011; Young and Carlson, 2020). The pelagic ecosystem is one of Earth's largest biomes and extends both horizontally and vertically, offering a vast three-dimensional habitat. Vertically, oceanic ecosystems go far beyond the epipelagic layer (~200 m) and host one of the largest animal biomass on Earth, the so called "deep scattering layer", composed of mesopelagic fishes and invertebrates (Aksnes et al., 2017; Davison et al., 2015; Proud et al., 2017). The deep scattering layer is a key component in trophic webs as a source of food for marine fauna (including sharks) that forage across large depth gradients (Braun et al., 2022; Madigan et al., 2018). Predators may find more diffuse and higher prey biomasses at mesopelagic depths than in the epipelagic zone (Figure 1-4), particularly in oligotrophic conditions (i.e., low primary production rates not supporting prey biomass in the epipelagic layer) (Braun et al., 2019; Gaube et al., 2018; Hazen and Johnston, 2010; Irigoien et al., 2014; Polovina et al., 2008).

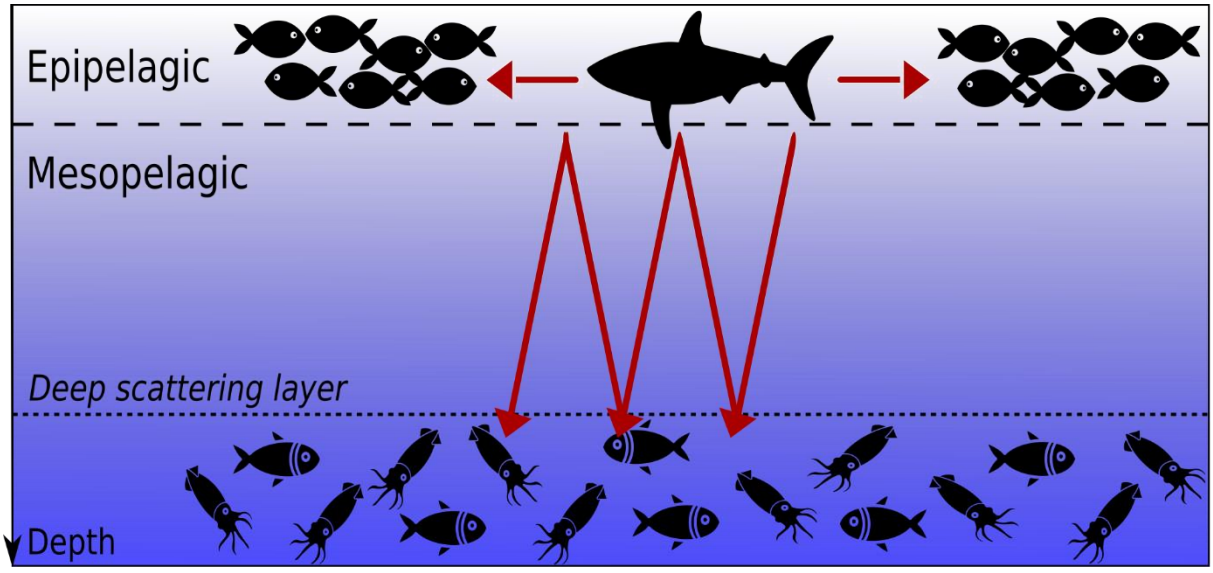


Figure 1-4 – Shark foraging strategies in offshore pelagic ecosystems. Sharks can either feed on concentrated epipelagic prey or diffused mesopelagic prey inside the boundaries of the deep scattering layer.

Coastal or oceanic large shark species can be highly migratory, connecting multiple habitats and biogeographic regions. In Australia, bull sharks are known for connecting tropical and temperate waters as well as coastal and offshore habitats (e.g., Heupel et al., 2015). Migrations can occur at the scale of ocean basins or at finer scale, with sharks targeting specific areas for reproduction (Fujinami et al., 2021) or foraging (Carlisle et al., 2012; Jorgensen et al., 2012). Movements can also be linked to environmental conditions (e.g., oxygen levels, sea surface temperature …) or topographic features (Schlaff et al., 2014; Vandeperre et al., 2016; Vögler et al., 2012).

b. Trophic ecology

The trophic role of sharks in marine food webs ranges from mesopredators to apex predators (Cortés, 1999; Heupel et al., 2014; Hussey et al., 2015; Munroe et al., 2014a). Owing to their size and hunting capacities, some shark species have the potential for wide fundamental trophic niches. For example, stomach content analysis of tiger sharks (*Galeocerdo cuvier*) from South Africa identified 193 different prey species (Dicken et al., 2017). However, fundamental trophic niches are generally not met, as apex predators are usually specialized on a limited diversity of prey (concentrated predation) compared to mesopredators (diffuse predation) (Heupel et al., 2014). These narrow realized trophic niches can be explained by different factors among which prey availability (spatial and temporal variations), ontogenetic diet shift, resource partitioning, energetic trade-off, prey selection, fear effect, climate change and anthropogenic pressures (Figure 1-5).

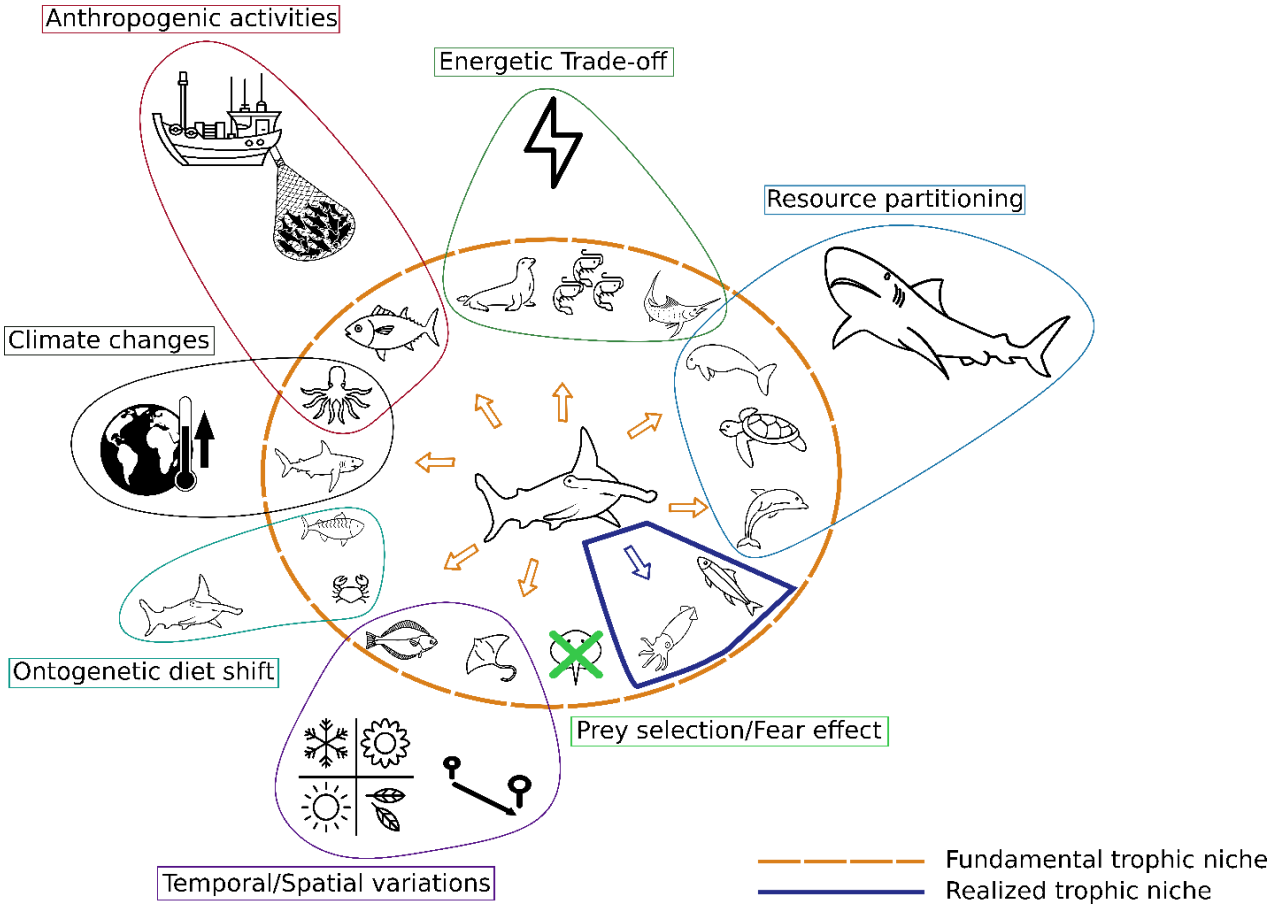


Figure 1-5 – Shark realized trophic niche (i.e., observed in its ecosystem) is generally narrower than all the prey theoretically available in its environment (or fundamental trophic niche).

Shark trophic niches first depend on the spatial and temporal availability in prey resources (e.g., Young et al., 2015). For migratory species, trophic niches might reflect ecosystem species composition rather than true dietary preferences (Lopez et al., 2010). For instance, different populations of scalloped hammerhead sharks (*Sphyrna lewini*) that use different nurseries with unique prey species composition, are characterized by major differences in the diet of young-of-the-year between spatially distanced areas (Bethea et al., 2011; Bush, 2003). The impact of spatial and temporal arrangement of food webs on the diet and foraging activities of sharks has also been reported for shortfin mako sharks (*Isurus oxyrinchus*). In the Atlantic Ocean, this species migrates seasonally from oceanic waters to continental shelf or inshore ecosystems, switching its diet from mostly squid to teleost species (Harford, 2013; Stillwell and Kohler, 1982). In the meantime, they are also known to opportunistically adapt their diet to locally high biomasses of certain prey, as observed for the “bloom”

of crustaceans in Portugal (Maia et al., 2006) or for increased abundances of squids in Californian waters (Preti et al., 2012; Vetter et al., 2008).

Shark observed trophic niches also depend on ontogenetic dietary and habitat shifts, which are common in elasmobranchs. Ontogenetic diet shifts are observed in large predator populations, due to increasing body length, mouth gap and stomach size, hunting capacities and energetic demands, or to avoid intra-specific competition. For example, bull sharks are known to switch from estuaries to marine environments throughout their growth in Florida to avoid intra-specific competition, an ontogenetic shift associated to dietary modifications (Belicka et al., 2012; Matich et al., 2010). Ontogenetic diet shifts also occur in oceanic species. For example, blue sharks adapt their diet to geographical conditions through ontogeny, feeding on easily accessible surface small pelagic fishes when juveniles, and later switching to deeper prey (McCord and Campana, 2003; Queiroz et al., 2010). In these cases, early life stages of top predator species are considered separately from adults in trophodynamic studies (Young et al., 2015). In some species, these ontogenetic changes are not homogeneous over length or age. This is for example the case for juvenile hammerheads frequently switching between coastal and offshore habitats (Estupiñán-Montaño et al., 2021b; Hussey et al., 2011; Raoult et al., 2019) or white sharks (*Carcharodon carcharias*) aggregating around marine mammal hotspots seasonally while actively foraging in the deep mesopelagic layers the rest of the year (Carlisle et al., 2012; Kerr et al., 2006; Le Croizier et al., 2020a).

Following the competitive exclusion principle, an increase in predator diversity often comes with a reduction in niche width, limiting inter-specific competition. In top predator species, niche separation between co-occurring species can occur spatially through differences in habitat use (Flores-Martínez et al., 2017; Hussey et al., 2011; Jorgensen et al., 2019; Kiszka et al., 2014). Sympatric sharks co-exist when the diet overlap is weak (Papastamatiou et al., 2006). Sometimes such habitat and trophic segregation can also be triggered by fear effects between co-existing marine top-predators as for white sharks shifting their foraging ground when orcas occur in the same area (Jorgensen et al., 2019). Resource partitioning has been observed in both early life stages of juvenile sharks with important trophic plasticity (e.g., Matich et al., 2017b) and in adult specimens (e.g., Bangley and Rulifson, 2017; Kubodera et al., 2006; Preti et al., 2012).

The optimal foraging theory predicts that predators will feed at maximum efficiency allowing an optimal energy intake compared to foraging efforts (Pyke, 1984). Therefore, foraging strategies depend on energetic trade-off between food energy gain and the risk/cost of predation and sharks will not target the entire prey spectrum available evenly. Depending on species, sharks can thus be either opportunists or specialists (i.e., using resources in different proportions than their availabilities in their habitats) affecting the width of realized trophic niches (Munroe et al., 2014a; Newman et al., 2012). Prey selection can be strong even in population of generalist species as they can be composed of specialist individuals, as observed locally for bull and tiger sharks (Dicken et al., 2017; Matich et al., 2011; Munroe et al., 2014a).

Sharks can also induce fear effect over prey species capable of switching their habitat to avoid shark presence. This effect has been observed in bottlenose dolphin (Heithaus and Dill, 2002) or loggerhead turtles (Hammerschlag et al., 2015) avoiding to share common ground with tiger sharks. Finally, a combination of current climate changes and anthropogenic pressures such as fisheries can also induce a shift in habitat and trophic niche of prey and predators impacting shark foraging ecology at a global scale (Chavez et al., 2003; Cury et al., 2011; Pinsky et al., 2011; Stramma et al., 2012; Worm et al., 2006).

The trophic structure of large shark assemblages is therefore highly complex, context-dependent and varies across time and regions. A given shark species or specimen will likely have disparate trophic and functional roles between the ecosystems it is connecting (Hussey et al., 2015). The different aforementioned mechanisms affecting shark realized trophic niches are difficult to study separately as they co-occur over different temporal and spatial scales. However, the complexity of probable top-down cascades initiated by the current removal of shark populations calls for a better characterization of the trophic ecology of sharks, requiring the use of novel approaches.

c. Approaches in shark trophic ecology

Direct field observations of feeding behavior provides the most accurate information regarding the trophic ecology of predators, although this approach is clearly limited in the marine environment (Nielsen et al., 2018). For instance, punctual observations of scars left by cephalopod beaks or suckers on shortfin mako sharks in California (Vetter

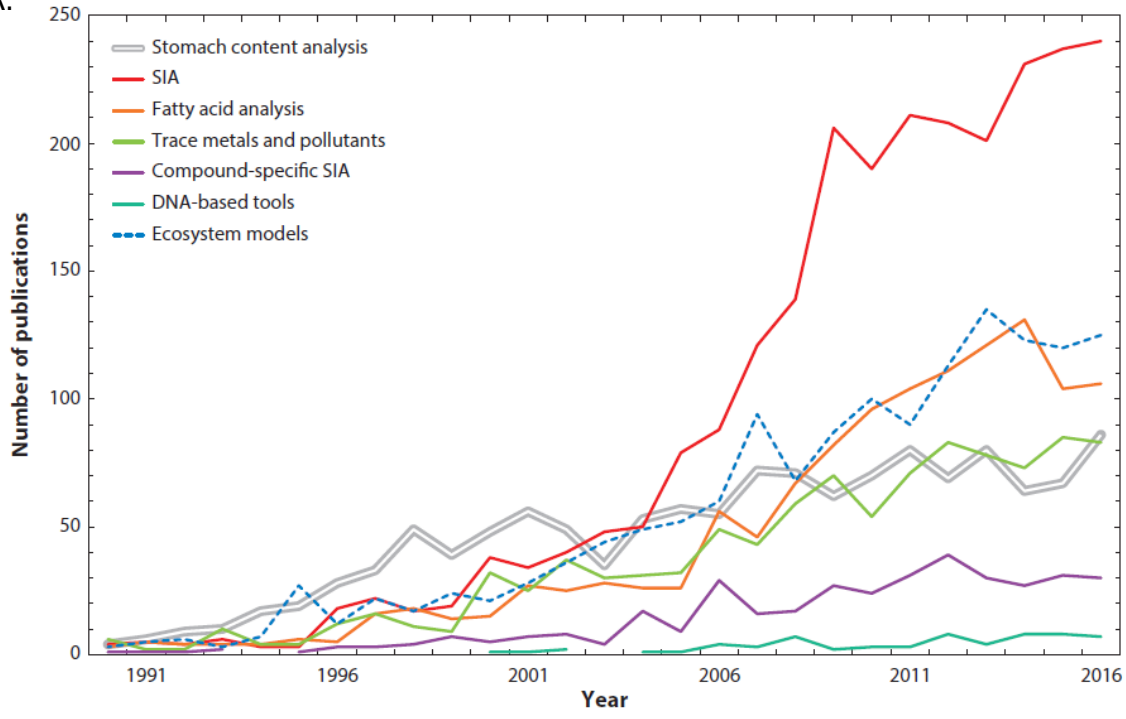
et al., 2008) and on white sharks in Guadalupe Island (Becerril-García et al., 2020) are direct evidences of shark predation on squids. However, visual tools often result from unusual sightings of trophic interactions and do not allow further quantitative or qualitative analysis (e.g., Hoyos-Padilla et al., 2013; Mourier et al., 2013; Sucunza et al., 2015), with the exception of the recent development of drone technologies (e.g., Doan and Kajiura, 2020).

The analysis of stomach contents has long been the main approach to study the trophic ecology of sharks and is the most direct way to identify the occurrence of prey species in the diet of a given predator (Cortés, 1999, 1997; Hyslop, 1980). However, it involves killing an important number of specimens to reach a significant number of full stomachs to analyze (stomachs are often empty either naturally or due to stress capture, Shiffman et al., 2012), a limitation that goes against the current effort of limiting lethal analyses in a context of global overfishing. Moreover, this approach requires a large number of samples and represents only a snapshot of the last meal(s). In top predator sharks, this analysis also frequently relies on hard structures that are weakly digested such as otoliths or cephalopod beaks (e.g., Kubodera et al., 2006) and differences in digestion rates may also bias the importance of prey items.

Sharks exhibit strong plasticity in horizontal and vertical movements (e.g., Klimley et al., 1993; Madigan et al., 2020a; Musyl et al., 2011). Movement characterization thanks to biotelemetry approaches allows the description of habitat use that can have applications in trophic ecology, as movements of sharks have been explained in part by foraging purposes (e.g., Papastamatiou et al., 2010; Papastamatiou and Lowe, 2012; Rogers et al., 2015; Shiffman et al., 2012). These methodologies include acoustic telemetry (Heupel et al., 2006) and satellite tracking via pop-up archival tags (PAT tags), or satellite-linked transmitters (SAT or SPOT) combined or not with additional data loggers recording swimming speed, sounds, muscle contraction, acceleration or environmental parameters (Hammerschlag et al., 2011). However, biotelemetry approaches can be limited by the temporal duration between tag deployment and data retrieval, cost per specimen tracked, and the associated tag burden precluding deployment on small individuals (Brownscombe et al., 2019; Jepsen et al., 2015), which has resulted in an overall bias towards the study of late life stages (Hammerschlag et al., 2011; Hazen et al., 2012).

Compared to other approaches, biomarker-based approaches target only the assimilated part of the diet, reducing biases due to differential digestibility and assimilation (Nielsen et al., 2018). Biomarkers usually offer the opportunity for non-lethal and relatively non-invasive tissue sampling, such as dorsal muscle or dermal samples which can be collected by biopsies (Daly and Smale, 2013; Jaime-Rivera et al., 2013; Meyer et al., 2018) or blood samples with syringes (Matich et al., 2015; Matich and Heithaus, 2014). They include the study of atomic tracers and biochemical compounds found in shark tissues such as stable isotopes, fatty acids, trace metals or pollutants. Over the last twenty years, the use of biomarkers has drastically increased in the literature to become the main methodologies used to assess the trophic ecology of marine species (Figure 1-6) including sharks.

A.



B.

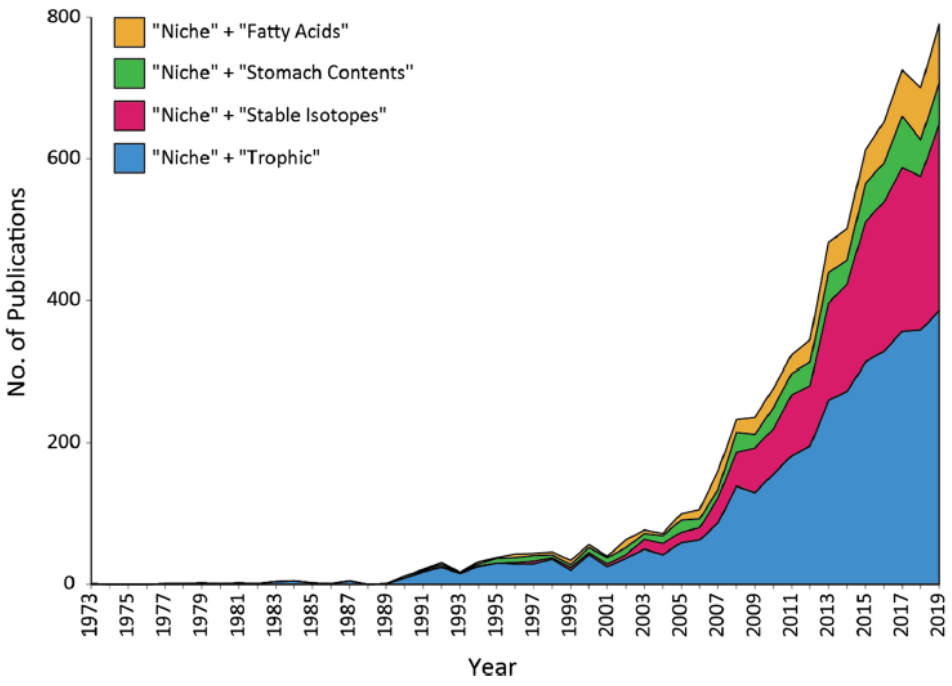


Figure 1-6 – (A.) Approaches used in marine trophic ecology publications from 1990 to 2016 (Pethybridge et al., 2018b). "SIA" stands for "Stable isotope analysis". (B.) Results from search of ISI Web of Science for studies using "Trophic", "Stable Isotopes", "Stomach Contents" and "Fatty Acids" to describe "Niche" (Shipley and Matich, 2020).

3. The marine ecosystem around the coast of Baja California Sur

Located on the west coast of Mexico, the Baja California peninsula is a narrow land stripe extending from the USA border to the city of Cabo San Lucas and separated in two different states: Baja California and Baja California Sur. The state of Baja California Sur (Figure 1-7) is a dry and low-urbanized region that covers 73 909 km² with a population of 798 447 (lower population density of Mexico ~10.8 inhabitants per km²) mainly dispatched in five municipalities (INEGI, 2020). This narrow arm of Mexico represents 22% of the country coastline and is surrounded on the west by the Pacific Ocean (with a coastline of approximately 920 km) and on the east by the Gulf of California (with a coastline of approximately 698 km).

Figure 1-7 – Map of the state Baja California Sur in Mexico. The state is shown in red and black lines delimit the bathyal 200 m depth limit.

a. The northeastern Pacific region

The northeastern Pacific region along the western coast of Baja California Sur is located at the extremity of the North Pacific subtropical gyre. It is mainly influenced by the southward extension of the California current, and its associated nearshore counter-current (García Huante et al., 2018; Lluch-Belda, 2000; Zaytsev et al., 2003; Appendix 1-1). The southward California current roughly influences the first 300 meters of the water body and is characterized by cold water enriched in dissolved oxygen and nutrient. Local micronekton is composed of cephalopods, lanternfishes (myctophids), cnidarians and pelagic shrimps, with lanternfishes representing a key trophic link between zooplankton and higher trophic level predators (Ibarra-Obando et al., 2001). The region is also affected by a strong coastal upwelling (Altabet et al., 1999; Ibarra-

Obando et al., 2001; Lluch-Belda, 2000; Thunell et al., 1994). Following northwest to north alongshore wind regimes, an offshore transport of surface water creates the upwelling dynamic injecting high nutrient concentrations into the euphotic zone and contributing to the overall high productivity of the region (Zaytsev et al., 2003). The northern portion of the Pacific coast of Baja California Sur is at the boundary of temperate and warm waters with sea surface temperature seasonally fluctuating between 18°C and 22°C while it varies from 22°C to 26°C in the warm southern regions (Ibarra-Obando et al., 2001). At depth, the Pacific coast of Baja California Sur is characterized by an important and permanent hypoxic zone (Helly and Levin, 2004). Despite that, large biomasses have been recorded inside the boundaries of the deep scattering layer, homogenously present below the current of California (Davison et al., 2015) and locally observed in Baja California Sur (e.g., Robinson et al., 1997).

The continental shelf is relatively narrow, the widest one being located between San Ignacio and northern Bahía Magdalena (~68.5 km). Coastal ecosystems in Baja California Sur are characterized by low river inputs (Thunell et al., 1994). They are also diversified and benefit from the pelagic water dynamic that transport nutrient into numerous lagoon ecosystems scattered along the Pacific coast of Baja California Sur (Zaytsev et al., 2003). Frequently, these lagoons are home to mangrove forests of *Rhizophora mangle* or *Laguncularia racemosa*. Most of these habitats are nearly pristine and provide protection and feeding grounds (Ibarra-Obando et al., 2001).

Combined, this mix of currents, high productivity, variety of habitats, bathymetry and topography lead to a strong diversity and biomass of marine species in the region. Global occurrence of major predator species like dolphins (*Delphinus capensis*, *Turniops truncatus*), killer whales (*Orcinus orca*), California sea lions (*Zalophus californianus*) and harbor seals (*Phoca vitulina*) are frequently reported. Gray whales (*Eschrichtius robustus*) are also common during the winter months, breeding in lagoon ecosystems. Besides, the Pacific coast of Baja California Sur hosts a hotspot of shark diversity, with 53 recorded species (Saldaña-Ruiz et al., 2019).

b. The Gulf of California

The Gulf of California is the only inland and marginal sea in the entire northeastern Pacific region. It is delimitated at the west by its peninsular shore (coast of Baja California and Baja California Sur) and at the east by its continental shore. Its depth

increases toward the mouth, reaching up to 3 000 m, with an important oxygen minimum zone (Lluch-Cota et al., 2007). The peninsular shores are mostly rocky with low river input due to a semi-arid climate while the continental shore is radically different with sandy beach, large lagoon and bay ecosystems with important freshwater inputs (Alvarez-Borrego, 2010). This leads to a unique series of diversified habitats with mangroves forests (Aburto-Oropeza et al., 2008), coral reefs in the southern end and important intertidal habitats up in the north (Lluch-Cota et al., 2007). Numerous coastal bays, lagoons, estuaries and wetlands have been identified as possible nurseries for a high number of fish species including sharks (Aburto-Oropeza et al., 2008; Salomón-Aguilar et al., 2009).

Compared to the water of the adjacent Pacific Ocean, sea surface temperature is warmer, fluctuating between 24°C to 32°C (Lluch-Cota et al., 2007). The Gulf of California is an area of high productivity mainly driven by an upwelling system in the central eastern region, tidal mixing (stronger in the northern areas) and water exchanges with the Pacific Ocean (Alvarez-Borrego, 2010). Of particular interest, the currents circulation forms mesoscale eddies (Lavín et al., 2014; Lluch-Cota et al., 2007) allowing the high eastern primary production to be spread to the entire Gulf of California (Alvarez-Borrego, 2010; Lluch-Cota, 2000).

Fishing, either industrial or artisanal, is the main activity in the region and is of major economic importance for the country and culturally rooted (Arreguín-Sánchez et al., 2017; Lanz et al., 2008; Lluch-Cota et al., 2007). Fisheries mainly target shrimp (e.g., *Forfantepenaeus californiensis*), small pelagic fishes (e.g., Pacific sardine, *Sardinops caeruleus*) and to a less extent squids (mainly *Dosidicus gigas*), tunas and sharks (Lluch-Cota et al., 2007). Major changes in species composition due to overfishing (notably in the 70s and early 80s) have been noted with a large decrease of fisheries landings (Sáenz-Arroyo et al., 2005; Sala et al., 2004).

The Gulf of California remains an important marine biodiversity hotspot (e.g., Arreguín-Sánchez et al., 2017). In their report on the region biodiversity, Morzaria-Luna et al., (2018) reported 12 105 species including 6 388 rare, 642 endemic and 386 threatened. The high primary productivity in the region is leading to high abundance of zooplankton including copepods (e.g., *Calanus pacificus*) and euphausids (e.g., *Nyctiphanes simplex*), food sources for fish larvae and carnivorous zooplankton. 36 different species of marine mammals are recorded, including iconic species as the region hosts

feeding and breeding sites for blue (*Balaenoptera musculus*) or humpback whales (*Megaptera novaeangliae*) (Lluch-Cota et al., 2007). Finally, 106 species of chondrychtians inhabit the Gulf of California, including 55 species of sharks, one of the most diversified sea in the world in this aspect (González-Acosta et al., 2021).

c. Artisanal elasmobranch fisheries

In 2015, Mexico ranked as the sixth-largest producer, in volume, of shark products worldwide (Food and Agriculture Organization of the United Nations (FAO), 2015). Even if both industrial and artisanal fisheries are responsible for sharks landing, the major part (~80%) of elasmobranch products sold in Mexican markets originates from artisanal fisheries (Arreguín-Sánchez et al., 2004; Cartamil et al., 2011). Artisanal fisheries have an economic, social, cultural and alimental importance in the Pacific coast of Mexico with a long history of shark fishing and consumption by the local population (e.g., Saldaña-Ruiz et al., 2017).

Baja California Sur harbors many artisanal fishing camps scattered along the coastline, from the Pacific coast (e.g., Cartamil et al., 2011; Ramírez-Amaro et al., 2013; Ramírez-Amaro and Galván-Magaña, 2019; Santana-Morales et al., 2020) to the peninsular (e.g., Bizzarro et al., 2009b, 2009a) and continental coasts of the Gulf of California (e.g., Galvan Magaña, 2009; Saldaña-Ruiz et al., 2017). Even though they are not the only fished species, elasmobranchs are most of the time targeted (e.g., Bizzarro et al., 2009a, 2009b; Cartamil et al., 2011). Artisanal fishing camps can take different forms, such as small temporary camps (Figure 1-8) or permanent ones with developed infrastructures and a higher number of boats. Fishermen can be self-employed or can work with cooperatives, can be licensed or not (Ramírez-Amaro et al., 2013). Fishing fleets are made of small fiberglass boats (~7-10 meters long) called “pangas” with outboard motors and fishing trips usually do not last more than a day (Castillo-Geniz and Tovar-Ávila, 2016; Galvan Magaña, 2009). Gillnets are the most common fishing gear used to capture elasmobranchs while longlines are restricted to the catch of large pelagic species (e.g., Ramírez-Amaro et al., 2013).

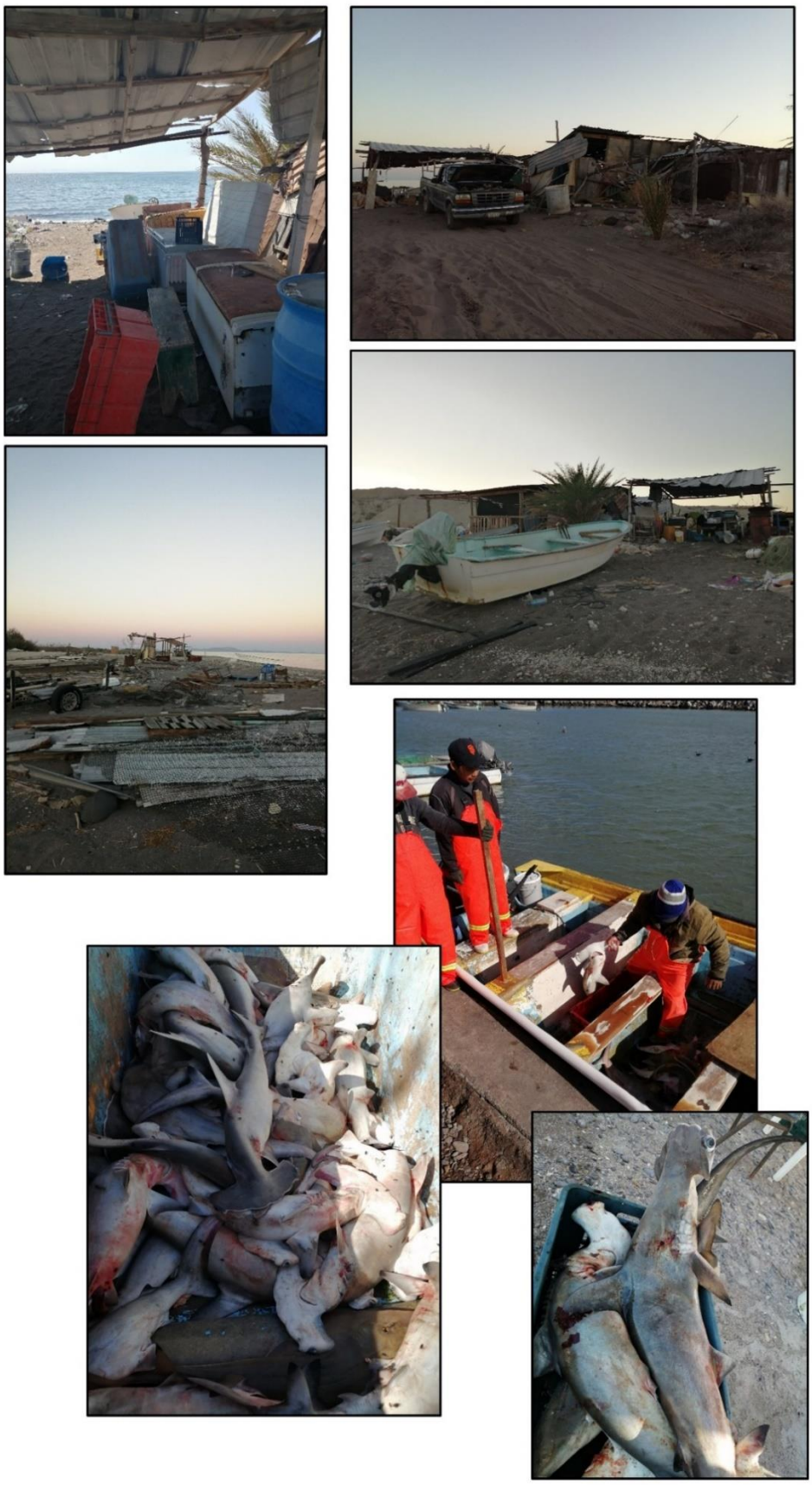


Figure 1-8 – Photographs of small temporary artisanal fishing camps in the Gulf of California with young hammerhead sharks caught by gillnet.

Artisanal shark fishing is passed on from generation to generation and is of critical social importance, bringing incomes to the poorest sectors of the Mexican society (Arreguín-Sánchez et al., 2004; Castillo-Geniz and Tovar-Ávila, 2016). Sharks can be sold as a whole or for their different parts mainly meat, liver or fins (Table 1-1), reaching the consumers through cooperatives or other intermediaries (detailed in Appendix 1-2).

Table 1-1 – Average price of sharks derived products for anglers in the Mexican market estimated by Castillo-Geniz and Tovar-Ávila in 2016.

Product	Average price
Whole shark (.kg^{-1})	22$MX (~1€)
Shark meat/fillet (.kg^{-1})	39 – 42$MX (~2€)
Oil/Liver (.L^{-1})	170$MX (~8€)
Fins (.kg^{-1})	130 – 650$MX (~6 – 29€) *up to 1,000$MX (~45€) depending on the fin quality*

Numerous claims have emerged that artisanal elasmobranch fisheries in the northeastern Mexican Pacific region were not sustainable and that the resilience of elasmobranch species (i.e., their capacity to recover) to high fishing pressures is probably low, calling for more management and conservation actions (e.g., Cartamil et al., 2011; Galvan Magaña, 2009; Ramírez-Amaro et al., 2013). Numerous factors might explain the threat artisanal fishery represents to elasmobranchs in the region. First, these fisheries appear not selective and target a large range of species from small nearshore to large pelagic ones, even if coastal accessible habitats are usually favored (Ramírez-Amaro et al., 2013; Saldaña-Ruiz et al., 2017; Salomón-Aguilar et al., 2009). The major part of the catches are early life stage specimens such as young-of-the-year or juvenile sharks which have not reached reproductive maturity (Bizzarro et al., 2009b, 2009c; Cartamil et al., 2011). A non-negligible part of the fished species are threatened and listed in CITES appendices (Castillo-Geniz and Tovar-Ávila, 2016). Moreover, there is a global lack of data and information on the landing of sharks by artisanal fisheries, probably due to their remoteness and difficulty to access (Saldaña-Ruiz et al., 2017). The mislabeling of sharks in the Mexican market also prevents the use of reliable data taken outside from the fishing camps (e.g., Galvan Magaña, 2009). Finally, the lack of knowledge on the ecology of sharks and rays across Baja California Sur marine ecosystems prevent the development of any informative management

planning (Galvan Magaña, 2009; Saldaña-Ruiz et al., 2017). Nevertheless, to slow down the harmful effects of fisheries, the Mexican jurisdiction (NOM-059-SEMARNAT-2010 and NOM-029-PESC-2006) prohibits from capturing some species (e.g., basking, whale, great white sharks or giant manta rays) (Diario Oficial de la Federación, 2019, 2010, 2007). Since 2012, one of the main measure to protect sharks and rays is the closing of shark fisheries during 3 months (May-July) to protect one part of the reproductive cycles of shark species (Diario Oficial de la Federación, 2012; González-Acosta et al., 2021).

4. Thesis objectives and structure

a. Aims and objectives

This thesis has objectives on several scales. The first one is the analysis of predator realized trophic niches following the principle of resource partitioning. It relies on the study of local sympatric shark species of equivalent trophic levels. We aim to characterize the drivers that are likely to reduce or promote food competition. Ultimately, this would help to address how the strength of top-down control could be modulated given the occurrence of intra-guild consumers and how the current decline of shark populations, specifically in the Mexican Pacific region but also worldwide, could affect marine food webs. We aim at:

- **Describing resource partitioning across different dimensions (i.e., food sources and habitat) in shark assemblages displaying similar trophic spectra.**
- **Characterizing shark trophic niches from nursery grounds to adult habitats.**

A second objective is to gather new knowledge on the ecology of shark species threatened by artisanal fisheries in Baja California Sur to address management plans and conservation issues, planning on:

- **Identifying the potential ecological and behavioral feature(s) that make sharks susceptible to interact with local fisheries.**

We chose to keep a special focus on large hammerhead shark species, particularly sensible to fishing exploitation and which have seen their population critically affected in the region (Castillo-Geniz and Tovar-Ávila, 2016; Gallagher et al., 2014a; Pérez-

Jiménez, 2014). We selected the case of smooth hammerhead sharks (*Sphyrna zygaena*) as this species mirror the situation of sharks harvested in Baja California Sur, that is to say frequently fished (e.g., Castillo-Geniz and Tovar-Ávila, 2016; Pérez-Jiménez et al., 2005) with no or little knowledge on their ecology preventing management actions (Gallagher and Klimley, 2018).

The final objective of this thesis is to question the use of different biomarkers in the study of highly mobile marine predators. It includes the analysis of biomarkers at inter-specific, intra-specific and community levels at different local or regional spatial scales where oceanographic conditions can vary. We intend at:

- **Using different biomarkers to construe trophic niches of highly mobile predators and define their complementarity or redundancy in regards of specific oceanographic conditions.**

b. Thesis Structure

To achieve these objectives, this manuscript starts by developing resource partitioning-related topics among sympatric predators, continues with the characterization of movements and ontogenetic diet shift of smooth hammerhead sharks and ends with the description of elasmobranch community trophic structures at a regional scale across different oceanographic conditions. **Chapter 3** to **6** have been written for publication in peer-reviewed scientific journals, which explains some overlaps between chapters:

- **Chapter 2** presents the study areas and species of interest. Laboratory protocols and methodologies are also detailed.
- **Chapter 3** combines stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) and fatty acids analysis in the muscle and blood of two hammerhead shark species, the scalloped hammerhead shark (*Sphyrna lewini*) and the smooth hammerhead shark (*Sphyrna zygaena*) in a shared coastal area near Santa Rosalía in the Gulf of California. The goal of this chapter is to assess the degree of overlap in habitat and trophic niches used by the two hammerhead species, using samples from co-occurring Pacific sharpnose shark (*Rhizoprionodon longurio*) as an outgroup.

* **Chapter 4** analyses the degree of competition in a pelagic shark assemblage between blue (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*) and smooth hammerhead shark (*Sphyrna zygaena*) in the Pacific coast of Baja California Sur. It demonstrates how mercury isotopes, by characterizing foraging depth, help identify resource partitioning in pelagic shark assemblages and reveal mercury accumulation pathways in the tissues of pelagic predators. This chapter has been published in *Environmental Pollution*.
* **Chapter 5** describes the movement of smooth hammerhead sharks (*Sphyrna zygaena*) in the northeastern Pacific region using a novel application of mercury isotopes as molecular clocks. It reveals smooth hammerhead sharks ontogenetic diet and habitat shift from coastal to offshore pelagic grounds. It uncovers that this species extensively relies on coastal resources, a critical new information that should be taken into account in its management. This chapter is currently under review in *Journal of Applied Ecology*.
* **Chapter 6** compares the trophic dynamics of coastal and pelagic elasmobranch species at two sites, one in Bahía Tortugas in the northern part of the Pacific coast and one in Santa Rosalía in the middle part of the Gulf of California. Complementary stable isotope analysis (mercury, nitrogen and carbon) identifies that oceanographic conditions (i.e., upwelling and oxygen minimum zone) drive elasmobranch trophic structures.
* **Chapter 7** will briefly summarize the thesis findings, discuss some of the limitations of the approaches used, suggest future work, and highlight how these results could support future fisheries management decision.

CHAPTER 2

APPROACHES

Species of interest, sampling strategy and methods.

1. Species of interest

a. Hammerhead sharks (Sphyrnidae)

Hammerhead sharks get their name from their vertically compressed and laterally expanded head structure called cephalofoil (Compagno, 1988). Such unique head evolution in the animal kingdom might result from diverse selective pressures (Lim et al., 2010). Cephalofoil could allow for better locomotion and manoeuvrability (Bertram et al., 2007; Kajiura et al., 2003), extended electroreceptor organs coverage (i.e., Lorenzini ampullae) favoring prey detection (Kajiura and Holland, 2002), or enhanced visual field (McComb et al., 2009). The higher encephalization quotient in hammerheads (i.e., larger brain compared to the body size) might have led to the higher development of cognitive capacities (Yopak et al., 2007) facilitating the evolution of complex behavioral traits such as sociability or large migration routes (Gallagher et al., 2014a).

Phylogenetically, hammerhead sharks are the last group to have diverged from Carcharhiniformes (Lim et al., 2010). They include nine species that are usually of small size (< 150 cm) except for three of them: *Sphyrna mokarran*, *Sphyrna lewini* and *Sphyrna zygaena*. The great hammerhead shark (*S. mokarran*) is the largest (up to 6 m total length) and is characterized by the shape of its dorsal fin. Scalloped hammerhead sharks (*S. lewini*) and smooth hammerhead sharks (*S. zygaena*) have very few morphological differences (Gallagher and Klimley, 2018). They mainly differ by their head's anterior margins (Figure 2-1), with scalloped hammerheads having two lobes and smooth hammerheads a unique one with no median separation (Gallagher and Klimley, 2018).

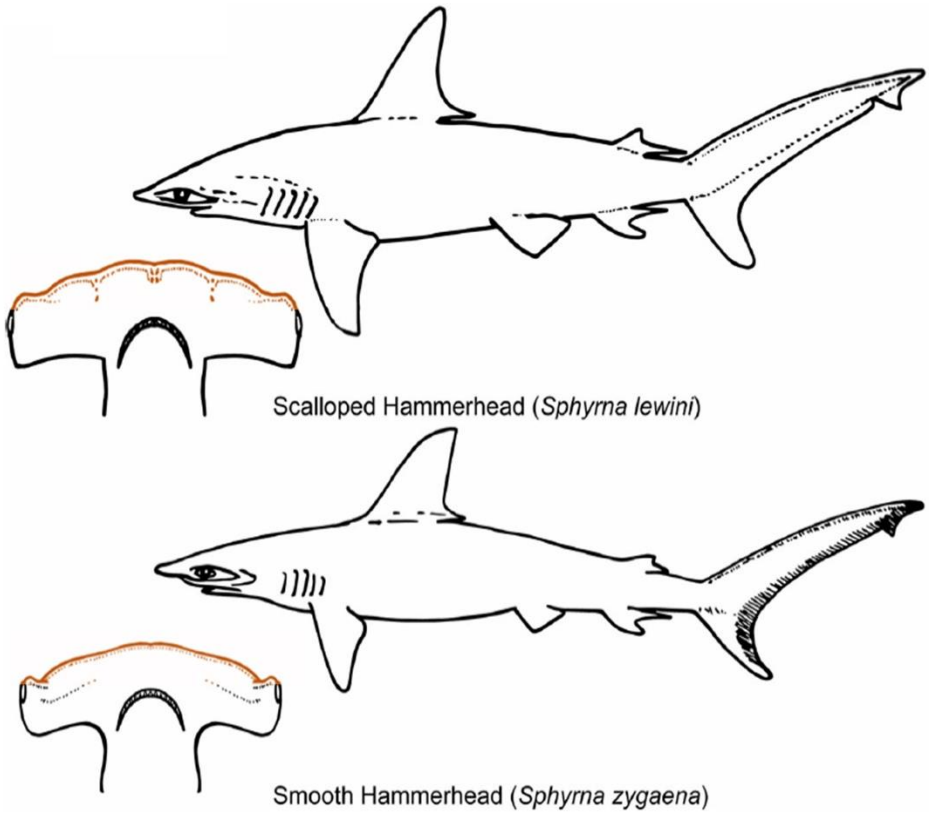


Figure 2-1 – Morphological differences (lobes colored in orange) between the scalloped hammerhead shark and the smooth hammerhead shark based on an illustration from Gallagher and Klimley, 2018.

Ecological knowledge on hammerhead sharks mainly originates from the studies carried out on great and scalloped hammerheads (Gallagher et al., 2014a; Gallagher and Klimley, 2018). The two species are recognized as among the most sensitive shark species to fishing pressure (Gallagher et al., 2014b), due to unique ecological, behavioral and functional specializations. Large hammerheads are easy to catch and highly harvested, mostly for their fins (Gallagher and Klimley, 2018). The high fishing pressure as well as their sensitivity has led hammerheads to be among the most declining sharks worldwide (Dulvy et al., 2021; Gallagher et al., 2014a).

Among all shark species from Baja California Sur, hammerheads are the species most likely to overlap with fishing activities due to the coastal phase(s) of their early life cycles (Castillo-Geniz and Tovar-Ávila, 2016), and are frequently reported in the catches of artisanal fishing camps (Bizzarro et al., 2009b, 2009a, 2009c; Cartamil et al., 2011; Saldaña-Ruiz et al., 2017). In the region, scalloped and smooth hammerhead sharks have been associated to the highest vulnerability and ecological risk indices, as great hammerhead sharks (along with three potential other Sphyrnidae species)

have already disappeared, likely as a result of overfishing (Pérez-Jiménez, 2014). Species-specific vulnerability is still difficult to assess for scalloped and smooth hammerhead sharks, often confused because of their morphological similarities. Reliable information is only available for scalloped hammerhead sharks, whose population levels are critically declining (Castillo-Geniz and Tovar-Ávila, 2016) while smooth hammerhead sharks are likely to display similar population trends.

i. Smooth hammerhead shark (*Sphyrna zygaena*)

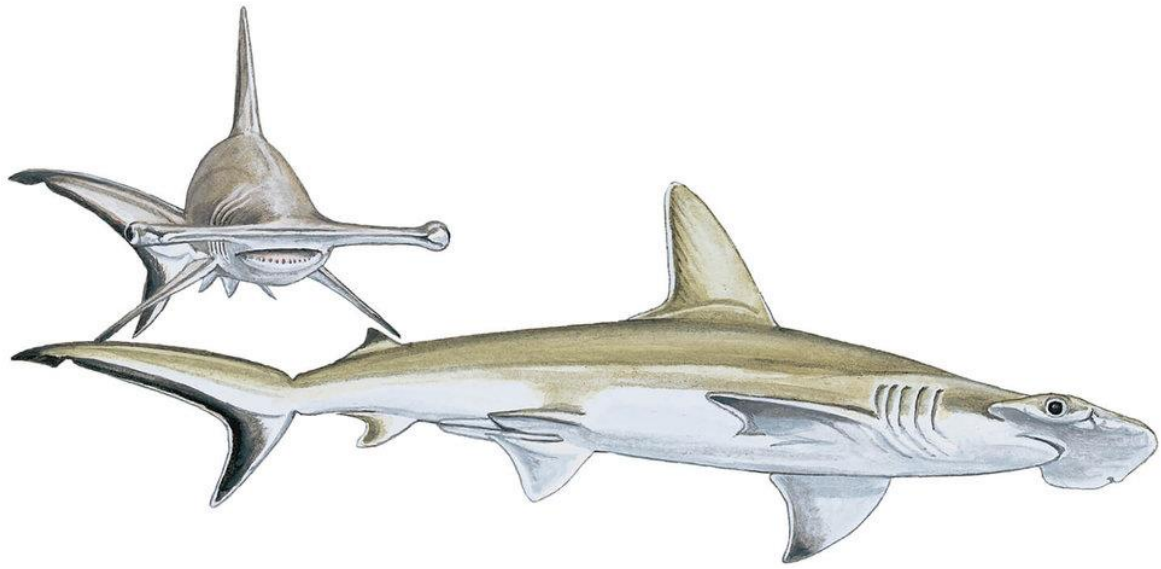


Figure 2-2 – Illustration of the smooth hammerhead shark ©Marc Dando.

Knowledge on smooth hammerhead sharks is scarce (Couto et al., 2018; Gallagher et al., 2014a; Gallagher and Klimley, 2018). This species can be found in temperate waters, and display an anti-tropical distribution in the Eastern Pacific (Bolaño-Martínez et al., 2019). Genetic information suggests that the species relies on coastal nursery habitats with potential female philopatry and maternal preference for birthing sites (Félix-López et al., 2019). Few information is available on life history traits but it is suggested to have the slowest growing of the three large hammerhead species (Gallagher and Klimley, 2018).

Coastal nursery areas, sheltering young-of-the-year and juvenile specimens, have been identified throughout smooth hammerhead shark's distribution range (e.g., Diemer et al., 2011; Francis, 2016; Segura-Cobeña et al., 2021). Individuals seem to undergo an ontogenetic habitat shift from coastal nurseries to offshore waters, where late juveniles or mature individuals are found in the Atlantic Ocean (Santos and Coelho,

2019), South Africa (Diemer et al., 2011; Smale, 1991), New Zealand (Francis, 2016) and in the Mexican Pacific (Li et al., 2016a). Tracking studies have been conducted in the Atlantic Ocean and have shown that they spend a major part of their time at the surface, with dives at depth increasing in frequency with size in the eastern basin (Santos and Coelho, 2018) and limited horizontal and vertical movements in the western basin (Logan et al., 2020).

The diet of smooth hammerhead sharks consists in a mix of cephalopods and teleosts in both the Atlantic (Bornatowski et al., 2007) and the Pacific Ocean (Gonzalez-Pestana et al., 2017). Around Baja California Sur, both juveniles and adults are teutophagous (i.e., mainly feeding on cephalopods) with a higher proportion of teleost fishes in the diet of juveniles (Díaz Ochoa, 2009). Epipelagic and mesopelagic prey cephalopods are dominated by three species: the Humboldt squid (*Dosidicus gigas*), the sharpear enope squid (*Ancistrocheirus leusueurii*) and the common clubhook squid (*Onychoteuthis banksii*) (Galván-Magaña et al., 2013). Generally, early life stages feed on coastal prey while adults switch to offshore pelagic ones, mostly mesopelagic cephalopods, suggesting both horizontal and vertical niche shift(s) (Estupiñán-Montaño et al., 2019; Gonzalez-Pestana et al., 2017; Smale and Cliff, 1998).

In artisanal fisheries, smooth hammerhead sharks are frequently caught by gillnets and longlines both in the Pacific coast of Baja California Sur (Cartamil et al., 2011; Castillo-Geniz and Tovar-Ávila, 2016; Ramírez-Amaro and Galván-Magaña, 2019) and in the Gulf of California (Bizzarro et al., 2009b, 2009c; Saldaña-Ruiz et al., 2017). The limited information about catch records suggests that they are fished at young-of-the-year and juvenile sizes while the species life history traits, ecological characteristics and population status are still unknown.

ii. Scalloped hammerhead shark (*Sphyrna lewini*)

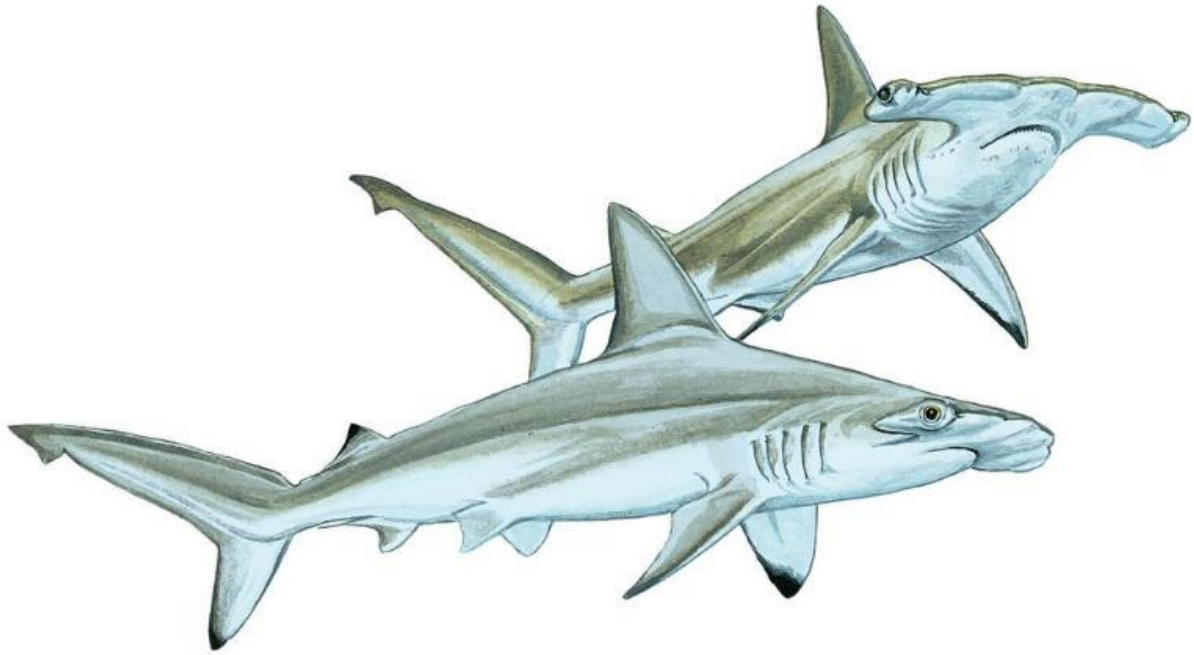


Figure 2-3 – Illustration of the scalloped hammerhead shark ©Marc Dando.

The scalloped hammerhead shark is a wide-ranging oceanic species known for its highly migratory behavior. In the Gulf of California, the species undergoes long migrations, connecting the region with remote islands in the eastern Pacific (Hoyos-Padilla et al., 2014; Ketchum et al., 2014b; Klimley, 1985). Similarly to smooth hammerheads, scalloped hammerhead shark's habitat and diet ontogenetic shifts from coastal and continental slopes to offshore ecosystems have been extensively described (e.g., Estupiñán-Montaño et al., 2021; Flores-Martínez et al., 2017; Hussey et al., 2011; Kiszka et al., 2014). Numerous coastal nurseries have been identified in the Mexican Pacific, such as in Sinaloa, Jalisco (Rosende-Pereiro et al., 2018; Torres-Rojas et al., 2013), the Gulf of California and the Gulf of Tehuantepec (Hoyos-Padilla et al., 2014; Torres-Rojas et al., 2015). Young sharks show high residency in these areas, where movements are limited to a small core habitat with rare foraging excursions (Rosende-Pereiro et al., 2018). Coastal habitats are therefore critical for the species, notably mangroves—identified as a feeding area for neonates and a breeding ground for adults (Estupiñán-Montaño et al., 2021b).

Late juvenile and mature individuals are known to regroup in large schools inside complex and organized social structures (Gallagher et al., 2014a; Gallagher and Klimley, 2018). They mostly reside in surface waters with frequent deep dives in the

Pacific Ocean (Jorgensen et al., 2009; Ketchum et al., 2014a; Klimley et al., 1993). These schools display strong residency around remote islands such as the Revillagigedo and the Galapagos archipelagos (Aldana- Moreno et al., 2020; Ketchum et al., 2014a). In the Gulf of California, early juveniles in coastal nurseries also migrate toward pelagic waters with ontogeny (Hoyos-Padilla et al., 2014) and important schooling behaviors have been observed near Espíritu Santo island (Klimley et al., 1993, 1988).

Scalloped hammerhead sharks are globally recognized as generalist predators feeding predominantly on cephalopods, fishes and crustaceans, with marked ontogenetic changes (reviewed in Gallagher and Klimley, 2018). Early life stages are opportunistic, feeding on the most abundant and available prey. For example, small fishes and shrimps have been reported to be the main preys in Florida (Bethea et al., 2011), gobies and shrimps in Hawaii (Bush, 2003) and small teleost fishes in South Africa (Hussey et al., 2011). During their time in nursery grounds, feeding on low-energy prey involves high daily rations (Lowe, 2002). Ontogenetic habitat shift is accompanied with a diet shift toward a higher proportion of mesopelagic preys (Gallagher and Klimley, 2018; Hussey et al., 2011). In the Mexican Pacific, the diet switch from teleost fishes such as chub mackerels (*Scomber japonicus*) and frigate tunas (*Auxis spp*), to crustaceans, mesopelagic cephalopods and deep demersal prey, suggests offshore vertical foraging behaviors for large scalloped hammerhead sharks (Flores-Martínez et al., 2017; Torres-Rojas et al., 2015). In the Gulf of California, late juveniles feed on neritic and mesopelagic prey (Klimley, 1987), especially cephalopods such as the Humboldt squid (*D. gigas*), *Abraliopsis affinis* and *Lolliguncula diomedeae* (Galván-Magaña et al., 2013).

In the catches of artisanal fishing camps, scalloped hammerhead sharks are more commonly reported in the Gulf of California than on the Pacific coast of Baja California Sur, which likely reflects their preference for warmer waters (Bizzarro et al., 2009b, 2009a, 2009c; Saldaña-Ruiz et al., 2017). The species was the first one to be recognized as strongly impacted by fisheries in the region, with population records decreasing over the years, leading to the implementation of time-closure areas to fisheries by the Mexican government (Diario Oficial de la Federación, 2012).

b. Blue shark (*Prionace glauca*)

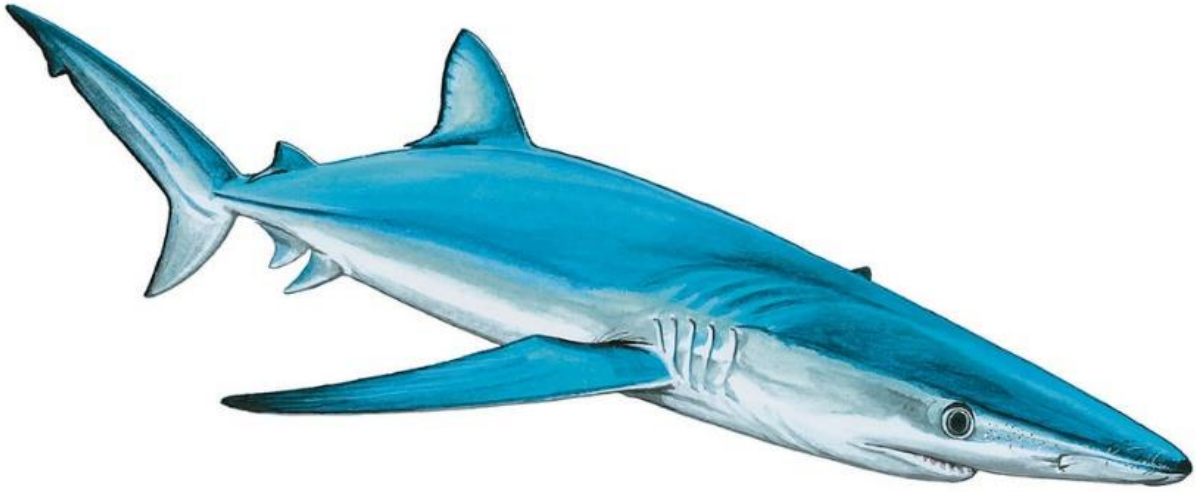


Figure 2-4 – Illustration of the blue shark ©Marc Dando.

Blue shark is a pelagic/oceanic species migrating over important horizontal distances (Musyl et al., 2011; Queiroz et al., 2010; Silva et al., 2010). It is frequently described as epipelagic (Clarke, 1996; Klimley et al., 2002; Vandeperre et al., 2014) even if it frequently dives in deep water layers down to 700-1000 meters (Carey et al., 1990; Musyl et al., 2011; Queiroz et al., 2010; Stevens et al., 2010). In the northeastern Pacific region, blue sharks appear to be resident, undergoing limited horizontal movements (Madigan et al., 2021; Maxwell et al., 2019).

Blue sharks are recognized as opportunistic predators, feeding on easily-catchable prey aggregations (e.g., Fujinami et al., 2018; Preti et al., 2012). In the Atlantic Ocean, they forage upon pelagic fishes and cephalopods with records of small epipelagic and large mesopelagic prey in their diet (Clarke, 1996; MacNeil et al., 2005; McCord and Campana, 2003). In the Pacific, feeding on deep or neritic cephalopods has been described in the northwestern (Fujinami et al., 2018; Kubodera et al., 2006), southeastern (Lopez et al., 2010) and northeastern regions (Preti et al., 2012). In Baja California Sur, opportunistic feeding behaviors have been observed with a seasonal consumption of epipelagic red crabs (*Pleuroncodes planipes*) (Hernández-Aguilar et al., 2016; Maya Meneses et al., 2016). However, blue sharks are mostly teutophagous feeding on common clubhook squids (*O. banksia*), California armhook squids (*Gonatus californiensis*), Humboldt squids (*D. gigas*) and sharpear enope squids (*A. lesueurii*). Deep foraging events are suggested in the region due to the occurrence of these deep

cephalopod species in their stomachs (Galván-Magaña et al., 2013; Hernández-Aguilar et al., 2016; Markaida and Sosa-Nishizaki, 2010).

The blue shark is the most fished shark species in artisanal fisheries of the Pacific coast of Baja California Sur, mainly caught by longlines (Cartamil et al., 2011; Castillo-Geniz and Tovar-Ávila, 2016; Ramírez-Amaro et al., 2013). Although less commonly landed, it is also fished in the Gulf of California (Bizzarro et al., 2009c, 2009a, 2009b).

c. Shortfin mako shark (*Isurus oxyrinchus*)

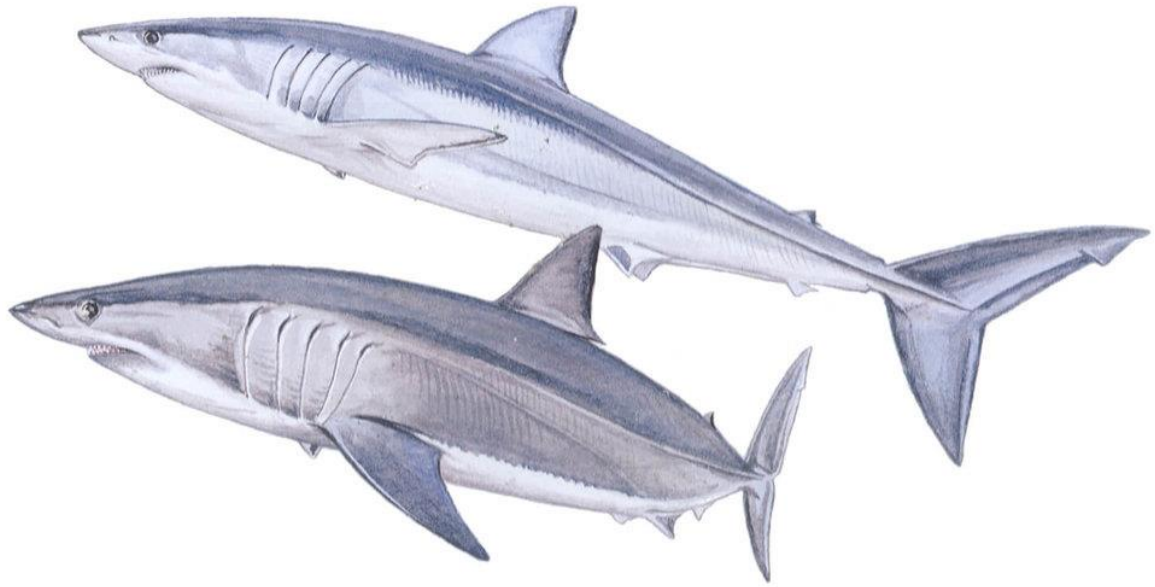


Figure 2-5 – Illustration of the shortfin mako shark ©Marc Dando.

Shortfin mako shark is a globally distributed pelagic and highly migratory species, which spend most of their time in the upper water layer, with frequent dives at depth (Casey and Kohler, 1992; Klimley et al., 2002; Musyl et al., 2011; Rogers et al., 2015; Vaudo et al., 2016). Diving behavior of shortfin mako sharks has been linked to foraging activities, allowing them to take advantage of their uncommon speed and counter-shading camouflage (Abascal et al., 2011; Loefer et al., 2005; Sepulveda et al., 2004; Vaudo et al., 2016).

Shortfin mako sharks are opportunistic generalists (MacNeil et al., 2005; Rosas-Luis et al., 2016; Vetter et al., 2008), feeding on teleost fishes, cephalopods, crustaceans, mammals, elasmobranchs and even birds (Lopez et al., 2009; Lyons et al., 2015; Maia et al., 2006). Throughout their distribution range, teleost fishes are consumed in greater

proportions than cephalopods, as reported in the Atlantic (Biton-Porsmoguer et al., 2014; Gorni et al., 2012; Maia et al., 2006; Stillwell and Kohler, 1982) and Pacific Ocean (Lopez et al., 2009; Preti et al., 2012; Rosas-Luis et al., 2016). In Baja California Sur, young juveniles are found in large coastal bays (Malpica-Cruz et al., 2013; Tamburin et al., 2019). Their diet is composed of teleost fishes like whitesnout searobins (*Prionotus albirostris*) or epipelagic Pacific makerels (*S. japonicus*). Mesopelagic cephalopods such as *D. gigas* or *A. lesueurii* are also consumed, although in a lesser extent (Maya Meneses et al., 2016; Velasco Tarelo and Galván-Magaña, 2005).

After blue sharks, the shortfin mako is the most fished species in the longline artisanal fisheries on the Pacific coast of Baja California Sur (Cartamil et al., 2011; Castillo-Geniz and Tovar-Ávila, 2016; Ramírez-Amaro et al., 2013; Vélez-Marín and Márquez-Farías, 2009) where catches are dominated by neonates and juveniles (Conde-Moreno and Galván-Magaña, 2006). In the Gulf of California, the species is less present and is therefore less fished (Bizzarro et al., 2009b, 2009c, 2009a).

d. Other species

In **Chapter 3**, the Pacific sharpnose shark (*Rhizoprionodon longurio*), a heavily exploited species in the Gulf of California (Bizzarro et al., 2009a, 2009b), is used as an outgroup to highlight the trophic dynamic of early juvenile hammerhead sharks. Indeed, adults (<120 cm) are neritic, occasionally inhabiting nursery grounds of scalloped and smooth hammerhead sharks. We sampled adult Pacific sharpnose sharks to describe its trophic niche width as a resident species with excepted low inter-individual dietary fluctuation compare to the potential occurrence, direction and amplitude of ontogenetic shift(s) in both hammerhead sharks.

In **Chapter 6**, other species are used to study coastal to pelagic elasmobranch assemblages on the Pacific coast of Baja California Sur and in the Gulf of California. Offshore pelagic species include the common thresher shark (*Alopias vulpinus*), the pelagic thresher shark (*Alopias pelagicus*) and the silky shark (*Carcharhinus falciformis*). For neritic shark species, the tope shark (*Galeorhinus galeus*), the gray smooth-hound shark (*Mustelus californicus*), the brown smooth-hound shark (*Mustelus henlei*) and the Pacific sharpnose shark (*R. longurio*) were sampled. Finally, to highlight the trophic ecology of resident coastal elasmobranch species, rays species were also

sampled and analyzed in this study, including the California butterfly ray (*Gymnura marmorata*), the bat ray (*Myliobatis californica*) and the shovelnose guitarfish (*Pseudobatos productus*).

2. Sampling strategy

a. Study sites

Sharks were sampled in five different artisanal fishing camps in Baja California Sur (Figure 2-6): Bahía Tortugas, Las Barrancas, San Lázaro, Punta Lobos and Santa Rosalía. Baja California Sur is surrounded by a narrow continental shelf, which is the largest in the area between Laguna San Ignacio and Bahía Magdalena (roughly corresponding to Las Barrancas fishing ground). Two of the sampling sites are located close to major lagoon ecosystems: 1) Bahía Sebastián Vizcaíno, included in the fishing area covered by fishermen from Bahía Tortugas, and 2) Bahía Magdalena, where San Lázaro fishing camp is located.

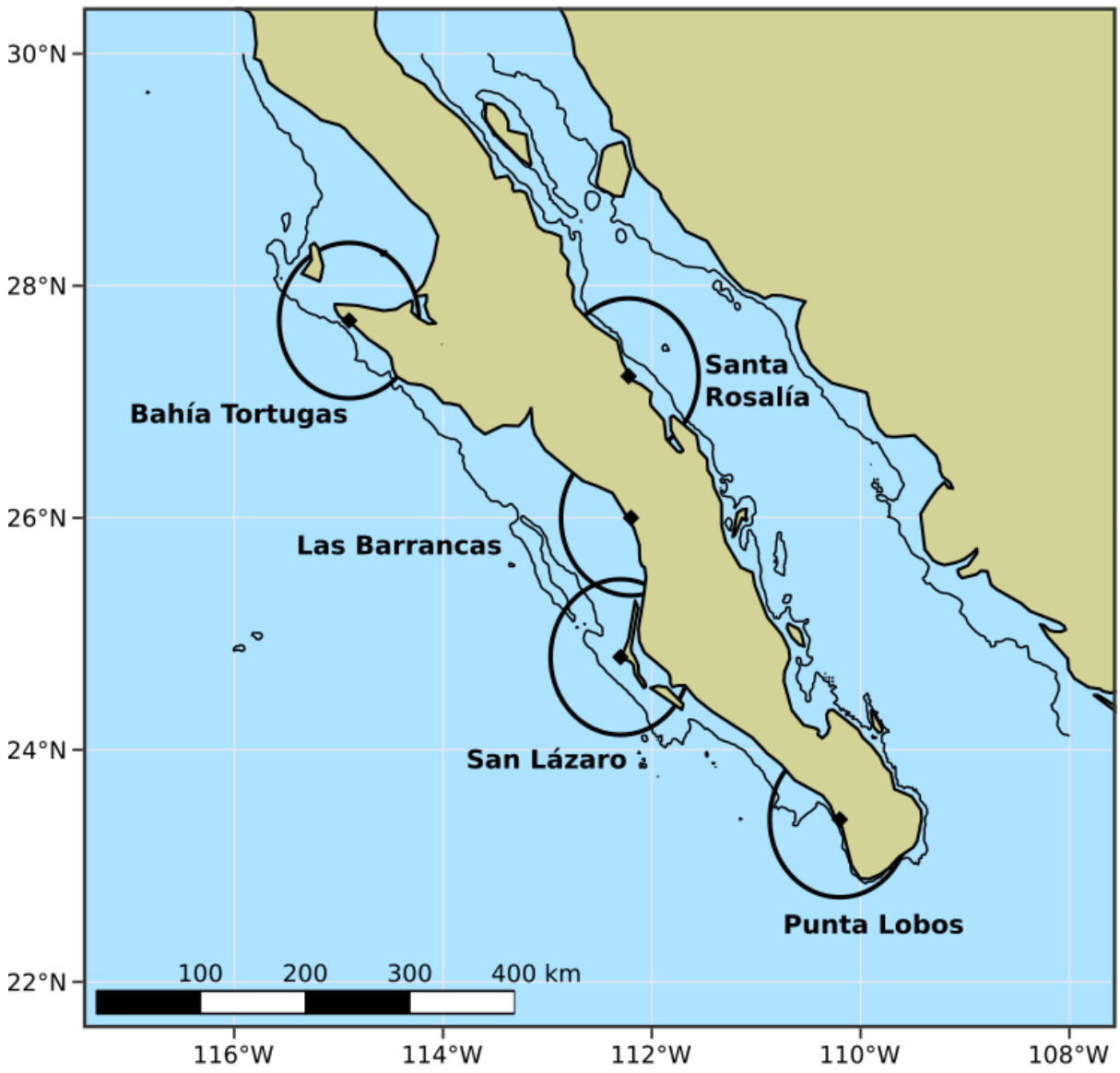


Figure 2-6 – Map of the sampling locations with the 200 m bathymetric line represented. All samples came from five artisanal fishing camps. Circle areas delineate the area covered by fishermen during their fishing activities (~40 nautical miles), an information obtained by interviews conducted by the CICIMAR laboratory (La Paz, Mexico).

b. Fishing gears

There were important variations in the equipment used between artisanal fishing camps and between boats/anglers, even though gillnet was the most commonly used fishing gear. In the Pacific coast of Baja California Sur, the length of gillnets varies from 200 to 800 m and from 7.6 to 25.4 cm in mesh size. Meanwhile, the length of longlines varies from 1.5 to 3 km with a number of J-hook ranging from 250 to 400 (Ramírez-

Amaro et al., 2013). In the fishing camp of Punta Lobos, samples from blue, shortfin mako and smooth hammerhead sharks (**Chapter 4**) were obtained using longlines.

c. Sharks tissue collection, measurement and sex determination

Whole sharks were brought back by fishermen and landed. Sampling always occurred on shore. After species identification, all individuals were measured for total length from the snout to the back of the tail. Sex was determined by the presence/absence of claspers. Approximately 1 g of dorsal muscle was extracted from each individual. Samples were placed into vials, labelled, stored in ice and transported from fishing camps to the laboratory, where they were conserved at -20°C until further processing (CICIMAR – Centro Interdisciplinario de Ciencias Marinas, La Paz, Baja California Sur; **Chapter 4-6**). Samples from Santa Rosalía (2019-2020) underwent a different methodology owing to **Chapter 3** multi-tissue stable isotope and fatty acid analyses (*see next section on biomarker analysis*): in addition to muscle, between 1.5 and 3 mL of blood was sampled from each shark using single-use syringes.

3. Biomarker analysis

a. C and N stable isotope analysis

Isotopes are atoms of a given element that differ in their number of neutrons. Stable isotope analysis relies on mass differences between isotopes of a given element, which are measured using isotope ratios mass spectrometers (IRMS). In this study, measurements were carried out using a continuous flow on a Thermo Scientific Flash EA 2000 elemental analyzer coupled to a Delta V Plus mass spectrometer (Pole Spectrométrie Océan, IUEM, Plouzané, France). Isotopic ratios were all calculated following international standards, which for $\delta^{13}C$ is Vienna Pee Dee Belemnite (a marine fossil of *Belemnitella americana* in its Vienna version as the previous one has been entirely used) and atmospheric air for $\delta^{15}N$. Values are accordingly expressed in per mil (‰) following:

$$\delta X\ (‰) = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Due to mass-related kinetic differences, the product of metabolic reactions is usually enriched in light isotopes compared to the substrate, a difference known as isotope fractionation. In the metabolic chain between nutrient assimilation and excretion/respiration, the highest fractionation occurs in the final reaction, resulting in consumers being isotopically enriched in heavy isotopes compared to their food source (breathed C and excreted N are isotopically lighter). Consequently, in food webs, basal species display the lowest C and N stable isotope ratios, while top-predators exhibit the highest ones.

Nowadays, stable isotope analysis is a central tool to study ecological niches, mostly based on C ($\delta^{13}C$) and N ($\delta^{15}N$) isotopes (Layman et al., 2012; Newsome et al., 2007; Pethybridge et al., 2018b; Shipley and Matich, 2020). Stable isotope composition of carbon and nitrogen established during photosynthesis by primary producers are transferred through the food web in a relatively predictable way, allowing the retrospective tracing of trophic interactions.

In marine ecosystems, $\delta^{13}C$ discriminates benthic from pelagic and coastal from offshore trophic habitats (Figure 2-7) (France, 1995; Peterson and Fry, 1987). At the base of the food web, $\delta^{13}C$ varies according to different inorganic carbon sources and metabolic pathways of photosynthesis, distinguishing between C_3 and C_4 plants, phytoplankton, macrophytes, seagrasses and mangroves (e.g., France, 1995; Fry and Sherr, 1984; Heithaus et al., 2011; Hemminga and Mateo, 1996). $\delta^{13}C$ generally remains relatively unaffected by trophic transfers (approximately +1‰ of enrichment) and is therefore used to infer food web bases (France and Peters, 1997). Major baseline $\delta^{13}C$ spatial variations occur, mainly resulting from changes in dissolved inorganic carbon and temperature (Magozzi et al., 2017). Such baseline fluctuations have been used to study shark spatial trophic ecology due to predictable $\delta^{13}C$ variations with latitudes (e.g., Bird et al., 2018).

The $\delta^{15}N$ values of primary producers depend on nitrogen inorganic sources (e.g., dinitrogen N_2, nitrate NO_3^-) and assimilation pathways (e.g., denitrification or fixation of atmospheric N_2), leading to spatial variations in $\delta^{15}N$ baselines (both horizontally and vertically) and allowing to characterize the habitats and movements of marine consumers (Pethybridge et al., 2018a; Somes et al., 2010; Trueman et al., 2014). Nonetheless, $\delta^{15}N$ is more commonly used for the characterization of trophic levels, as it poorly discriminates between primary producers but shows stepwise enrichments

through the food chain (Figure 2-7) (Cabana and Rasmussen, 1994; Hussey et al., 2014; Post, 2002).

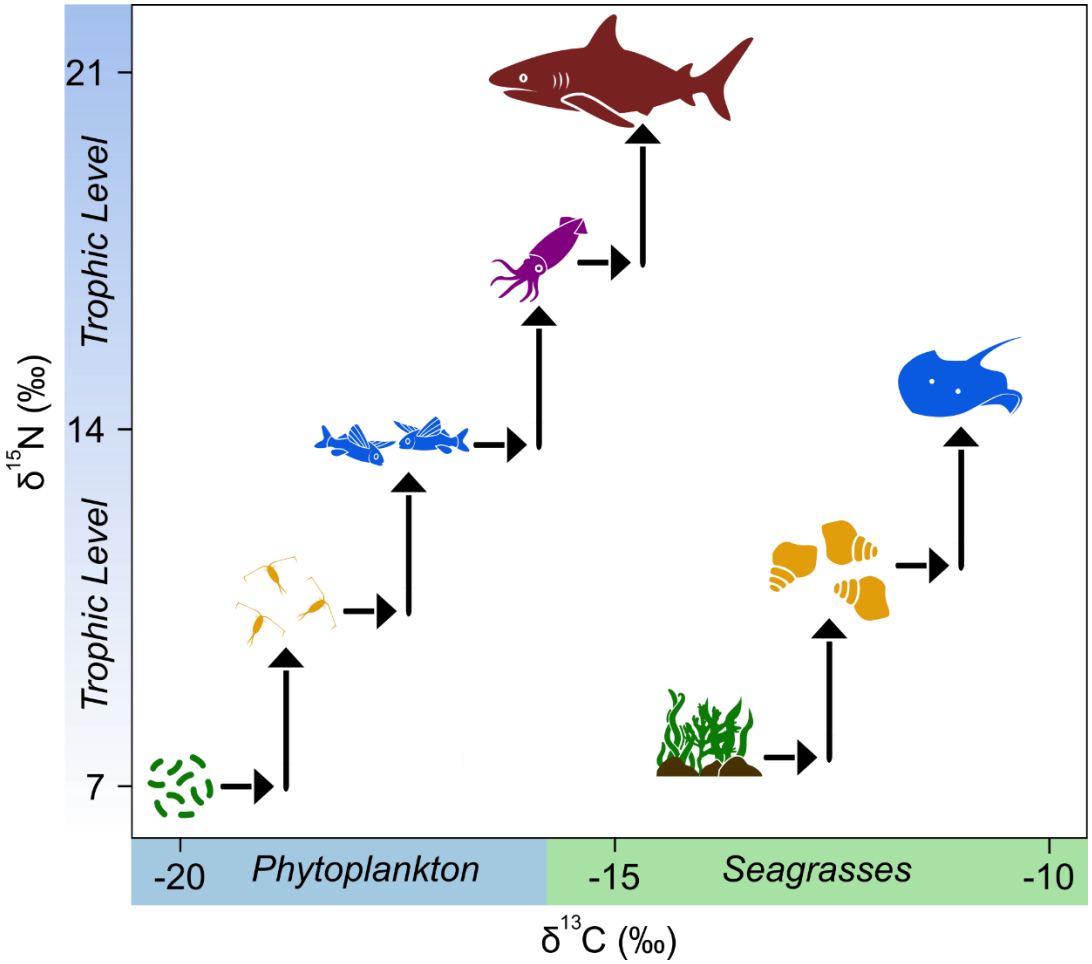


Figure 2-7 – Enrichment in ^{13}C and ^{15}N isotopes throughout trophic transfers in a putative pelagic (on the left) and coastal (on the right) trophic chain. Colors match the different taxon trophic levels. Panels provide hypothetical stable isotope values that could differ given spatial variations, as described in the text.

Other isotopes used in marine ecology include sulphur isotopes, $\delta^{34}S$ ($^{34}S/^{32}S$). $\delta^{34}S$ can further distinguish between pelagic and benthic and between marine and fresh-water sources (Croisetière et al., 2009; Layman et al., 2012). $\delta^{34}S$ thus complement $\delta^{13}C$ values and has been used to trace habitat use or quantify maternal provisioning in shark species (Niella et al., 2021; Raoult et al., 2019). Other tools include hydrogen $\delta^{2}H$ ($^{2}H/^{1}H$ or δD for deuterium) or oxygen $\delta^{18}O$ ($^{18}O/^{16}O$), which exhibit important spatial variations and can be used to track large-scale dietary patterns/migration across ocean basins (Layman et al., 2012; Shiffman et al., 2012) or discriminate movements between freshwater and marine ecosystems (Solomon et al., 2009).

Stable isotopes present practical advantages, such as their low cost, and are a relatively simple methodology that can be performed on living, dead and even museums archived shark specimens (Kerr et al., 2006). In the field, sampling can be non-lethal and minimally invasive, which is essential for endangered species (Shiffman et al., 2012). Their main advantages lie in their capacity to integrate the elementary compositions of preys through wider time scales than stomach content analysis, allowing a better view of the feeding habits throughout time. Consumers acquire the stable isotope composition of their diet within a time period depending on the incorporation rate of the analyzed tissue (Carter et al., 2019), whereby metabolically active tissues integrate new isotopic information faster than those that are less metabolically active (Thomas and Crowther, 2015; Vander Zanden et al., 2015). Short time integrating tissues include liver and blood plasma, while integration rates of skin, muscle or bone collagen are longer (Caut et al., 2013; Kim et al., 2012; Logan and Lutcavage, 2010; MacNeil et al., 2006; Malpica-Cruz et al., 2012). Meanwhile, hard structures with apparent growth marks, such as vertebrae in sharks or otoliths in fishes, allow the characterization of ontogenetic niche shift(s) at the scale of individual's life histories, without sampling many organisms of different size classes (Estupiñán-Montaño et al., 2021b; Kerr et al., 2006; Raoult et al., 2019; Trueman et al., 2012).

Stable isotopes also allow the implementation of quantitative analyses to characterize a consumer's diet. A classical way of analyzing stable isotope data is to characterize isotopic niches as the area included within projected coordinates in a δ-space (Layman et al., 2007; Newsome et al., 2007). Prey contribution to the diet of a consumer can be retraced thanks to its isotopic values using mixing models (Caut et al., 2013; Hussey et al., 2010b; Le Croizier et al., 2020a). Finally, stable isotopes can also help to trace migration patterns using latitudinal $\delta^{13}C$ and $\delta^{15}N$ spatial gradients, given the fact that isotopic signals are incorporated gradually in animal tissues (Graham et al., 2010; Hobson, 1999; Madigan et al., 2021; Magozzi et al., 2021; Trueman and St John Glew, 2019). Animals moving between two isotopically distinct regions and foraging throughout the process exhibits stable isotope compositions reflecting a mix of both systems, but will ultimately reach isotopic steady stage with the arrival habitat, after a sufficient residence time (Madigan et al., 2020b; Trueman and St John Glew, 2019). Under the hypothesis of diet consistency, animals whose tissues isotopic composition

does not reflect local baselines are considered to have immigrated from another habitat (Graham et al., 2010).

Measuring stable isotopes of carbon and nitrogen in the tissues of sharks and rays requires taking into account the biochemical composition of their tissues. Elasmobranch osmoregulation mechanisms involves the retention of ^{15}N-depleted urea ($CO(NH_2)_2$) and/or trimethylamine *N*-oxide (TMAO, $(CH_3)_3NO$) potentially impairing bulk $\delta^{15}N$ values interpretation. Lipids are also ^{13}C-depleted compared to proteins and carbohydrates (DeNiro and Epstein, 1977), and can modify bulk $\delta^{13}C$ values with no connection to dietary patterns (i.e., the fatter the tissue, the lower its $\delta^{13}C$ value). Debates are still ongoing on the necessity of lipid extraction in consumers (Post et al., 2007) and some studies chose not to account for lipid effects in sharks, as their tissues (especially muscle) are generally lean (e.g., Malpica-Cruz et al., 2013). Meanwhile, repeatedly washing samples repeatedly with deionized or MiliQ water to avoid urea and TMAO effects is a common methodology (Kim and Koch, 2012). These effects must be considered to avoid biased ecological conclusions and to standardize isotopic values in the literature, either by chemical extraction or by mathematical corrections of untreated tissue (e.g., Bird et al., 2018; Le Croizier et al., 2016). According to a previous study on our main species of interest (i.e., smooth hammerhead, scalloped hammerhead, blue and shortfin mako sharks), lipid and urea extractions were performed for each sample using Folch solution (Folch et al., 1957) and distilled water, respectively (Li et al., 2016b).

b. Mercury (Hg) stable isotope analysis

i. Hg cycle and accumulation in marine fauna

Mercury (Hg) is a major pollutant of marine ecosystems, mainly emitted by anthropogenic activities since pre-industrial times (Bowman et al., 2020; Outridge et al., 2018) with harmful neurotoxic effects on marine fauna (Eisler, 2006; Krey et al., 2015). Atmospheric Hg is deposited to surface waters through inorganic Hg(II) dry and wet deposition (i.e., via particles and rainfall, respectively) or ocean uptake of gaseous Hg(0) (Jiskra et al., 2021). In coastal ecosystems, river Hg exports dominate atmospheric inputs (Liu et al., 2021) and Hg is subsequently transformed to methylmercury (MeHg) by bacteria in sediment (using Hg(II) as a substrate). In the open ocean, Hg arises from nearly equal contribution of atmospheric Hg(II) deposition

and Hg(0) uptake (Jiskra et al., 2021). Hg methylation occurs in the water column (i.e., via Hg(II) methylation, following oxidation of Hg(0) in the case of gaseous uptake), particularly in hypoxic and high remineralization layers where anaerobic microbial activity is enhanced (Blum et al., 2013; Fitzgerald et al., 2007; Sunderland et al., 2009).

MeHg is the most bioavailable form of Hg, it is assimilated by phytoplankton after bacterial methylation and transferred through the entire food web (Choy et al., 2009; Hammerschmidt and Bowman, 2012). Therefore, diet is the primary pathway for MeHg exposition, and is generally the primary form of Hg in fish species. After consumption, MeHg is absorbed through the digestive tract, penetrates blood circulation and is distributed to the different organs (Li et al., 2020). MeHg is characterized by a strong affinity to the thiol groups of amino acids such as cysteine (Lemes and Wang, 2009), leading to long-term binding to muscle proteins, a tissue where MeHg is therefore particularly concentrated in sharks (O'Bryhim et al., 2017).

Due to its low excretion rate in marine fauna, Hg bioaccumulates in organisms with size and age (Figure 2-8), a pattern globally observed in sharks (Biton-Porsmoguer et al., 2018; Chouvelon et al., 2018; Le Bourg et al., 2019; Matulik et al., 2017; McKinney et al., 2016). In the meantime, due to both efficient trophic transfer of MeHg in aquatic food webs and weak Hg elimination rate in marine biota, long-lived apex predators tend to accumulate higher Hg concentrations in their tissues than baseline organisms, a mechanism referred to as biomagnification (Figure 2-8). Biomagnification of Hg is commonly observed in nearly all aquatic food-webs (Lavoie et al., 2013) with trophic position representing the principal factor of MeHg or total Hg concentrations in higher consumers (Biton-Porsmoguer et al., 2018; Le Bourg et al., 2019; Matulik et al., 2017; McKinney et al., 2016; Senn et al., 2010). As long-lived predators at the top of food webs, sharks naturally exhibit high mercury concentrations (Le Bourg et al., 2019; Schartup et al., 2019).

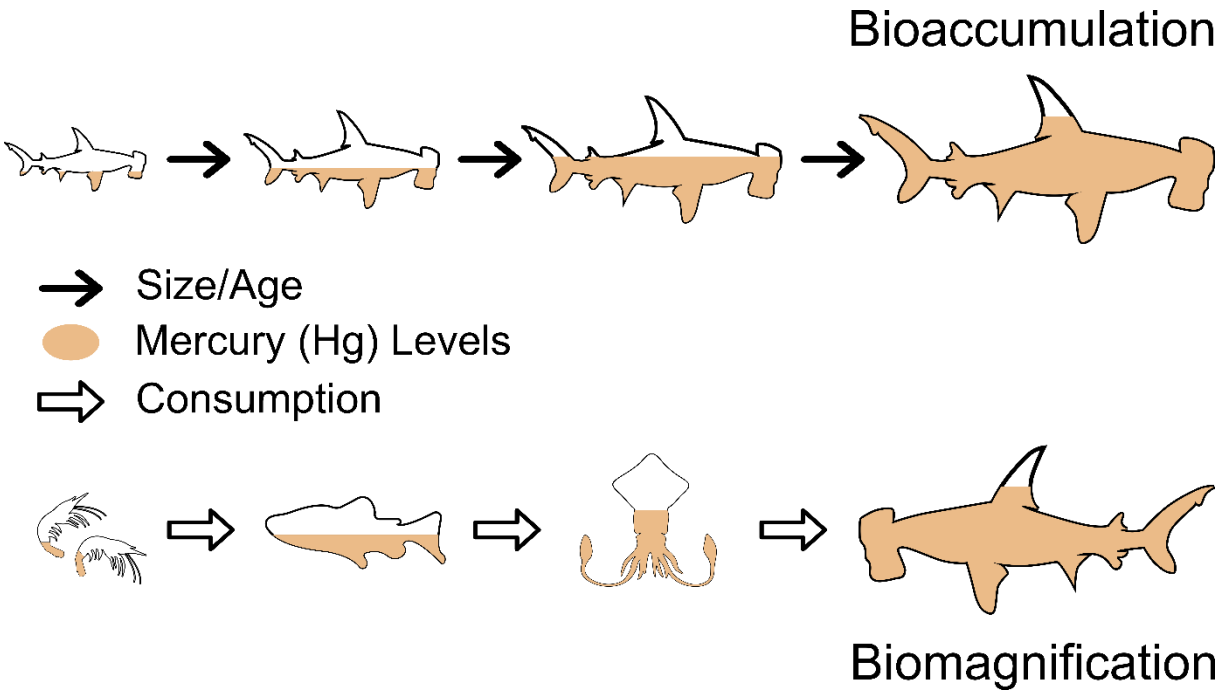


Figure 2-8 – Mercury bioaccumulation and biomagnification mechanisms in sharks.

Hg concentrations in sharks are influenced by their trophic habitats. Coastal demersal and bathyal species have been observed to concentrate more Hg than pelagic species (Le Bourg et al., 2019; Le Croizier et al., 2019). Oceanic predators feeding at depth, closer to the hotspot of MeHg production, had higher Hg concentrations than epipelagic species (Choy et al., 2009). Ecosystem characteristics also drive Hg accumulation patterns. Changes in sea temperature, increasing primary production and diminishing dissolved oxygen levels lead to higher levels of MeHg in the water column (Ferriss and Essington, 2014; Houssard et al., 2019; Schartup et al., 2019). The trophic structure (e.g., number of trophic levels) affects the strength of biomagnification (Ferriss and Essington, 2014). Oligotrophy (i.e., low productivity) generally increases Hg concentrations as the pool of Hg in productive systems is diluted in the strong biomass of first trophic level species (Chouvelon et al., 2018; Lavoie et al., 2013). Hg concentration in marine fauna is also affected by physiological characteristics such as longevity, fasting, metabolism, growth and feeding rates (Bolea-Fernandez et al., 2019; Houssard et al., 2019; Peterson et al., 2018). Finally, high Hg concentrations in marine predators are detected in areas where strong anthropogenic inputs occur, such as observed in the northwestern Pacific Ocean, which is particularly subject to local atmospheric emissions (McKinney et al., 2016; Médieu et al., 2022).

ii. Hg isotopes

Hg has seven naturally occurring stable isotopes (^{196}Hg = 0.16%, ^{198}Hg = 10.00%, ^{199}Hg = 16.90%, ^{200}Hg = 23.10%, ^{201}Hg, =13.20%, ^{202}Hg = 29.70%, and ^{204}Hg = 6.83%, Bergquist and Blum, 2007). In the water column, Hg is subjected to mass-independent isotopic fractionation (MIF) and to mass-dependent isotopic fractionation (MDF). In this study, Hg isotopes were measured using an inductively coupled plasma mass spectrometry (MC-ICP-MS, Thermo Finnigan Neptune) with continuous-flow cold vapor (CV) generation using Sn(II) reduction, CETAC HGX-200 (Observatoire Midi-Pyrénées, Toulouse, France). Hg isotopic composition is reported in per mil (‰) deviation from the NIST-SRM-3133 standard and determined by sample-standard bracketing:

$$\delta^{XXX}Hg\ (‰) = \left(\frac{^{XXX}Hg\ /\ ^{198}Hg_{sample}}{^{XXX}Hg\ /\ ^{198}Hg_{NIST-SRM-3133\ standard}} - 1 \right) \times 1000$$

where XXX represents the different masses of Hg isotopes. MDF corresponds to δ^{202}Hg values. MIF (Δ notation) is subsequently calculated as the difference between the measured δ value and the predicted δ value (i.e., calculated by multiplying the δ^{202}Hg value by the kinetic fractionation factor established for each isotopes) (Bergquist and Blum, 2007):

$$\Delta^{199}Hg\ (‰) = \delta^{199}Hg - (\delta^{202}Hg \times 0.252)$$

$$\Delta^{200}Hg\ (‰) = \delta^{200}Hg - (\delta^{202}Hg \times 0.502)$$

$$\Delta^{201}Hg\ (‰) = \delta^{201}Hg - (\delta^{202}Hg \times 0.752)$$

$$\Delta^{204}Hg\ (‰) = \delta^{204}Hg - (\delta^{202}Hg \times 1.493)$$

MIF of even-mass isotopes (i.e., Δ^{200}Hg) is thought to occur through atmospheric Hg transformations in the tropopause (Chen et al., 2012). At the ocean/atmosphere interface, Hg inputs can occur through dry and wet depositions via Hg(II) or dissolution of gaseous Hg(0) (Zhang et al., 2014). Δ^{200}Hg values differ between Hg(II), with slightly positive values, and Hg(0), with slightly negative values (Enrico et al., 2016; Gratz et

al., 2010). These values are conserved in the water column, making it a good tracer to characterize Hg atmospheric origin (Jiskra et al., 2021; Lepak et al., 2015), even in upper trophic levels (Le Croizier et al., 2022; Masbou et al., 2018). In some regions, coastal areas are more influenced by continental Hg(0) uptake introduced via riverine and terrestrial runoff, while pelagic ecosystems are characterized by approximatively equal contribution of Hg(0) and Hg(II) (Figure 2-9) (Jiskra et al., 2021; Meng et al., 2020).

MIF of odd-mass isotopes (i.e., assessed by Δ^{199}Hg values but also expressed in Δ^{201}Hg values) is a consequence of Hg photochemical degradation (Blum et al., 2013). In the open ocean, light intensity is high at the surface and decreases with depth until the aphotic water layer, a pattern reflected in the Δ^{199}Hg signatures of marine fauna (Blum et al., 2013; Motta et al., 2019; Sackett et al., 2017). Δ^{199}Hg values have been used to characterize the foraging depth of pelagic predators, at both the inter- and intra-specific level, offering a new perspective in the characterization of the trophic habitat, which was not previously provided by traditional isotopic approaches (Le Croizier et al., 2022, 2020b; Madigan et al., 2018). Moreover, coastal Hg from sediments or turbid waters (where light penetration is restricted) displays low Δ^{199}Hg values compared to oceanic Hg, discriminating between coastal and offshore foraging habitats (Figure 2-9) (Meng et al., 2020; Senn et al., 2010).

MDF (i.e., δ^{202}Hg) results from photochemical transformation, but also from other abiotic and biotic processes such as volatilization (Zheng et al., 2007) and methylation/demethylation (Janssen et al., 2016; Perrot et al., 2016). δ^{202}Hg is therefore a useful tool to study the metabolism of MeHg demethylating species. Indeed, *in-vivo* demethylation (i.e., degradation of MeHg to Hg(II)) occurs in some organs (e.g., intestine, liver) of birds, fishes and marine mammals to detoxify MeHg and mitigate its deleterious effects (Figure 2-9) (Bolea-Fernandez et al., 2019; Li et al., 2020; Wang et al., 2017).

During trophic transfers, Δ^{199}Hg values are conserved while δ^{202}Hg values generally increase from prey to predator due to Hg metabolism, with varying trophic discrimination factors depending on the consumer species considered (Kwon et al., 2013, 2012; Laffont et al., 2011; Li et al., 2014).

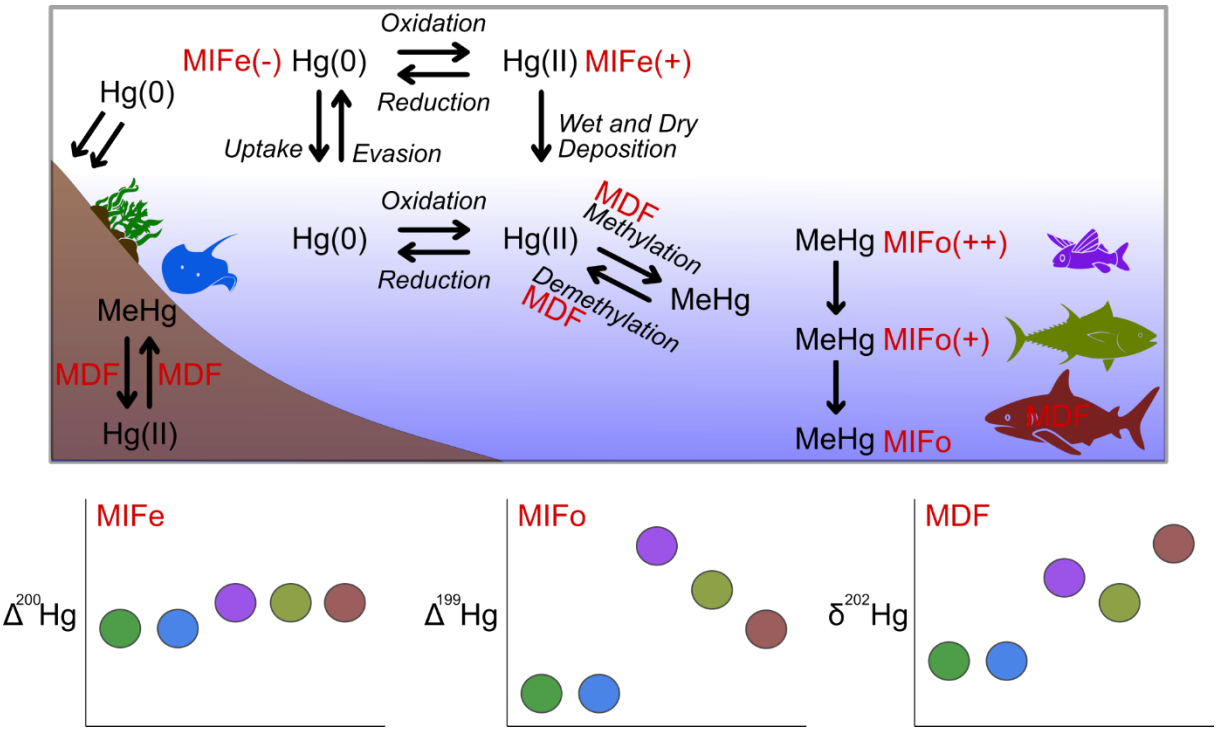


Figure 2-9 – Hg cycle and fractionation in marine ecosystems. MIFe refers to mass-independent isotopic fractionation of even-mass isotopes ($\Delta^{200}Hg$), MIFo to mass-independent isotopic fractionation of odd-mass isotopes ($\Delta^{199}Hg$) and MDF to mass-dependent isotopic fractionation ($\delta^{202}Hg$). Colored points represent the Hg isotopic patterns between species. MDF in the shark corresponds to potential biotic demethylation of MeHg.

In the present work, Hg concentration and isotope measurements were performed on muscle samples. Total Hg concentration was determined on a 20 mg aliquot of the sample. Measurements were carried out using a Direct Mercury Analyzer (DMA-80, Milestone, USA) (Observatoire Midi-Pyrénées, Toulouse, France). Measured total Hg concentration was used as a proxy for MeHg as it is the dominant form in shark muscle (e.g., Matulik et al., 2017) especially for the species of interests analyzed in this work (i.e., smooth hammerhead, blue and shortfin mako sharks) (Carvalho et al., 2014; Kim et al., 2016; Storelli et al., 2003). According to Hg concentration in each sample, successive acid digestions were performed on another dry muscle sample to convert solubilized MeHg to inorganic Hg and reach a Hg concentration of 1 ng·mL^{-1} in the final mixture analyzed by MC-ICP-MS. In marine fishes, $\Delta^{199}Hg$ and $\Delta^{201}Hg$ values are highly correlated (Blum et al., 2013) and their relationship was used to check for the reliability of the analytical results, along with the frequent measurement of blanks, certified materials and procedural standards and the constant monitoring of the ^{202}Hg signal provided by MC-ICP-MS.

c. Fatty acid composition

Fatty acids (FA) are saturated or unsaturated linear carbon chains ending with a carboxyl group. They are named following the traditional C:An-B nomenclature, with C the number of carbon, A the number of double bonds and B the position of the first double bound starting from the methyl end group (Figure 2-10) (Iverson, 2009). FA, which are the main components of complex lipids, cover an important range of functions in marine organisms. Membrane lipids (also known as polar lipids) enter the composition of cell membranes (e.g., phospholipids). Reserve lipids (also named neutral lipids), mostly triacylglycerol, are the densest form of energy storage intended for oxidation or stored (Dalsgaard et al., 2003; Parrish, 2013). The FA composition of membrane lipids is highly regulated for homeostasis purpose and does not reflect dietary inputs dietary inputs. In contrast, neutral lipids FA are deposited with less selectivity from dietary inputs, and reflect the composition of food sources integrated over a period of time depending of the tissue, season, species and reproductive status considered (Iverson, 2009).

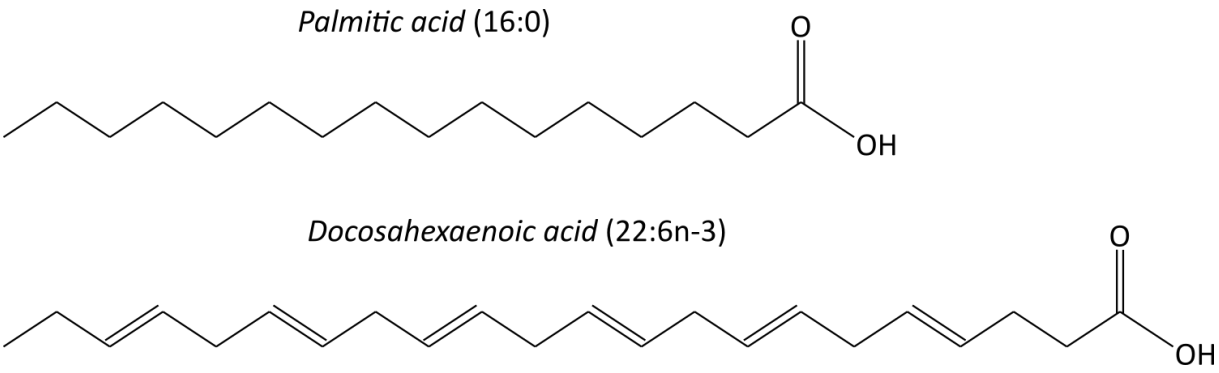


Figure 2-10 – Examples of FA nomenclature.

FA in marine animals can be either synthesized *de novo*, incorporated from diet without modification, or modified from existing precursors. *De novo* synthesis is limited to short and monounsaturated FA in marine fishes. FA can be modified from existing precursors thanks to elongation, desaturation or β-oxidation reactions thanks to different enzymes, which differ according to the taxa considered. Primary producers (algae/plants) are the only organisms containing the Δ^{15} desaturase and Δ^{12} desaturase enzymes (Dalsgaard et al., 2003) allowing the synthesis of polyunsaturated fatty acids (PUFA) from linoleic acid, 18:2n-6, and α-linoleic acid, 18:3n-3. Whereas 18:2n-6 and 18:3n-3 are known as essential FA for terrestrial food web,

phytoplankton/algae in the marine world contained all the desaturases allowing the synthesis of long-chain PUFA. Long-chain PUFA include FA such as eicosapentaenoic acid (EPA, 20:5n-3), docosahexaenoic acid (DHA, 22:6n-3) and arachidonic acid (ARA, 20:4n-6). These FA are recognized as essential to fulfill key functions (i.e., reproduction, development, growth), cannot be synthetized by most animals and have to be obtained from the diet (e.g., Arts et al., 2011; Parrish, 2013; Sardenne et al., 2017).

FA composition in fishes therefore originates from both endogenous and exogenous sources. Nevertheless, their capacity of *de novo* synthesis is limited to a few structurally simple FA and is rapidly inhibited whenever physiological requirements are met in the diet, leading to a predominant influence of dietary inputs in the composition of FA in animals (Iverson, 2009; Nelson, 1992). Apart from characterizing predator-prey relationships, FA can also distinguish between phytoplanktonic groups (diatoms *vs* dinoflagellate), macroalgae and bacteria, and can be marker of certain zooplankton orders (Dalsgaard et al., 2003; Iverson, 2009; Parrish, 2013).

FA were used combined to stable isotope analysis to compare the dietary habits of scalloped hammerhead, smooth hammerhead and Pacific sharpnose sharks, as previously achieved in the study of resource partitioning among predator assemblages (e.g., Belicka et al., 2012; Segura-Cobeña et al., 2021). Metabolically active tissues are preconized in the analysis of FA to assess animal diet, as neutral lipids (reserve lipids) are more concentrated in these tissues. In this context, the use of muscle or skin is not optimal compared for example to adipose tissues (Iverson, 2009). For the present study, we analyzed whole blood as a highly metabolically active, easy to sample in the field, “tissue”. Muscle was still analyzed as its FA composition might reflect long-term differences in diet and metabolic regulations (Iverson, 2009). In addition, during experiment under controlled environment, shark muscle tissues have been shown as a reliable diet indicator (Beckmann et al., 2013b), even if the major storage site of lipids is localized in the liver (Beckmann et al., 2013a; Belicka et al., 2012).

Muscle and whole blood samples were transferred in glass tubes containing a chloroform/methanol mixture (2/1, v/v) (Folch et al., 1957) immediately after sample collection in the field and stored on ice to avoid sample denaturation during transportation (Couturier et al., 2020; Parrish, 1999). Once in the laboratory, each

solution containing tissues was flushed with N_2 and tubes were stored at -20°C until further processing or analysis. Lipid extraction from muscle tissues was completed using manual grinding with a Dounce homogenizer. Due to the limited time to process samples in the field, we could not weigh the amount of muscle and blood extracted from each shark. Therefore, this study FA analysis is qualitative, with each FA expressed as the percentage of the total FA content of the sample.

CHAPTER 3

RESOURCE PARTITIONING IN HAMMERHEAD SHARK SPECIES OUT-MIGRATING FROM COASTAL ECOSYSTEMS IN THE GULF OF CALIFORNIA.

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IN PREP.

1. Abstract

Large hammerhead sharks occupy coastal nurseries in the first months of their life cycle before migrating to offshore pelagic regions. In the Gulf of California, artisanal elasmobranch fisheries have reported the catch of early life stages of scalloped (*Sphyrna lewini*) and smooth (*Sphyrna zygaena*) hammerhead sharks. Given the continuous fishing pressure and the observed decrease of hammerhead abundance in the region, a local assessment of both species habitat use is needed to promote conservation and improve management planning. In this study, we used an approach based on the dynamic foraging strategy of hammerhead shark species to characterize their dietary reliance to coastal ecosystems in the central occidental coast of the Gulf of California. We compared the stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) and fatty acid composition in two tissues, whole blood and muscle, of two hammerhead sharks and another permanent coastal resident, the Pacific sharpnose shark (*Rhizoprionodon longurio*). Scalloped hammerhead sharks were sampled at smaller size (~97 cm) than smooth hammerhead sharks (~126 cm). Smooth hammerhead sharks were characterized by lower $\delta^{13}C$ values and higher level of docosahexaenoic acid (DHA) in neutral lipids in both muscle and blood, suggesting that they relied more on pelagic prey and have already performed their ontogenetic habitat shift. Scalloped hammerhead sharks showed higher variation in stable isotopes and fatty acid compositions between tissues. In the long-term integrating muscle, the species occupied a wider isotopic niche with higher $\delta^{13}C$ range than smooth hammerhead sharks. In blood, a short-term integrating tissue, its isotopic niche was narrower and closer to the pelagic signal observed in smooth hammerhead sharks. These results suggest scalloped hammerhead sharks had recently initiated their ontogenetic transition with muscle still reflecting coastal foraging signal, probably from nurseries. Therefore, dietary tracers revealed different stages of ontogenetic habitats shift in the two hammerhead sharks. Such resources partitioning between life stages in a shared ecosystem could allow for the reduction of competition between morphologically and ecologically similar hammerhead species, and could be considered for setting science-based management plans for the two hammerhead species.

2. Introduction

Coastal ecosystems are among the most productive and valued ecosystems, providing major goods and services to human populations (Barbier et al., 2011; Costanza et al.,

1997). They are highly variable over different spatial and temporal scales, and include a diversity of habitats, which marine biota uses for feeding and/or reproduction (Gray, 1997). In many fish species, juvenile and adult's habitats are separated to avoid intra-specific competition, and coastal ecosystems are frequently used as nursery areas. Nurseries are mainly characterized by the high abundances of neonate, young-of-the-year or juvenile specimens in a sheltered and productive area, which ultimately results in higher rates of recruitment into adult populations (Beck et al., 2001). Sharks are among the species using coastal ecosystems as nurseries (Heupel et al., 2007), especially large-bodied species because of their low productivity (i.e., slow growth, late maturity, limited number of pups), which involves a need to maintain juvenile populations with low mortality rates in the absence of maternal care (Heupel et al., 2018; Knip et al., 2010).

Among large hammerhead shark species, scalloped hammerhead sharks (*Sphyrna lewini*) and smooth hammerhead sharks (*Sphyrna zygaena*) are recognized to use coastal nurseries (Diemer et al., 2011; Duncan and Holland, 2006; Estupiñán-Montaño et al., 2021b; Francis, 2016). Both species share common life histories: early juveniles inhabit nursery areas before migrating toward offshore pelagic waters where individuals regroup and eventually reproduce (Gallagher and Klimley, 2018). In the northeastern Pacific, young-of-the-year and juvenile specimens of both species are frequently reported in the catches of coastal artisanal fisheries in the Gulf of California (Saldaña-Ruiz et al., 2017; Torres-Rojas et al., 2015). The region is characterized by high fishing pressure on coastal habitats, which results in depleted scalloped and smooth hammerhead shark populations and has led to the local disappearance of four other hammerhead shark species (i.e., *S. corona*, *S. media*, *S. mokarran* and *S. tiburo*) from the Mexican Pacific (Pérez-Jiménez, 2014). While movements of late juveniles in the pelagic habitat have been characterized (e.g., Jorgensen et al., 2009; Klimley et al., 1993), the dependence on coastal and offshore food webs in the young stages of these species, especially during their ontogenetic habitat shift, remains yet to be fully understood while critical for their conservation (Kinney and Simpfendorfer, 2009).

The study of trophic ecology regroups indirect, spatially and temporally integrating approaches to characterize dietary sources and partitioning in marine predators. Trophic biomarkers, such as stable isotopes (SI, here $\delta^{13}C$ and $\delta^{15}N$) and fatty acids (FA), provide a powerful approach to describe consumer trophic niches and can easily

be carried out on samples collected from fisheries catches. In marine ecosystems, $\delta^{13}C$ values efficiently discriminate coastal from offshore primary producers due to different inorganic carbon sources and photosynthesis pathways between phytoplankton and coastal basal producers (e.g., seagrasses, macrophytes) (Miller et al., 2010). Baseline $\delta^{13}C$ values are reflected in consumers with little or no trophic enrichment between prey and predator, and are used to infer food web bases in higher consumers (Bird et al., 2018). $\delta^{15}N$ values are classically considered as proxies of trophic levels, due to ^{15}N-stepwise enrichment throughout the food webs (Hussey et al., 2014). FA, the main component of lipids, can also be used to infer food sources and can help to retrace food web origin (Dalsgaard et al., 2003; Meyer et al., 2019; Parrish, 2013). In trophic ecology, the FA composition of neutral lipids (i.e., storage lipids) are preferred to the one of polar lipids, as they are transferred with limited modifications from prey to predators (Robin et al., 2003). Among FA, polyunsaturated FA (PUFA), such as docosahexaenoic acid (DHA, 22:6n-3), eicosapentaenoic acid (EPA, 20:5n-3), and arachidonic acid (ARA, 20:4n-6) are essentials for the development of shark early life stages, as they support somatic growth (Tocher, 2010), cognitive functions (Sugasini et al., 2017) and behavioral competences (Pilecky et al., 2021). In marine ecosystems, primary producers are the only species able to *de novo* synthesize PUFA (Parrish, 2013). Therefore, they have to be acquired from the diet in predators (Belicka et al., 2012; Sargent et al., 1995) and can inform on the nutritional resources of an organism (Rangel et al., 2021b). Combined, SI and FA offer the opportunity to describe trophic niches on multiple dimensions and efficiently address resources partitioning.

In this study, we aimed to describe the trophic niches of scalloped and smooth hammerhead sharks to assess their overlap in dietary resources and use of coastal habitats. As young hammerhead sharks exhibit multiple trophic shifts from maternal provisioning to active foraging in nursery grounds and migration in offshore ecosystems, we decided to use a multi-tissue approach, analyzing muscle and whole blood. Indeed, sharks acquire dietary signals within a different timeframe between the metabolically active blood, which integrates prey biochemical composition at shorter time scale than less metabolically active tissues, such as muscles (Beckmann et al., 2014; Bierwagen et al., 2019; Malpica-Cruz et al., 2012). In addition to scalloped and smooth hammerhead sharks, we used a third co-occurring species for comparison, the Pacific sharpnose shark (*Rhizoprionodon longurio*). The Pacific sharpnose shark is a

small-bodied coastal species (<160 cm total length) living on the continental shelf of the Gulf of California, where it is traditionally fished along with hammerhead sharks (Alatorre-Ramirez et al., 2013; Márquez-Farías et al., 2005; Saldaña-Ruiz et al., 2017). *Rhizoprionodon spp.* are very productive species (i.e., fast growing with important fecundity) and consequently do not rely on nursery areas (Heupel et al., 2018; Knip et al., 2010). They exhibit broad movement within coastal ecosystems (Carlson et al., 2008; Heupel et al., 2019; Munroe et al., 2014b) and were used as a proxy of the coastal ecosystem dietary signal.

This study improves our knowledge on the habitat use of hammerhead sharks during their early life stages, including variation in trophic inputs and movements between habitats. We hypothesize that co-occurring scalloped and smooth hammerhead sharks would present related dietary signals given the similarity of their foraging habitats at early life stages. We also expected that fine-scale differences in sampled shark stage of ontogenetic habitat and dietary shift to offshore ecosystems might be observed in whole blood SI and FA compositions. Such new ecological information could help to conserve these species, which face intense fishing pressure, and serve as a baseline for future research aiming at delineating hammerhead nursery areas in the Gulf of California.

3. Materials and Methods

a. Sample collection

Sharks were fished using gillnets by fishermen from the artisanal fishing camp of Santa Rosalía (27°20’26”N; 112°15’54”W), located in the western coast of the Gulf of California, in March and November 2019. Three species were sampled: the scalloped hammerhead shark, *Sphyrna lewini* (n=20), the smooth hammerhead shark, *Sphyrna zygaena* (n=19), and the Pacific sharpnose shark, *Rhizoprionodon longurio* (n=20). Total length (TL) measurements were taken, and sharks were sexed. Scalloped hammerhead sharks were caught from 76 to 143 cm (TL), smooth hammerhead sharks from 94 to 138 cm (TL) and Pacific sharpnose sharks from 92 to 125 cm (TL).

Tissue sampling took place as soon as the sharks were landed on shore. Whole blood and muscle were sampled for each specimen. Between 1 and 3 mL of blood was drawn via caudal venipuncture using a 10 mL single-use syringe and approximately 1 g of muscle was sampled from the shark dorsal region. Both tissues were transferred into

7 mL glass tubes previously heated at 450°C and closed with Teflon liners to avoid contamination. Then, they were immediately immersed in 6 mL of Folch $CHCl_3$/MeOH mixture (2:1, v/v) to initiate lipid extraction (Folch et al., 1957). Solutions were held on ice during the transport to the laboratory (CIBNOR – Centro de Investigaciones Biológicas del Noroeste, La Paz, Baja California Sur). There, mixtures containing the tissue and the Folch solution were vortexed for 5 minutes, flushed with N_2 and stored at -80°C until further treatments. For muscle samples, mechanical crushing using a Dounce homogenizer was performed in order to enhance lipids extraction. Then, for all samples, the Folch solution (i.e., containing the lipids) and the tissues were separated and transferred into different 7 mL glass tubes. Tubes containing lipid extracts were immediately flushed with N_2 and stored at -80°C while blood and muscle samples were stored at -20°C and freeze-dried until further treatments.

b. Stable isotope analysis

Prior to stable isotope analysis, we ensured a good lipid removal and chemically extracted urea from muscle samples, as they are known to impair both $\delta^{15}N$ and $\delta^{13}C$ interpretations respectively (Li et al., 2016b; Post et al., 2007; Shipley and Matich, 2020). Despite lipid extraction initiated at the sampling location, we ensured a good lipid removal by immersing the tissues in 6 mL of Folch $CHCl_3$/MeOH solution (2:1, v/v). The solution was vortexed 1 minute, left overnight at room temperature and centrifuged 10 minutes before removal of the Folch solution, a process repeated three times. Urea was then extracted, immersing the muscle sample into 6 mL of distilled water. The solution was subsequently vortexed for 1 minute, left at room temperature for 24 hours and centrifuged for 5 minutes before water removal, a process also repeated three times. All samples were dried and homogenized prior to analysis.

We weighted approximately 0.50 mg of dry muscle or blood powder into tin cups. Stable isotope ratios (δ notation) are expressed relatively to international standards: Vienna Pee Dee Belemnite for $\delta^{13}C$ and atmospheric air for $\delta^{15}N$. Samples were analyzed using a Thermo Scientific Flash EA 2000 elemental analyzer coupled to a Delta V Plus mass spectrometer at the Pole Spectrométrie Océan (IUEM, Plouzané, France). Values are expressed in per mil (‰) with R the $^{13}C/^{12}C$ or the $^{15}N/^{14}N$ ratios and X the corresponding ^{13}C or ^{15}N:

$$\delta X\ (‰) = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1000$$

Values of international standards (IAEA-600 Caffeine, IAEA-CH-6 Sucrose, IAEA-N-1 and IAEA-N-2 Ammonium Sulphate) were measured throughout the samples run and validated correct isotopic measurements. Analytical uncertainties were calculated using an Acetanilide in-lab certified substance and were ± 0.17‰ for $\delta^{13}C$ and ± 0.11‰ for $\delta^{15}N$. All samples presented a C:N ratio below 3.5, validating a good lipid and urea removal as pure protein sample is expected to be around 3.0 (Hussey et al., 2012; Post et al., 2007).

c. Fatty acid composition

Lipid extracts were shaken for 20 minutes at room temperature and centrifuged at 3000 rpm (~738 *g*) for 15 minutes. An aliquot of 250 µL of each muscle extracts and of 500 µL of each whole blood extracts were transferred to new glass vials and evaporated to dryness under N_2 flux. Dry extracts were recovered by three consecutive re-suspension in 500 µL of $CHCl_3$/MeOH (98:2, v/v) and deposited at the top of a silica gel micro-column (40 mm × 4 mm, silica gel 60A, previously heated at 450°C, 63-200 µm rehydrated with 6% H_2O; 70-230 mesh). Neutral lipids (NL) were eluded using 10 mL of $CHCl_3$/MeOH (98:2, v/v) and collected in glass vials (Le Grand et al., 2014, 2011). Before elution, 2.3 µg of a 23:0 internal standard (i.e., tricosanoic acid) was added to each glass vial. Following elution, NL fractions were evaporated to dryness using an EZ-2 centrifugal evaporator (Genevac). NL fractions were subsequently recovered by three consecutive re-suspension in 500 µL of $CHCl_3$/MeOH (2:1, v/v), transferred to 7 mL glass vials and evaporated to dryness under N_2 flux.

Blood NL underwent a basic transmethylation directly followed by an acidic transmethylation, while muscle samples underwent acidic transmethylation alone. Basic transmethylation consisted in the addition of 1 mL of KOH/MeOH (0.5M); the solution was flushed under N_2, vortexed and incubated at 80°C for 30 minutes. After cooling at room temperature, acidic transmethylation was achieved by adding 1600 µL of H_2SO_4/MeOH (3.4%, v/v) and incubation at 100°C for 10 minutes. Then, after cooling at room temperature, 800 µL of hexane was added to recover fatty acids methyl esters (FAME) and this organic phase was washed three times with 1.5 mL of hexane-

saturated distilled water. The organic phase was then transferred to 2 mL tapering vials, flushed under N_2 flux and stored at -20°C prior FAME analysis.

Organic phase was evaporated to dryness under N_2 flux and recovered by adding 150 µL of hexane. FAME were then purified (Marty et al., 1999) on a Dionex P680 HPLC system equipped with an ASI-100 auto-sampler, detected with a DAD-detector at 205 nm to isolate FAME from sterols, squalene and fatty alcohols. Two columns aligned in series were used: a Lichrospher Si 60 (Merck) and a Lichrospher 100 Diol (both 250 mm x 4 mm I.D., 5 µm). The mobile phase was composed of a mixture of two solvents, 1) hexane and 2) hexane/isopropanol (90:10, v/v), at 1 mL.min^{-1}. The gradient was as follows: 100% (1), 0-2 min, 85% (1), 2-10 min; 50% (1), 10-16 min; 100% (1), 16-35 min. FAME were collected from 12 to 18 minutes with an Isco Foxy Jr. fraction collector in 7 mL glass vials, evaporated to dryness under N_2 flux and finally recovered by resuspension into 800 µL of hexane.

FAME analysis was performed using a CP 8400 (Varian) gas chromatograph-flame ionization detection (GC-FID). Samples run was programmed in temperature (from 0°C to 150°C at 50°C min^{-1}, then to 170°C at 3.5°C min^{-1}, to 185°C at 1.5°C min^{-1}, to 225°C at 2.4°C min^{-1}, and finally to 250°C at 5.5°C min^{-1} for 15 min). The GC-FID was equipped with an auto-sampler, two split-less injectors regulated at 220°C and two flame-ionization detectors (280°C) using hydrogen as vector gas.

FAME were separated simultaneously on two different capillary columns, a polar (DBWAX -30 m × 0.25 mm i.d., 0.25-µm thickness, Agilent) and an apolar (DB5 -30 m × 0.25 mm i.d., 0.25-µm thickness, Agilent). FAME were identified by comparison of their retention time with those of commercial standards (Supelco 37 Component FAME Mix, the PUFA No.1 and No.3, and the Bacterial Acid Methyl Ester Mix from Sigma) and in-house standard mixtures from marine bivalves, micro- and macroalgae. Peak integration was realized with the software Galaxy Chromatography Data System (v. 1.9, Varian). Individual FA contents are expressed as the mass percentage (%) of the total FA content.

d. Data analysis

Species isotopic niches were described using Layman metrics based on convex hull areas (Layman et al., 2007). We estimated isotopic ranges (δ^{13}C rg and δ^{15}N rg) as the distance between the highest and lowest δ^{13}C and δ^{15}N values respectively, the

total area (TA) as the surface of the convex hull area and the mean distance to the centroid (CD) as the mean distance of each individual to the $\delta^{13}C/\delta^{15}N$ centroid. Core region of the isotopic niches were described based on 40% kernel density plots from which we calculated the area using the rKIN package (Eckrich et al., 2020).

FA accounting for less than 1.5% of the total FA contents were removed from the analysis. In blood, 14 FA were selected (14:0, 16:0, 18:0, 16:1n-7, 18:1n-7, 18:1n-9, 20:1n-9, 24:1n-9, 20:4n-6, 20:5n-3, 22:4n-6, 22:5n-3, 22:5n-6 and 22:6n-3) with 3 more FA for the muscle, which were not considered in blood samples (16:1n-9, 18:2n-6 and 16:0DMA). Principal component analyses (PCA) were separately performed for both tissues to investigate the variation in FA compositions among shark species. To avoid giving excessive weight to rare FA, Euclidean distances were calculated (Legendre and Gallagher, 2001) and the most discriminant FA (here selected as accounting for more than 90% of the dissimilarities between species) were identified through a test of similarity percentages (SIMPER).

After checking for normality and variances homogeneity, one-way ANOVAs were performed followed by post-hoc Tukey's HSD tests to assess statistical differences in muscle $\delta^{13}C$ values between species, and Kruskal-Wallis tests, followed by Dunn's post hoc tests with Bonferroni's adjustment, were used to assess statistical differences in total length, FA composition, $\delta^{15}N$ and blood $\delta^{13}C$ values between species. Intra-specific statistical differences in isotopic values between tissues and sexes were tested using Student's *t*-tests or the non-parametric analogue, the Wilcoxon singed rank test (α=0.05 for all statistical tests).

Finally, we estimated the overlap between species niches (i.e., both SI and FA) using the nicheROVER package (Swanson et al., 2015). The package's functions allow estimating different niche regions in multivariate space and calculating overlap between them as the probability for an individual from one species to be found in the niche region of a second species. Here, niche regions were set as a 95% probability region using $\delta^{13}C$, $\delta^{15}N$ and the coordinates of the first two most explaining dimensions of the PCA performed on FA composition. To account for uncertainty, 1000 Monte Carlo draws of niche region projections were used in overlap estimation in a Bayesian framework. This analysis was run separately for muscle and blood tissues to compare overlap estimations between them. All analyses were performed using R (R Core Team, 2022).

4. Results

a. Carbon and nitrogen stable isotopes

Significant differences were found in the size of the three shark species ($\chi^2_{58,2}$ = 22.9, p < 0.001). Smooth hammerhead sharks ranged from 94 to 138 cm (TL), scalloped hammerhead sharks from 76 to 143 cm (TL) and Pacific sharpnose shark were comprised between 92 and 125 cm (TL) (Table 3-1). For hammerhead shark species, no differences in $\delta^{13}C$ nor $\delta^{15}N$ values were observed between sexes for both tissues (Table 3-1), excepted for scalloped hammerhead shark blood $\delta^{15}N$ values (t_{18} = -2.28, p < 0.05). For the Pacific sharpnose shark, significant differences in $\delta^{13}C$ values between female and male specimens were found for blood and muscle tissues (t_{18} = -2.52, p < 0.05 and t_{17} = -2.14, p < 0.05, respectively), as well as for $\delta^{15}N$ values in the muscle (W = 89, p < 0.01). Because the Pacific sharpnose shark was not the main focus of our study and considered an outgroup for comparison with the two hammerhead species, such $\delta^{13}C$ and $\delta^{15}N$ differences were not explored in this study, and both sexes were presented altogether.

Table 3-1 – Number of individuals (N) and mean values ±standard deviations (SD) of total length (TL) for scalloped hammerhead, smooth hammerhead and Pacific sharpnose sharks. Values in bold correspond to overall average by species. C and N isotope values for muscle and blood are presented and expressed in mean values (±SD). Upper case letters indicate significant differences between species and lower case letters between females (F) and males (M).

Species	N	Sex	TL (cm)	Muscle		Blood	
				$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Scalloped hammerhead	**20**	**-**	**97 (± 22)**	**-14.59 (± 0.43)^{A}**	**22.22 (± 0.43)^{A}**	**-14.58 (± 0.37)^{A}**	**20.95 (± 0.41)^{A}**
	10	*F*	*92 (± 20)*	*-14.43 (± 0.42)*	*22.16 (± 0.40)*	*-14.52 (± 0.43)*	*21.14 (± 0.39)^{a}*
	10	*M*	*103 (± 23)*	*-14.76 (± 0.41)*	*22.27 (± 0.48)*	*-14.65 (± 0.30)*	*20.76 (± 0.35)^{b}*
Smooth hammerhead	**19**	**-**	**126 (± 11)**	**-15.27 (± 0.25)^{B}**	**21.78 (± 0.45)^{B}**	**-15.22 (± 0.29)^{B}**	**20.58 (± 0.38)^{B}**
	4	*F*	*130 (± 4)*	*-15.36 (± 0.23)*	*21.96 (± 0.11)*	*-15.15 (± 0.26)*	*20.75 (± 0.28)*
	15	*M*	*126 (± 12)*	*-15.25 (± 0.26)*	*21.74 (± 0.50)*	*-15.24 (± 0.30)*	*20.54 (± 0.39)*
Pacific sharpnose	**20**	**-**	**105 (± 9)**	**-14.94 (± 0.42)^{C}**	**22.00 (± 0.54)^{AB}**	**-14.50 (± 0.56)^{A}**	**21.37 (± 0.64)^{C}**
	10	*F*	*111 (± 10)*	*-14.76 (± 0.43)^{a}*	*21.63 (± 0.52)^{a}*	*-14.22 (± 0.50)^{a}*	*21.33 (± 0.67)*
	10	*M*	*100 (± 4)*	*-15.13 (± 0.33)^{b}*	*22.37 (± 0.20)^{b}*	*-14.78 (± 0.49)^{b}*	*21.42 (± 0.64)*

At the intra-specific scale, muscle samples were ^{15}N-enriched compared to blood samples for all three species (t_{38} = -9.6, p < 0.001 for scalloped hammerhead shark, W = 6, p < 0.001 for smooth hammerhead shark and W = 86.5, p < 0.01 for Pacific

sharpnose sharks). In hammerhead sharks, $\delta^{13}C$ values remained similar across tissue (t_{37} = 0.1, p > 0.05 for scalloped hammerhead shark and t_{35} = 0.6, p > 0.05 for smooth hammerhead shark), while Pacific sharpnose shark muscle was ^{13}C-depleted (t_{35} = 2.8, p < 0.01) compared to blood samples (Figure 3-1).

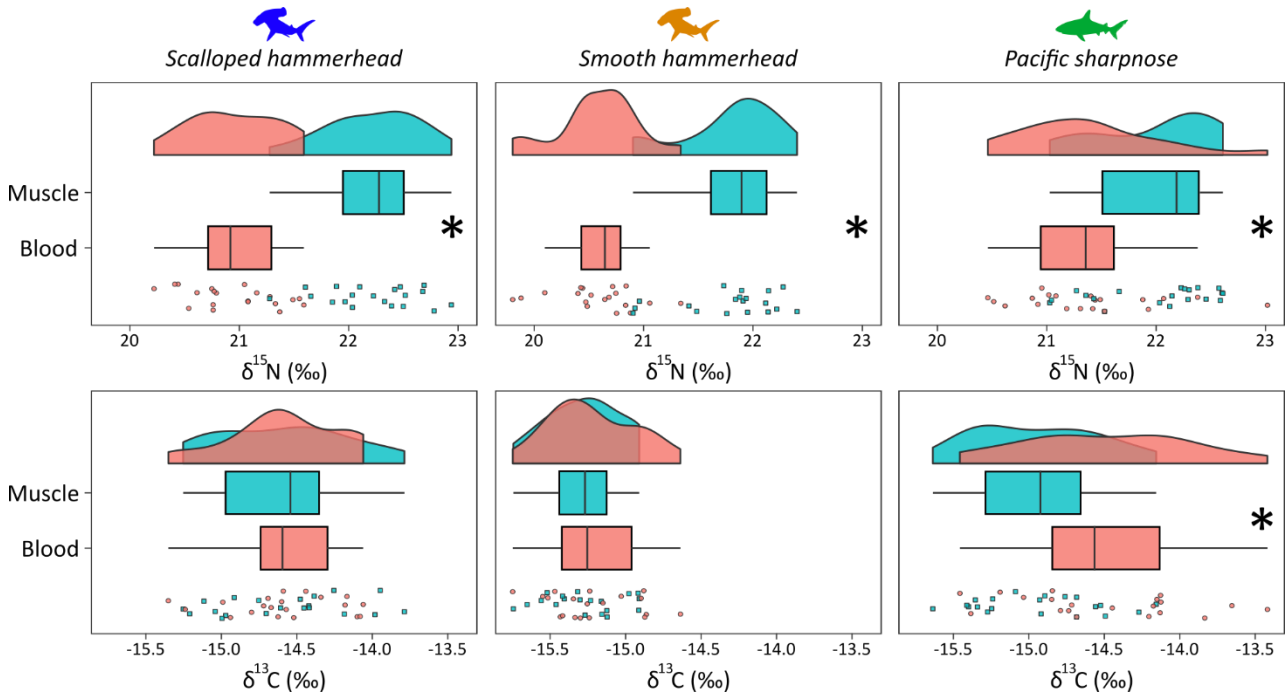

Figure 3-1 – Density-plots, boxplots and raw data points of $\delta^{15}N$ and $\delta^{13}C$ values in the muscle (blue) and whole blood (red) of scalloped hammerhead, smooth hammerhead and Pacific sharpnose sharks. Asterisks indicate significant differences between muscle and blood isotopic values for each species.

In muscle tissue, $\delta^{15}N$ values were significantly different between scalloped and smooth hammerhead sharks ($\chi^2_{58,2}$ = 7.9, p < 0.05) (Table 3-1). In blood, $\delta^{15}N$ differed among all species ($\chi^2_{58,2}$ = 18.4, p < 0.001). Pacific sharpnose shark had the highest values followed by scalloped and smooth hammerhead sharks. Muscle $\delta^{13}C$ values also differed between species from ^{13}C-depleted smooth hammerhead to Pacific sharpnose and ^{13}C-enriched scalloped hammerhead sharks ($F_{58,2}$ = 15.6, p < 0.001). Smooth hammerhead sharks had also significantly ^{13}C-depleted blood values compared to both scalloped hammerhead and Pacific sharpnose sharks ($\chi^2_{58,2}$ = 23.4, p < 0.001).

Overall, species isotopic niches overlapped in both tissues (represented by convex hull areas on Figure 3-2). This was mainly due to Pacific sharpnose sharks, which displayed the largest niche for both muscle and blood tissues, almost entirely

encompassing the niche of scalloped hammerheads (particularly for blood values), and significantly overlapping with the niche of smooth hammerheads. The overlap between the two hammerhead species only concerned less than half of their respective niches. While the core of the Pacific sharpnose (represented by 40% kernel density plots on Figure 3-2) was larger in blood than in muscle, a relative consistency was observed between tissues for the two hammerheads.

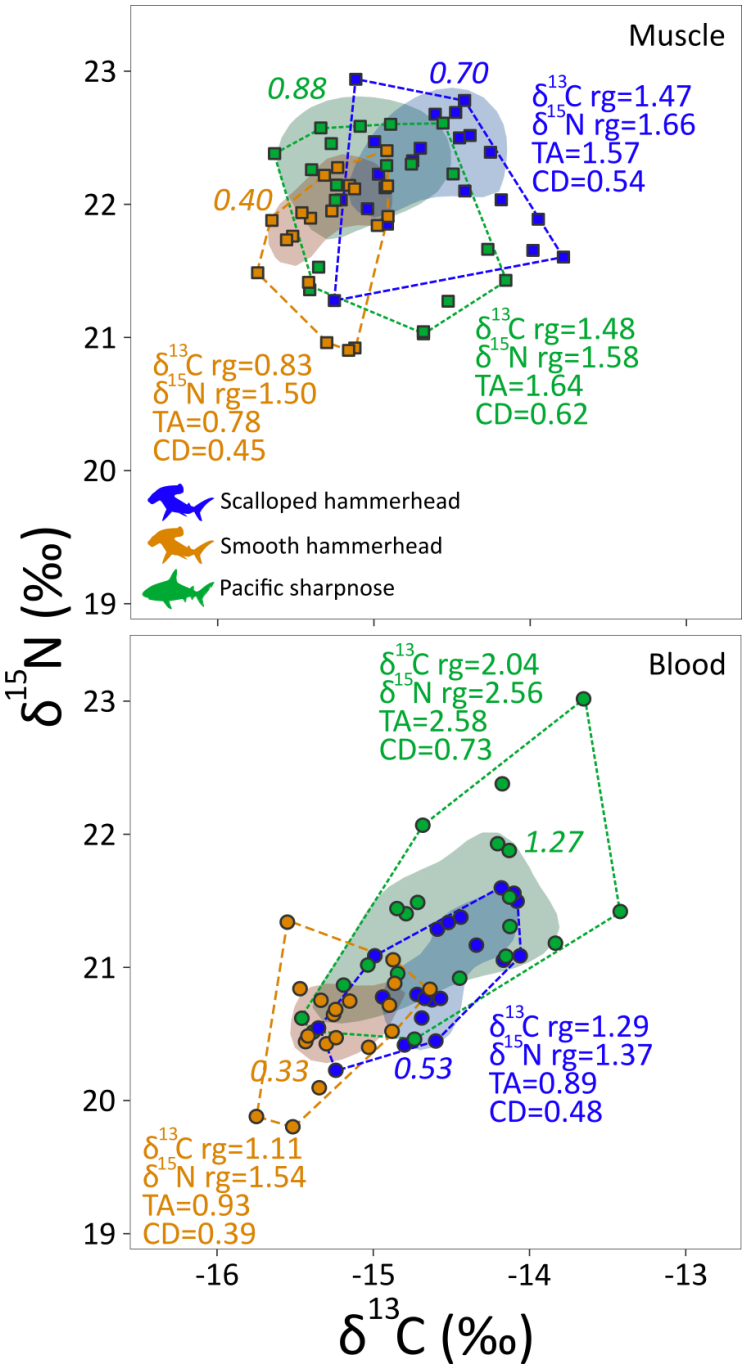

Figure 3-2 – Muscle and blood $\delta^{13}C$ and $\delta^{15}N$ values of scalloped hammerhead (blue), smooth hammerhead (orange) and Pacific sharpnose (green) sharks. 40%

kernel density plot are represented (with associated surface estimation in italic) along with convex hull areas and their associated Layman metrics ($\delta^{13}C$ range, $\delta^{15}N$ range and mean distance to the centroid in ‰ except for total area in ‰²) for each species.

Based on convex hull area estimations, smooth hammerhead sharks systematically occupied a smaller isotopic niche with lower $\delta^{13}C$ rg, $\delta^{15}N$ rg, TA and CD (Figure 3-2). A similar trend was observed in 40% kernel density surface estimations. The only exception was the isotopic niche of the scalloped hammerhead shark in the blood that was characterized by the lowest TA estimations, while the smooth hammerhead shark displayed the smallest 40% kernel density surface estimation. Compared to the muscle, the blood isotopic niche of scalloped hammerhead sharks had a narrower niche while the one of Pacific sharpnose sharks was wider.

b. Fatty Acid composition

Among the FA accounting for more than 1.5% of the total FA contents, 13 were selected based on SIMPER analyses for muscle tissue, while 10 were used for blood tissue. The discrimination between species was more pronounced based on blood tissue FA composition, and mostly opposed the Pacific sharpnose to the two hammerheads (Figure 3-3). In both tissues, this inter-specific distinction was mostly expressed according to the second most explanatory PCA axis (18.62% and 21.40% of total variance explained for muscle and blood, respectively). The FA contributing to the first two axes differed depending on the tissue considered. While the 22:5n-3 and EPA (20:5n-3) (along with the 22:4n-6, 18:1n-9 and 18:1n-7) were the main contributors to the first axis for muscle tissue (hence did discriminate within, more than among, species), they were the main contributors for the second axis for blood tissue (hence supported most of inter-specific differences, along with 22:5n-6, ARA (20:4n-6) and 18:0). In contrast, 16:0 and DHA (22:6n-3) supported the difference among species for muscle, but not for blood (contributors to the first axis).

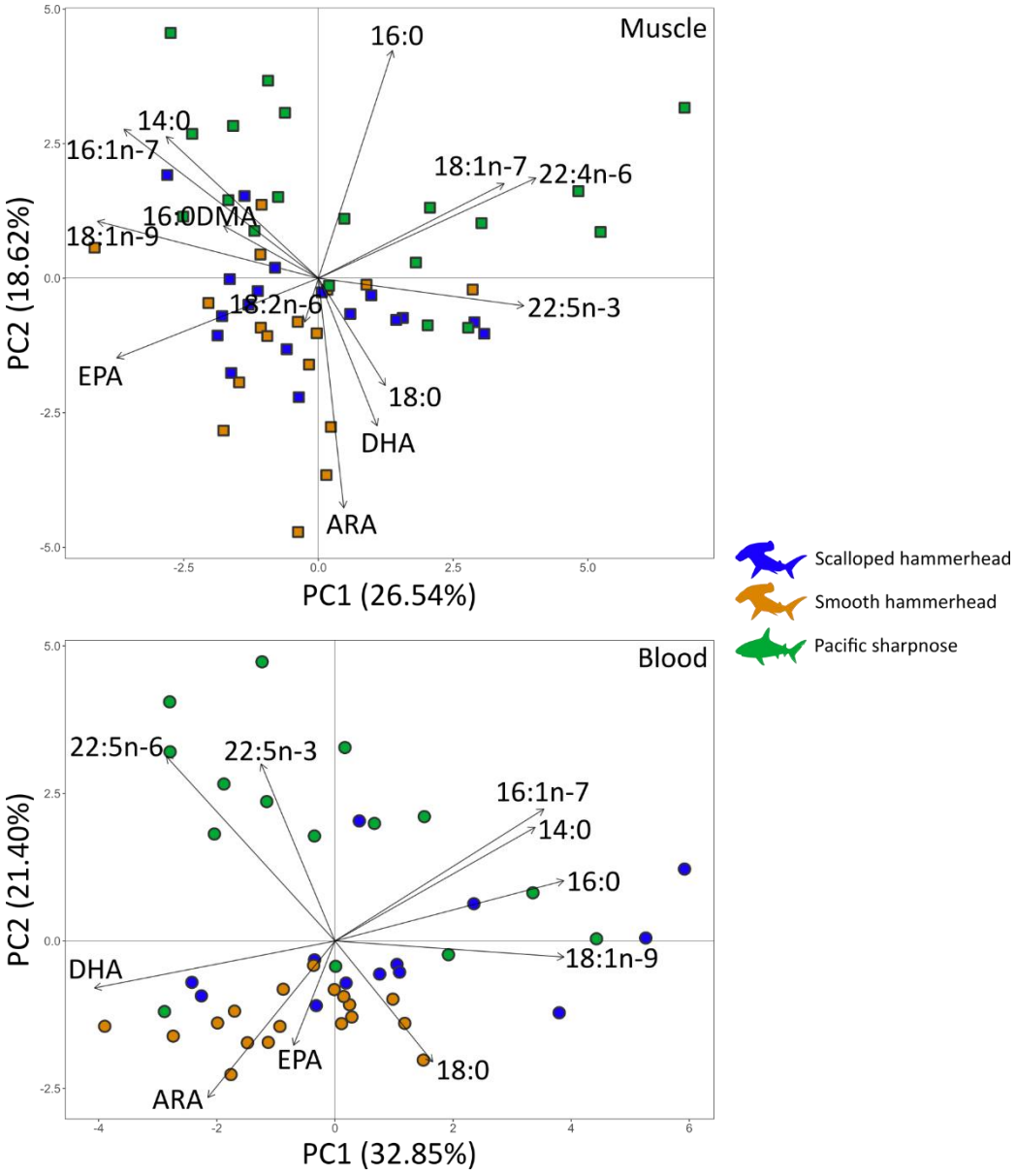

Figure 3-3 – Principal component analyses using fatty acid profiles (%) of sharks among species separately performed for muscle and blood samples. Fatty acids that account for >90% of the contribution of dissimilarity between species in the similarity of percentages analyses (SIMPER) are represented.

Similar inter-specific patterns were observed between muscle and blood FA composition (Figure 3-4). All three species accumulated high level of PUFA, mostly DHA followed by oleic acid (18:1n-9) with intermediate levels of ARA and EPA. DHA was significantly more accumulated by smooth hammerhead sharks than scalloped hammerhead sharks in muscle tissue ($\chi^2_{53,2} = 15.3$, $p < 0.001$), as in the blood ($\chi^2_{45,2} = 7.3$, $p < 0.05$) (Figure 3-4). 18:1n-9 was the second most abundant FA in this group but levels did not significantly differ between species. Both hammerhead sharks had significant higher amount of ARA than Pacific sharpnose sharks in the muscle ($\chi^2_{53,2} =$

26.0, $p < 0.001$) while it was the case only for smooth hammerhead shark in the blood ($\chi^2_{45,2} = 10.0$, $p < 0.01$). Proportions of EPA were significantly different among species only in muscle with higher proportion in smooth hammerhead compared to Pacific sharpnose shark ($\chi^2_{53,2} = 8.7$, $p < 0.05$). In the muscle, proportions of 22:4n-6 were higher in Pacific sharpnose shark compared to hammerheads ($\chi^2_{53,2} = 25.3$, $p < 0.001$) and proportions of 16:0DMA higher in smooth hammerhead sharks ($\chi^2_{53,2} = 11.2$, $p < 0.01$). In the blood, proportions of 22:5n-3 were higher in Pacific sharpnose sharks ($\chi^2_{45,2} = 10.2$, $p < 0.01$) and proportions of 16:1n-7 the lowest in smooth hammerhead sharks ($\chi^2_{45,2} = 14.0$, $p < 0.001$).

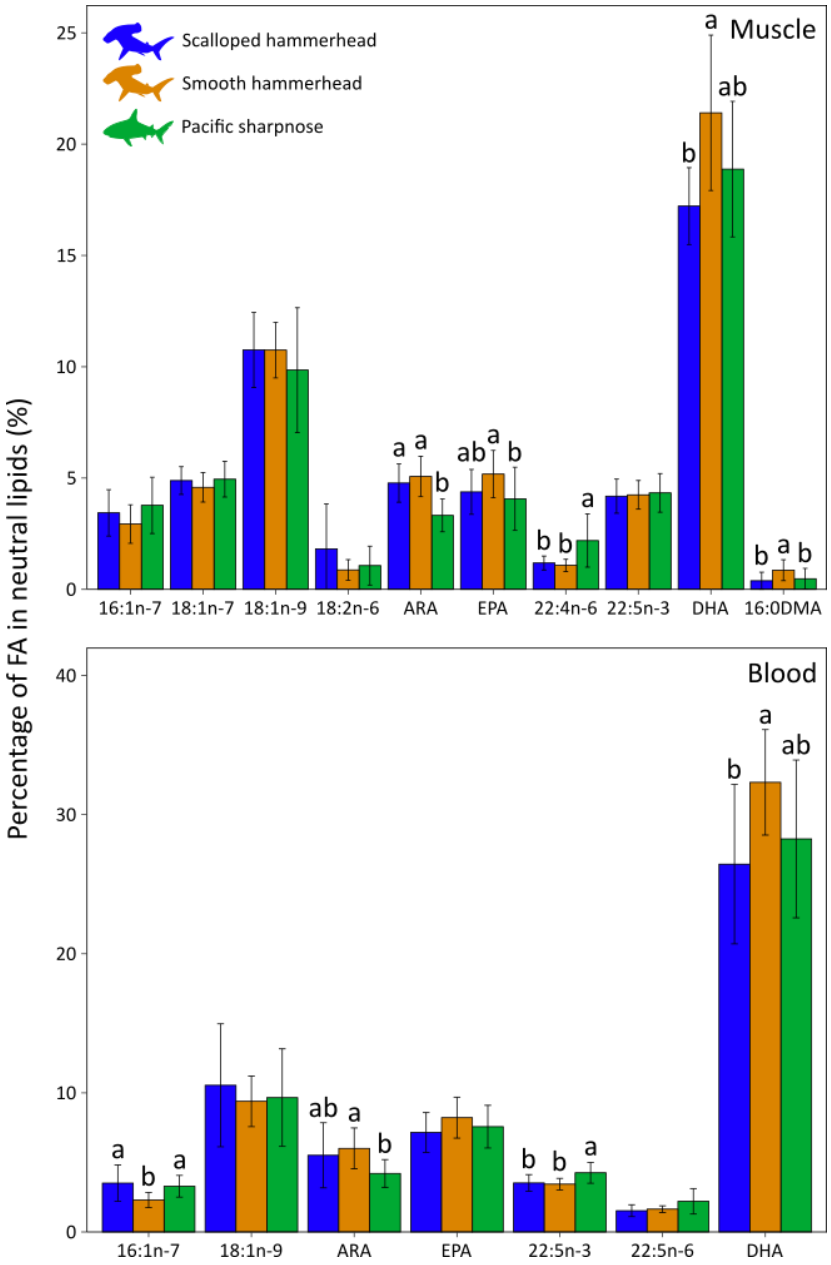

Figure 3-4 – Percentage of fatty acid contents in neutral lipids (mean ± standard deviation) accounting for >90% of the contribution of dissimilarity between species (SIMPER) in the muscle and blood of hammerhead and Pacific sharpnose sharks. Saturated FA are not shown in the histograms and significant differences (KW tests) between species are indicated by lower case letters.

c. Overlap between trophic niches

The mean probability of hammerhead sharks to be found within the niche of Pacific sharpnose sharks, based on $\delta^{13}C$, $\delta^{15}N$ and PCA first two explaining dimensions for FA compositions, systematically decreased from muscle to blood estimations (i.e., from 24.79% to 20.36% for scalloped hammerhead sharks and from 22.36% to 1.73% for smooth hammerhead sharks) (Figure 3-5A and Figure 3-5B). The probability to find Pacific sharpnose sharks within the niche of scalloped hammerhead sharks increased between muscle and blood estimates (i.e., 46.93% and 63.27% respectively) (Figure 3-5A). However, both tissues estimated equivalent probability to find Pacific sharpnose sharks within the niche of smooth hammerhead sharks (47.82% in muscle and 42.31% in blood) (Figure 3-5B). Finally, the probability of encountering scalloped hammerhead sharks in the niche of smooth hammerhead sharks varied from 26.89% in the muscle to 45.26% in the blood and the opposite from 28.89% in the muscle to 10.31% in the blood (Figure 3-5C).

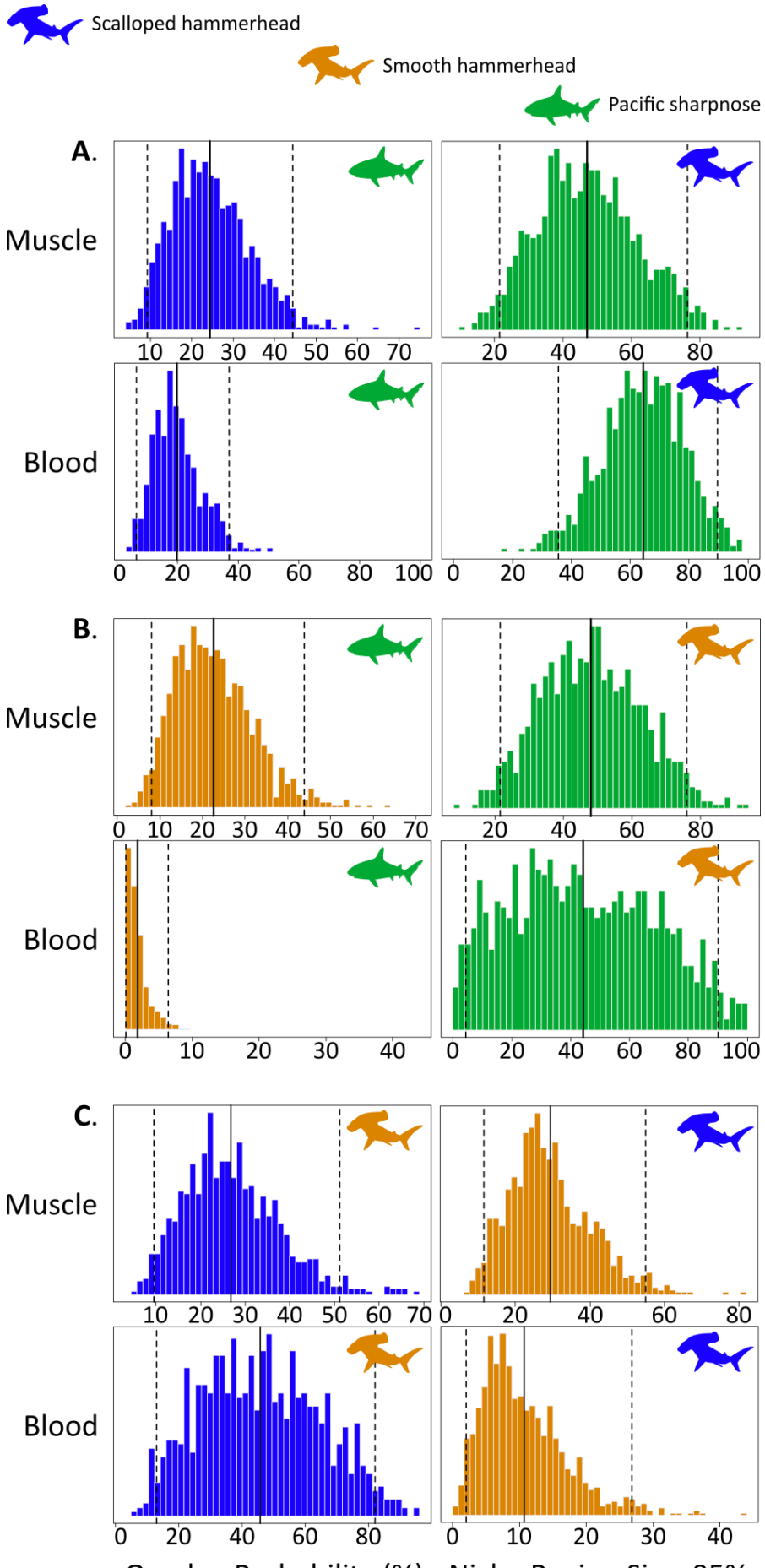
Scalloped hammerhead
Smooth hammerhead
Pacific sharpnose
A.
Muscle
Blood
B.
Muscle
Blood
C.
Muscle
Blood
Overlap Probability (%) - Niche Region Size: 95%

Figure 3-5 – Posterior distributions of the probabilistic niche overlap metrics of four variables ($\delta^{15}N$, $\delta^{13}C$ and the first two dimensions of the PCA using FA compositions of the three species) separately performed for muscle and blood tissues. Means are presented in full lines and 95% credible intervals in dash lines. Overlaps are estimated as the probability of one shark (i.e., color of the histogram) being found within the niche of another shark (i.e., shark icon). For example, the first top left panel represents the probability distribution of the scalloped hammerhead shark being found in the niche of the Pacific sharpnose shark using muscle values.

5. Discussion

Although our results suggest that the three species rely on a same coastal food web, slight, yet significant, differences in SI and FA composition among species suggest differences in resource use. Inter-specific mean $\delta^{13}C$ and $\delta^{15}N$ values did not differ by more than 1‰ between species, suggesting sharks relied on similar prey deriving their carbon from an homogeneous pool of primary producers and foraging at equivalent trophic levels (Bird et al., 2018; Hussey et al., 2014). The range of isotopic values suggest sharks were tertiary consumers foraging mainly on coastal areas in accordance with published values of marine biota in the Gulf of California (i.e., $\delta^{15}N$ higher than 20‰ and $\delta^{13}C$ from -15 to -12‰ for coastal tertiary consumers in Aurioles-Gamboa et al., 2013) and supported by the overlapping niches of hammerheads and coastal mesopredator Pacific sharpnose sharks (Alatorre-Ramirez et al., 2013). Although largely overlapping, FA compositions differed between hammerheads and Pacific sharpnose sharks. As FA are transferred along the food webs trough dietary intakes, different prey and/or metabolic requirement can lead to inter-specific differences in FA composition (Dalsgaard et al., 2003; Gladyshev et al., 2018; Iverson, 2009). The similar spectrum of FA observed between the three species, their high contents in DHA which cannot be synthetize by sharks (Sargent et al., 1995), and the analysis performed on neutral lipids known to reflect dietary inputs with a lower influence of internal processes (Arts et al., 2001), likely point to a dietary assimilation. Observed inter-specific differences in FA proportions are therefore likely to reflect differences in diet, as generally assumed in shark species assemblages (Meyer et al., 2019; Pethybridge et al., 2010; Rangel et al., 2019). Such contrasted diet is further supported by the slight but significant inter-specific isotopic niche differences observed in both tissues.

The trophic niche of juvenile smooth hammerhead sharks suggested they already initiated their ontogenetic shift toward offshore ecosystems, owing to a stronger reliance on pelagic resources. Here, sampled smooth hammerhead sharks were around 120 cm (TL), which corresponds to 4 years old individuals based on growth model established in the region (Villatoro and Maythé, 2018). Smooth hammerhead sharks were systematically characterized by the lowest $\delta^{13}C$ (and to a lesser extent $\delta^{15}N$) values. Contrary to the other two species, their isotopic niche was similar for both muscle and blood tissues (i.e., similar kernel surface, TA, $\delta^{15}N$ rg, although slightly increasing $\delta^{13}C$ rg in blood values). Lower $\delta^{13}C$ values may indicate a stronger influence of pelagic prey, where carbon originates from ^{13}C-depleted phytoplankton (Fry and Sherr, 1984; Magozzi et al., 2017). This species was also characterized by higher level of DHA in both tissues and lower levels of 16:1n-7 in blood. DHA is recognized as a biomarker of dinoflagellate based food web (along with lower levels of 16:1n-7), which supports the hypothesis of a stronger reliance towards a pelagic food web (Dalsgaard et al., 2003; Gladyshev et al., 2018; Parrish et al., 2015). Besides, the probability of encountering smooth hammerhead sharks inside the niche of coastal Pacific sharpnose sharks was the lowest. This may suggests that the size classes sampled in this study for smooth hammerhead sharks have already performed the transition between their coastal nursery and their juvenile offshore habitat. In the northeastern Pacific, movement studies of the species established the switch from a coastal-dominant to a mesopelagic-dominant diet happened around 3 years old (detailed in **Chapter 5**). Given muscle turnover rate (i.e., months to years) (Logan and Lutcavage, 2010), the fact that sampled smooth hammerhead shark have already initiated their ontogenetic diet switch at 120 cm (i.e., still overlapping with coastal species but with clear markers of a pelagic diet) is in direct accordance with a switch occurring around 3 years old for the species as demonstrated in **Chapter 5**.

The scalloped hammerhead shark isotopic niche was not consistent when analyzed in muscle or whole blood, reflecting a more recent transition towards a phytoplankton based food web than the smooth hammerhead shark. The species had higher $\delta^{13}C$ values in muscle compared to the smooth hammerhead shark suggesting it more extensively relies on coastal prey (Bird et al., 2018; Fry and Sherr, 1984). In blood, scalloped hammerhead sharks trophic niche was narrower (i.e., smaller kernel density surface and TA) and closer to the one of smooth hammerhead sharks than in the

muscle. Evidence for a diet shift towards pelagic sources was therefore found only in whole blood tissue. Blood has a shorter turnover and should therefore reflect more recent diet source compare to muscle (Malpica-Cruz et al., 2012), suggesting that if scalloped hammerhead sharks sampled in this study have already initiated their ontogenetic diet shift, this was more recent than for smooth hammerhead sharks.

The different muscle SI and FA composition observed in scalloped hammerhead sharks could be explained by the residual trophic signal of coastal nurseries and/or maternal provisioning (Belicka et al., 2012; Olin et al., 2011). Even if not explicitly tested in this study, we believe that scalloped hammerhead sharks in the size classes sampled here do not reflect maternal provisioning. Indeed, the mean size of scalloped hammerhead sharks was 97 cm (TL) corresponding to approximately 2 to 3 years old shark according to growth model estimations of the species in the eastern Pacific (Anislado-Tolentino and Robinson-Mendoza, 2001). Maternal signal in scalloped hammerhead sharks muscle have been observed in individuals from 0 to 1 year old, corresponding to individuals not exceeding 75 cm (TL) not sampled in this study (Estupiñán-Montaño et al., 2021b). Moreover, umbilical scars were healed for all sampled individuals and it has been shown that maternal resources are rapidly consumed and compensated by active foraging in neonate hammerhead sharks (Duncan and Holland, 2006; Lyons et al., 2020). FA composition of shark muscle did not reflect maternal provisioning, as previously identified in elasmobranch species (e.g., high level of ARA or FA deficiency marker such as 20:3n-9 due to decreasing reliance on maternal provisioning and poorly developed foraging skills Belicka et al., 2012; Rangel et al., 2021a). Therefore, differences observed in the scalloped hammerhead shark isotopic niches between muscle and blood likely resulted from a shift in dietary resources used. The pronounced coastal signal in the muscle could potentially originate from nursery grounds. Within nurseries, hammerhead shark movements are limited to a small core area (Duncan and Holland, 2006; Rosende-Pereiro et al., 2018). Therefore, while coastal nursery signal might explain higher $\delta^{13}C$ ranges, the wider isotopic niche of scalloped hammerheads in muscle is likely to be explained by some individuals already showing a post-nursery ontogenetic signal toward more pelagic foraging grounds (increasing $\delta^{13}C$ and possibly $\delta^{15}N$ range). This hypothesis is supported by the degree of decreasing estimated probability between

muscle and blood of encountering scalloped hammerhead sharks inside the trophic niche of the coastal Pacific sharpnose shark.

In the central Gulf of California, scalloped and smooth hammerhead sharks co-exist at different stages of their ontogenetic shift. Smooth hammerhead sharks show a more important reliance to pelagic dietary resources in both tissues and likely left nursery grounds earlier than scalloped hammerhead sharks, for which coastal resources (probably from nurseries) were still detectable. Scalloped hammerheads were sampled closer to size at birth (~50 cm) while smooth hammerhead sharks were older juveniles, yet none of the sampled individuals has reached the size at sexual maturity (beyond 150 cm) (Estupiñán-Montaño et al., 2021a; Francis, 2016; Nava Nava and Márquez-Farías, 2014). Therefore, the smallest sampled scalloped hammerhead sharks were more likely to rely on coastal resources, in agreement with the observed mismatch between stages of ontogenetic shifts between hammerhead species. Resource and habitat partitioning are generally observed among shark juveniles (Heupel et al., 2019; Kinney et al., 2011; Legare et al., 2015; Shaw et al., 2016), including between large and small-bodied coastal hammerhead species (Bethea et al., 2011; Galindo et al., 2021). However, scalloped and smooth hammerhead sharks are morphologically close species (Gallagher and Klimley, 2018) with similar opportunistic feeding strategies at early life stages (Bethea et al., 2011; Bush and Holland, 2002; Estupiñán-Montaño et al., 2019). The observed mismatch in species ontogenetic shifts in a shared ecosystem could allow for the optimization of resource partitioning, favoring the fitness of sensible early life stages.

While we would expect that hammerhead sharks, connecting coastal and pelagic ecosystems, would encompass a larger trophic niche than coastal resident Pacific sharpnose sharks, the opposite was found, especially for blood. Trophic niches of Pacific sharpnose sharks were larger, explaining the high probability of the species to be found in the niche of both hammerhead shark species. Even if not migratory, sharpnose sharks (*Rhizoprionodon spp.*) can display significant movement throughout coastal ecosystems (Carlson et al., 2008; Heupel et al., 2019; Munroe et al., 2014b) with important trophic plasticity (Drymon et al., 2012). In southern regions of the Mexican Pacific, the Pacific sharpnose shark has been described as an opportunistic species foraging upon a wide range of coastal prey (Alatorre-Ramirez et al., 2013). A combination of movement and diversified diet could therefore explain such wide trophic

niches. In the meantime, it suggests that scalloped and smooth hammerhead sharks are more specialized after their ontogenetic diet shift, potentially resulting from lower prey diversity in the pelagic environment where scalloped and smooth hammerhead sharks target principally mesopelagic cephalopods (Estupiñán-Montaño et al., 2019; Galván-Magaña et al., 2013; Torres-Rojas et al., 2015).

This study conclusions are in accordance with data from larger scalloped hammerhead sharks tagged in the Gulf of California, that showed a dominant offshore habitat in juveniles close to sexual maturity (Jorgensen et al., 2009; Klimley et al., 1993). Hoyos-Padilla et al. (2014) recorded the movement of a single female on the occidental coast of the Gulf of California, captured at 95 cm (TL) and recaptured at 123 cm (TL) in the Bay of La Paz, 360 km south of our sampling site. Its movement pattern was characterized by an increasing exploration of pelagic grounds with increasing use of mesopelagic layers probably for foraging purposes with horizontal migration up to this study's sampled site.

Once leaving nursery grounds, early life stages of hammerhead shark species seem to initiate their movement toward offshore habitats after a prolonged period during which they still rely on coastal resources. Here, both hammerhead shark species are supposed to be still in transition between coastal and offshore habitats. This hypothesis is particularly supported by the overall coastal signal of the three species and by the similar overlapping probabilities between scalloped and smooth hammerhead sharks. Such prolonged reliance on coastal ecosystems could be one of the reason of the decline of hammerhead shark species observed in the region (Hoyos-Padilla et al., 2014; Pérez-Jiménez, 2014) as shark fishing mainly target coastal habitats in the Gulf of California (Saldaña-Ruiz et al., 2017). While rigorous testing of hammerhead shark nursery criteria are needed to clearly identify nursery grounds, overall coastal areas extensively used by juveniles, should also be considered as a conservation priority if we were to maintain hammerhead shark populations at sustainable levels.

CHAPTER 4

FORAGING DEPTH DEPICTS RESOURCE PARTITIONING AND CONTAMINATION LEVEL IN A PELAGIC SHARK ASSEMBLAGE: INSIGHTS FROM MERCURY STABLE ISOTOPES.

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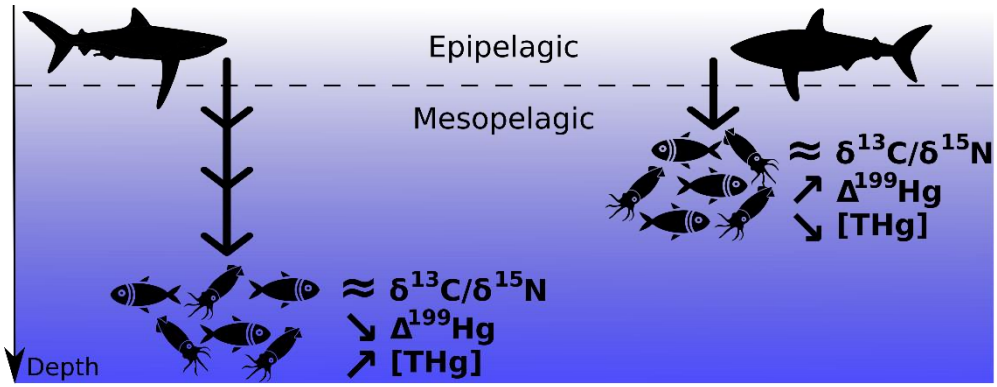
1. Abstract

The decline of shark populations in the world ocean is affecting ecosystem structure and function in an unpredictable way and new ecological information is today needed to better understand the role of sharks in their habitats. In particular, the characterization of foraging patterns is crucial to understand and foresee the evolution of dynamics between sharks and their prey. Many shark species use the mesopelagic area as a major foraging ground but the degree to which different pelagic sharks rely on this habitat remains overlooked. In order to depict the vertical dimension of their trophic ecology, we used mercury stable isotopes in the muscle of three pelagic shark species (the blue shark *Prionace glauca*, the shortfin mako shark *Isurus oxyrinchus* and the smooth hammerhead shark *Sphyrna zygaena*) from the northeastern Pacific region. The Δ^{199}Hg values, ranging from 1.40 to 2.13‰ in sharks, suggested a diet mostly based on mesopelagic prey in oceanic habitats. We additionally used carbon and nitrogen stable isotopes (δ^{13}C, δ^{15}N) alone or in combination with Δ^{199}Hg values, to assess resource partitioning between the three shark species. Adding Δ^{199}Hg resulted in a decrease in trophic overlap estimates compared to those based on δ^{13}C/δ^{15}N alone, demonstrating that multi-isotope modeling is needed for accurate trophic description of the three species. Mainly, it reveals that they forage at different average depths and that resource partitioning is mostly expressed through the vertical dimension within pelagic shark assemblages. Concomitantly, muscle total mercury concentration (THg) differed between species and increased with feeding depth. Overall, this study highlights the key role of the mesopelagic zone for shark species foraging among important depth gradients and reports new ecological information on trophic competition using mercury isotopes. It also suggests that foraging depth may play a pivotal role in the differences between muscle THg from co-occurring high trophic level shark species.



2. Introduction

Sharks are facing worldwide a large variety of threats such as overfishing, pollution, ecosystem degradation and others (Dulvy et al., 2014; Hazen et al., 2013; Queiroz et al., 2019). In recent years, the decline of many shark populations in the global ocean has raised public concern due to the iconic nature of these top predators and their influence on marine ecosystems over various temporal and spatial scales (Ferretti et al., 2010; Heithaus et al., 2008). Since the consequences of their removal are difficult to assess and predict (Baum and Worm, 2009; Ferretti et al., 2010), ecological information on habitat use and foraging grounds is needed to better assess future changes in marine ecosystems (Shiffman et al., 2012).

Large sharks, such as most marine predators, influence their ecosystem mainly through trophic interactions, either by predation on mesopredators, i.e. top-down control (Baum and Worm, 2009; Ferretti et al., 2010), competition with sympatric (i.e. co-occurring) high trophic level predators (Matich et al., 2017a), or more complex interactions (Heithaus et al., 2008; Jorgensen et al., 2019). Competition for a shared trophic resource can result in lower food availability, change in physiological condition, and ultimately, reduced fitness (Jorgensen et al., 2019). Therefore, evolutionary processes tend to favor resource partitioning in co-occurring top predators (Heithaus et al., 2013). Tracking studies have highlighted differences in habitat use between shark species suspected to compete for food (Meyer et al., 2010; Musyl et al., 2011), but this method appears limited to discriminate the diet of species sharing a same trophic ground. Isotopic trophic tracers, such as stable carbon and nitrogen isotopes, have been used to assess resource partitioning between sympatric predators (Heithaus et al., 2013). However, contrary to coastal ecosystems, pelagic trophic webs are most of the time based on phytoplankton production only resulting in homogeneous isotopic signatures and in overlapping isotopic niches between predators (Kiszka et al., 2015; Klarian et al., 2018; Rosas-Luis et al., 2017). Rather than competition, overlapping regions of isotopic niches might therefore be due to some inherent approach limitations. For instance, stable isotopes have a poor ability to discriminate foraging depth for top predators likely to feed in deep oceanic habitats (Choy et al., 2015; Kiszka et al., 2015) and only few studies have investigated the vertical dimension of resource partitioning in pelagic predator assemblages (Le Croizier et al., 2020b, 2020a).

The mesopelagic zone (200-1000 m below the ocean surface) contains one of the most important animal biomass on earth (Aksnes et al., 2017; Irigoien et al., 2014), principally gathered inside the “deep scattering layer” community (Costello and Breyer, 2017). It is mainly composed of fishes and invertebrates that are commonly targeted by marine megafauna (Aksnes et al., 2017; Davison et al., 2015; Hazen and Johnston, 2010). Among these predators, some pelagic shark species display typical deep diving patterns suggesting that they rely on this compartment, such as great white (Le Croizier et al., 2020a), blue (Braun et al., 2019) or scalloped hammerhead sharks (Jorgensen et al., 2009). Surprisingly, although the combined effect of climate change and fishing pressure is dramatically changing epipelagic fish biomass and dynamic (Pinsky et al., 2011; Tu et al., 2018), little attention has been paid to the mesopelagic zone which is also predicted to be affected by climate change (Proud et al., 2017). In this context, the importance of deeper mesopelagic prey for different oceanic shark species must be better assessed.

Mercury is a globally distributed atmospheric pollutant (Fitzgerald et al., 2007) having deleterious toxic effects on marine fauna (Eisler, 2006). Entering the ocean in its inorganic form, its bioavailability increases through methylation by microbial activity (Sunderland et al., 2009). The resulting methylmercury (MeHg) is incorporated and bioaccumulated, i.e. increase in concentration with age/length, naturally in marine organisms as well as biomagnified, i.e. increase in concentration with trophic position (Biton-Porsmoguer et al., 2018; Lavoie et al., 2013; Le Bourg et al., 2019). As long-lived predators at the top of food webs, sharks naturally exhibit high mercury concentrations (Schartup et al., 2019), predominantly in the MeHg form (Carvalho et al., 2014; Kim et al., 2016; Storelli et al., 2003). Alongside these processes, mercury accumulation in marine predators appears to be also driven by other physiological (e.g. metabolism, ontogeny, detoxification mechanisms) (Bolea-Fernandez et al., 2019; Li et al., 2020), ecological (e.g. habitat, systems productivity, food web structure, foraging depth) (Ferriss and Essington, 2014; Lavoie et al., 2013; Le Croizier et al., 2019; Senn et al., 2010) and physical parameters (e.g. oxygen level, sea temperature) (Houssard et al., 2019; Le Bourg et al., 2019; Schartup et al., 2019). In the ocean, mercury is subject to mass-independent isotopic fractionation (“MIF”, generally represented through Δ^{199}Hg values) due to its photochemicaltransformation in the water column (Bergquist and Blum, 2007). Following light attenuation with depth, Δ^{199}Hg values

decrease from the surface to aphoticwaters (Blum et al., 2013). Δ^{199}Hg values are also conserved during trophic transfer between a prey and its predator (Kwon et al., 2016; Laffont et al., 2011), making this nontraditional isotope a powerful proxy to address trophic resources and feeding depth in marine predators (Le Croizier et al., 2020b; Madigan et al., 2018). Mercury isotopic composition is also affected by mass-dependent fractionation ("MDF"), studied through δ^{202}Hg values (Bergquist and Blum, 2007; Blum et al., 2013). δ^{202}Hg is modified during physico-chemical processes such as photoreduction (Bergquist and Blum, 2007) and volatilization (Zheng et al., 2007), but also during biological processes such as methylation (Janssen et al., 2016) and demethylation (Perrot et al., 2016). It is therefore a useful tool to study mercury metabolism in species capable of demethylating MeHg (Bolea-Fernandez et al., 2019; Li et al., 2020).

In this study, we used a combination of carbon, nitrogen and mercury stable isotope analyses to address resource partitioning in three sympatric pelagic shark species (blue, shortfin mako and smooth hammerhead sharks) off the west coast of the Baja California peninsula (Mexico) in the northeastern Pacific. Based on stomach contents and carbon and nitrogen stable isotopic analyses, these three species have previously been reported to display highly overlapping trophic niches (Klarian et al., 2018; Kone et al., 2014). However, because these sharks display different diving behavior patterns (Logan et al., 2020; Musyl et al., 2011; Santos and Coelho, 2018) leading to different abilities to access potential prey in the mesopelagic layer, we tested the hypothesis that resource partitioning occurs along the vertical dimension of their habitat. From an ecological perspective, this would confirm the key importance of the mesopelagic compartment even for predators spending most of their time in the upper layers (Le Croizier et al., 2020b, 2020a). It would also highlight the limitations of studying only carbon and nitrogen isotopic composition in pelagic assemblages to assess the degree of trophic similarities and the importance of the addition of relevant biomarkers to better address resource partitioning. Finally, as vertical habitat has been suspected to influence mercury contamination in marine predators (Choy et al., 2009; Le Bourg et al., 2019), we sought to evaluate if the total mercury levels found in these shark species could be related to foraging depth.

3. Materials and Methods

a. Sampling strategy

From 2014 to 2016, samples were collected in the artisanal fishing camp of Punta Lobos (southern Baja California Sur, Mexico, northeast Pacific). Sharks were fished using longlines equipped with hooks. Sex and total length (TL) were recorded for each shark and approximately 1 g of muscle was extracted from the dorsal muscle between the first dorsal fin and the snout. Immediately after collection, samples were transported to the laboratory on ice packs, preserved at -20°C and freeze-dried prior to analysis. In total, 13 blue sharks (*Prionace glauca*), 10 shortfin mako sharks (*Isurus oxyrinchus*) and 13 smooth hammerhead sharks (*Sphyrna zygaena*) were sampled.

b. Carbon and nitrogen stable isotopes

Following the methodology proposed by Li et al. (2016b), two extractions were performed prior to isotopic ratio determination. To avoid $\delta^{13}C$ misinterpretation, lipids were extracted by placing each sample in 6 mL of a 2:1 chloroform:methanol Folch solution (Folch et al., 1957). Mechanical crushing using a Dounce homogenizer enhanced the extraction. The mixture was then vortexed for 1 min, left overnight at room temperature and centrifuged for another 10 min before tissue extraction. This process was repeated three times. For $\delta^{15}N$ determination, urea was also removed from the samples. Samples were immerged in 5 mL of distilled water, vortexed for 1 min and left at room temperature for 24 h. The aqueous phase was separated from the tissue after another 5 min centrifugation and this process was repeated three consecutive times. Samples were then re-dried and homogenized prior to analysis.

A sample of 0.50 mg of muscle powder was weighted into tin cups using a XPR10 microbalance (METTLER TOLEDO). Stable carbon and nitrogen isotope measurements were carried out using a continuous flow on a Thermo Scientific Flash EA 2000 elemental analyzer coupled to a Delta V Plus mass spectrometer (Pole Spectrométrie Océan, IUEM, Plouzané, France). Based on international standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$), isotopic ratio (δ) are expressed in per mil (‰) following: $\delta X = ([R_{sample}/R_{standard}] - 1) \times 1000$ where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. We repeatedly measured known international isotopic standards (i.e. IAEA-600 Caffeine, IAEAeCHe6 Sucrose, IAEA-N-1 and IAEA-N-2 Ammonium Sulphate) and an in-lab certified standard substance (i.e. Acetanilide) indicating analytical uncertainties of ± 0.23‰ for

$\delta^{13}C$ and ± 0.16‰ for $\delta^{15}N$. C:N ratios for all samples were ranging from 3.07 to 3.36, validating good extractions as shown by Li et al. (2016b) (i.e. mean C:N ratio after lipid and urea removal of 3.2 for blue and smooth hammerhead shark and 3.1 for shortfin mako shark).

c. Total mercury concentration

As total mercury concentration (THg) is known to be almost exclusively in the MeHg form in shark muscle, including for the species analyzed here, e.g. 95-98% in blue sharks (Carvalho et al., 2014; Kim et al., 2016; Storelli et al., 2003), THg was used as a proxy for MeHg. THg is expressed on a dry weight basis with an analytical detection limit of 0.005 $mg \cdot g^{-1}$ dw. A 20 mg aliquot section of dry muscle was analyzed using a DMA80 analyzer (Milestone, USA) after combustion, gold trapping and atomic absorption spectrophotometry detection. The analysis accuracy and reproducibility was assessed from repeated measurements of two reference materials, a lobster hepatopancreas (TORT 3, NRCC, 0.292 ± 0.022 $mg \cdot g^{-1}$ dw) and a homogenate of tuna flesh (IAEA 436, INMM, 4.19 ± 0.36 $mg \cdot g^{-1}$ dw). Both reference materials were reproduced within the confidence limits (i.e. 0.286 ± 0.024 $mg \cdot g^{-1}$ dw for TORT 3, n=10, and 4.20 ± 0.09 $mg \cdot g^{-1}$ dw for IAEA 436, n=10).

d. Mercury isotopes

A segment of 20 mg of dry muscle was immersed into 3 mL of pure bi-distilled nitric acid (HNO_3) and left at room temperature overnight. Samples were then digested at 85°C for 6 h in pyrolyzed glass vessels closed by Teflon caps on a hotplate. After the addition of 1 mL of hydrogen peroxide (H_2O_2), digestion continued for another 6 h and 100 mL of BrCl were added to complete the extraction. Finally, the solution was diluted in an inverse aqua regia (3:1 HNO_3:HCl with 20 vol% MilliQ water) to reach a total mercury concentration of 1 $ng \cdot mL^{-1}$.

Mercury isotopic compositions were measured at the Observatoire Midi-Pyrenées (Toulouse, France) using inductively coupled plasma mass spectrometry (MC-ICP-MS, Thermo Finnigan Neptune) with continuous-flow cold vapor (CV) generation using Sn(II) reduction (CETAC HGX-200), according to a previously published method (e.g. Le Croizier et al., 2020b). Mercury isotopic composition is expressed in δ notation, reported in per mil (‰) deviation from the NIST SRM 3133 standard and determined

by sample-standard bracketing according to the following equation: $\delta^{XXX}Hg$ (‰) = ([($^{XXX}Hg/^{198}Hg)_{sample}/(^{XXX}Hg/^{198}Hg)_{standard}$] - 1) × 1000 where XXX represents mercury isotope different masses. $\delta^{202}Hg$ represents Hg MDF, and Δ notation is used to express Hg MIF by the following equation: $\Delta^{XXX}Hg$ (‰) = $\delta^{XXX}Hg$ - ($\delta^{202}Hg$ × a) (Bergquist and Blum, 2007), where a=0.252, 0.502, 0.752 and 1.493 for isotopes 199, 200, 201 and 204, respectively.

Blanks as well as certified materials (i.e. NRC-TORT-3 and ERM-BCR- 464) were analyzed with the same procedure. Total mercury concentration in the diluted digest mixtures was monitored by the ^{202}Hg signals provided by MC-ICP-MS. A recovery rate of 96 ± 7% (n=37) for shark samples and 95 ± 6% (n=7) for certified reference materials was obtained. Reproducibility of mercury isotope measurements was assessed by analyzing UM-Almadén (n=4), ETH-Fluka (n=4) and the biological tissue procedural standards NRC-TORT-3 (n=3) and ERM-BCR-464 (n=4). Only one analysis was performed per sample, but measured isotope signatures as well as analytical reproducibility of standards agreed with previously published values (Appendix 4-1).

e. Data analysis

For comparison between shark species, data was first checked for normality using Shapiro-Wilk test and for equality of variances using Bartlett's test. When both conditions were met, one-way ANOVA were performed followed by a post-hoc Tukey's HSD test. Otherwise, we used its non-parametric analogue, the Kruskal-Wallis test, followed by Dunn's post hoc test with Bonferroni's adjustment in the presence of several groups. Between-sex comparisons (Student t-test or its non-parametric analogue Wilcoxon test) are described in Appendix 4-2.

We used 2D ($\delta^{13}C$ and $\delta^{15}N$) ellipse areas encompassing 95% of the data (EA) calculated using the SIBER package (Jackson et al., 2011) from R programming language (R Core Team, 2020). 3D ($\delta^{13}C$, $\delta^{15}N$ and $\Delta^{199}Hg$) ellipsoid volumes encompassing 95% of the data (EV) were calculated using the SIBER-derived model described by Skinner et al. (2019) for three-dimensional coordinate systems. To allow for comparison between the two model outputs, we expressed isotopic overlap as a proportion of the non-overlapping area of the two 2D ellipses (EA) or 3D ellipsoids (EV).

Pearson correlation test was used to describe the linear correlation between THg and Δ^{199}Hg. Generalized linear models (GLMs) were used to evaluate the influence of species, total length, C, N and Hg isotope values on muscle mercury levels. GLMs were built with the LME4 package (Bates et al., 2015) using THg as the response variable. Based on diagnostic plots of the residuals, a Gaussian distribution and identity link function were used in the GLMs. Predictor variables were species, age, δ^{13}C, δ^{15}N, Δ^{199}Hg and δ^{202}Hg. Age was estimated for each individual using growth parameters established for blue (Blanco-Parra et al., 2008), shortfin mako (Ribot-Carballal et al., 2005) and smooth hammerhead sharks (Morán-Villatoro et al., 2018) in the studied region. Models were built using backward stepwise selection which consists in building a model containing all predictor variables and removing gradually each predicator variable until no variable is left in the model (i.e. null model). Akaike's Information Criterion (AIC) was used to define the order of deletion as the model with the lowest AIC is retained for the next step. All models were ranked based on Akaike's Information Criterion adjusted for small sample sizes (AICc) and Akaike weights (w) using the R package WIQID (Meredith, 2020). Marginal R^2 were applied to assess each model predictive power using the R package R2GLMM (Jaeger, 2017).

4. Results and discussion

a. Carbon and nitrogen isotopic composition

A summary of the results is presented in Table 1. For all variables (TL, δ^{13}C, δ^{15}N, Δ^{199}Hg, δ^{202}Hg and THg), no significant difference between sexes within species was detected (Appendix 4-2). In marine ecosystems, δ^{13}C is known to vary between habitats (e.g. coastal versus oceanic), according to primary producers supporting the food webs (e.g. benthic producers versus phytoplankton) (Fry and Sherr, 1984). Here, no significant difference in δ^{13}C was detected between the three species ($\chi^2_{35,2}$ = 6.1, $p > 0.05$). These similarities in δ^{13}C profiles (Table 4-1) suggest that they forage on equivalent pelagic food webs derived from phytoplankton production, in accordance with reported data on shortfin mako and blue sharks in the study area (Hernández-Aguilar et al., 2016; Tamburin et al., 2019).

Table 4-1 – Number of individuals, total length, C, N and Hg isotope composition, and total mercury concentration (THg) in the muscle of blue, shortfin mako and smooth hammerhead sharks. Data are means (±standard deviation). THg is expressed on a dry weight basis. Different letters indicate significant differences between species for each variable.

Species	N	Total length (m)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\Delta^{199}Hg$ (‰)	$\delta^{202}Hg$ (‰)	THg ($ng \cdot g^{-1}$)
Blue	13	1.98 (± 0.36)	-16.81 (± 0.91) ^{A}	18.15 (± 1.07) ^{A}	1.56 (± 0.10) ^{A}	0.63 (± 0.16) ^{AB}	7804 (± 2699) ^{A}
Shortfin mako	10	1.49 (± 0.43)	-16.36 (± 0.55) ^{A}	19.13 (± 1.10) ^{B}	1.94 (± 0.23) ^{B}	0.53 (± 0.15) ^{A}	4772 (± 3892) ^{B}
Smooth hammerhead	13	1.67 (± 0.16)	-16.25 (± 0.85) ^{A}	20.30 (± 0.60) ^{C}	1.82 (± 0.15) ^{B}	0.71 (± 0.12) ^{B}	3600 (± 1524) ^{B}

We found significant $\delta^{15}N$ differences between species ($F_{35,2} = 17.2$, $p < 0.001$). The smooth hammerhead shark presented significantly higher $\delta^{15}N$ than both the shortfin mako (Tukey's HSD test, $p < 0.05$) and the blue shark (Tukey's HSD test, $p < 0.001$). In contrast, the blue shark was ^{15}N-depleted compared to the shortfin mako shark (Tukey's HSD test, $p < 0.05$). In the case of mobile top predator species evolving in the pelagic habitat, these differences in $\delta^{15}N$ can reflect either differences in relative trophic position (Cabana and Rasmussen, 1994) or foraging in different regions with contrasted $\delta^{15}N$ baselines (Lorrain et al., 2015). In the northeastern Pacific region, no information is available on smooth hammerhead shark movement, while both blue and shortfin mako are known to perform limited horizontal movements without a clear seasonal pattern that could suggest foraging on broad different $\delta^{15}N$ ecosystem baselines (Musyl et al., 2011; Queiroz et al., 2019; Sepulveda et al., 2004). Therefore, their isotopic signatures likely represent an integrated signal of these shared habitat baselines. The significant differences observed in $\delta^{15}N$ signature between the three species might overall be due to differences in trophic levels, with blue sharks occupying the lowest trophic level and smooth hammerhead sharks the highest. In the study region, all three species are known to principally rely on different cephalopod species as observed in previous stomach content analyses. Shortfin mako sharks feed on *Dosidicus gigas* (Velasco Tarelo and Galván-Magaña, 2005), blue sharks on *Onychoteuthis banksii*, *Gonatus californiensis* and *D. gigas* and smooth hammerhead sharks on *D. gigas*, *Ancitrocheirus lesueurii* and *O. banksii* (Galván-Magaña et al., 2013). The apparent differences between the trophic levels of the three shark species

could be the result of broad differences in cephalopod trophic levels. Indeed, the observed mean difference in $\delta^{15}N$ values between blue and smooth hammerhead sharks (2.15‰) matches the important variation in $\delta^{15}N$ signatures previously observed for cephalopod species sampled in the region (Madigan et al., 2012).

b. Inter-specific differences in foraging depth

Both $\Delta^{199}Hg$ and $\delta^{202}Hg$ values vary vertically throughout the water column due to the photochemical transformation of Hg, which follows the decrease in solar radiation from surface to deep water layers (Bergquist and Blum, 2007; Blum et al., 2013). However, while $\Delta^{199}Hg$ is only affected by photochemical reactions and is conserved from prey to predator, $\delta^{202}Hg$ is also modified by physiological processes like methylation or demethylation of mercury (Bolea-Fernandez et al., 2019; Janssen et al., 2016; Li et al., 2020; Perrot et al., 2016) and undergoes inconstant trophic discrimination factors from prey to predator (Kwon et al., 2016; Laffont et al., 2011), especially in shark species (Le Croizier et al., 2020b). Moreover, metabolic MeHg detoxification pathways seem to occur for blue, shortfin mako and smooth hammerhead sharks. Indeed, the $\Delta^{199}Hg/\delta^{202}Hg$ slope is traditionally used to assess the influence of photodegradation versus microbial transformation on the isotopic signature of mercury before its incorporation into the food web (Blum et al., 2013; Madigan et al., 2018). Here, no significant linear regression could be obtained between $\Delta^{199}Hg$ and $\delta^{202}Hg$ for all shark species at the inter- or intraspecific level (Appendix 4-3). This lack of correlation between $\Delta^{199}Hg$ and $\delta^{202}Hg$ is observed in species showing in vivo demethylation modifying the $\delta^{202}Hg$ values (Li et al., 2020) and suggests possible MeHg detoxification processes in the shark species studied here (Le Croizier et al., 2020b). Therefore, as $\delta^{202}Hg$ in all three shark species appeared to depend on both trophic and physiological features, this isotopic ratio was not taken into account to assess differences in trophic ecology and subsequently to study the possible food competition between species.

In nearshore ecosystems, $\Delta^{199}Hg$ can vary seasonally and spatially due to coastal phenomena affecting water turbidity (Senn et al., 2010). In this study, the fact that all three sharks were pelagic species using oceanic habitats (as inferred by $\delta^{13}C$ values) confirms that reported $\Delta^{199}Hg$ may vary primarily over a vertical gradient depending on photochemical processes affected by depth (Blum et al., 2013). Therefore, the range of individual $\Delta^{199}Hg$ values (1.40-2.13‰) observed in this study highlights the

importance of mesopelagic prey in the diet of all three oceanic species. In the north Pacific oceanic region, similar Δ^{199}Hg signatures in fish muscle have been observed for species foraging in the twilight zone near Hawaii, i.e. 1.00-2.56‰ (Blum et al., 2013), and off the coast of California, i.e. 0.95-2.31‰ (Madigan et al., 2018), including for the great white shark, *Carcharodon carcharias*, i.e. 1.25-1.95‰ (Le Croizier et al., 2020a). This conclusion is supported by the consistent presence of mesopelagic species in stomach contents of blue (Hernández-Aguilar et al., 2016; Markaida and Sosa-Nishizaki, 2010), shortfin mako (Lopez et al., 2009; Preti et al., 2012) and smooth hammerhead sharks (Estupiñán-Montaño et al., 2019; Galván-Magaña et al., 2013) sampled off the west coast of Baja California and across the Pacific Ocean. As mercury has a similar turnover rate as carbon and nitrogen in fish muscle, i.e. 1 year or more (Kwon et al., 2016), deep foraging appears as a constant strategy through time. The three shark species remain most of the time inside the boundaries of the surface mixed layer but exhibit differences in their diving behaviors in the study length range. Indeed, while blue sharks perform frequent deep dives (Campana et al., 2011; Queiroz et al., 2010), shortfin mako sharks seem to exploit deep water more sporadically and to undergo less frequent dives in the mesopelagic zone (Abascal et al., 2011; Musyl et al., 2011). Finally, although no study reported depth habitat use in smooth hammerhead sharks in the Pacific region, data from the Atlantic Ocean demonstrated limited diving frequency associated with shallower dives than both shortfin mako and blue sharks (Logan et al., 2020; Santos and Coelho, 2018). Here, Δ^{199}Hg corroborates the deep diving behavior observed for blue and shortfin mako sharks and proves that they are associated with foraging in the mesopelagic layer. It also suggests that smooth hammerhead sharks might feed at depth and that populations from the northeastern Pacific region might differ from the Atlantic ones by using deeper water layers (Logan et al., 2020; Santos and Coelho, 2018).

There were significant inter-specific differences in Δ^{199}Hg ratio between species ($\chi^2_{35,2} = 17.8$, $p < 0.001$) revealing differences in mean foraging depth. Blue sharks presented Δ^{199}Hg values significantly lower than shortfin mako sharks (Dunn's test, $p < 0.001$) and smooth hammerhead sharks (Dunn's test, $p < 0.01$). These variations could not be explained by different isotope fractionation between prey and predator, as Δ^{199}Hg values are conserved during trophic transfers (Kwon et al., 2016; Laffont et al., 2011). Thus, the significant gap in Δ^{199}Hg between species suggests systematic differences

in foraging depth (Le Croizier et al., 2020b). The lower Δ^{199}Hg of the blue shark suggests constant foraging in deeper water than the two other species. This conclusion is supported by stomach content analyses, which revealed that this species was the only one with bathypelagic prey in its gut (Galván-Magaña et al., 2013). On the other hand, epipelagic prey were also commonly reported in the stomach of the three shark species (Galván-Magaña et al., 2013; Hernández-Aguilar et al., 2016; Wood et al., 2009). Δ^{199}Hg signatures observed in this study may thus be the result of the consumption of both epi- and mesopelagic prey as reported for the Pacific bluefin tuna, *Thunnus orientalis* (Madigan et al., 2018). Differences in the relative importance of prey from these two compartments could therefore result in the observed Δ^{199}Hg differences between sharks. Compared to deeper species, epipelagic prey may form dense aggregations with higher nutritive and energetic value (Madigan et al., 2018; Spitz et al., 2010a). However, they are more scattered across time and space resulting in shark feeding opportunistically on them depending on the season, geographic position and maturity stage (Hernández-Aguilar et al., 2016; Maia et al., 2006; Rosas-Luis et al., 2017). This behavior is frequently observed in shortfin mako sharks, which favor a diet dominated by shallower teleost when seasonally and locally available (Harford, 2013; Maia et al., 2006). Compared to the shortfin mako, blue sharks display a more consistent diet targeting less nutritive but more reliable mesopelagic prey (Preti et al., 2012; Vollenweider et al., 2011). The mesopelagic food web indeed appears more stable through time and supports high prey biomasses in the northeast Pacific (Davison et al., 2015; Hazen and Johnston, 2010). Therefore, foraging on these deeper prey might represent a more reliable feeding strategy and involve less metabolic costs associated to foraging on more scattered epipelagic prey. Overall, the higher Δ^{199}Hg of blue sharks compared to shortfin mako sharks might be the result of different foraging strategies, with the blue shark occupying a deeper ecological niche and the shortfin mako shark favoring opportunistic foraging on epipelagic prey. Smooth hammerhead shark Δ^{199}Hg was not significantly different from the shortfin mako shark (Dunn's test, $p > 0.05$), hence, suggesting feeding at shallower depths than blue sharks and/or at equivalent rates on deeper organisms than shortfin mako sharks.

c. Resource partitioning between co-occurring predators

The overlaps between the three species EA (i.e. δ^{13}C and δ^{15}N, Figure 4-1) and EV (i.e. δ^{13}C, δ^{15}N and Δ^{199}Hg, Figure 4-2) are presented in Table 4-2. The limited

differences between $\delta^{13}C$ and $\delta^{15}N$ isotopic compositions resulted in significant isotopic overlaps between species except between blue and smooth hammerhead sharks (16.8%). The overlap systematically decreased by adding $\Delta^{199}Hg$ for all pairs of species. This decrease was the strongest for shortfin mako and blue sharks (from 42.0% to 23.0%). A smaller overlap decrease was observed between shortfin mako and smooth hammerhead sharks, which presented no significant difference in $\Delta^{199}Hg$, and between blue and smooth hammerhead sharks, already well separated by $\delta^{15}N$ and to a lesser extent by $\delta^{13}C$ (i.e. 5.9% and 3.9% decrease respectively). In the latter case, even if significant differences occurred in $\Delta^{199}Hg$, EA and EV overlapping areas appeared equivalent suggesting that carbon and nitrogen isotopic ratios can be sufficient to depict resource partitioning in the case of co-existing shark species feeding on different habitats or prey (Curnick et al., 2019), although always overlooking the vertical dimension.

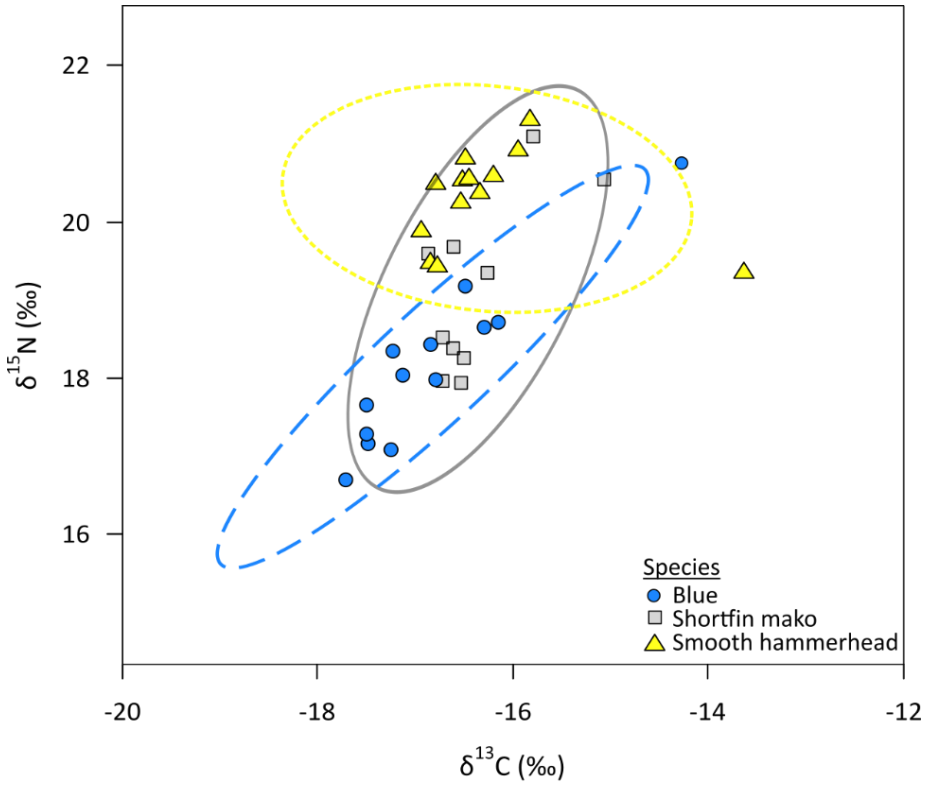


Figure 4-1 – $\delta^{13}C$ and $\delta^{15}N$ of blue (●), shortfin mako (□), and smooth hammerhead (△) sharks. The represented ellipses encompass 95% of the data.

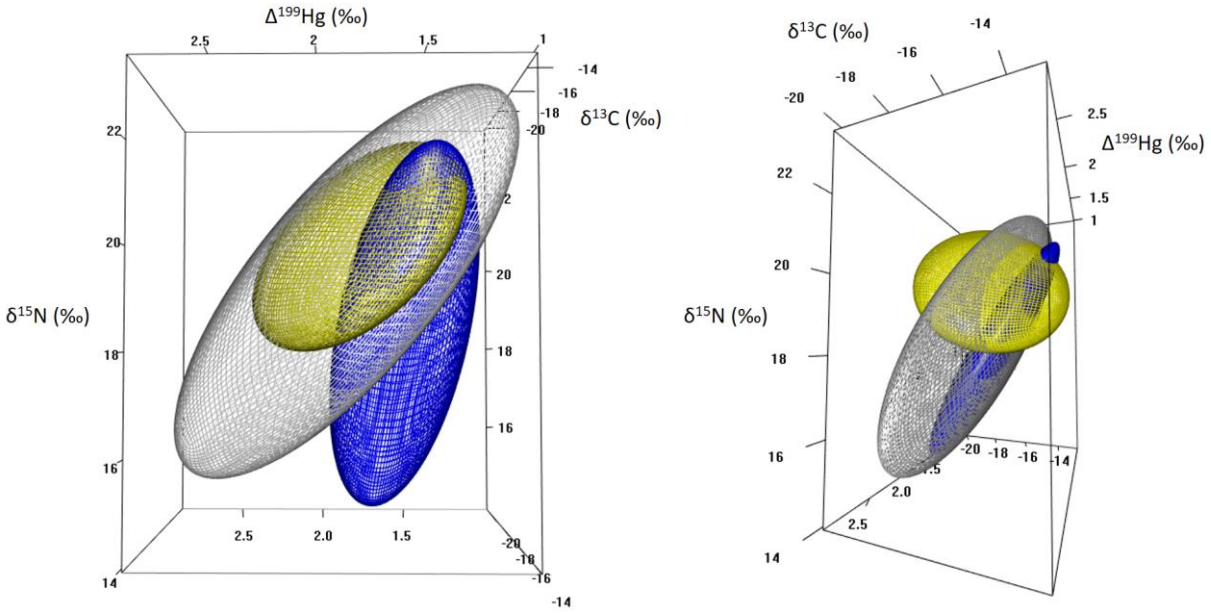


Figure 4-2 – 95% ellipsoids using $\delta^{13}C$, $\delta^{15}N$ and $\Delta^{199}Hg$ for blue, shortfin mako and smooth hammerhead sharks respectively represented in blue, grey and yellow.

Table 4-2 – Isotopic overlaps between blue, shortfin mako and smooth hammerhead sharks. Comparison is made between the SIBER ellipse metric for $\delta^{13}C$ and $\delta^{15}N$ (EA) (Jackson et al., 2011) and the ellipsoid approach combining $\delta^{13}C$, $\delta^{15}N$ and $\Delta^{199}Hg$ (EV) (Skinner et al., 2019).

	$\delta^{13}C/\delta^{15}N$	**$\delta^{13}C/\delta^{15}N/\Delta^{199}Hg$**
Blue | Shortfin mako	42.0%	23.0%
Shortfin mako | Smooth hammerhead	33.3%	27.4%
Blue | Smooth hammerhead	16.8%	12.9%

Resource partitioning within pelagic shark assemblages has been extensively studied using $\delta^{13}C$ and $\delta^{15}N$, yielding frequent records of important overlapping areas (Kiszka et al., 2015; Li et al., 2016a) suggesting similar foraging niches. In the eastern Pacific, such overlaps were recorded between shortfin mako and blue shark (Klarian et al., 2018; Rosas-Luis et al., 2017). From a methodological perspective, these similarities could however be expected in the case of these pelagic species. Indeed, by foraging in the same region and on similar phytoplankton-derived food web, sympatric pelagic sharks would exhibit similar $\delta^{13}C$ values (Bird et al., 2018), and possibly similar $\delta^{15}N$ depending on prey trophic position, even when feeding on different prey. The observed similarities in carbon and nitrogen isotopic niches between blue and shortfin mako sharks (overlapping at 42.0%) in this study may therefore be due to these processes,

rather than to a clear similarity in dietary habits. Moreover, important overlaps in isotopic signatures are not in accordance with previous stomach content analysis of both species in the northeastern Pacific region (Preti et al., 2012; Rosas-Luis et al., 2017). Hence, the differences in mean foraging depth between the two species increased resource partitioning estimation between the blue shark and the shortfin mako shark (19.0% decrease in overlapping area).

Our results demonstrate that carbon and nitrogen isotopic signatures overestimate overlapping areas by not reflecting the importance of foraging depth. In the case of pelagic sharks migrating vertically, carbon and nitrogen stable isotope analysis has shown some limitations in its capacity to address foraging depth issues. Indeed, even if vertical patterns in nitrogen isotopic baselines have been reported in zooplankton (Hannides et al., 2013), such patterns are rarely observed for top predators (Choy et al., 2015). However, the vertical foraging component has been suspected of being of critical importance in the ecology of marine predators. For example, computational models based on prey distribution systematically resulted in the emergence of vertical movements in tropical oceanic predatory fishes (Dagorn et al., 2000). Furthermore, differences in vertical movement patterns in sympatric pelagic top predators, including sharks, have already been demonstrated (Choy et al., 2015; Musyl et al., 2011). In our study, the systematic decrease in overlapping area for all pair of comparisons after the incorporation of Δ^{199}Hg demonstrates that differences in foraging depth better explain trophic niche partitioning between pelagic shark species.

d. Influence of foraging depth on mercury exposure

Muscle THg (Table 4-1) significantly differed between the three species ($\chi^2_{35,2} = 15.2$, $p < 0.001$). Blue sharks presented higher THg compared to shortfin mako (Dunn's test, $p < 0.05$) and smooth hammerhead sharks (Dunn's test, $p < 0.001$), as already observed in a previous study in the area (Maz-Courrau et al., 2012). The blue shark was the species presenting both higher THg and lower Δ^{199}Hg. Regardless of the species, THg was higher for individuals foraging on the deepest mesopelagic prey (i.e. exhibiting the lowest Δ^{199}Hg) as shown by the significant and negative correlation between the two variables (Figure 4-3). In the open Pacific Ocean, MeHg, the most bioavailable form of mercury, is mainly produced in the mesopelagic layer and especially in the Oxygen Minimum Zone (Blum et al., 2013; Fitzgerald et al., 2007). As

MeHg is trophically incorporated in food webs, sharks feeding in the mesopelagic zone will be exposed to higher MeHg levels compared to shallow feeding sharks, as highlighted by our results. This is in agreement with previous observations on fish (Monteiro et al., 1996), seabirds (Thompson et al., 1998) and pelagic predators (Choy et al., 2009; Houssard et al., 2019; Le Bourg et al., 2019; Madigan et al., 2018) that demonstrated higher mercury contamination in deeper foraging individuals or species.

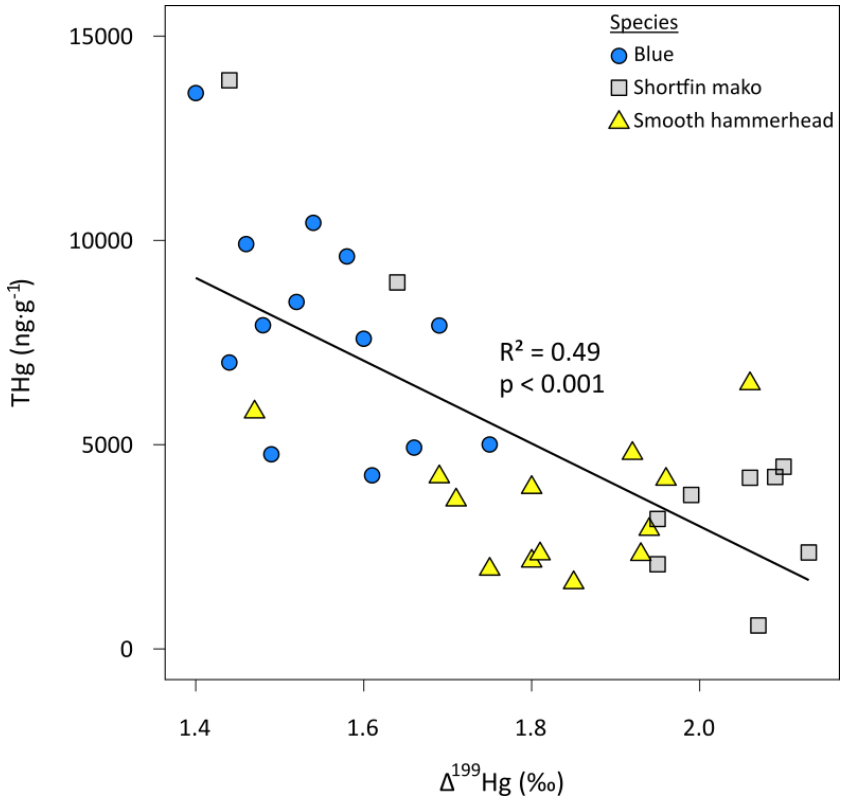


Figure 4-3 – Variation of THg with Δ^{199}Hg values in the muscle of blue (●), shortfin mako (□) and smooth hammerhead (△) sharks. Data fit a linear curve. Pearson correlation (R^2 value) was significant as indicated by its p-value.

In generalized linear models (GLMs), Δ^{199}Hg and species were the main factors explaining shark THg compared to other variables (Appendix 4-4), confirming that foraging depth was a key driver of shark mercury concentration in our dataset. Foraging depth has rarely been assessed in THg accumulation studies of marine predators except by qualitative approaches such as attributing a median depth of occurrence (Choy et al., 2009) or habitat preference (Le Bourg et al., 2019) to the studied species. It is interesting to note that this approach would not have been relevant for blue, shortfin mako and smooth hammerhead sharks that remain in the upper oceanic layers and occasionally undergo deep bounce dives to feed on mesopelagic prey (Abascal et al., 2011; Campana et al., 2009; Queiroz et al., 2010;

Sepulveda et al., 2004). In our study, mercury isotopic composition offers new opportunities to implement quantitative approaches of foraging depth. As $\Delta^{199}Hg$ was the main driver of THg (along with species), we suggest that this factor should be investigated in future research regarding mercury accumulation patterns in elasmobranchs.

In shark species, the pattern observed for THg in muscular tissue has been generally linked to changes in trophic level, generally estimated through $\delta^{15}N$ values (Biton-Porsmoguer et al., 2018; Le Bourg et al., 2019). Here, $\delta^{15}N$ did not explain THg variation. Although the limited number of samples may not cover the entire spectrum of length and trophic levels for all shark species, influence of such small $\delta^{15}N$ spectrum on THg has been previously demonstrated (Le Croizier et al., 2019). This therefore implies that foraging depth could affect more significantly THg in pelagic shark species than their respective trophic levels, but further investigations at a specific level or with broader size and $\delta^{15}N$ range are needed to confirm this effect.

THg in marine organisms depends not only on trophic features (Ferriss and Essington, 2014; Le Bourg et al., 2019; Thompson et al., 1998) but also on species physiological characteristics such as longevity, metabolic, growth and feeding rates and/or possible detoxication processes (Bolea-Fernandez et al., 2019; Houssard et al., 2019; Li et al., 2020; Senn et al., 2010). This can be seen in our results as the best-fitted model incorporated species as a key variable explaining THg (along with $\Delta^{199}Hg$). However, all these parameters could not be tested in this study, except for longevity and demethylation mechanisms which are known to increase $\delta^{202}Hg$ values (Bolea-Fernandez et al., 2019; Senn et al., 2010). Here, $\delta^{202}Hg$ values varied significantly between species (Table 4-1; $F_{35,2} = 4.4$, $p < 0.05$), as previously observed for other co-occurring shark species (Le Croizier et al., 2020b). Still, $\delta^{202}Hg$ variations did not affect THg in GLMs (as it can also be seen in the relation between the two variables in Appendix 4-5) showing no link between mercury contamination and the demethylation process previously highlighted by the absence of correlation between $\Delta^{199}Hg$ and $\delta^{202}Hg$ (Appendix 4-3). Age was also not affecting THg while differences between species were also significant ($F_{35,2} = 8.6$, $p < 0.001$), with blue sharks encompassing the oldest individuals and shortfin mako sharks the youngest ones (Appendix 4-6). Overall, the fact that metabolic demethylation and individual age did not critically affect THg strengthens the hypothesis that ecological characteristics were mainly driving

muscle mercury contamination. As all physiological characteristics could not be analyzed in this study, future investigations on physiological intra-specific differences between blue, shortfin mako and smooth hammerhead sharks might help to identify the entire mechanisms behind their THg.

e. Insights into mercury cycle

In the northeastern Pacific region, atmospheric mercury deposition dominates mercury inputs to the water column as river influence appears negligible (Masbou et al., 2018; Zhang et al., 2014). This deposition at the atmosphere/ocean interface has two different origins: inorganic mercury (iHg) via precipitation and atmospheric gaseous mercury (Hg(0)) through dissolution (Gratz et al., 2010; Zhang et al., 2014). While the mechanisms causing mass-independent isotopic fractionation (MIF) of even-mass Hg isotopes are still poorly understood, processes such as photooxidation of Hg(0) to iHg in the atmosphere (e.g. tropopause) may be involved leading to isotopic fractionation (Chen et al., 2012). Therefore, iHg deposition by precipitation presents slightly different Δ^{200}Hg values ranging from 0 to 0.3‰ than atmospheric Hg(0) dissolution characterized by Δ^{200}Hg between -0.11 and -0.01‰ (Enrico et al., 2016; Gratz et al., 2010). Once in the water column, Δ^{200}Hg values are conserved, making it a robust tracer of atmospheric deposition pathways even when analyzed in top-predator species (Enrico et al., 2016; Le Croizier et al., 2020b). Here, Δ^{200}Hg values ranged from -0.07 to 0.14‰ with no significant differences between species ($F_{35,2} = 1.4$, $p > 0.05$; i.e. 0.05 ± 0.05‰ for blue and smooth hammerhead sharks and 0.02 ± 0.05‰ for shortfin mako sharks). These values are similar to those observed in bottomfish from Hawaii, i.e. -0.04 to 0.10‰ (Sackett et al., 2017), and to other coastal shark species sampled off La Réunion Island, i.e. 0.08 ± 0.04‰ in bull sharks, *Carcharhinus leucas*, and 0.06 ± 0.04‰ in tiger sharks, *Galeocerdo cuvier* (Le Croizier et al., 2020b). For the three shark species, Δ^{200}Hg values suggest a common origin in the mercury precursors of MeHg in shark tissues, probably from a combined source of both iHg and Hg(0) because of both positive and negative Δ^{200}Hg (Le Croizier et al., 2020b).

Due to solar radiation, photodemethylation can transform dissolved MeHg into iHg and photoreduction can convert iHg into Hg(0) in the water column. Both of these reactions are characterized by a Δ^{199}Hg/Δ^{201}Hg ratio of respectively 1.36 and 1.00 (Bergquist and Blum, 2007). All shark species considered, Δ^{199}Hg/Δ^{201}Hg slope was 1.16

(Appendix 4-7), not clearly indicating the prevalence of one reaction over another. Surprisingly this is not in accordance with previous studies reporting the dominance of MeHg demethylation in oceanic island marine ecosystems (Le Croizier et al., 2020b; Sackett et al., 2017). Indeed, the ratio observed here seems to represent a mixed signature of both phenomena. Interestingly, in Hawaii, deep-foraging species exhibit a flatter $\Delta^{199}Hg/\Delta^{201}Hg$ slope (1.05 ratio) compared to shallower species (1.21 ratio) (Blum et al., 2013; Masbou et al., 2018). The intermediate slope in this study is therefore consistent with shark species foraging on mesopelagic prey exhibiting a flatter slope than epipelagic ones, reinforcing the conclusion that all three shark species foraged mainly at depth.

5. Conclusions

Based on $\delta^{13}C$, $\delta^{15}N$ and $\Delta^{199}Hg$, this study provided new information on the trophic ecology of blue, shortfin mako and smooth hammerhead sharks in the eastern Pacific region. Mesopelagic prey appeared as a major component in the diet of the three species. Our study demonstrated the importance of considering foraging depth when studying resource partitioning between co-occurring pelagic predators. In the northeastern Pacific, blue sharks appeared to forage deeper than mako and smooth hammerhead sharks and these foraging strategies seemed to reduce trophic competition between them. Since carbon and nitrogen isotopes did clearly underestimate resource partitioning, this study confirmed the usefulness of multi-isotopic approaches to help fine scaling resource partitioning in top predators depending on the ecology of the studied species. Our results highlighted the underexploited potential of mercury stable isotopes for marine ecology studies. This new tool has the potential to elucidate possible ontogenetic variation in depth utilization for these species, as deep diving at early life stages is a rare pattern for blue and shortfin mako sharks (Nosal et al., 2019) and could be limited inside shallow coastal nursery areas for smooth hammerhead sharks (Francis, 2016; Santos and Coelho, 2018). Moreover, there are increasing evidences of vertical habitat partitioning between different predator species in other pelagic ecosystems (Madigan et al., 2020a) and mercury stable isotopes could help to precise the mechanisms behind such vertical structuring. As foraging depth appeared as a key factor influencing mercury exposure for the three species, it should be more extensively studied to understand mercury accumulation in top predators. In the context of climate change, Oxygen Minimum

Zones are observed at shallower depth in tropical and subtropical regions, acting as a physical barrier and preventing sharks to forage deeper in the water column (Vedor et al., 2021), particularly in the tropical eastern Pacific (Trucco-Pignata et al., 2019). This habitat compression could therefore limit the possibility for co-occurring shark species to forage at significant different depths and could lead to new competition processes between pelagic predators that should be carefully monitored.

CHAPTER 5

MERCURY ISOTOPE CLOCKS PREDICT COASTAL RESIDENCY AND MIGRATION TIMING OF HAMMERHEAD SHARKS.

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1. Abstract

The management of migratory taxa relies on the knowledge of their movements. Among them, ontogenetic habitat shift, from nurseries to adult habitats, is a behavioral trait shared across marine taxa allowing resource partitioning between life stages and reducing predation risk. As this movement is consistent over time, characterizing its timing is critical to implement efficient management plans, notably in coastal areas where nurseries mostly occur. In the Mexican Pacific, habitat use of the smooth hammerhead shark (*Sphyrna zygaena*) is poorly described, while the species is heavily harvested. Given the large uncertainties associated with the timing of out-migration from coastal nursery grounds to offshore waters prior to reproductive maturity, an assessment of smooth hammerhead shark movements is needed. Photochemical degradation of mercury imparts mass-independent isotope fractionation (Δ^{199}Hg) which can be used to discriminate between coastal shallow and offshore deep foraging patterns. Here, we present the application of muscle Δ^{199}Hg as molecular clocks to predict the timing of ontogenetic habitat shifts by smooth hammerhead sharks, based on their isotopic compositions at the initial and arrival habitats and on muscle isotopic turnover rate. We observed decreases in Δ^{199}Hg values with shark body length, reflecting increasing reliance on offshore mesopelagic prey with age. Coastal residency estimates indicated that smooth hammerhead sharks utilize coastal resources for up to three years prior to offshore migration, suggesting longer residency in these ecosystems than previously assumed.

Policy implications: This study demonstrates how mercury stable isotopes and isotopic clocks can be implemented as a complementarity tool for stock management by predicting the timing of animal migrations—a key aspect in the conservation of marine taxa. In the Mexican Pacific, fishing pressure on shark species occurs in coastal habitats depleting juvenile stocks. Consequently, management decision support tools are imperative for effectively maintaining early life stage population levels over time. The finding that juvenile smooth hammerhead sharks extensively rely on highly fished coastal habitats for three years after parturition have important management consideration. Particularly, it supports the relevance of establishing permanent marine reserves, as the current seasonal time-area closure of coastal habitat to fisheries could lack efficiency.

2. Introduction

Managing mobile species relies on the knowledge of their non-random predictable movements as individuals connect habitats with different levels of threats and protections (Harrison et al., 2018; Lascelles et al., 2014; Queiroz et al., 2019). Among these movements, ontogenetic habitat shift from coastal nursery grounds to offshore adult habitats is a common behavior-trait of marine fauna (Beck et al., 2001; Nagelkerken et al., 2015). Its main drivers are the diminution of predation risk, juveniles inhabiting nursery areas with less predators, and the enhancement of intra-specific resource partitioning between life stages (Sánchez-Hernández et al., 2019). Ontogenetic migrations are highly consistent in routes and timing, allowing management priorities to be set when these movements are characterized (Beck et al., 2001; Nagelkerken et al., 2015).

More than one-third of all chondrichthyan species are threatened by overfishing (Dulvy et al., 2021). Due to their slow growth, late maturity, habitat, behavior (e.g., schooling in large groups, site fidelity, seasonal residency) and by-catch sensitivity, hammerhead sharks are among the most threatened families of chondrichtyans (Gallagher et al., 2014a; Gallagher and Klimley, 2018). While still extensively fished in the Mexican Pacific, the smooth hammerhead shark (*Sphyrna zygaena*) is the least studied of all large hammerhead species, and effective management requires the characterization of movement trajectories and their associated timing (Cartamil et al., 2011; Castillo-Geniz and Tovar-Ávila, 2016; Ramírez-Amaro and Galván-Magaña, 2019). In the northeastern Pacific, movement data are currently unavailable for smooth hammerhead sharks, hindering knowledge on core habitats utilized through ontogeny.

Biochemical tracers, such as naturally occurring stable isotopes, offer a retrospective, rapid and low cost solution for studying the location and the timing of habitat shifts in organisms (Madigan et al., 2020b; Madigan et al., 2014; Trueman and St John Glew, 2019). The isotopic composition of an animal mainly reflects that of its diet, the local ecosystem where the diet was consumed and physiological processes that can elicit distinct patterns of isotopic fractionation (Shipley and Matich, 2020). The isotopic composition of primary producers (i.e., isotopic baselines) is driven by local environmental conditions (e.g., temperature, dissolved CO_2 concentrations, denitrification), biochemical proprieties (e.g., phytoplankton growth rate, cell size, NO_3^- uptake and community dynamics) and varies significantly across space (e.g., Magozzi

et al., 2017). Thus, the tissues of animals migrating between two isotopically distinct regions reflect a mixture of multiple isotopic baselines and will ultimately reach isotopic steady-state over time.

After migration, the rate at which an organism's tissues reach steady-state with a new isotopic baseline is determined by the isotopic turnover rate, which varies between metabolically active tissues (e.g., liver and blood plasma) integrating new isotopic information faster than less metabolically active (e.g., muscle and bone collagen) (Carter et al., 2019; Thomas and Crowther, 2015). This information can be leveraged to determine the timing of animal movements between regions with distinct isotopic baselines. Following this principle, isotopic clocks have been applied in marine ecosystems to study both fine habitat-scale (Shipley et al., 2021) and ocean-basin scale movement dynamics (Madigan et al., 2014) using nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes, due to their distinct regional variability (Madigan et al., 2020b; Magozzi et al., 2017; Somes et al., 2010). Isotopic clocks calculate the timing of an animal movements into a new habitat as a function of the differences between its own isotopic composition and the baseline isotopic compositions at the initial and arrival habitats, taking into account the tissue isotopic turnover rate (Klaassen et al., 2010). However, traditional isotope systems are limited if migrations occurs over isotopically homogenous environments like in the Pacific coast of Mexico (Besnard et al., 2021).

Mercury (Hg) bioaccumulates in marine fauna primarily in the form of monomethylmercury (MeHg) (Storelli et al., 2003). MeHg undergoes photochemical degradation, which imparts mass-independent isotope fractionation, represented by $\Delta^{199}Hg$ signatures (Bergquist and Blum, 2007). In surface waters, light penetration drives high $\Delta^{199}Hg$ values, which subsequently decrease with depth until the aphotic water layer. This vertical isotopic gradient is reflected in marine fauna (Blum et al., 2013; Sackett et al., 2017) and $\Delta^{199}Hg$ values have been subsequently used to characterize the foraging depth of marine predators (Besnard et al., 2021; Le Croizier et al., 2020b; Madigan et al., 2018). Unlike traditional isotopes, $\Delta^{199}Hg$ values are conserved during trophic transfers between consumer and their prey such that isotopic baseline values are directly reflected in the tissues of predators (Kwon et al., 2016; Laffont et al., 2011). Moreover, turnover rates of Hg isotopes are slow in large-bodied fish species (Kwon et al., 2016), holding the potential to depict ontogenetic migrations. The application of isotopic clocks using Hg isotopes therefore represents a new

opportunity to assess movements across vertical gradients without the constraints related to diet-tissue discriminator factors (Madigan et al., 2020b; Shipley et al., 2021).

This study demonstrates how Hg isotopes ($\Delta^{199}Hg$) can be used as molecular clocks to characterize movement across habitats in smooth hammerhead sharks. In the Mexican Pacific, coastal sharks are particularly vulnerable due to higher fishing efforts compared to offshore habitats. Juvenile smooth hammerhead sharks display an ontogenetic habitat shift, whereby pups and young juveniles feed on shallow prey within coastal nursery areas and close-to-maturity individuals forage at depth in oceanic waters (Besnard et al., 2021; Francis, 2016; Li et al., 2016a; Santos and Coelho, 2018). Using samples obtained during artisanal fisheries surveys, we estimated the timing of smooth hammerhead shark migration into offshore pelagic habitats and inferred its coastal residency periods during which sharks are particularly sensitive to fishing activities.

3. Materials and Methods

a. Study sites and sample collection

Research was conducted along the western coast of Baja California Sur (Mexico), an area influenced by the southern extension of the California Current and scattered with productive lagoon systems (Ibarra-Obando et al., 2001). Juvenile smooth hammerhead sharks were caught by gillnets and longlines in 2009 and from 2014 to 2018. Sharks (n=102) were sampled in artisanal fishing camps at four locations: Bahía Tortugas, Las Barrancas, San Lázaro and Punta Lobos (Figure 5-1). For each individual, approximately 1 g of dorsal white muscle tissue was sampled from sharks ranging from 66 to 192 cm (total length). Samples were transported on ice, stored at -20°C at the laboratory (Centro Interdisciplinario de Ciencias Marinas, La Paz, B.C.S., México) and ultimately freeze-dried prior to transport and further treatments.

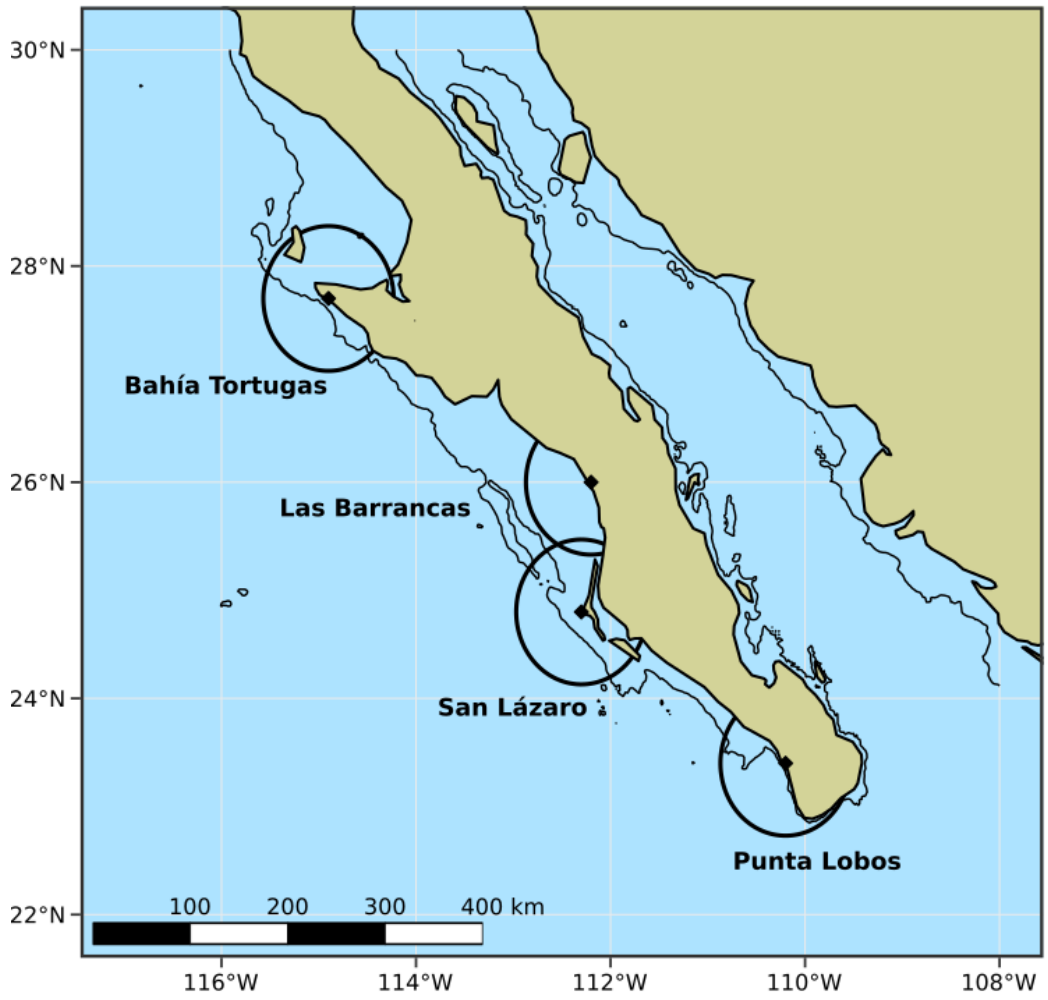

Figure 5-1 – Map of the sampling locations in the Mexican Pacific, with the 200 m bathymetric line represented. All samples came from four artisanal fishing camps. Circled regions delineate the area covered by fishermen during their fishing activities.

b. Mercury isotope analysis

Total Hg concentration (THg) was used as a proxy for MeHg concentration as MeHg represents more than 85% of THg in smooth hammerhead shark muscle (Storelli et al., 2003). THg was determined in a 20 mg aliquot of each sample using a Direct Mercury Analyzer (DMA-80, Milestone, USA), by combustion, gold trapping and atomic absorption spectrophotometry detection (Observatoire Midi-Pyrénées, Toulouse, France). THg analytical detection limit was 0.005 $\mu g \cdot g^{-1}$ dw (dry weight). Repeated measurements of a tuna flesh homogenate (BCR-464, Institute for Reference Materials and Measurements, 5.24 ± 0.10 $\mu g \cdot g^{-1}$ dw) tested the analysis reproducibility and accuracy. BCR-464 measurements (n=9) were reproduced within the confidence limits: 5.30 ± 0.44 $\mu g \cdot g^{-1}$ dw.

Another 20 mg muscle sample was then diluted into 3 mL of pure bi-distilled nitric acid (HNO_3), left overnight at room temperature and digested at 100°C for 6 hours in pyrolyzed glass vessels closed by Teflon caps on a hotplate. We added 1 mL of hydrogen peroxide (H_2O_2), left the digestion to continue for another 6 hours and completed the extraction with 100 µL of bromine monochloride (BrCl), to convert solubilized MeHg into inorganic Hg. Depending on THg concentration in each sample, we reached a Hg concentration of 1 ng·mL^{-1} by dilution of the solution in an inverse aqua regia (3:1 HNO_3:HCl with 20 vol.% of MilliQ water). Hg isotope composition was measured at the Observatoire Midi-Pyrénées (Toulouse, France) by inductively coupled plasma mass spectrometry (MC−ICP−MS, Thermo Finnigan Neptune) with continuous-flow cold vapor (CV) generation using Sn(II) reduction (CETAC HGX-200). Hg isotopic compositions are expressed in δ notation (‰). Sample values are expressed relatively to their deviation from the National Institute of Standards and Technology (NIST) SRM-3133 standard and calculated by sample-standard bracketing:

$$\delta^{XXX}Hg\ (‰) = \left(\frac{^{XXX}Hg\ /\ ^{198}Hg_{sample}}{^{XXX}Hg\ /\ ^{198}Hg_{NIST-SRM-3133\ standard}} - 1 \right) \times 1000$$

where XXX represents Hg isotope masses. Hg isotopic composition is affected by mass-dependent fractionation (δ^{202}Hg) and by mass-independent fractionation (e.g., Δ^{199}Hg). This study focuses on Δ^{199}Hg which is expressed in regards of its fractionation factor (Bergquist and Blum, 2007; Blum et al., 2013):

$$\Delta^{199}Hg\ (‰) = \delta^{199}Hg - (\delta^{202}Hg \times 0.252)$$

Along the procedure, THg in the solution was monitored by the ^{202}Hg signal provided by MC-ICP-MS. We measured blanks and BCR-464 certified materials following the same procedure as for shark samples. We recovered 84 ± 19% of Hg in shark samples and 90 ± 2% in BCR-464 replicates (n=10). Isotopic measurement reproducibility was assessed by analyzing UM-Almadén (n=8), ETH-Fluka (n=8) and the biological tissue procedural standards BCR-464 (n=10). Measured isotope signatures as well as analytical reproducibility of standards agreed with previously published values (Appendix 5-1). We simultaneously estimated Δ^{200}Hg and Δ^{201}Hg values for each sample (detailed in Appendices). Measured δ^{202}Hg and Δ^{199}Hg variability was typical of marine biota and the Δ^{199}Hg/Δ^{201}Hg slope characteristic of photochemical MeHg

breakdown in the marine environment (Blum et al., 2013), further validating smooth hammerhead shark Hg isotopes measurement (Appendix 5-2 and 5-3).

c. Isotopic clock model parameterization

The isotopic clock was parameterized following Klaassen et al., (2010):

$$t_i = \frac{ln\left(\frac{\Delta_{0_i} - \Delta_{f_i}}{\Delta_{t_i} - \Delta_{f_i}}\right)}{\lambda_i}$$

where t can be expressed as residency, or time-since-immigration of an individual into the arrival/new habitat, Δ_0 is the isotopic composition of the organism at isotopic steady-state with the initial habitat, Δ_f is the isotopic composition of the organism at isotopic steady-state with the arrival habitat, Δ_t is the measured isotopic composition of the organism in the arrival habitat and λ is the isotopic incorporation rate of the analyzed tissue—i represents the statistical resampling from n iterations.

In this study, isotopic clocks were used to estimate the time-since-immigration of smooth hammerhead sharks to the offshore pelagic habitat (t_i). Young-of-the-year smooth hammerhead sharks inhabit inshore bays or lagoon ecosystems, where they feed in shallow water, before migrating into pelagic ecosystems prior to reaching sexual maturity, where individuals forage on deeper mesopelagic prey (Besnard et al., 2021; Li et al., 2016a; Santos and Coelho, 2018). This ontogenetic habitat and diet shift is expressed vertically (i.e., shallow to deep foraging) and is traceable via Δ^{199}Hg values (Blum et al., 2013; Sackett et al., 2017) (Figure 5-2).

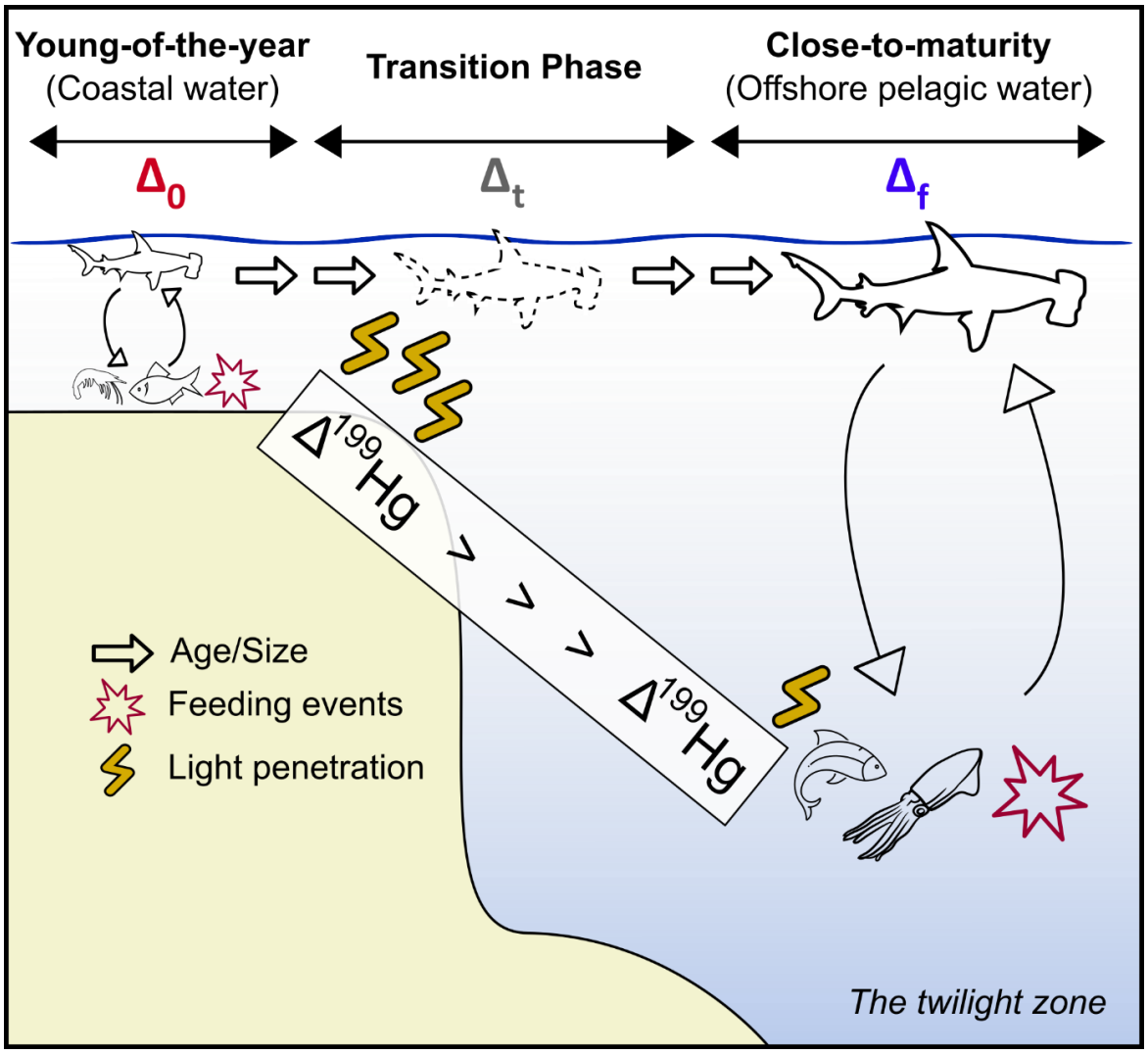

Figure 5-2 – Proposed migration of juvenile smooth hammerhead sharks in the northeastern Pacific region in relation to parameters used in the isotopic clock approach (Δ_0, Δ_t and Δ_f). Young-of-the-year inhabit coastal nurseries where they feed on shallow water prey before migrating offshore where close-to-maturity specimens feed on deep mesopelagic prey. In shallow water, light penetration is strong which drives high Δ^{199}Hg values compared to deeper water layers.

Age was estimated from the total length of each individual (Appendix 5-4). Δ_0 was parametrized by the Δ^{199}Hg values from the six individuals identified as young-of-the-year (Δ^{199}Hg comprised between 2.12 and 2.24‰). Young-of-the-year are expected to be at isotopic steady-state with the inshore coastal habitat as they actively forage in their nurseries (e.g., Lyons et al., 2020). As smooth hammerhead shark sexual maturity has been estimated to be between 9 and 10 years old in adjacent regions (Nava Nava and Márquez-Farías, 2014), close-to-maturity individuals were selected as ranging from 8 to 9 years old. Δf was parametrized by the Δ^{199}Hg values from the identified nine close-to-maturity individuals expected to be at isotopic steady-state with the

offshore pelagic environment (Δ^{199}Hg comprised between 1.43 and 1.96‰). Following normality and variances homogeneity, Wilcoxon singed rank test was used to assess statistical differences in median Δ^{199}Hg among Δ_0 and Δ_f and Student's *t*-test was used to test for statistical differences in mean Δ^{199}Hg between sexes (α=0.05).

Coastal MeHg from sediments or turbid waters (where light penetration is restricted) can display low Δ^{199}Hg values in coastal ecosystems (Meng et al., 2020; Senn et al., 2010). Here, young-of-the-year Δ^{199}Hg values (2.17 ± 0.05‰) were similar to that of other shark species (2.08 ± 0.16‰) foraging on coastal shallow prey in ecosystems where MeHg did not originate from coastal sediment or turbid water but from the water column (Le Croizier et al., 2020b). Observed Δ^{199}Hg differences between Δ_0 and Δ_f individuals therefore originate from the photochemical breakdown of MeHg in the water column and Δ^{199}Hg values are assumed to vary with foraging depth, allowing the isotopic clock model to efficiently characterize shark ontogenetic migration from shallow coastal habitats to offshore deeper ecosystems. Other Hg isotopes (δ^{202}Hg or Δ^{200}Hg) were not applied due to potential biotic fractionation or absence of variability in sharks (Appendix 5-5).

In the first months of their life, newborn sharks exhibit a rapid ontogenetic diet switch from maternal energy sources to active foraging (Lyons et al., 2020; Matich et al., 2015). This maternal provisioning comes with the transfer of both Hg (Lyons et al., 2013) and heavy ^{13}C and ^{15}N isotopes from the mother to the tissue of neonates (Matich et al., 2015; Olin et al., 2011). This effect was nevertheless not included in the isotopic clock model due to the absence of data on Hg isotope maternal transfers, high uncertainty about the trophic habitat of large female smooth hammerhead sharks (Gallagher and Klimley, 2018), and as active feeding starts early and maternal energy is quickly consumed in hammerhead neonates (Lyons et al., 2020).

The isotopic clock model parametrization assumes that the time at which smooth hammerhead sharks leave coastal areas for pelagic grounds is unknown and could be reflected in sharks ranging from 1 to 8 years old. For these individuals, Δ^{199}Hg values were subsequently assigned to Δ_t (n=87, Table 5-1). The isotopic turnover rate, λ, was 0.0028 ± 0.001 day^{-1} based on estimates derived from Pacific bluefin tunas, *Thunnus orientalis*, held captive during a 2,914 days experiment (Kwon et al., 2016), as there are no direct estimates for elasmobranchs. While physiological differences between juvenile hammerhead sharks and Pacific bluefin tuna might lead to different λ, their

similarities in body mass, life span, diet and Hg concentration make this λ estimate the most reasonable to use (Madigan et al., 2018; Shimose et al., 2009; Thomas and Crowther, 2015).

Table 5-1 – Parameterization of the isotopic clock model to estimate smooth hammerhead shark time-since-immigration in the offshore pelagic habitat.

	Mean values ± standard deviation	**Samples analyzed**
Δ_0	2.17 ± 0.05‰	Muscle Δ^{199}Hg values of young-of-the-year smooth hammerhead sharks sampled in the area of Bahía Tortugas (*This study*)
Δ_t	1.92 ± 0.19‰	Muscle Δ^{199}Hg values of 1 to 8 years old smooth hammerhead sharks sampled across the Pacific coast of Baja California Sur, Mexico (*This study*)
Δ_f	1.77 ± 0.16‰	Muscle Δ^{199}Hg values of close-to-maturity (8 to 9 years old) smooth hammerhead sharks sampled across the Pacific coast of Baja California Sur, Mexico (*This study*)
λ	0.0028 ± 0.001 day^{-1}	White muscle Δ^{199}Hg isotopic incorporation rate of captive Pacific bluefin tunas, *Thunnus orientalis* (Kwon et al., 2016). Standard deviation was originally estimated at ± 0.0008 but we instead used ± 0.001 to make the parameter more conservative.

For each Δ_t individual, we computed 10,000 estimates of t_i by resampling from the mean ($\bar{x}_i$) and standard deviation (σ_i) of each input parameter (i.e., $\Delta 0_i$, Δf_i, Δt_i and λ_i) assuming a Gaussian distribution. As this function can produce a large range of values, a rejection sampling algorithm was used to resample ecologically implausible simulated t_i values (von Neumann, 1951). Estimates that were considered implausible include: 1) when t_i cannot be solved because Δt_i values fell outside the mixing space (e.g., when $\Delta_f > \Delta_t$ while $\Delta_0 > \Delta_f$); 2) when t_i were negatives; 3) when t_i exceeded Δ^{199}Hg time to steady-state in muscle (i.e., 1,070 days) (Kwon et al., 2016); 4) when simulated λ_i were negatives. In these cases, the rejection sampling algorithm rejected t_i estimates and recalculated new ones based on the distribution of the parameters. This procedure was iteratively repeated until no t_i was left to be rejected. Rejection sampling rates were calculated to assess the appropriateness of model parameterization, with higher rejection rates indicating poorer model performance (i.e., more individuals falling beyond the mixing space). For each individual, we extracted the median t_i values to

obtain a better measure of the distribution central tendency relative to the mean and calculated their 95% confidence intervals (95% CI), assuming *t*-distribution.

d. Timing of migration from coastal to offshore pelagic habitat

Ordinary least squares linear regression was used to describe the relationship between median t_i and shark total length. Median t_i estimates underwent min-max normalization procedure to scale values between 0 and 1 (referred to as 'normalized medians'). Values were scaled down to 0 being a fully coastal resident individual (t_i = 0 days) and 1 being the maximum median t_i exhibited by juvenile smooth hammerhead sharks. We applied a Michaelis-Menten model to the change in normalized median t_i following shark age, assuming that differences in t_i were diminishing approaching isotopic steady-state:

$$Normalized\ medians\ of\ t_i\ \epsilon\ [0;1] = a \times \frac{Age}{Age + b}$$

where a generally corresponds to the model maximum value of normalized median of t_i and b to the value in days corresponding to half of the maximum value of normalized median of t_i (i.e., $^1/_2\ a$). We used a nonlinear least square method to fit the Michaelis-Menten model to the data and estimate the mean and standard error of a and b (Bates and Watts, 1988). Based on these estimates, a time of departure from coastal areas was calculated ($Age_{50\%}$) corresponding to the age, in days, at which more than half of the population showed an offshore mesopelagic signature. The analysis was performed using R software (R Core Team, 2021) and the Tidyverse package (Wickham et al., 2019).

4. Results

Median $\Delta^{199}Hg$ values were significantly different between Δ_0 (2.15‰) and Δ_f (1.80‰) individuals (W=54, p < 0.01). Among Δ_t sharks, $\Delta^{199}Hg$ values ranged from 1.34 to 2.35‰ (Figure 5-3A) with no significant differences in mean $\Delta^{199}Hg$ values between females (1.89 ± 0.19‰) and males (1.93 ± 0.19‰) (t(62)=0.96, p > 0.05).

The isotope clock model simulated 870,000 t_i estimates of time-since-immigration to the offshore pelagic habitat for juvenile smooth hammerhead sharks (Figure 5-3B). The rejection sampling procedure resulted in the random resampling of 31 ± 22% of t_i estimates on average. At the individual level, rejection rates varied from 2 to 95% (all

individuals were kept for the final analysis). Rejection rate appeared to increase when Δ_t fell outside of the isotopic clock mixing space consistent with the rejection sampling procedure. Most rejections were explained by low Δ^{199}Hg Δ_t values relative to Δ^{199}Hg Δ_f (Figure 5-4). At the population scale, mean values of each individual median t_i was 242 (95% CI 227 – 258) days.

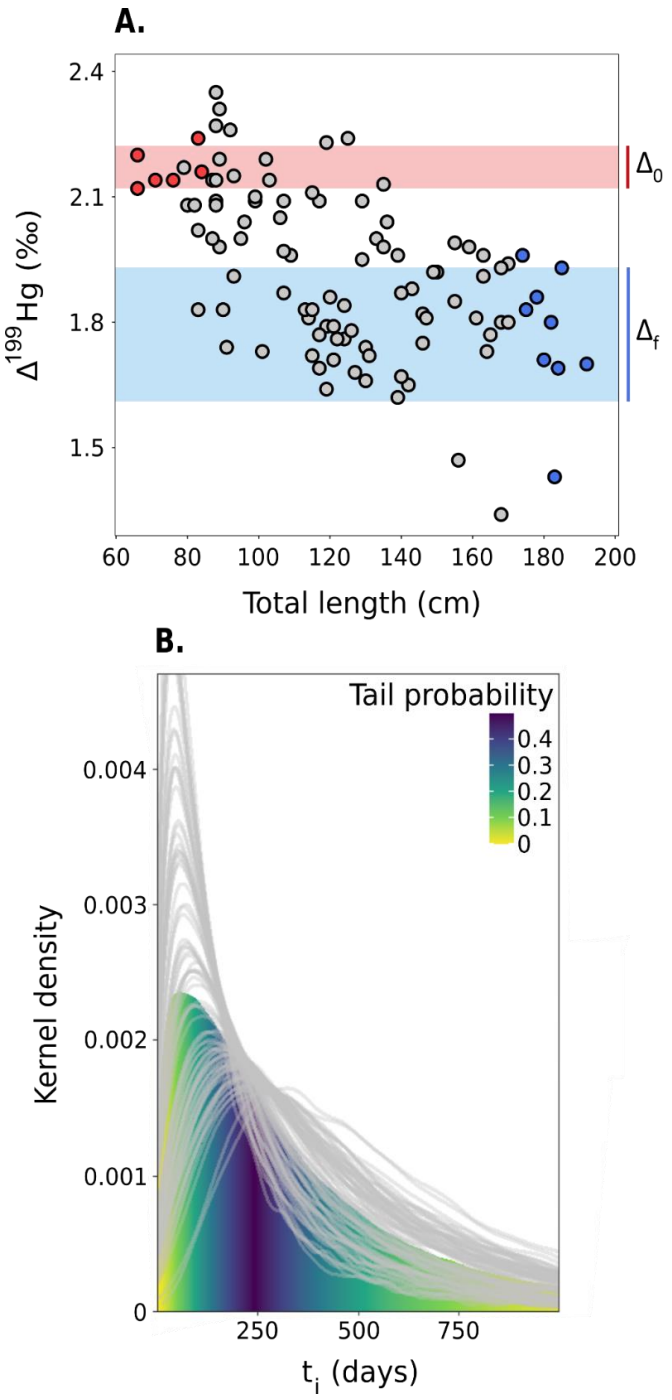

Figure 5-3 – (A.) Change in muscle Δ^{199}Hg values in relation to the total length of juvenile smooth hammerhead sharks. Red dots correspond to young-of-the-year and blue dots to close-to-maturity individuals that were used to respectively define Δ_0 and Δ_f in the isotopic clocks model parametrization. The red bar characterizes Δ_0 and the blue bar Δ_f based on the mean and standard deviation of Δ^{199}Hg values. Grey dots are values from 1 to 8 years old individuals that were assumed in possible transition state between coastal and offshore pelagic habitats (Δ_t). (B.) Kernel density distribution of time-since-immigration in the offshore pelagic habitat (t_i). Gray lines represent density t_i estimates for each Δ_t individual. Tail probability is color-coded using the empirical cumulative function for the joint distribution of t_i. Probability between 0.05 and 0.5 represents 2.5 to 97.5% of the distribution.

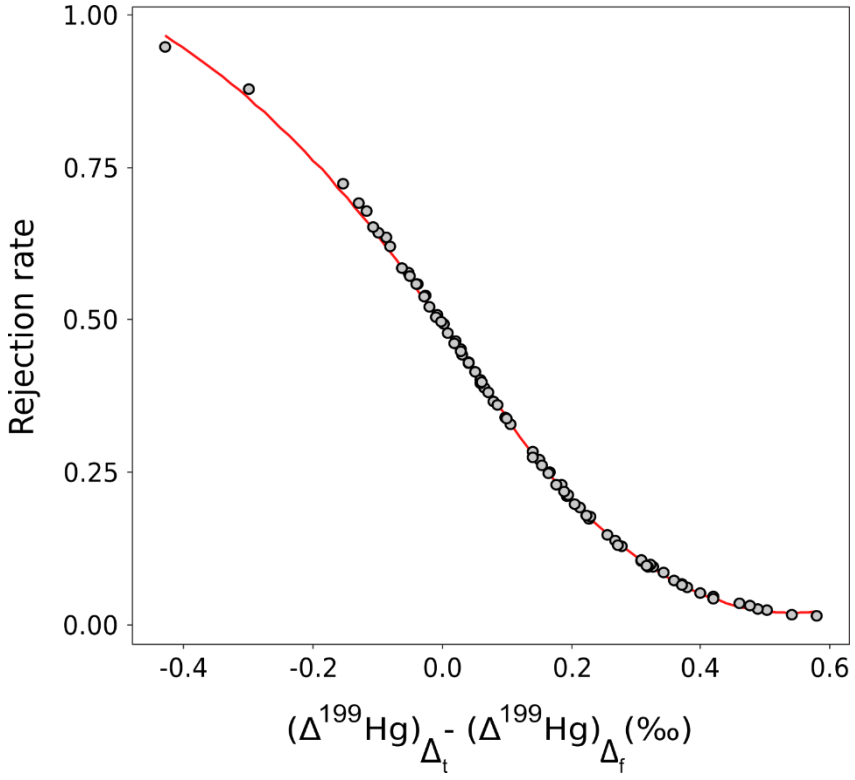

Figure 5-4 – Mean proportion of rejected t_i values according to the difference between mean $\Delta^{199}Hg$ values of Δ_t and Δ_f for all Δ_t individuals.

Individually, both the mean and the distribution (i.e., minimum and maximum estimates) of medians of t_i shifted with shark age (Table 5-2) with median estimates of t_i increasing with smooth hammerhead shark total length (Figure 5-5A). After normalization of the medians and based on the Michaelis-Menten model, $Age_{50\%}$ was estimated at 1,121 days corresponding to approximately 3 years (Figure 5-5B). Based on the standard errors of a and b, $Age_{50\%}$ varied between 1,005 and 1,163 days.

Table 5-2 – Output of the isotopic clock model according to juvenile smooth hammerhead shark age classes. Mean total length (TL), number of individuals (N), mean rejection rates (± standard deviation) and median t_i estimates are presented (i.e., mean minimum/maximum of the medians and the overall mean of the medians with 95% confidence intervals written in italic).

Age class (in years)	**Mean TL (in cm)**		**N**	**Mean rejection rate (± SD)**	**Median t_i estimates after rejection sampling procedure (in days)**		
	♀	♂			**min**	**mean**	**max**
]1;2]	89	85	13	0.15 ± 0.15	93 (*90 – 96*)	171 (*137 – 204*)	332 (*327 – 336*)
]2;3]	104	93	15	0.18 ± 0.16	102 (*99 – 105*)	188 (*156 – 220*)	342 (*338 – 346*)
]3;4]	116	109	10	0.28 ± 0.24	110 (*107 – 113*)	224 (*169 – 279*)	372 (*368 – 376*)
]4;5]	126	119	17	0.40 ± 0.19	108 (*105 – 111*)	280 (*248 – 312*)	353 (*349 – 357*)
]5;6]	137	136	12	0.39 ± 0.24	137 (*133 – 140*)	274 (*229 – 320*)	392 (*388 – 396*)
]6;7]	152	151	9	0.39 ± 0.22	198 (*194 – 202*)	280 (*234 – 326*)	436 (*431 – 440*)
]7;8]	167	166	11	0.43 ± 0.21	217 (*213 – 221*)	294 (*258 – 330*)	447 (*443 – 452*)
Global	**127**	**119**	**87**	**0.31 ± 0.22**	**93 (*90 – 96*)**	**242 (*227 – 258*)**	**447 (*443 – 452*)**

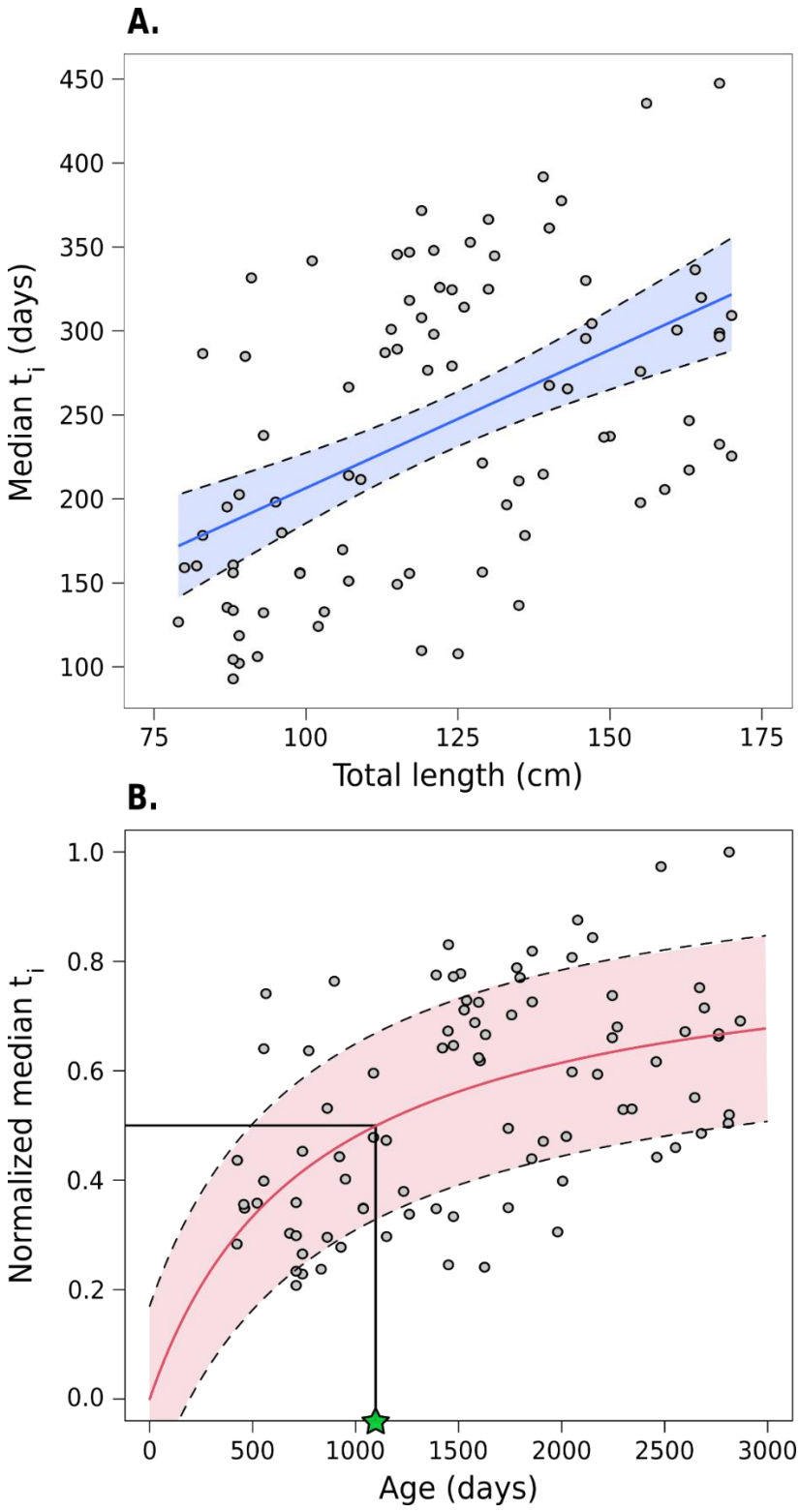

Figure 5-5 – (A.) Median time-since-immigration in the offshore habitat (t_i) in Δ_t smooth hammerhead sharks. A linear regression (R^2=0.25, F=28.9, p < 0.001) was applied to describe the increase of median t_i with shark total length with associated standard error in blue. (B.) Change in normalized t_i median values as a function of shark age. Michaelis-Menten model constants were a = 0.85 (± 0.10) and b = 784.43 (± 262.07). The red area represents the model standard error. The star icon shows the pivotal point for the determination of $Age_{50\%}$.

5. Discussion

In the Mexican Pacific, time-since-immigration estimates suggest that smooth hammerhead sharks rely on shallow water prey in coastal food webs for approximately three years following parturition. Optimal foraging theory predicts a tradeoff between movement and resource use to optimize fitness (Pyke, 1984). Foraging in coastal ecosystems might benefit smooth hammerhead shark compared to offshore dietary opportunities. Inshore prey are usually more abundant and lipid-rich (Spitz et al., 2010b), representing an energy gain for the species to fulfill its requirements compared to shark mesopelagic diet in offshore ecosystems (Madigan et al., 2018; Spitz et al., 2012). Extended dietary reliance on coastal habitats could therefore maximize growth and promote larger size at maturity (Gallagher and Klimley, 2018; Sánchez-Hernández et al., 2019). Reliance of smooth hammerhead sharks on coastal waters could be driven by the existence of secondary nurseries inhabited by older sharks. These areas could be distinct from primary nursery areas (i.e., where newborns spend the first months of their lives) but could also overlap spatially (and isotopically) (Chapman et al., 2009; Heupel et al., 2007). In the Mexican Pacific region, smooth hammerhead sharks could therefore either forage on a range of productive systems scattered along the coast (Ibarra-Obando et al., 2001) or could remain highly reliant on their birthing area.

In the Atlantic Ocean, late juveniles (>160 cm TL) inhabit pelagic waters but occasionally exploit coastal ecosystems (Logan et al., 2020; Santos and Coelho, 2018). Similar back and forth movement patterns could probably occur in the northeastern Pacific and explain the Δ^{199}Hg variability observed for juvenile sharks. However, the absence of data on early life stages in the Atlantic prevented the precise estimation of the age or length at ontogenetic shift. In the southwestern Pacific region, a previous study based on commercial fishing records and research trawl surveys estimated that the species inhabit shallow coastal area for about two years (Francis, 2016). Our study therefore suggests that smooth hammerhead sharks may spend more time in coastal habitats than previously thought, at least in the northeastern Pacific region.

The life cycles of most hammerhead shark species are generally poorly known with the exception of scalloped hammerhead sharks (*Sphyrna lewini*) and, to a lesser extent, great hammerhead sharks (*Sphyrna mokarran*) (Gallagher and Klimley, 2018).

These two species are highly sensitive to fishing pressure due to their unique ecological (i.e., slow growth, late sexual maturity, low reproductive rate, relatively low number of offspring), functional (i.e., increase in physiological disturbances following catch resulting in high mortality rates even if the sharks are released post-capture) and behavioral (i.e., schooling, alternation between coastal and pelagic habitats) specificities (Gallagher et al., 2014a, 2014b). The present study suggests that smooth hammerhead sharks share one of these behavioral traits, with long periods of coastal residency increasing vulnerability to fisheries in the Pacific coast of Mexico. The studied region has an important community of artisanal anglers who are responsible for the major part of shark captures in coastal areas (Cartamil et al., 2011; Ramírez-Amaro et al., 2013). This fishing pressure has led to the disappearance of four other hammerhead shark species from the Mexican Pacific (Pérez-Jiménez, 2014). As smooth hammerhead sharks remain heavily fished in the region (Cartamil et al., 2011; Castillo-Geniz and Tovar-Ávila, 2016; Ramírez-Amaro and Galván-Magaña, 2019), limiting their interaction with fishing gears should become a conservation priority to maintain population levels in the future (Gallagher et al., 2014a). Since 2012, the Mexican law forbids shark fishing from May to July to protect elasmobranch reproductive cycles (Diario Oficial de la Federación, 2012). This study suggests that this seasonal time-area closure of core habitat (e.g., inshore nurseries) to fishing boats might not be sufficient for smooth hammerhead sharks relying on coastal habitats for consecutive years and that the creation of coastal marine reserves could be needed to significantly decrease fishing mortality (Gallagher and Klimley, 2018).

Our approach, combining isotope clocks and Hg isotopes, represents promising insights into the development of future management and conservation measures for marine migratory species. Biotelemetry approaches, the main approach to assess species movements so far, can be limited by the temporal duration between tag deployment and data retrieval, cost, and the associated tag burden precluding deployment on small species or early life stages (Hazen et al., 2012; Jepsen et al., 2015). In the framework of ontogenetic habitat shifts, we demonstrate that the combination of mercury stable isotopes and isotopic clock can allow for a rapid estimation of migration timing and habitat use, providing insights for management decisions. This approach is a powerful tool that can be applied to a broad number of predator species with the opportunity to be more systematic than biotelemetry studies

as based on various tissue types routinely sampled in traditional field procedures (Madigan et al., 2020b).

6. Conclusions

When used in an isotopic clocks framework, Hg isotopes allow to evaluate the movement and foraging habitats of top predators during their life cycle. By identifying different degrees of habitat reliance between species, this approach offers promising perspectives in coastal management to target conservation issues. In order for this method to be broadly applied, there is a need for more feeding experiments under controlled conditions to gain data on Hg isotope turnover rates in tissues of marine species. In the Mexican Pacific, smooth hammerhead sharks exhibit unexpected long-term reliance to coastal habitats. This has direct management implications, as hammerhead species are particularly sensitive to coastal fishing pressure in the region.

CHAPTER 6

VARIATION IN THE TROPHIC STRUCTURE OF ELASMOBRANCH ASSEMBLAGES REVEALED BY COMPLEMENTARY MERCURY, NITROGEN AND CARBON STABLE ISOTOPE ANALYSES.

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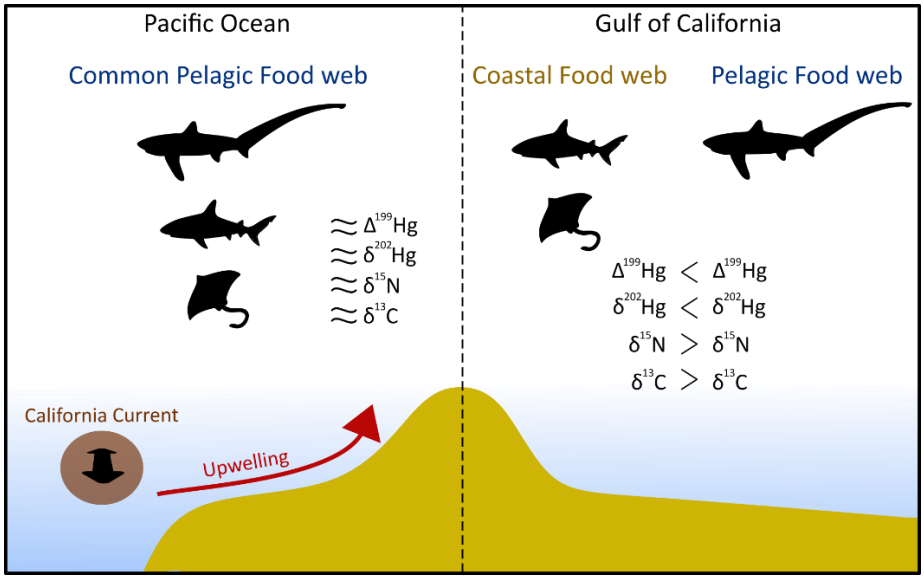
IN PREP.

1. Abstract

The resilience of marine ecosystems facing climate variations and anthropogenic disturbances depends largely on their trophic structure. Marine food webs are dynamic systems including many species with complex trophic interactions. Elasmobranchs occupy meso- to top-predator positions and their interactions with associated communities have mainly been examined from a fisheries perspective, while the mesoscale diversity of their trophic structures remains poorly documented. In this study, we described and compared the trophic structure of elasmobranch assemblages in two systems from the Mexican Pacific and the Gulf of California, including coastal rays and large pelagic sharks, using mercury, nitrogen and carbon stable isotope analyses. Despite being composed of similar species, the trophic structure of the two assemblages differed. On the Pacific side of the Baja California peninsula, all elasmobranchs relied on pelagic basal food sources, probably reflecting the upwelling influence. Overlapping trophic spectra between large apex predators and small mesopredator rays were unraveled through homogeneous $\delta^{13}C$ and $\delta^{15}N$ values and a dominant source of Hg for all co-occurring species. In the Gulf of California, coastal rays and small neritic sharks relied on a coastal food web distinct from the pelagic one, as highlighted by the differences in $\delta^{13}C$ and $\delta^{15}N$ patterns. Hg origin also differed between pelagic sharks and coastal rays, the later characterized by low $\Delta^{199}Hg$ and $\delta^{202}Hg$ values probably reflecting a sedimentary origin. This study demonstrates that the trophic structure of elasmobranch assemblages can vary spatially, which may affect their resilience to climate and fishing pressures.



2. Introduction

Global environmental changes, including overfishing (Chavez et al., 2003; Frank et al., 2005; Utne-Palm et al., 2010), are major destabilizing forces that marine food webs have to face worldwide (Tunney et al., 2014; Walther et al., 2002). The resilience of marine ecosystems to such pressures partly depends on their trophic structure, which can be defined as the biodiversity, network of interactions and distribution of biomass across trophic levels. Resilience has been mainly linked to biodiversity, as it influences the potential for redundant species to compensate for taxa losses (Loreau and de Mazancourt, 2013; Peterson et al., 1998). However, food webs are shaped by the balance between biomass-related top-down and bottom-up controls, and trophic interactions play a pivotal role in marine ecosystem resilience (Rooney et al., 2008).

The strength of top-down and bottom-up controls within marine food webs fluctuates over time and space, resulting in a variety of community structure and dynamics (Baum and Worm, 2009; Hunter and Price, 1992). In most upwelling systems, trophic regulation is generally initiated by intermediate trophic levels, like planktivorous fishes, controlling the biomass of their predators via bottom-up linkages and of their prey via top-down processes, in the so-called wasp-waist ecosystems (Cury et al., 2000). Food webs are therefore dynamic structures where consumers diet shifts depend on the environmentally induced range of available resources (Briand and Cohen, 1987; McCann and Rooney, 2009; McMeans et al., 2015). Temporal and spatial variations in current, temperature and oxygen level in pelagic ecosystems, terrestrial organic matter inputs in estuaries, bleaching in coral habitats or sea ice cover in polar regions have been associated to major changes in species compositions, trophic interactions and ultimately food web structures (Hempson et al., 2018; Kortsch et al., 2019; Liu et al., 2020; Michel et al., 2019; Pethybridge et al., 2018a; Shin et al., 2022).

Elasmobranch species nearly cover the entire spectrum of marine food webs with large-bodied carnivorous sharks being apex predators, while small-bodied rays occupy secondary consumers to higher mesopredator positions (Cortés, 1999; Flowers et al., 2021; Heupel et al., 2014). The analysis of elasmobranch assemblages therefore represents a relevant integrative approach to assess the structure and dynamics of marine food webs. Moreover, overfishing is currently driving many elasmobranch populations to near collapse (Dulvy et al., 2021) and their functional role in marine ecosystem is often used as an argument supporting their conservation despite a lack

of clear empirical data. New investigations on their trophic roles and interactions are therefore needed to clearly define the ecological function of elasmobranchs (Jorgensen et al., 2022). This topic has been studied through the prism of anthropogenic stressors (e.g., Baum and Worm, 2009; Ferretti et al., 2010), while naturally occurring spatial variations in trophic structure are still unclear and could influence the potential cascading effects of elasmobranch reduction or complete removal.

Trophic interactions within elasmobranch assemblages have mostly been addressed through the use of dietary tracers such as stable isotopes (Bird et al., 2018; Hussey et al., 2015). Specifically, the combination of $\delta^{13}C$ and $\delta^{15}N$ values represents a proxy for trophic niches, allowing the characterization of species trophic interactions at the scale of communities (Layman et al., 2007). Carbon and nitrogen stable isotopes allow describing habitat use, as isotopic baselines are driven by local environmental conditions (e.g., phytoplankton growth rate, cell sizes, temperature, denitrification), which vary spatially depending on the habitat characteristics and primary producers (Bird et al., 2018; Lorrain et al., 2015). Of particular interest, $\delta^{13}C$ values efficiently discriminate between coastal and pelagic foraging habitats, higher values being reported in coastal primary producers (e.g., algae, macrophytes, seagrasses) compared to pelagic phytoplanktonic species (Fry and Sherr, 1984; Magozzi et al., 2017). While also varying spatially, the most common use of $\delta^{15}N$ is the characterization of trophic levels due to stepwise ^{15}N-enrichment through the food web (Cabana and Rasmussen, 1994; Post, 2002).

Methylmercury (MeHg), the most bioavailable and toxic form of mercury, is mostly assimilated by sharks and rays from dietary sources (Barone et al., 2021; Kim et al., 2016). MeHg is subject to mass-dependent isotope fractionation (expressed as $\delta^{202}Hg$) and mass-independent fractionation of odd-mass (e.g., $\Delta^{199}Hg$) and even-mass (e.g., $\Delta^{200}Hg$) isotopes (Bergquist and Blum, 2007). Mass-independent fractionation of odd-mass isotopes happens during aquatic photochemical reactions, resulting in high $\Delta^{199}Hg$ where light penetration is high, such as in surface and oligotrophic sub-surface waters (Blum et al., 2013; Le Croizier et al., 2020b), while turbid and deep waters, as well as sediments, are characterized by lower $\Delta^{199}Hg$ (Meng et al., 2020; Senn et al., 2010). As $\Delta^{199}Hg$ values are conserved during trophic interactions (Kwon et al., 2016), they allow the foraging habitat of high trophic level consumers to be traced by

distinguishing between species feeding in coastal versus oceanic ecosystems, or at different depths in pelagic environments (Besnard et al., 2021, **Chapter 4**). Photochemical reactions also affect δ^{202}Hg fractionation along with other processes, both abiotic, such as volatilization (Zheng et al., 2007), or biotic, like demethylation (Perrot et al., 2016) and methylation (Janssen et al., 2016). Finally, mass-independent fractionation of even-mass isotopes occurs in the upper atmosphere (Chen et al., 2012) and Δ^{200}Hg values discriminate between atmospheric gaseous Hg(0) and inorganic Hg(II) wet and dry deposition at the ocean-atmosphere interface (Jiskra et al., 2021). As coastal habitats are more prone to indirect Hg(0) inputs via terrestrial runoff, Δ^{200}Hg have been locally used as a coastal to pelagic horizontal dietary tracer (Le Croizier et al., 2022).

In the present study, we combined Hg, N and C isotope analyses to assess the trophic structure of elasmobranch assemblages in two contrasted region in terms of environmental parameters. We aimed to characterize to which extent the coastal and pelagic food webs overlapped and to infer the degree of resource partitioning within predatory assemblages. Such aspects are likely to affect the ecological function of elasmobranch within marine ecosystems, driving the intensity of top-down control on the whole biological community and the vulnerability of these organisms to coastal fisheries or extreme climatic events. For that purpose, we sampled a large diversity of elasmobranch species from the Pacific coast of Baja California Sur (Mexico), a region strongly influenced by upwelling impulses, and compared the trophic structure with a largely similar assemblage from the Gulf of California.

3. Materials and Methods

a. Study area and sample collection

Elasmobranchs were sampled in two different locations of the Baja California peninsula (Mexico). Sharks and rays (n=169 individuals) were fished on the Pacific coast around Bahía Tortugas from 2013 to 2017 and on the western coast of the Gulf of California around Santa Rosalía from 2019 to 2020. Both sites correspond to artisanal fishing camps where sharks and rays were fished using gillnets or longlines. Samples were collected upon fishing boats return. Sex and total length (TL) were recorded for each specimen and a muscle sample extracted from the dorsal region. Samples were kept in vials and transported on ice to the laboratory (Centro Interdisciplinario de Ciencias

Marinas, La Paz, B.C.S., México) where they were stored at -20°C until further treatments. These two areas were selected based on the similarities of their respective elasmobranch assemblages and on the occurrence of upwelling impulses on the Pacific coast (Ibarra-Obando et al., 2001; Zaytsev et al., 2003), while absent from the western coast of the Gulf of California (Figure 6-1).

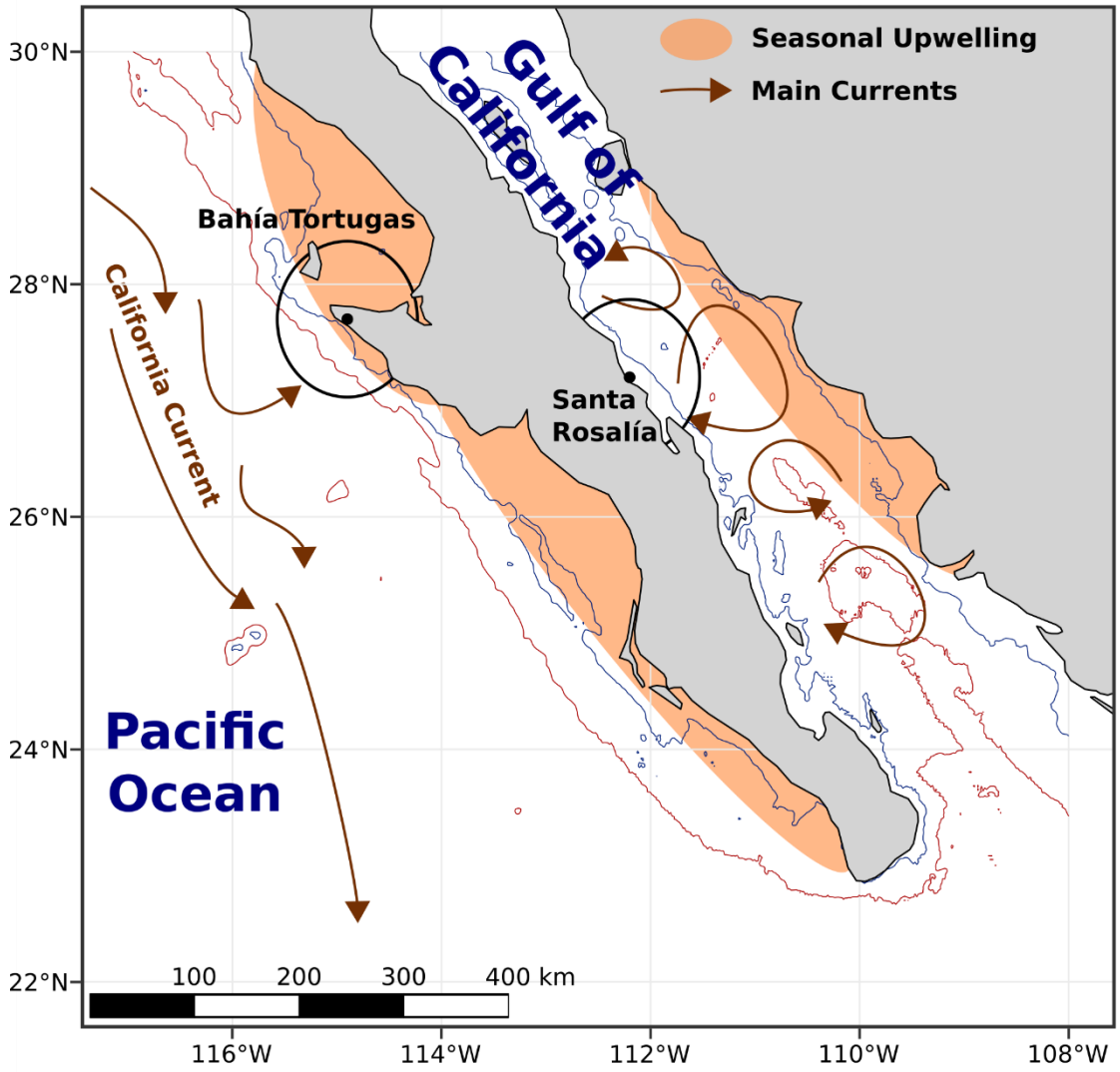


Figure 6-1 – Map of the sampling locations with the 200 m (in blue) and the 2000 m (in red) isobaths represented. Circle areas delineate the areas covered by anglers in the two artisanal fishing camps where the elasmobranch samples came from. The approximate locations of coastal upwelling, as well as the main currents, are represented.

b. Species theoretical trophic habitats

Species were classified as pelagic sharks (i.e., offshore, including oceanic species), neritic sharks or coastal rays owing to their theoretical established habitats in previous

published studies (Appendix 6-1). A total of 10 different species were sampled in Bahía Tortugas (Pacific Ocean) while 9 different species were sampled in Santa Rosalía (Gulf of California). Pelagic sharks from the Pacific Ocean included the common thresher shark, *Alopias vulpinus* (n=8), the shortfin mako shark, *Isurus oxyrinchus* (n=9) and the blue shark, *Prionace glauca* (n=10). Pelagic sharks from Santa Rosalía were the pelagic thresher shark, *Alopias pelagicus* (n=10), the silky shark, *Carcharhinus falciformis* (n=8) and one specimen of shortfin mako shark. Neritic sharks from the Pacific Ocean were the tope shark, *Galeorhinus galeus* (n=8), the grey smooth-hound shark, *Mustelus californicus* (n=10), the brown smooth-hound shark, *Mustelus henlei* (n=8) and the smooth hammerhead shark, *Sphyrna zygaena* (n=10). Neritic sharks from the Gulf of California were the brown smooth-hound shark (n=10), the Pacific sharpnose shark, *Rhizoprionodon longurio* (n=10) and the scalloped hammerhead shark, *Sphyrna lewini* (n=10). The same species of coastal rays were sampled in both locations: the California butterfly ray, *Gymnura marmorata* (n=10 in both sites), the bat ray, *Myliobatis californica* (n=10 in the Pacific Ocean and n=9 in the Gulf of California) and the shovelnose guitarfish, *Pseudobatos productus* (n=9 in the Pacific Ocean and n=10 in the Gulf of California).

c. C and N stable isotope analysis

In elasmobranch muscle, lipids and urea are known to affect $\delta^{13}C$ and $\delta^{15}N$ values (Carlisle et al., 2016; Li et al., 2016b) and were therefore chemically extracted following the approach described by Li et al. (2016). Samples were then freeze-dried and homogenized prior to stable isotope measurements. Between 0.30 and 0.50 mg of muscle powder was weighted into tin cups. The measurements were carried out using a continuous flow on a Thermo Scientific Flash EA 2000 elemental analyzer coupled to a Delta V Plus mass spectrometer at the Pole Spectrométrie Océan (Plouzané, France). Based on international standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$), isotopic ratio (δ) are expressed in per mil (‰) following: $\delta X = ((R_{sample}/R_{standard}) - 1) \times 1000$ where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. We repeatedly measured known international isotopic standards (i.e. IAEA-600 Caffeine, IAEA-CH-6 Sucrose, IAEA-N-1 and IAEA-N-2 Ammonium Sulphate) to ensure correct isotopic measurements throughout the samples run. Repeated measurements of an in-lab Acetanilide certified standards estimated the analytical uncertainties at ± 0.24‰ for $\delta^{13}C$ and ± 0.09‰ for $\delta^{15}N$.

d. Hg stable isotope analysis

Total Hg concentrations were first determined on a 10 to 20 mg aliquot section of dry muscle using a Direct Mercury Analyzer (DMA-80, Milestone, USA) after combustion, gold trapping and atomic absorption spectrophotometry detection, with an analytical detection limit of 0.005 $\mu g \cdot g^{-1}$ dw (dry weight). Repeated measurements of a tuna flesh homogenate (BCR-464, Institute for Reference Materials and Measurements, 5.24 ± 0.10 $\mu g \cdot g^{-1}$ dw) tested the analysis reproducibility and accuracy. BCR-464 measurements (n=18) were reproduced within the confidence limits (i.e., 5.21 ± 0.30 $\mu g \cdot g^{-1}$ dw) validating the accuracy of the analysis.

Elasmobranch muscle Hg concentrations varied between 0.07 and 8.07 $\mu g \cdot g^{-1}$ dw (Appendix 6-6). For samples with Hg concentrations between 0.57 and 8.07 $\mu g \cdot g^{-1}$ dw, an aliquot of 17 to 45 mg of dry muscle was immersed into 3 mL of pure bi-distilled nitric acid (HNO_3) and left at room temperature overnight. Samples were then digested at 85°C for 6 hours in pyrolyzed glass vessels closed by Teflon caps on a hotplate. After the addition of 1 mL of hydrogen peroxide (H_2O_2), digestion continued for another 6 hours. A volume of 100 µL of BrCl was then added to ensure a full conversion of MeHg to inorganic Hg. Finally, the solution was diluted in an inverse aqua regia (3:1 HNO_3:HCl with 20 vol.% MilliQ water) to reach a total Hg concentration of 1 $ng \cdot mL^{-1}$. For samples with Hg concentrations below 0.07 $\mu g \cdot g^{-1}$ dw, the protocol was adapted to reach the same 1 $ng \cdot mL^{-1}$ concentration without saturating the reaction by an excess of biological tissue. For these samples, the analysis relied on an aliquot of 21 to 185 mg of muscle tissue immersed in 1.6 mL of HNO_3 with same quantity of BrCl and dilution in an inverse aqua regia.

Hg isotopic compositions were measured using inductively coupled plasma mass spectrometry (MC−ICP−MS, Thermo Finnigan Neptune) with continuous-flow cold vapor (CV) generation using Sn(II) reduction (CETAC HGX-200) at the Observatoire Midi-Pyrenées (Toulouse, France). Values are expressed in δ notation, reported in per mil (‰) deviation from the SRM-3133 standard (National Institute of Standards and Technology) and determined by sample-standard bracketing according to the following equation: $\delta^{XXX}Hg$ (‰) = $(((^{XXX}Hg/^{198}Hg)_{sample} / (^{XXX}Hg/^{198}Hg)_{standard}) - 1) \times 1000$ where XXX represents Hg isotope different masses. Hg mass-dependent fractionation is expressed as $\delta^{202}Hg$ and mass-independent fractionation is expressed in Δ notation

following: $\Delta^{XXX}Hg$ (‰) = $\delta^{XXX}Hg$ - ($\delta^{202}Hg \times a$) (Bergquist and Blum, 2007), where *a* is 0.252, 0.502, 0.752 and 1.493 for isotopes 199, 200, 201 and 204, respectively.

Along with elasmobranch muscles, blanks and certified materials (i.e., UM-Almadén, ETH-Fluka and BCR-464) were analyzed following the same procedure. Total Hg concentration in the diluted digest mixture was monitored by the ^{202}Hg signal provided by MC-ICP-MS. Hg recovery rate was 89 ± 13% (n=169) for elasmobranch samples, 89 ± 6% (n=10) for UM-Almadén, 96 ± 8% (n=14) for ETH-Fluka and 95 ± 3% (n=10) for BCR-464. One analysis was performed per sample and measured isotope values as well as analytical reproducibility of the certified materials agreed with previously published values (see Appendix 6-2 and details of stable isotope values and total length for each species in Appendix 6-3).

e. Data analysis

Data were first checked for normality (Shapiro–Wilk test) and homogeneity of variances (Bartlett test). When these conditions were met, one-way ANOVA followed by a post-hoc Tukey's HSD test was used to test for statistical differences in isotopic values between elasmobranch species (for $\delta^{13}C$, $\Delta^{200}Hg$, $\delta^{15}N$ in the Pacific Ocean, and $\Delta^{199}Hg/\delta^{202}Hg$ in the Gulf of California). Otherwise, Kruskal-Wallis tests followed by Dunn's post hoc test with Bonferonni adjustment were used (for $\delta^{15}N$ in the Gulf of California and $\Delta^{199}Hg/\delta^{202}Hg$ in the Pacific Ocean). For all statistical tests, a significance threshold of 0.05 was admitted.

Standard ellipse areas encompassing 40% of the data, based on $\Delta^{199}Hg$ and $\delta^{202}Hg$ values, were performed using the SIBER package to quantify the overlap between coastal rays, neritic sharks and pelagic sharks (Jackson et al., 2011). Isotopic overlaps were expressed as a proportion of the non-overlapping area of the two ellipses.

Classification trees were used to evaluate how stable isotopes discriminate between pelagic, neritic and coastal individuals and were built using the rpart package (Therneau et al., 2022). Classification trees were run separately for the Pacific Ocean and Gulf of California assemblages using theoretical individual habitat as the response variable. Predictor variables were first $\delta^{13}C$ and $\delta^{15}N$ and $\delta^{13}C$, $\delta^{15}N$, $\Delta^{199}Hg$ and $\delta^{202}Hg$. Each tree explanatory power was assessed by its accuracy and Kappa statistics, and graphically represented by chord diagrams using the confusion matrix (observed *vs* predicted values) of each tree. Accuracy is calculated as the number of

agreements between theoretical and predicted habitats divided by the total number of predictions. Kappa measures the rate of agreement between theoretical and predicted habitats taking into account the hypothetical probability of random agreement(s). Both values vary between 0 (i.e., no agreement) and 1 (i.e., perfect agreement). Random forest analyses (i.e., numerous iterations of classification trees) were also tested. However, owing to accuracy and Kappa statistics, classification trees were systematically preferred to random forests as they performed better in each site and for all different combination of stable isotope values (Appendix 6-4). All analyses were performed under R programming language (R Core Team, 2021).

4. Results

a. Stable isotope analysis

In the Pacific Ocean, $\delta^{13}C$ values ranged from -18.3‰ to -14.0‰, whereas in the Gulf of California $\delta^{13}C$ values ranged from -16.7‰ to -13.4‰. Patterns of $\delta^{13}C$ values from pelagic shark to coastal rays were different between assemblages from the Pacific Ocean and the Gulf of California (Figure 6-2). In the Pacific Ocean, significant differences existed between species ($F_{90,9}$=16.2, $p < 0.001$) but were mainly explained by the lower values exhibited by *P. glauca* (-17.78 ± 0.38‰) and the higher value of *G. marmorata* (-15.16 ± 0.73‰) as the rest of the species presented equivalent values. In the Gulf of California, $\delta^{13}C$ values significantly differed between many species ($F_{76,7}$=31.3, $p < 0.001$). Pelagic species exhibited similar $\delta^{13}C$ values that were lower than for the rest of the species, while *G. marmorata*, *M. californica* and *S. lewini* presented the highest values (Tukey's HSD test).

A similar pattern was observed for $\delta^{15}N$ values with more homogeneous values in the assemblage from the Pacific Ocean compared to the one in the Gulf of California (Figure 6-2). While values were significantly different ($F_{90,9}$=16.4, $p < 0.001$), they overlapped between sampled species in the Pacific Ocean. Lowest $\delta^{15}N$ values were observed for *P. glauca* and *M. californica* and highest values for *I. oxyrinchus* and *G. galeus* (Tukey's HSD test). In the Gulf of California, significant differences ($\chi^2_{76,7}$=64.8, $p < 0.001$) highlighted highest values for the neritic *R. longurio* and *S. lewini*. Interestingly, there were no significant differences in $\delta^{15}N$ values between *C. falciformis* and *M. californica* and between *A. pelagicus* and *P. productus* (Dunn's test).

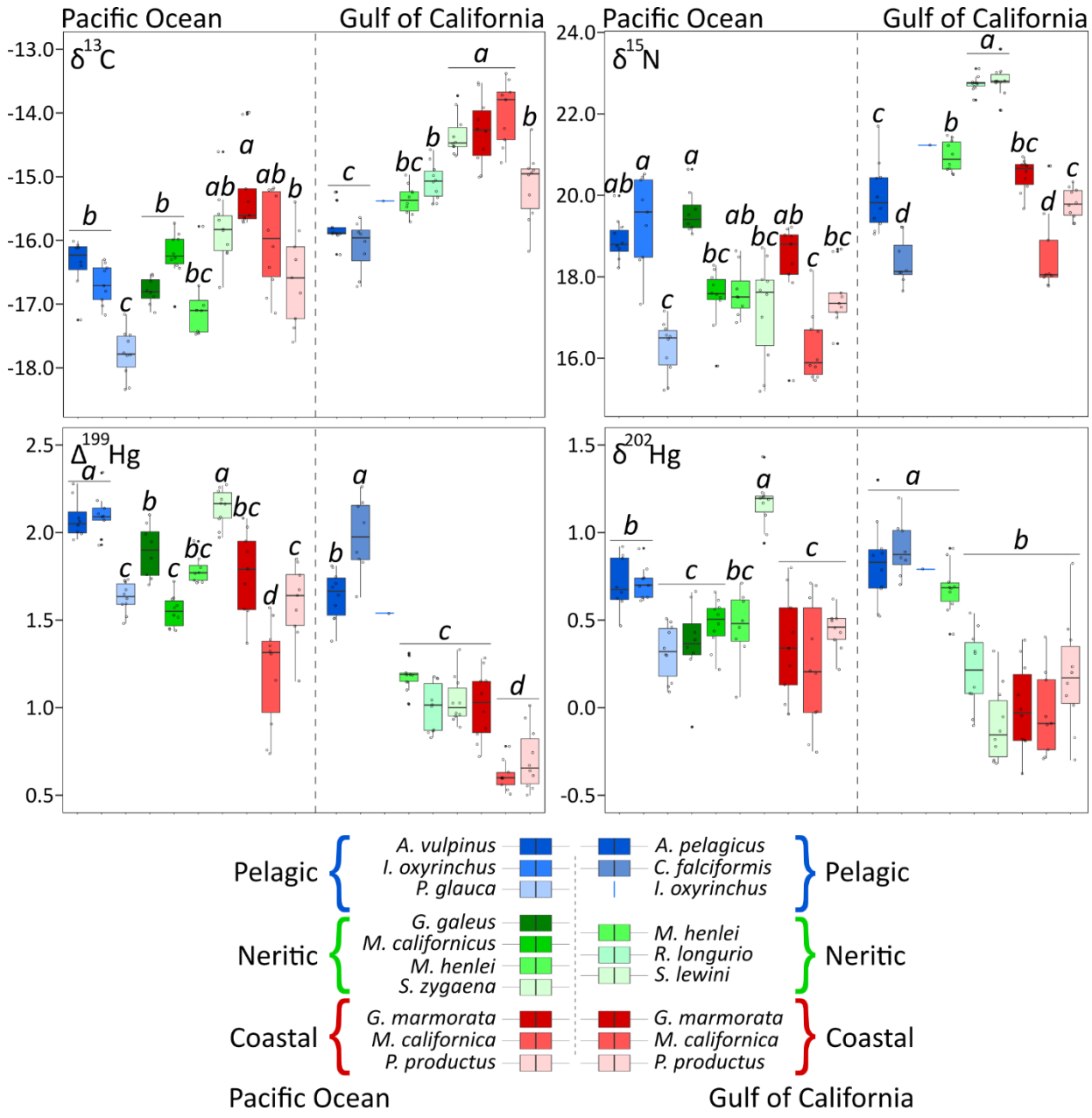


Figure 6-2 – Boxplots of muscle $\delta^{13}C$, $\delta^{15}N$, $\Delta^{199}Hg$ and $\delta^{202}Hg$ values (in ‰) for each sampled species in the Pacific Ocean (on the left) and in the Gulf of California (on the right). Colors correspond to the species theoretical trophic habitat with pelagic sharks in blue, neritic sharks in green and coastal rays in red.

As for $\delta^{13}C$ and $\delta^{15}N$, $\Delta^{199}Hg$ and $\delta^{202}Hg$ values clearly differed between species in the Gulf of California ($F_{76,7}$=80.1, $p < 0.001$ for $\Delta^{199}Hg$ and $F_{76,7}$=28.7, $p < 0.001$ for $\delta^{202}Hg$), while overlapping values between species with different theoretical foraging habitats were observed in the Pacific Ocean despite significant differences ($\chi^2_{90,9}$=71.2, $p <$ 0.001 for $\Delta^{199}Hg$ and $\chi^2_{90,9}$=51.0, $p < 0.001$ for $\delta^{202}Hg$) (Figure 6-2). In the Gulf of California, pelagic species were characterized by higher $\Delta^{199}Hg$ than neritic sharks and *G. marmorata*, while *M. californica* and *P. productus* had the lowest values (Tukey's

HSD test). Two groups were separated by δ^{202}Hg values with the highest values measured in pelagic species and *M. henlei*. Finally, Δ^{200}Hg values did not significantly vary between studied sites or among species theoretical trophic habitats ($F_{168,5}$=0.7, p > 0.05) (Appendix 6-7).

Contrasted patterns between sampling locations were observed in the Δ^{199}Hg-δ^{202}Hg niche space (Figure 6-3). In the Pacific Ocean, pelagic, neritic and coastal individuals had higher overlapping regions in the δ-space compared to the Gulf of California. In the Pacific Ocean, overlap estimates were 20% between neritic sharks and coastal rays, 10% between pelagic sharks and coastal rays and 27% between neritic and pelagic sharks. Furthermore, a limited number of individuals had Δ^{199}Hg values below 1.00‰ (n=3 coastal rays only) or negative δ^{202}Hg values (n=4 coastal ray and n=1 neritic shark). In the Gulf of California, coastal ray and neritic shark values weakly overlapped (8%), exhibiting overall Δ^{199}Hg values between 0.5‰ and 1.33‰ and δ^{202}Hg values between -0.38‰ and 0.91‰. Pelagic sharks in the δ-space had a singular profile with higher Δ^{199}Hg and δ^{202}Hg values (i.e., 1.38‰ ≤ Δ^{199}Hg ≤ 2.26‰ and 0.52‰ ≤ δ^{202}Hg ≤ 1.30‰ and not overlapping with neither of the coastal or neritic specimens).

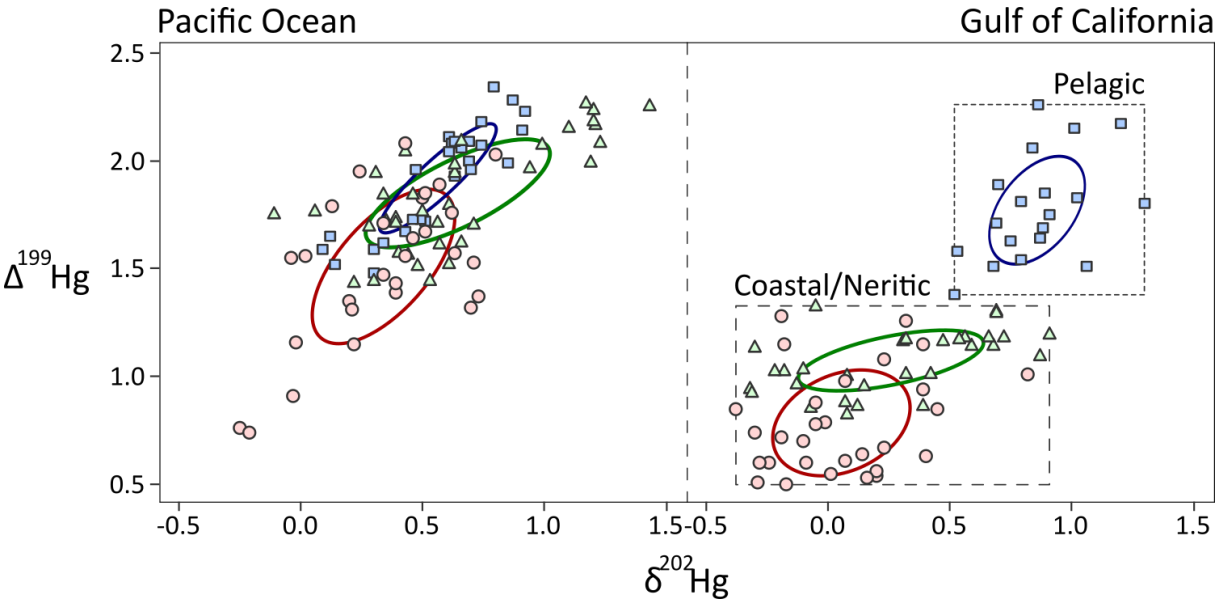


Figure 6-3 – Δ^{199}Hg values (‰) in relation to δ^{202}Hg values (‰) in the muscle of shark and ray species from the Pacific Ocean (on the left) and from the Gulf of California (on the right). Blue square points correspond to pelagic sharks, green triangle points to neritic sharks and red circle points to coastal rays.

b. Classification trees

Classification trees performed differently in their ability to categorize individuals as pelagic, neritic or coastal species based on stable isotope compositions (Figure 6-4). The distinction between foraging habitats was systematically more efficient in the Gulf of California compared to the Pacific Ocean (i.e., accuracy and kappa statistics), regardless of the combination of stable isotope values used. At each site, combining $\delta^{13}C$, $\delta^{15}N$, $\Delta^{199}Hg$ and $\delta^{202}Hg$ values resulted in better foraging habitat characterization compared to $\delta^{13}C$ and $\delta^{15}N$ values alone (details of each classification trees in Appendix 6-8 to 6-10).

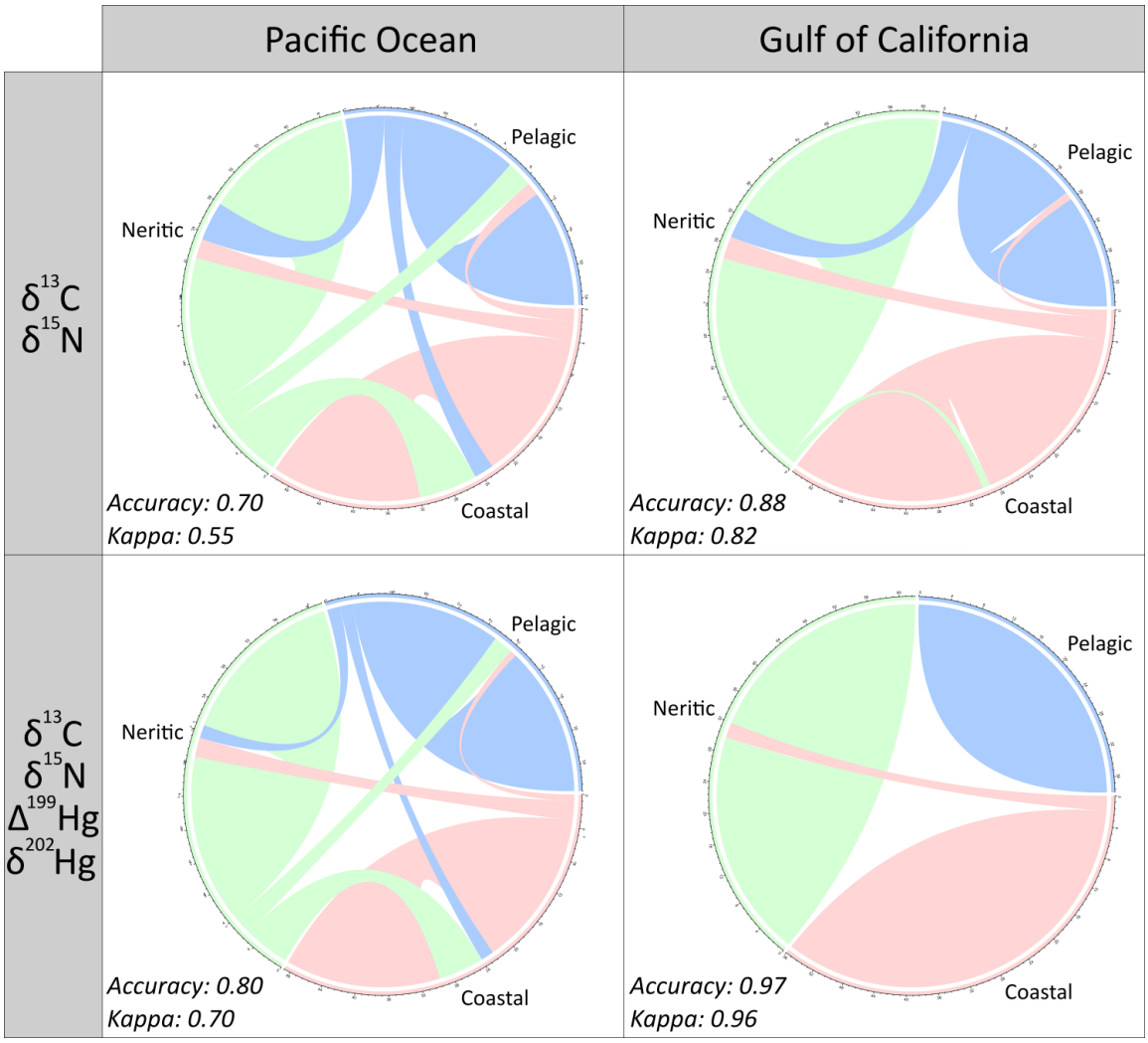


Figure 6-4 – Chord diagrams of the links between theoretical and predicted pelagic (in blue), neritic (in green) and coastal (in red) elasmobranchs established by classification trees. Each line represents an individual classified differently between its theoretical and predicted trophic habitat. Lines thickness is proportionated to the number of individuals concerned.

In the Pacific Ocean, the classification tree based on the analysis of $\delta^{13}C$ and $\delta^{15}N$ values misclassified twenty-seven individuals (~30% of the individuals) including five coastal (*M. californica* and *P. productus*), thirteen neritic (*M. californicus*, *M. henlei* and *S. zygaena*) and nine pelagic (*I. oxyrinchus*, *P. glauca* and *A. vulpinus*). By adding Hg isotopes, this number decreased to eighteen individuals (~20% of the individuals) including four coastal (*P. productus*), ten neritic (*G. galeus*, *M. californicus*, *M. henlei* and *S. zygaena*) and four pelagic (*I. oxyrinchus*, *P. glauca* and *A. vulpinus*).

In the Gulf of California, classification tree based on the analysis of $\delta^{13}C$ and $\delta^{15}N$ values misclassified nine individuals (~12% of the individuals) including four coastal (*P. productus*), one neritic (*M. henlei*) and four pelagic (*C. falciformis*, *I. oxyrinchus* and *A. pelagicus*). Using $\delta^{13}C$, $\delta^{15}N$, $\Delta^{199}Hg$ and $\delta^{202}Hg$ values, only two *P. productus*, theoretically coastal, were classified as neritic.

5. Discussion

a. Separated coastal and pelagic food webs in the Gulf of California

In the Gulf of California, stable isotope analyses differentiated between a benthic coastal food web and a pelagic one. This was explained by the unique composition of rays and neritic sharks, suggesting they foraged upon a different baseline than pelagic species. Broad differences in $\Delta^{199}Hg$ and $\delta^{202}Hg$ values between compartments revealed that MeHg exposure was derived from different sources (Figure 6-2 and 6-3). Neritic and coastal species had significantly lower $\Delta^{199}Hg$ and $\delta^{202}Hg$ values, suggesting MeHg was less influenced by photoreduction before incorporation in tissues compared to pelagic species (Bergquist and Blum, 2007; Blum et al., 2013). Previous reports of coastal to offshore Hg isotopic gradients have generally found lower photochemical degradation in coastal environments, due to the higher turbidity induced by river discharge (Meng et al., 2020; Senn et al., 2010). Except for large riverine inputs in the northern and eastern shores of the Gulf of California, no major terrestrial inputs is likely to induce turbidity increases on the coast of Santa Rosalía. Our interpretation of such low $\Delta^{199}Hg$ (and $\delta^{202}Hg$ values) in coastal/neritic elasmobranchs is that they reflect MeHg produced by microbial activity at the sediment interface that has not been subjected to photochemical degradation prior to its integration in the food web (Gantner et al., 2009; Meng et al., 2020; Yin et al., 2015).

Higher $\Delta^{199}Hg$ values in pelagic sharks implied their MeHg were more affected by photochemical degradation, a characteristic pattern of sharks foraging within offshore food webs (Besnard et al., 2021).

The different origin of MeHg concurs to trophic niches described by traditional C and N stable isotope analysis, and support the fact that pelagic sharks fed on a different baseline than other species. Indeed, $\delta^{13}C$ decreased from coastal to pelagic species (Figure 6-2), which is classically observed across marine biota as a result of the different inorganic carbon sources and subsequent metabolic pathways mobilized among primary producers, with lower $\delta^{13}C$ values in pelagic specimens, deriving C from phytoplankton (Magozzi et al., 2017; Miller et al., 2010). The same difference in baseline foraging grounds was observed in $\delta^{15}N$ values. Under the hypothesis of a common foraging ground with homogeneous baseline, $\delta^{15}N$ would likely reflect differences between trophic levels (Hussey et al., 2011; Post, 2002), whereas, here, numerous mismatches were observed between $\delta^{15}N$ and the known diet of these species (Figure 6-2). Indeed, highest values were observed in mesopredatory species such as *R. longurio* (Alatorre-Ramirez et al., 2013) and early life stages *S. lewini* (**Chapter 3**), while pelagic top-predators had similar $\delta^{15}N$ values as coastal rays, like between the cephalopod-feeding *C. falciformis* and *M. californica* foraging on small mollusks or polychaetes (Bezerra et al., 2021; Bizzarro et al., 2017). This supports the finding that coastal and pelagic food webs were separated in the Gulf of California and suggests that the $\delta^{15}N$ baseline was higher in the coastal food web.

Within the coastal food web, the significant difference between neritic shark and coastal ray $\delta^{15}N$ values revealed a clear-cut difference in their trophic levels, in accordance with their respective documented diet (Bezerra et al., 2021; Bizzarro et al., 2017; Curiel-Godoy et al., 2016; de la Cruz Agüero et al., 1997). This implies limited competition for resource, a conclusion supported by their contrasted $\delta^{13}C$ values. Under such segregation between trophic habitats (both between pelagic and coastal species, and between trophic levels within the coastal food web), competition for dietary resources is likely to be reduced. This was observed in classification trees performed in the Gulf of California that efficiently discriminated between theoretical foraging habitats (Figure 6-4). While incorporation of the isotopic composition of MeHg sources enhanced the discrimination of foraging grounds, $\delta^{13}C$ and $\delta^{15}N$ values alone also showed a good accuracy, with ~88% of individuals correctly classified.

Consequently, whenever baselines are sufficiently discriminating and resource partitioning significant, such as around Santa Rosalía in the Gulf of California, $\delta^{13}C$ and $\delta^{15}N$ efficiently characterize trophic niches.

b. Elasmobranch assemblage supported by pelagic subsidies in the Pacific upwelling system

In the Pacific Ocean, Hg, N and C isotopes revealed that pelagic production was the main source of nutrients and Hg inputs in elasmobranch assemblage. The analysis of Hg isotopes ($\Delta^{199}Hg$ and $\delta^{202}Hg$) revealed no major difference in MeHg exposure source between individuals of different foraging habitats (Figure 6-3). MeHg affected by photochemical degradation in the pelagic environment is characterized by $\Delta^{199}Hg$ values higher than 1.00‰, as observed in teleost fishes (Blum et al., 2013; Sackett et al., 2017), birds (Renedo et al., 2020) and sharks (Besnard et al., 2021; Le Croizier et al., 2022). In the present study, such values were found in pelagic sharks (1.92 ± 0.25‰), as well as in small-bodied neritic sharks (mostly <100 cm TL) (1.84 ± 0.25‰) and coastal rays (1.51 ± 0.35‰) (Figure 6-2) suggesting that all species mainly derived their MeHg from pelagic subsidies.

Pathways to nutrient acquisition also led to more homogeneous $\delta^{15}N$ and $\delta^{13}C$ values compared to species from the Gulf of California (Figure 6-2). Indeed, $\delta^{13}C$ values were globally similar and did not vary between foraging habitats such as observed in the Gulf of California. Homogeneous $\delta^{15}N$ values were also found, except for the case of ^{15}N-depleted *P. glauca* and *M. californica* and ^{15}N-enriched *I. oxyrinchus* and *G. galeus*. Pelagic shark species sampled in the Pacific Ocean are known to be migratory but show limited horizontal movement in the studied region (Madigan et al., 2021; Musyl et al., 2011; Nosal et al., 2019; Sepulveda et al., 2004). It is therefore unlikely that differences in $\delta^{15}N$ baseline could explain the observed values between species due to the limited dispersal capacity of small-bodied sharks and rays. Regardless of metabolic differences that could not have been tested in this study (e.g., diet-tissue discrimination factor), we suggest elasmobranch $\delta^{15}N$ values reflect an integrated signal of foraging at intermediate trophic levels (Hussey et al., 2011; Post, 2002). Sharks, especially the large-bodied pelagic species, can feed on high trophic level prey (predatory fishes, cephalopods), which small coastal rays are unlikely to do (Flowers et al., 2021; Galván-Magaña et al., 2013). Consequently, we suggest that the similar

trophic levels displayed by elasmobranchs sampled in this area reflect average foraging, where large sharks are characterized by a highly omnivorous diet (Madigan et al., 2012) feeding on both high and low trophic levels, while coastal rays feed on intermediate trophic levels. For instance, stomach content analyses carried out on blue sharks, *P. glauca*, revealed a diet mainly composed of the pelagic red crab, *Pleuroncodes planipes*, and secondarily by large mesopelagic cephalopods (Galván-Magaña et al., 2013; Hernández-Aguilar et al., 2016; Maya Meneses et al., 2016). Furthermore, high omnivory in top predator species agrees with the description of the pelagic upwelling system associated to the California Current made by Madigan et al. (2012).

The pelagic signature of elasmobranch MeHg (Δ^{199}Hg and δ^{202}Hg) coupled to homogeneous δ^{13}C and δ^{15}N values between the different species are likely to be a result of the strong upwelling activity observed in the study region (Ibarra-Obando et al., 2001). Indeed, in this area, the transport of pelagic nutrients to coastal habitats is enhanced by the coupling of coastal upwelling (Figure 6-1) and tidal pumping of surface waters (Zaytsev et al., 2003). For instance, the reliance of coastal invertebrates towards pelagic production has been highlighted inside the lagoon of Ojo de Liebre (included in the sampling area) for the suspension-feeding bivalve *Spondylus crassisquama* (Mathieu-Resuge et al., 2019). Upwelling impulses in marine ecosystems are generally shifting δ^{15}N and δ^{13}C baselines, ultimately affecting marine consumers isotopic signatures over different spatial (i.e., distance from the upwelling core area) and temporal (i.e., upwelling seasonality) scales (Chouvelon et al., 2012; Lopez-Lopez et al., 2017). Such confounding effects could be one reason of homogeneous δ^{13}C and δ^{15}N values observed for elasmobranchs, especially as we measured stable isotopes inside muscle tissues, which provide an integrated signal beyond seasonal variations (Thomas and Crowther, 2015). As a result, classification trees poorly performed in the study region located on the Pacific coast compared to the Gulf of California (Figure 6-4). Rather than a poorly discriminatory power of Hg, N and C stable isotope analyses, we suggest that the observed values reflect local ecological dynamics due to the presence of the upwelling scattering pelagic subsidies from offshore to coastal habitats. This result reinforces the idea that special attention must be paid to local environmental conditions when studying the ecology of marine consumers using stable isotopes. On the other hand, while complementary Hg isotope

analysis offer a better precision in depicting foraging habitats, common MeHg sources between pelagic and coastal species could limit the discriminatory power of such approach.

c. Atmospheric Hg origin, incorporation in the water column and potential biotic fractionation in elasmobranch:

In marine ecosystems, Hg is supplied by atmospheric deposition following two mechanisms: gaseous Hg(0) uptake and wet or dry inorganic Hg(II) deposition (Jiskra et al., 2021). Dissolution of Hg(0) is characterized by slightly negative Δ^{200}Hg values while precipitation and dry deposition of Hg(II) are characterized by positive Δ^{200}Hg values (> 0.10‰) (Enrico et al., 2016). Even if Δ^{200}Hg variation remains small in environmental samples (Blum and Johnson, 2017), values are conserved and are ultimately reflected in the MeHg bioaccumulated by marine biota, allowing the use of Δ^{200}Hg values as a tracer of atmospheric Hg entry points in marine ecosystems (Le Croizier et al., 2022; Masbou et al., 2018). Here, elasmobranch mean Δ^{200}Hg values were 0.04 ±0.05‰ from the Pacific Ocean and 0.05 ±0.04‰ from the Gulf of California, suggesting approximately equal contribution of both deposition pathways in these two contrasted marine ecosystems, as indicated in a recent global analysis of Δ^{200}Hg latitudinal variations in seawater, sediment and marine biota (Jiskra et al., 2021).

Continental ecosystems (i.e., flora and soil) have been suspected to be more prone to Hg(0) dissolution than Hg(II) deposition, leading to lower Δ^{200}Hg values in marine biota foraging in coastal ecosystems where terrestrial inputs can be exacerbated (e.g., terrestrial runoff trough rivers) (Meng et al., 2020; Obrist et al., 2017). However, Δ^{200}Hg values did not significantly changed from coastal to oceanic species with similar values than reported for other shark species in the eastern Pacific region (e.g., 0.06‰ Le Croizier et al., 2022, 0.05‰ Besnard et al., 2021). Homogeneous Δ^{200}Hg in elasmobranchs is likely the result of a common atmospheric origin of Hg in marine ecosystems with no Δ^{200}Hg spatial differences between coastal and offshore species. This hypothesis is supported by both the global low contribution of rivers to the total Hg in the Pacific Ocean (Masbou et al., 2018; Zhang et al., 2014) and the absence of major river-brought terrestrial inputs to marine environments in the studied region (Alvarez-Borrego, 2010; Thunell et al., 1994).

The $\Delta^{199}Hg/\Delta^{201}Hg$ slope (Appendix 6-11) is characteristic of MeHg photochemical transformation in marine environments prior to incorporation in the food webs (Bergquist and Blum, 2007). Two photoreduction reactions result in different $\Delta^{199}Hg/\Delta^{201}Hg$ ratios: Hg(II) photoreduction to Hg(0) with a ratio of 1.00 (±0.02, 2 SE) and the photodegradation of MeHg to Hg(II) with a ratio of 1.36 (±0.02, 2 SE) (Bergquist and Blum, 2007). In the elasmobranch species sampled from the Pacific Ocean and the Gulf of California, this ratio was 1.26 and 1.30, respectively, suggesting that photodegradation of MeHg is the main mechanism affecting $\Delta^{199}Hg$ in both sites, such as previously reported in the eastern Pacific region (Blum et al., 2013; Le Croizier et al., 2022; Sackett et al., 2017).

Photochemical transformation of Hg in the water column leads to both $\Delta^{199}Hg$ and $\delta^{202}Hg$ fractionations, explaining the similar pattern observed at both sites (Figure 6-2) (Bergquist and Blum, 2007; Blum et al., 2013). The smaller differences in $\delta^{202}Hg$ values between pelagic, neritic and coastal elasmobranchs compared to $\Delta^{199}Hg$ could be explained by an effect of metabolic detoxication. Detoxication of Hg in waterbirds and marine mammals has been reported to involve tissue-dependent mechanisms including in-vivo hepatic MeHg demethylation, increasing $\delta^{202}Hg$ values in an Hg pool redistributed to less metabolically active tissues such as muscle (Bolea-Fernandez et al., 2019; Li et al., 2020; Perrot et al., 2016; Poulin et al., 2021). As only $\delta^{202}Hg$ values are affected by biotic processes, high muscle $\delta^{202}Hg$ values and a $\Delta^{199}Hg/\delta^{202}Hg$ slope equal to 0 are expected following Hg detoxification (e.g., Li et al., 2020). Such a pattern has been observed in different shark species (Besnard et al., 2021; Le Croizier et al., 2022, 2020b). Besides, fish muscle $\Delta^{199}Hg/\delta^{202}Hg$ slope was 0.96 (Sackett et al., 2017), 1.50 or 1.77 (Madigan et al., 2018) in species which supposedly do not undergo demethylation. For the species analyzed in this study, $\Delta^{199}Hg$ and $\delta^{202}Hg$ values were mostly not significantly correlated with putative slopes varying between 0.01 to 1.74, suggesting possible Hg demethylation even for some small-bodied sharks and rays (Appendix 6-5).

6. Conclusions on ecosystem resilience

Based on the complementarity between Hg, N and C stable isotope analyses, this study shows that the trophic structure of elasmobranch assemblages can spatially differ. Even if not directly tested here, the strong pelagic signal observed in all individuals of the region of Bahía Tortugas in the Pacific coast is likely the result of

coastal upwelling processes. Trophic interactions are likely to diverge between these two assemblages, implying that the same species would not play the same functional role in both food webs (Hussey et al., 2015). In the Gulf of California, separated pelagic and coastal compartments lead to separate trophic niches, probably reducing dietary competition. In the Pacific Ocean, shark trophic plasticity is leading to omnivory and potentially higher degree of interaction between species. Such foraging habits among sharks could lead to overlapping trophic niches, increasing dietary competition within the assemblage. As sharks are major predators in the ecosystems, such a competition could have important ecological implications for the resilience of marine ecosystems facing fishing pressure and climatic perturbations, either periodic (Pacific Decadal Oscillations, El Niño Southern Oscillations) or chronic (climate change). Despite potential competition, one could argue that the strength of top-down control is expected to be attenuated in the Pacific coast, due to strong trophic connectivity and redundancy through omnivory. Conversely, a more complex trophic structure could imply a mosaic of responses to perturbations that could stabilize the ecosystem against the loss of predatory taxa (Gross et al., 2009; Rooney et al., 2008). In the Gulf of California, due to separate niches, strong cascading effects could therefore be expected following the loss of shark species, decreasing the overall ecosystem resilience. Finally, this study shows the limitation of traditional stable isotope analysis whenever baselines are not sufficiently discriminating, or when resource partitioning not marked enough. Additional compounds such as Hg or S (which will be later incorporated to this study) provide a promising insight in this situation to unravel food web structure and ecological mechanisms at play, with potentially a major influence on the regulation of marine ecosystems resilience.

CHAPTER 7

DISCUSSION AND PERSPECTIVES

Vertical and horizontal dimension of trophic niches, the smooth hammerhead shark life cycle and management perspectives in the Mexican Pacific.

Understanding what drives the limitation of fundamental trophic niches toward realized trophic niches in predators is a major challenge in ecology, as it depends on different mechanisms that occur over different spatial (both horizontal and vertical) and temporal scales. Among these mechanisms, resource partitioning is probably one of the most important ecological drivers underlying the maintenance of species diversity and ecosystem services (Chesson, 2000). Resource partitioning in sharks occurs at many different scales. At the intra-specific level, some shark species tend to separate habitat and resource use between life stages. At the inter-specific level, similar patterns exist between co-occurring species to avoid competitive exclusion forces, a mechanism observed in both shared nurseries and adult habitats. The resulting plasticity in shark realized trophic niche may modify the control top-predators exert on the entire ecosystem via top-down cascading effects. Characterizing highly-complex realized trophic niches in top-predatory shark species is therefore needed to understand such effects and their variability, all the more urgent when considering the alarming rate of declining shark populations worldwide under the effect of overfishing and climate change (Dulvy et al., 2021). In the Mexican Pacific, such considerations are particularly urgent as the region harbors a multitude of artisanal fishing camps, main actors of shark fishing in Mexico, leading the country among the top 10th producers of shark-derived products worldwide. Recent calls for action following observed decreased abundance of shark species have led the Mexican jurisdiction to take decision in prohibiting the catch of some species (e.g., giant manta rays and great white sharks) or the fishing ban from May to July to allow some species to reproduce. However, these efforts may as well be ineffective in the absence of ecological knowledge on local shark populations.

In this context, the first objective was to describe the partitioning of food and habitat across different shark assemblages. This issue was at the center of the scientific questions tackled in this thesis and was transverse to all chapters. Using a combination of trophic tracers adapted to the studied species, resource partitioning was assessed at the intra-specific scale, studying the segregation in resource used and trophic habitat across hammerhead shark juvenile stages both in the Gulf of California (**Chapter 3**) and on the Pacific coast of Baja California Sur (**Chapter 5**). Resource partitioning was also addressed for co-occurring shark species displaying putative similar trophic spectra, as with the case of sympatric juvenile scalloped and smooth

hammerhead sharks in the Gulf of California (**Chapter 3**) or pelagic species in the northeastern Pacific region (**Chapter 4**). Finally, a focus was made on the potential differences in resource partitioning at the scale of the elasmobranch assemblage, from pelagic top-predator shortfin mako sharks to mesopredator coastal rays, by comparing the trophic dynamic of elasmobranch communities of both coasts of Baja California Sur with contrasted environmental and oceanographic dynamics (**Chapter 6**). Another objective of this thesis was to characterize the trophic niches of shark species at different stages of their life, from young juveniles to adults. We were finally able to focus only on the juvenile phases of most species, as we relied on samples obtained in artisanal fishing camps, for which catch composition is dominated by juvenile specimens (Ramírez-Amaro et al., 2013; Saldaña-Ruiz et al., 2017). Still, important ontogenetic shifts in trophic niches were observed in the case of hammerhead sharks (**Chapter 3 and 5**). Owing to the high fishing pressure sharks are facing in the Mexican Pacific, this thesis also seeks to assess the ecological drivers that could increase their vulnerability. This question was mainly targeted by studying the reliance of smooth hammerhead sharks to coastal habitats, highly targeted by fishing activities, before their migration to oceanic regions (**Chapter 5**). From a methodological perspective, different biomarkers were analyzed throughout this document (fatty acid composition, carbon, nitrogen and mercury isotopes, and two studies will be completed by sulfur isotopes). Their insights and complementarity in regards of species ecology and oceanographic conditions is a consideration extending across all studies and will be particularly discussed in the following chapter.

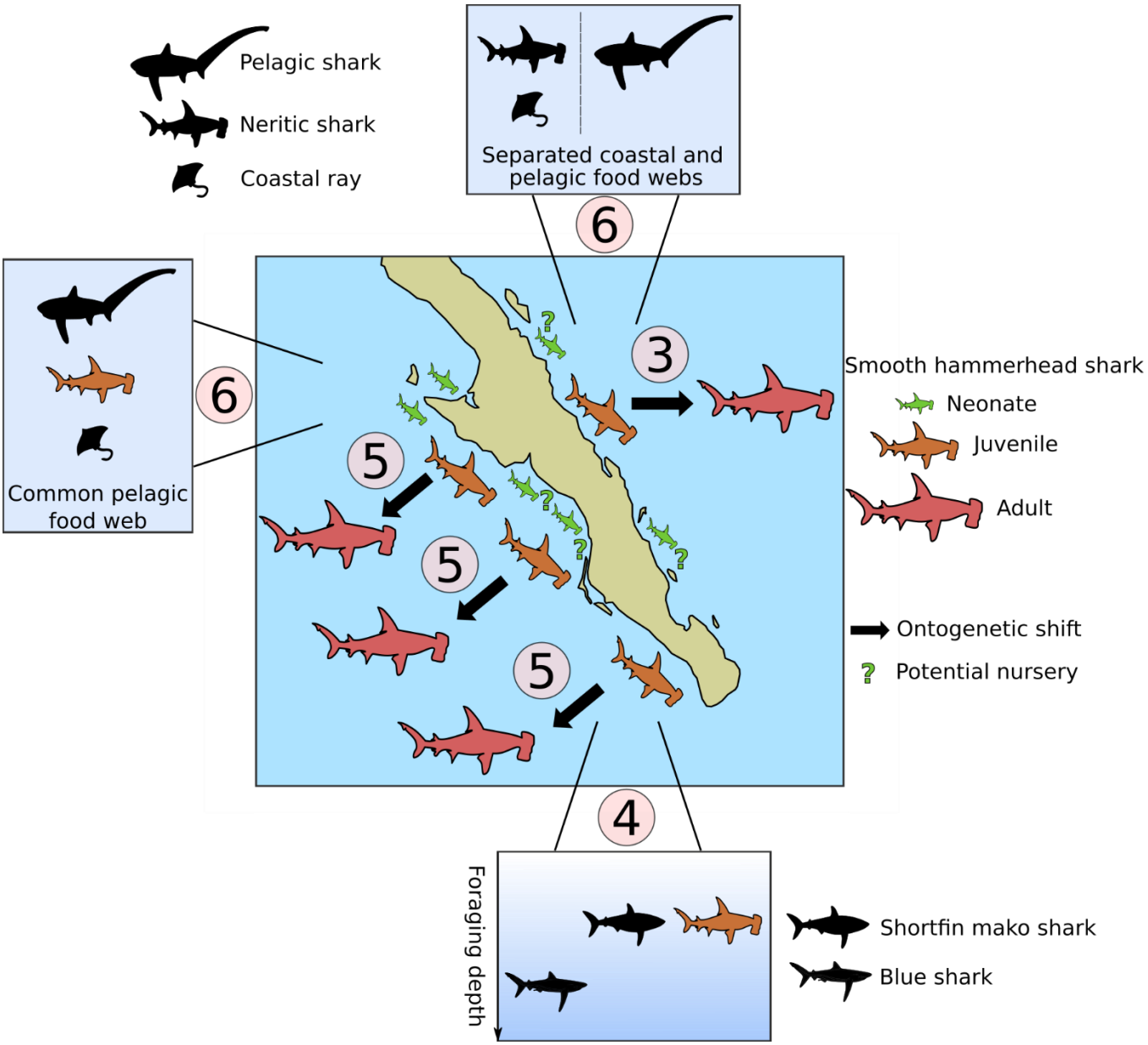


Figure 7-1 – Summary scheme of the four different studies (Chapters 3, 4, 5 and 6) exploring the trophic niches of shark species in Baja California Sur with a central focus on the case of the smooth hammerhead shark.

1. Shark trophic niches

a. Resource partitioning and foraging depth

For hammerhead shark species, the realized trophic niche variability did mainly depend on habitat and resource partitioning between life stages. As demonstrated in **Chapter 3 and 5**, the ontogenetic shift allows for the distinction of separated ecological niches between neonates and juveniles in habitat use (i.e., from coastal areas to offshore and oceanic habitats) and dietary habits (i.e., increasing reliance on

mesopelagic prey). These studies (especially **Chapter 5**) further highlighted that such a switch is gradual. Hammerhead sharks did not move from their nurseries straight to offshore habitats, but did exhibit long-term reliance to coastal ecosystems (i.e., estimated at three years for the smooth hammerhead shark in the Pacific coast). The resulting differences in prey composition between life stages imply that hammerhead sharks play a different trophic role within distinct food webs throughout their life. It would be crucial to take into account such trophic complexity in ecosystem modelling to assess the effects of species removal from overfishing or environmental variations (Heithaus et al., 2008; Hussey et al., 2015). It is also important to note that ontogenetic diet shift is a common trait of mesopredator to top-predator marine fishes and does not necessary occur along with a clear habitat separation between life stages (Sánchez-Hernández et al., 2019). Indeed, ontogenetic diet shifts also result from increasing body length, mouth gap and stomach size, hunting capacities and energetic demands, a commonly observed trait of small mesopredator species (e.g., Besnard et al., 2022). The integration of trophic intra-specific variability within ecosystem models will be crucial to understand the spatial and temporal variability of marine food web structure.

In marine ecosystems, horizontal movements generally come with a change in the extent of vertical niche available, an aspect overlooked in the characterization of predator ecological niches. Addressing depth range changes in sharks at the intra-specific scale is particularly intuitive and relevant in the context of coast-to-offshore movements (as for juvenile hammerhead sharks) but also for oceanic migrations, due to different bathymetric structures, thermal conditions or concentrations of dissolved oxygen within the water column (Queiroz et al., 2010; Rogers et al., 2015; Vaudo et al., 2016). At the inter-specific scale, vertical habitat segregation is also occurring among pelagic predators exhibiting different patterns in depth use (Madigan et al., 2020a). The most likely explanation for deep diving in shark species is foraging on mesopelagic prey (e.g., Braun et al., 2019; Jorgensen et al., 2009). **Chapter 4** highlighted the importance of the vertical dimension for assessing segregation in trophic niches between similar pelagic species spending most of their time in upper water layers and frequently deep diving. Such an importance of foraging depth was until then difficult to assess and was revealed in the present work thanks to Hg isotopes, which hold the power to explore a dimension of the niche of marine predators critically unexplored.

In **Chapter 4 and 5**, Δ^{199}Hg was used as a tracer of foraging depth. In long-term integrating tissues such as muscle (Kwon et al., 2016), Hg isotopes could first help to characterize the mean foraging depth. In marine species, attributing a mean depth for habitat use is particularly challenging. While some studies have used median depth of occurrence (Blum et al., 2013; Choy et al., 2009) or putative habitat preference (Le Bourg et al., 2019), Δ^{199}Hg is the first explicit (i.e., directly results from what is assimilated, not from an associated behavior) and non-ambiguous (δ^{15}N has sometimes been used for this purpose, although no clear global depth-related pattern has been reported to date) proxy to address this crucial dimension in the trophic ecology of pelagic predators. Deep-diving is a trait shared across birds, reptiles, elasmobranchs, teleosts and mammals and has been linked to diverse functions, namely foraging on the mesopelagic layer, avoiding predators, identifying migration pathways (e.g., light, bathymetric structure, magnetic/electrical fields), saving energy, avoiding parasitic infections, thermoregulating or interacting trough social bounds (reviewed in Braun et al., 2022). While the use of biologging sensors equipped with camera and telemetry receivers could help disentangle such processes from one another (e.g., Papastamatiou et al., 2022), Hg isotopes, when correctly applied and under the right assumptions, could offer the opportunity for a first assessment of why a given species exhibit frequent deep diving patterns. Such opportunity for a new vision of marine species movement could be notably enhanced by coupling tracking devices and Hg isotopes, and analyze the mismatch or correspondence between information provided by both approaches. Better than using long-term integrating muscle, such studies could rely on blood samples providing a foraging signal at short time scale, as previously analyzed in birds (Renedo et al., 2021) or mammals (Bolea-Fernandez et al., 2019).

In the context of climate change, Oxygen Minimum Zones (OMZ) are observed at shallower depth and spatially-extending both horizontally and vertically (Stramma et al., 2008). Large pelagic sharks are known to commonly dive at depth to forage on mesopelagic taxa sometimes even beyond OMZ (Coffey et al., 2017; Jorgensen et al., 2009) but still favor normoxic waters (Vedor et al., 2021). As suggested in **Chapter 4**, habitat compression could limit the vertical resource partitioning between co-occurring oceanic species but could also affect hammerhead shark trophic niches owing to the gradually increasing importance of mesopelagic prey in juveniles (**Chapter 3 and 5**).

Inter-specific differences in the physiological capacities to forage in deoxygenized water could influence foraging grounds (both horizontally and vertically) in sharks, with some species able to forage on prey that developed capacities to live outside normoxic water boundaries, like cephalopods (Rosa and Seibel, 2010). As long-term tracking data are limited and most of the time unavailable to trace back changes in diving depth, the study of archived shark muscle samples could enable to potentially retrace such effects and anticipate on future vertical migration of foraging grounds in the next years.

b. Complementarity in trophic tracers

The more co-existing species are ecologically close, the more efficient the combined use of different biomarkers is likely to depict resource partitioning. This was particularly the case for pelagic species that can display similar isotopic niches for some elements, despite having contrasted diets. This was largely due to the lack of discrimination according to $\delta^{13}C$, as a result of carbon originating from phytoplankton for most oceanic food chains. As seen in **Chapter 4** for such co-existing pelagic species, $\delta^{15}N$ could explain some part of the resource partitioning, while ecological drivers of such differences can be difficult to identify unambiguously (i.e., horizontal/vertical baseline variations, trophic level, metabolism). In the end, an overall better picture of the separation of trophic niches was obtained once $\Delta^{199}Hg$ was considered in the analysis. Ultimately, combining carbon and nitrogen isotopes with other isotopic signatures (e.g., $\delta^{34}S$, Skinner et al., 2019), fatty acids (Pethybridge et al., 2010), organic contaminant analysis (Lyons et al., 2019), or with direct observations from stomach content analysis (i.e., to gain a qualitative diet description) or from tracking studies (i.e., to assess differences in vertical or horizontal habitat use) might be necessary to clearly identify resource partitioning between sympatric species. However, most of these methodologies will often overlook the vertical dimension of trophic niches, except for tracking studies, whose drawbacks are discussed in **Chapter 5**. Hg isotopes as a complementary tool for trophic ecology studies therefore offer the opportunity to better highlight the dietary niches and interactions of species inside marine food webs, taking Hg contamination as a proxy for feeding. It is still important to consider that while all of these biomarkers have a dietary origin, their accumulation pattern and metabolic fate can drastically differ. C and N isotopes, as well as fatty acids, are associated to nutrients and can have a very diverse fate within animals' tissues due to the different metabolic pathways they may be involved in. In contrast, Hg is a contaminant that

bears no physiological interest, not homogeneously distributed within potential food sources, whose detoxication is limited in many taxa, and whose fate within animals' tissues is relatively independent from the nutrients along with it was assimilated. Consequently, although both assimilation and metabolization pathways of C, N and fatty acids are relevant to explain their distribution in animals, exposure sources are dominant in explaining the distribution of contaminant-based biomarkers.

While $\Delta^{199}Hg$ is a relevant proxy for foraging depth, it is important to acknowledge that the composition of other stable isotopes varies vertically from the epipelagic layer to deep-sea ecosystems. Indeed, microbial degradation and the recycling of sinking POM can result in heavy isotope enriched values in benthic consumers compared to pelagic ones, notably for $\delta^{15}N$ (Trueman et al., 2014). Such vertically changing $\delta^{15}N$ values have been observed in suspended particle and zooplankton (Hannides et al., 2013) but not systematically in higher order consumers, probably because they forage across broad vertical dimensions, which, associated to limited baseline contrasts and confounding factors, such as trophic fractionation, buffers such signals (Choy et al., 2015). In smooth hammerhead sharks sampled on the Pacific coast of Baja California Sur (i.e., juveniles sampled for **Chapter 5** and additional 10 mature specimens), muscle $\delta^{15}N$ values significantly increased with decreasing $\Delta^{199}Hg$ values (Figure 7-2). Such pattern highlights potential ^{15}N-enriched foraging baseline at depth for the species. However, any definitive conclusion on a potential redundancy in the ecological information provided by both isotopic signals in the northeastern Pacific is difficult. Indeed, $\Delta^{199}Hg$ values is known to be only impacted by photochemical reaction in the water column (Bergquist and Blum, 2007), whereas $\delta^{15}N$ values could result from the interplay between baseline changes (both vertically and horizontally), trophic levels and metabolism.

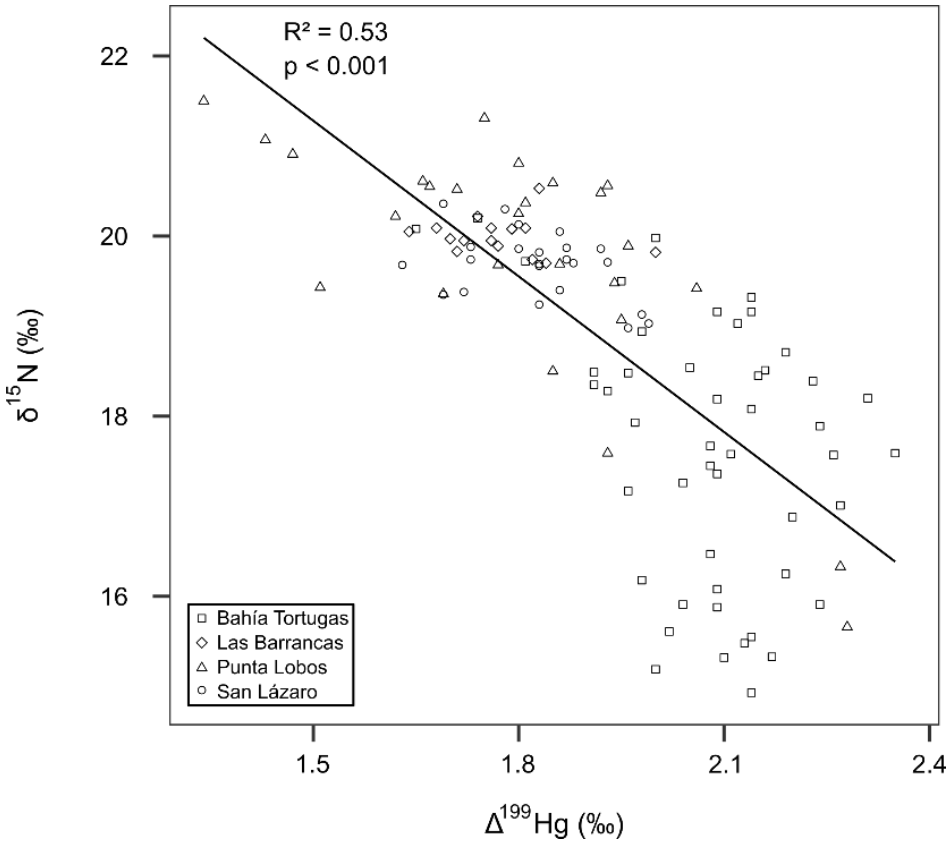


Figure 7-2 – Correlation between $\delta^{15}N$ and $\Delta^{199}Hg$ values in the muscle of juvenile and adult smooth hammerhead sharks sampled on the Pacific coast of Baja California Sur. A linear regression was applied to describe the decrease in $\delta^{15}N$ values as a function of increasing $\Delta^{199}Hg$ values (R^2 and p-value reported in the figure, F=125.2). Point shapes correspond to the different sampling sites.

The complementarity between stable isotope analyses to understand basal biochemical processes affecting nutrient cycles and the functioning of local food web is particularly needed in dynamic ecosystems. This was particularly observed in **Chapter 6** in the case of upwelling system mixing the water column. In the Pacific coast of Baja California Sur, the upwelling system supports a food web on which the whole elasmobranch assemblage relies, resulting in $\delta^{13}C$, $\delta^{15}N$ and $\Delta^{199}Hg$ values poorly discriminating among species (e.g., chord diagram **Chapter 6**).

One of the challenging aspect of studying elasmobranch ecology is the delimitation between their coastal and offshore life stages, as such delimitation can be important for conservation purposes given the actual anthropogenic pressures exercised on nearshore ecosystems (Knip et al., 2010). Such aspects are traditionally assessed from $\delta^{13}C$ but could be also completed in the future from $\Delta^{199}Hg$ values, given the fact that some coastal ecosystems are characterized by Hg entering the food web without

being impacted by strong mass-independent fractionation of odd-mass Hg isotope (such as in the Gulf of California, **Chapter 6**). We sought to investigate coastal to offshore isotopic patterns with $\delta^{34}S$ signatures and compare the outcomes with both $\delta^{13}C$ values and $\Delta^{199}Hg$ values in **Chapter 3 and 6**. Unfortunately, as a result of late samples acquisition after COVID restrictions, this analysis could not have been achieved in time for being included in this manuscript.

An explanatory approach presented in this document concerned the use of $\Delta^{199}Hg$ values to estimate the migration timing of juvenile smooth hammerhead sharks using isotopic clocks. Such an approach offers promising perspectives, on one hand as ontogenetic diet shifts from coastal shallow water nurseries to pelagic grounds is a common trait in fish species and on the other hand as isotopic clocks are relatively easy to settle (i.e., the methodology used in **Chapter 5** will soon be edited as an R package). The benefits of using $\Delta^{199}Hg$ compared to traditional stable isotopes mainly lies in its sole dependence on baseline effects. An example of such effect was particularly highlighted by the described relationship between $\Delta^{199}Hg$ and $\delta^{15}N$ values (Figure 7-2). In the absence of prey data, using $\delta^{15}N$ in a similar isotopic clock approach would have relied on better-established isotopic turnover rate (Shipley et al., 2021) but observed ontogenetic shift could have been linked to the well-described increasing trophic level with size, and not to vertical or horizontal changes in baseline values. The study of predators movement using stable isotopes often relies on isoscapes (Graham et al., 2010; Trueman and St John Glew, 2019). Isoscapes represent the horizontal variations in baseline stable isotope composition that allow the reconstruction of animal migrations. Considering pelagic ecosystems, existing data suggest that $\Delta^{199}Hg$ values principally vary with foraging depth or with depth of MeHg production. Consequently, although Hg isotopes yielded original information on shark migration at the regional scale (e.g., coastal to offshore movements), traditional stable isotopes remain probably a more efficient approach to investigate animal migration across larger scales.

Overall, the application of Hg isotopes in movement studies and their long-lasting implementation in shark trophic ecology studies remain dependent on future experimental developments. For the isotopic clock approach, we had to rely on the $\Delta^{199}Hg$ turnover rate of the Pacific bluefin tuna in the absence of estimation for shark species. As it has been achieved for $\delta^{13}C$ and $\delta^{15}N$ values (e.g., Hussey et al., 2010;

Kim et al., 2012; Malpica-Cruz et al., 2012), experiments evaluating Hg isotope turnover rates and further confirming the absence of diet-tissue discrimination factors from prey to sharks (Kwon et al., 2016, 2013) are needed. Hg isotopes are likely to reflect the largest dietary Hg intake, which depend on prey Hg concentration and consumption rates. To what extend Hg concentration will affect Hg isotope composition in top-predator species such as sharks with a diversified diet made of epipelagic and mesopelagic prey yet remains also to be tested. Under natural conditions, our studies also call for more investigations on Hg stable isotopes composition of zooplankton across the water column and in prey species exhibiting diel vertical migration. Indeed, shark mesopelagic prey performing such migrations could present similar Δ^{199}Hg signal than epipelagic prey if they were to consistently feed at the surface.

2. Management perspectives in the Mexican Pacific

a. Unraveling the life cycle of smooth hammerhead sharks

Hammerheads are globally highly threatened (Dulvy et al., 2021) and include the smooth hammerhead shark, which is the least known species of the three large hammerhead species (Gallagher and Klimley, 2018). The smooth hammerhead shark was considered in this study as a model species, critically affected by overfishing (Castillo-Geniz and Tovar-Ávila, 2016; Pérez-Jiménez, 2014; Saldaña-Ruiz et al., 2017) and largely data deficient, which impedes the implementation of effective management plans. The case of the smooth hammerhead shark could further be regarded as an illustration of emergent research priorities for shark conservation across marine ecosystems worldwide, where conservation often suffer from a lack of ecological data (Dulvy et al., 2021; Jorgensen et al., 2022). Based on biomarkers analyzed on readily available samples obtained from artisanal fishing camps, **Chapters 3 to 5** provide new elements on the species life cycle in the region, mostly at juvenile stages, and potential inferences on adult habitats could be drawn for the rare large specimens that we were able to sample.

Smooth hammerhead sharks were highly suspected to use nursery areas (Francis, 2016; Santos and Coelho, 2018; Segura-Cobeña et al., 2021). On the Pacific coast of Baja California Sur, samples from young-of-the-year (**Chapter 5**) all came from the fishing camp of Bahía Tortugas, including the region of Bahía Sebastián Vizcaíno. Bahía Sebastián Vizcaíno was already hypothesized as a nursery ground for other

species such as shortfin mako or great white sharks (García-Rodríguez and Sosa-Nishizaki, 2020; Tamburin et al., 2019). The area is characterized by a wide continental shelf covering the entire embayment with shallow waters that expand up to a lagoon ecosystem (Laguna Ojo de Liebre). Neonates and early juveniles of smooth hammerhead sharks were previously reported in the Bay (Castillo-Geniz and Tovar-Ávila, 2016; García-Rodríguez et al., 2021). Bahía Sebastián Vizcaíno and the Laguna Ojo de Liebre could satisfy the major roles of nursery areas for this species, namely the protection from predators (i.e., shallow water with potential utilization of lagoon ecosystems as shelters and co-occurrence of only juvenile size large-bodied sharks) and food availability (García-Rodríguez et al., 2021), even if strict nursery criteria remain to be tested (Heupel et al., 2007).

In the Gulf of California, we found smooth hammerhead sharks at juvenile sizes probably having already left their nurseries (**Chapter 3**). Along the continental coast of the Gulf of California, smooth hammerhead sharks have been found at neonate sizes along the coastline of Sonora (Bizzarro et al., 2009c), while it was not the case in the occidental coast studied in **Chapter 3** (Bizzarro et al., 2009b). These differences in observed ontogenetic stages could therefore result from the use of the continental coast as nurseries and the rest of the Gulf of California as secondary foraging ground for juveniles. Interestingly, the catch of smooth hammerhead sharks was reported in the northern part of the Gulf of California (Figure 7-3), supporting the idea that this epicontinental sea also remains a possible important foraging or nursery ground for the species.

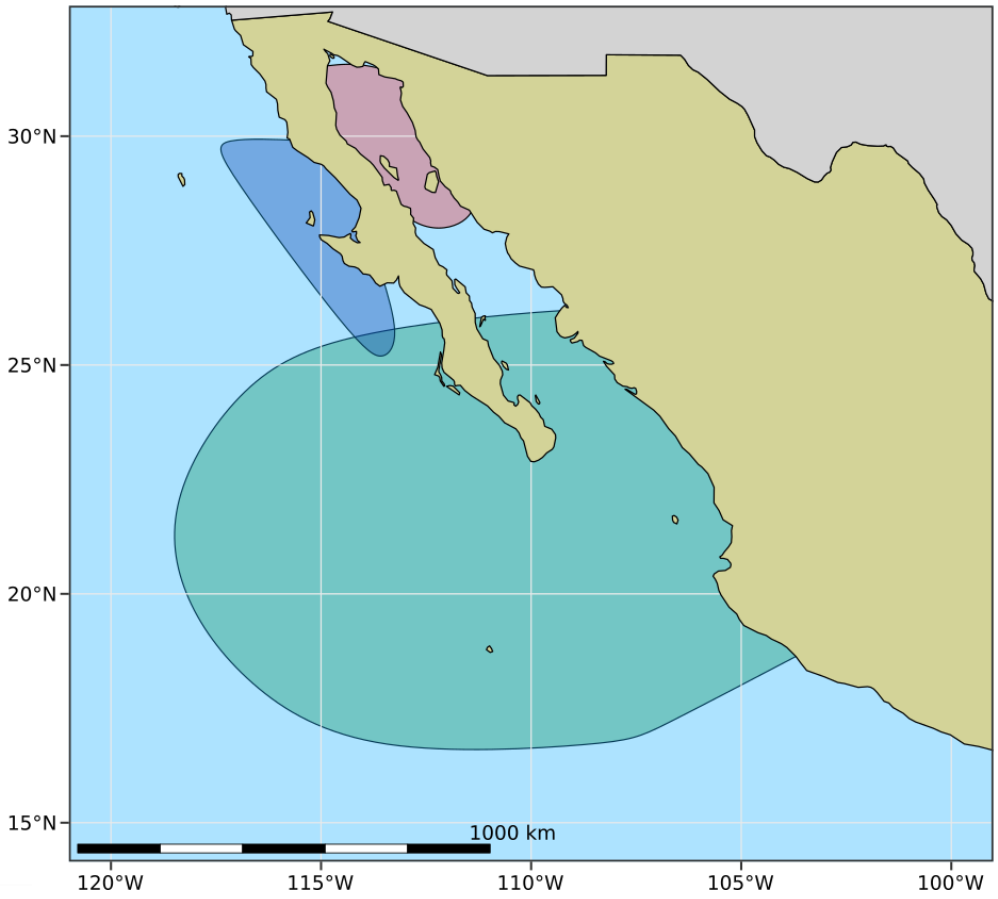


Figure 7-3 – Geographic regions where smooth hammerhead sharks were caught by medium-sized fleets using longlines and nets in the Mexican Pacific based on data from Castillo-Geniz and Tovar-Ávila (2016). Different colors correspond to different fishing fleets and monitored years: in blue the fleet of Ensenada (2006-2014), in green the fleet of Mazatlán (2006-2014) and in red the fleet of Puerto Peñasco (2006-2009).

Using multiple nursery grounds could allow smooth hammerhead sharks to gain benefit from “portfolio effects”. As different nurseries would provide different levels of benefits, using multiple ones would allow a good maintenance of shark biomass through time (Heupel et al., 2018). Both the Pacific coast of Baja California Sur and the Gulf of California offer a mosaic of diversified environments where sharks are known to settle nursery grounds like mangroves, coastal bays, lagoons, estuaries and wetlands, which could also be used by smooth hammerhead sharks (Aburto-Oropeza et al., 2008; Lluch-Cota et al., 2007; Salomón-Aguilar et al., 2009).

In **Chapter 5**, the coastal residency of juvenile smooth hammerhead sharks in the Pacific coast was estimated around three years, exceeding previous estimations for the species based on catch data (e.g., Francis, 2016). The potential use of secondary nurseries by the species fit in the “seascape nurseries” concept developed by

Nagelkerken et al. (2015). Seascape nurseries are defined as a framework of multiple habitat patches functionally connected by mobile organisms of a given species with irregular density hotspots. Such pattern could occur over large spatial scale for the smooth hammerhead shark given its mobility (Logan et al., 2020; Santos and Coelho, 2018). In scalloped hammerhead sharks, females have been hypothesized to leave coastal nursery grounds earlier than males to maximize their growth and reach larger size at maturity (Gallagher and Klimley, 2018). Differences in the use of coastal ecosystems between females and males could not have been directly tested in the isotopic clock approach in **Chapter 5**, as outcomes of the models for females were not robust enough due to lower sample size. Nevertheless, the lower regression slope between $\Delta^{199}Hg$ (or $\delta^{15}N$) and total length in females (Figure 7-4) could suggest that females were not leaving coastal areas before males, but this hypothesis needs to be specifically addressed. At size close to sexual maturity, **Chapter 4** demonstrated that smooth hammerhead sharks relied on mesopelagic prey, although less significantly than for co-occurring blue sharks.

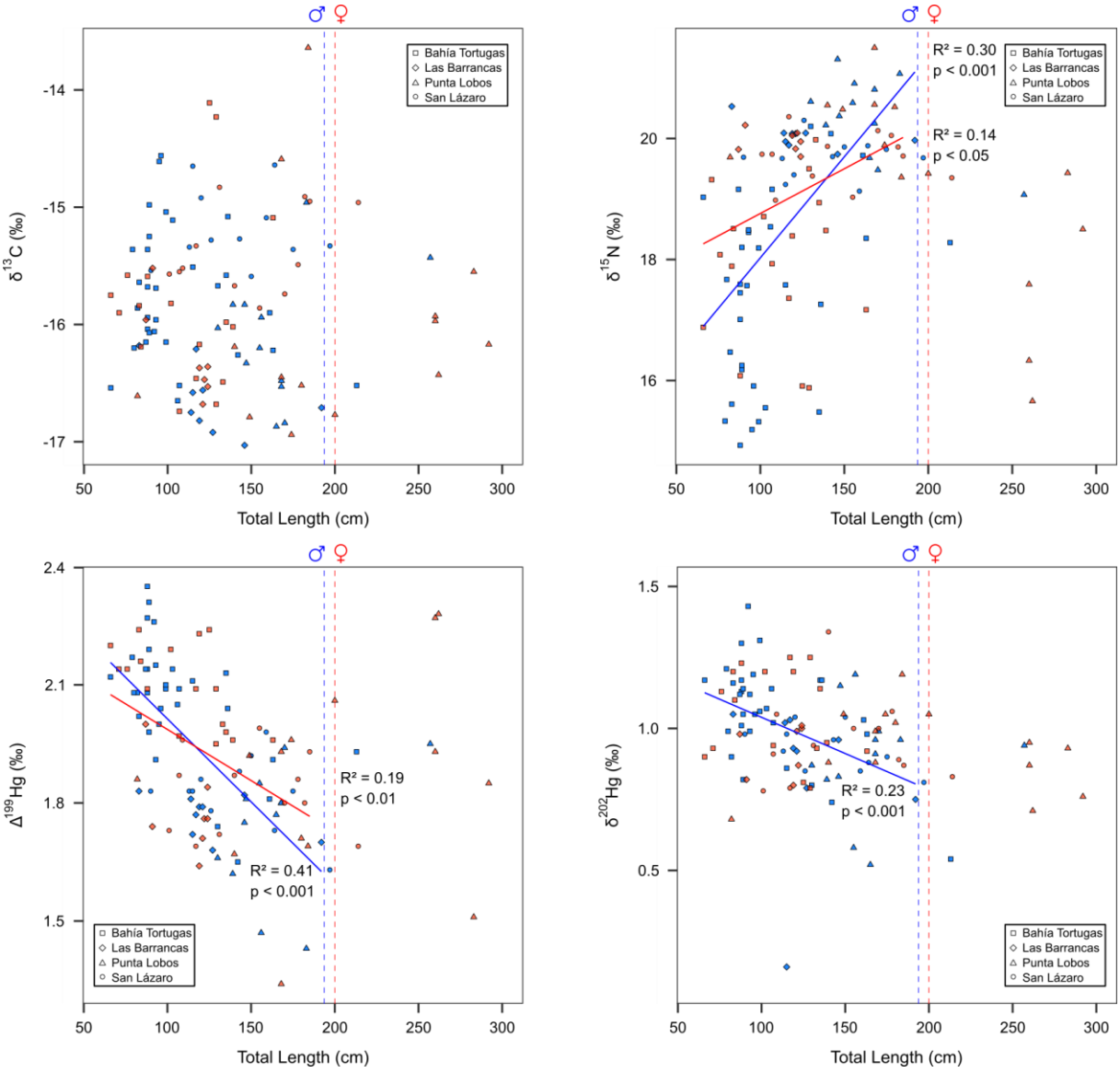


Figure 7-4 – Scatter plots of muscle $\delta^{13}C$, $\delta^{15}N$, $\Delta^{199}Hg$ and $\delta^{202}Hg$ values as a function of smooth hammerhead shark total length on the Pacific coast of Baja California Sur. The different point shapes correspond to the different sampling sites. Females and males are represented in red and blue, respectively. Dashed lines for each sex represents size at maturity ($L_{50\%}$) owing to previous published data in the studied region (Nava Nava & Márquez-Farías, 2014). For each sex, linear regressions were applied to describe the decrease or increase in isotopic values with shark length in juvenile individuals, with R^2 and p-value reported in the Figure. Regressions were significant for $\delta^{15}N$ (F=6.8 for females and F=25.6 for males), $\Delta^{199}Hg$ (F=10.0 for females and F=41.9 for males) and $\delta^{202}Hg$ for males (F=17.6).

Based on the capture of 10 mature smooth hammerhead sharks (the furthermost right data points in Figure 7-4), some hypotheses can be formulated regarding the trophic niche and movements of adult smooth hammerhead sharks. Most of these large individuals were caught in Punta Lobos, a site with a very specific bathymetry

characterized by the narrowest continental shelf of the southern peninsula of Baja California leading to an abrupt slope where fisherman are fishing with longlines in deeper waters compared to other fishing camps. Higher occurrence of large adults in deeper water is in accordance with the ontogenetic shift described throughout this thesis as well as reports of the catch of large smooth hammerhead sharks in deep oceanic regions (Li et al., 2016 and Figure 7-3). Interestingly, large smooth hammerhead sharks had highly variable Δ^{199}Hg values with some females presenting unexpected high values, similar to the ones of neonates sampled in shallow coastal areas (Figure 7-4). Such values could correspond to the comeback of females around parturition within (or close to) coastal nursery grounds. Indeed, previous data on the genetic structure of this species in the northeastern Pacific suggested that females were characterized by natal philopatry, preferentially returning to their birthing site for parturition (Félix- López et al., 2019).

There are many parallels between the life cycle of smooth and scalloped hammerhead sharks. The scalloped hammerhead shark also inhabits nursery areas (Bush and Holland, 2002; Duncan and Holland, 2006; Lyons et al., 2020) and undergoes an ontogenetic shift toward offshore regions (Gallagher and Klimley, 2018; Hussey et al., 2011), as suggested in **Chapter 3** based on stable isotopes and fatty acid composition. In the eastern Pacific, movement and connectivity have been established for the scalloped hammerhead shark by tracking devices, allowing the implementation of conservation measures. Moreover, scalloped hammerhead sharks form large schools near oceanic seamounts in the Pacific tropical regions where marine protected areas have been established, in part, for their protection (e.g., Aldana- Moreno et al., 2020; Gallagher and Klimley, 2018). Schooling of similar scales have not yet been observed for the smooth hammerhead shark and its movements have still not been clearly characterized through tracking approaches in the region, providing the implementation of management measure for this species. **Chapter 5** offers what we think is a reasonable ground to establish enhanced protection of coastal habitat for the species. The habitat use of smooth hammerhead sharks in oceanic region of the northeastern Pacific remains unresolved, while it is a key aspect for the conservation of this species.

b. Ecological gap and future directions

As detailed above, both the Pacific coast and the Gulf of California offer a large diversity of potential nurseries for many shark species. These nurseries seem to overlap with fishing activities as artisanal fishing camp catches are dominated by early juvenile and neonate specimens (Ramírez-Amaro et al., 2013; Saldaña-Ruiz et al., 2017). However, an important biomass of early life stages in an area is not sufficient to confirm the presence of a nursery (Heupel et al., 2007). Identifying nursery resides mainly in understanding the benefice of one area compared to another for the recruitment of juveniles into adult population. Therefore, future surveys within and outside suspected nurseries could be conducted with acoustic tagging or capture-recapture approaches to specifically assess the three criteria of shark nursery, which, given the scale of artisanal fishing in coastal habitats and under limited management budget, could become conservation hotspots (Heupel et al., 2018).

Protecting coastal habitats could have cascading beneficial effects to many small-bodied species massively fished in the region and that are known to spend their entire life in coastal ecosystems over the shelf area like *Rhizoprionodon spp.* or *Mustelus spp.* (Ramírez-Amaro et al., 2013; Ramírez-Amaro and Galván-Magaña, 2019; Saldaña-Ruiz et al., 2017). However, for large-bodied shark species using nursery for early life stages with a more pelagic adult phase, the question of where to focus management efforts remains open. For such species, not protecting late juvenile phases has been shown to reverse the beneficial effect of nursery protection (Kinney and Simpfendorfer, 2009). There is a global lack of ecological information on shark late life stages in the region and future research should focus on establishing their habitat use and trophic niche. A first step towards a global management of the area would be to collect more reliable fisheries data, from artisanal to industrial fleets, to gain information on the threats faced by sharks throughout their life cycle and to allow the implementation of effective conservation plans (Galván-Magaña et al., 2019).

The studied region is home to a high diversity of sharks, suggesting the area is particularly profitable in terms of environmental conditions and food supply. Of particular interest, the highly migratory species studied here are known to exhibit high level of fidelity to restricted areas in the northeastern Pacific. This was the case for blue and shortfin mako sharks (Madigan et al., 2021; Nosal et al., 2019). Understanding what environmental variables drive this site fidelity is also a major challenge. By demonstrating the importance of foraging depth in the resource

partitioning between pelagic sharks, **Chapter 4** suggests that the expanding OMZ present all around the coast of Baja California Sur could increase competition among species. **Chapter 6** also shows that the coastal upwelling in the Pacific coast of Baja California Sur was likely to lead to a different trophic structure than in the Gulf of California. Both these features could modify the trophic role and control a single shark species can exercise through space and time. Such effects of environmental variables remain to be specifically addressed in the region. A possible approach would be to establish stable isotope time series with regards to environmental data indices (e.g., strength of the upwelling, OMZ, Pacific oscillation, ENSO) to understand food web architecture and how the removing of sharks could induce top-down cascading effects under different scenarios.

3. Conclusion

The results obtained during this thesis demonstrate the need to further investigate shark trophic niches. We have highlighted the importance of resource partitioning in shaping shark realized trophic niche both at the intra- and at the inter-specific level. This mechanism reduces competitive pressures in juvenile sharks, and appears to be driven by the use of distinct habitats between early life stages and close to sexual maturity individuals in smooth hammerhead sharks. Moreover, sympatric species in pelagic regions might reduce competition by foraging at different depth. Dietary habits are at the basis of the trophic control and cascading effects a predator can have on its entire associated community. Understanding such control is becoming urgent, notably in the Mexican Pacific where sharks are overfished. All the studies conducted here illustrate how trophic biomarkers can fill ecological gaps over multiple scales and the key vision such approaches can provide to resolve trophic niches and ecological controls. Multi-biomarker approaches should be used more consistently in the field of marine predator conservation. Moreover, the development of Hg isotopes offers promising grounds to tackle the future challenges of understanding shark trophic niches evolutions facing anthropogenic global changes, such as the expansion of OMZ. The use of such tracers can be viewed as a preliminary or complementary approach to many different tools, such as nowadays frequently used tracking devices, as they rely on low amount of tissue that can easily be sampled during tagging campaigns, fishery surveys or animal stranding. A key role that mobile predatory species play in the stability of marine food webs reside in their capacity to link distinct

food webs or different energy channels inside a single food web (Rooney et al., 2006). The trophic control exerted by sharks on Baja California Sur marine ecosystems is likely to be preponderant, as they appear to link coastal and pelagic or epipelagic and mesopelagic habitats. However, such effects might be dependent on local environmental forcing. Direct evidences of shark trophic control are still difficult to clearly demonstrate due to the highly dynamic properties of marine ecosystems, yet is frequently used as a keystone argument for shark conservation. Bringing together data from multidisciplinary approaches and integrating them into a global framework of analysis will ultimately help to predict the consequences of the removal of elasmobranch predation effects on the overall ecosystems.

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APPENDICES

RELATED SCIENTIFIC PRODUCTION

Appendix 0-1 – List of scientific production not included in the thesis document

Publications (First author):

Besnard, L., Duchatelet, L., Bird, C. S., Le Croizier, G., Michel, L., Pinte, N., Lepoint, G., Schaal, G., Vieira, R. P., Gonçalves, J. M. S., Martin, U., & Mallefet, J. (2022). Diet consistency but large-scale isotopic variations in a deep-sea shark: The case of the velvet belly lantern shark, Etmopterus spinax, in the northeastern Atlantic region and Mediterranean Sea. Deep Sea Research Part I: Oceanographic Research Papers, 182, 103708. https://doi.org/10.1016/j.dsr.2022.103708. IF = 2.955.

Publications (Co-author):

Le Croizier, G., Lorrain, A., Sonke, J.E., Hoyos-Padilla, E.M., Galván-Magaña, F., Santana-Morales, O., Aquino-Baleytó, M., Becerril-García, E.E., Muntaner-López, G., Ketchum, J., Block, B., Carlisle, A., Jorgensen, S.J., **Besnard, L.**, Jung, A., Schaal, G., Point, D., 2020. The Twilight Zone as a Major Foraging Habitat and Mercury Source for the Great White Shark. Environ. Sci. Technol. https://doi.org/10.1021/acs.est.0c05621. IF=9.028.

Le Croizier, G., Lorrain, A., Sonke, J.E., Jaquemet, S., Schaal, G., Renedo, M., **Besnard, L.**, Cherel, Y., Point, D., 2020. Mercury isotopes as tracers of ecology and metabolism in two sympatric shark species. Environmental Pollution 265, 114931. https://doi.org/10.1016/j.envpol.2020.114931. IF=8.071.

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Conferences (Oral presentation):

European Elasmobranch Association annual conference

Leiden, Netherlands (3rd – 5th of November 2021)

Besnard, L., Lucca, B. M., Shipley, O. N., Le Croizier, G., Sonke, J., Galván-Magaña, F., Kraffe, E., Point, D., Martinez Rincon, R.O., Ketchum, J., Schaal, G. Mercury isotope clocks estimate dispersal timing from natal area in hammerhead shark species.

IsoEcol Interlude 11.5 - Applications of Stable Isotope Techniques to Ecological Studies

Gaming, Austria (Virtual Meeting; 19th – 21st of May 2021)

Besnard, L., Le Croizier, G., Galván-Magaña, F., Point, D., Kraffe, E., Ketchum, J., Martinez Rincon, R.O., Schaal, G. Foraging depth depicts resource partitioning and

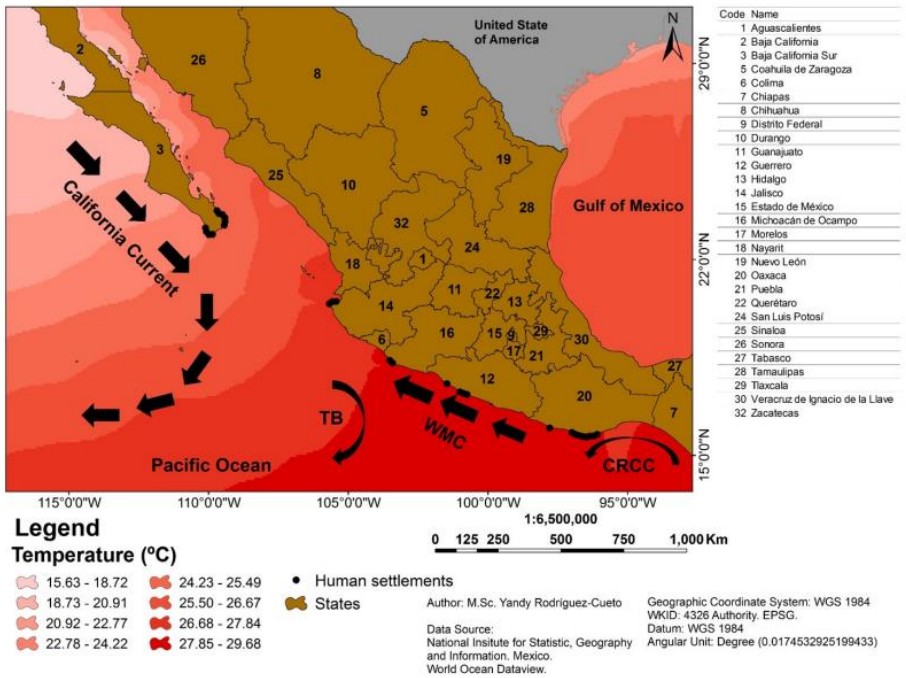
contamination level in a pelagic shark assemblage: Insights from mercury stable isotopes.

Northeast Pacific shark symposium IV (Seattle Aquarium)

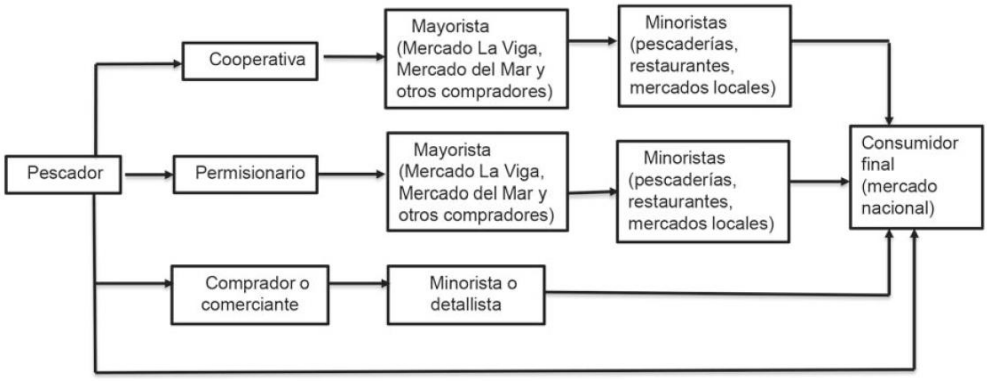
La Paz, Mexico (5th – 7th of March 2020)

Besnard, L., Schaal, G., Le Croizier, G., Galván-Magaña, F., Ketchum, J., Martinez Rincon, R.O., Kraffe E. Using mercury isotopes to characterize the trophic ecology of sympatric shark species in the Pacific coast of Baja California Sur, Mexico.

CHAPTER 1



Appendix 1-1 – Mexican current by (García Huante et al., 2018) "Circulation patterns in the Eastern Tropical Pacific Ocean. Nomenclature: TB (Tehuantepec Bowl), WMC (Western Mexican Current) and CRCC (Costa Rica Coastal Current)".



Appendix 1-2 – Main canals of commercialization of shark meat in the Mexican market (Castillo-Geniz et Tovar-Avila et al., 2016).

CHAPTER 4

Appendix 4-1 – Summary Table (mean ± 2SD) of mercury isotopic ratios measured in certified reference materials (CRM).

References:

(1) Blum, J.D., Popp, B.N., Drazen, J.C., Anela Choy, C., Johnson, M.W., 2013. Methylmercury production below the mixed layer in the North Pacific Ocean. Nat. Geosci. 6, 879–884. https://doi.org/10.1038/ngeo1918

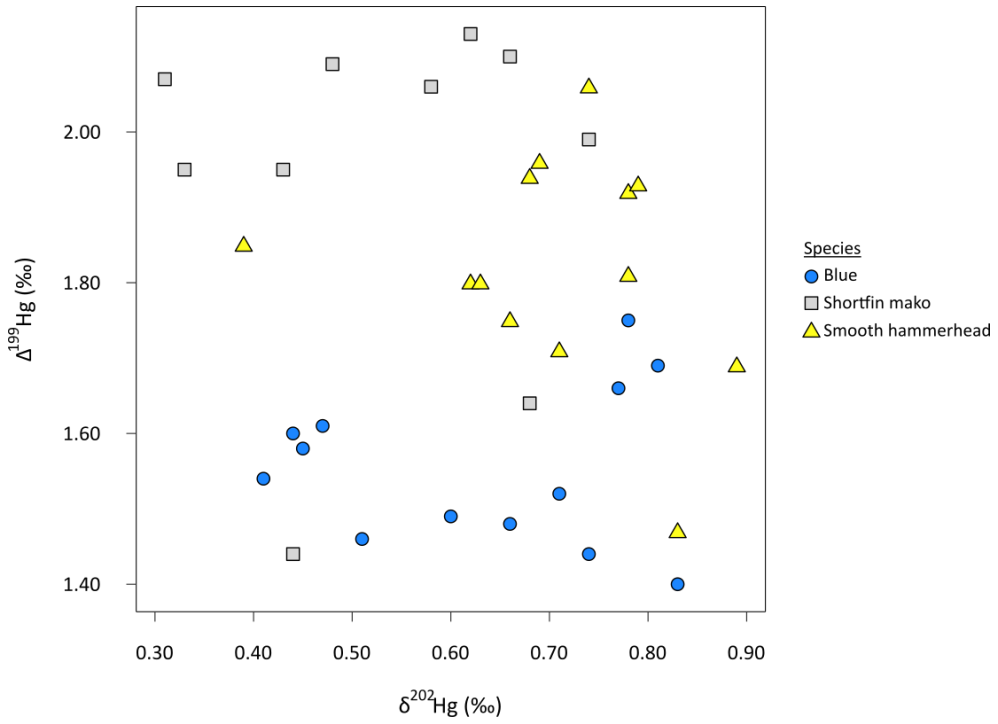
(2) Jiskra, M., Wiederhold, J.G., Skyllberg, U., Kronberg, R.-M., Kretzschmar, R., 2017. Source tracing of natural organic matter bound mercury in boreal forest runoff with mercury stable isotopes. Environ. Sci. Process. Impacts 19, 1235–1248. https://doi.org/10.1039/C7EM00245A

(3) Li, M., Schartup, A.T., Valberg, A.P., Ewald, J.D., Krabbenhoft, D.P., Yin, R., Balcom, P.H., Sunderland, E.M., 2016. Environmental origins of methylmercury accumulated in subarctic estuarine fish indicated by mercury stable isotopes. Environ. Sci. Technol. 50, 11559–11568. https://doi.org/10.1021/acs.est.6b03206

CRM	n	δ^{202}Hg (‰)	Δ^{199}Hg (‰)	Δ^{200}Hg (‰)	Δ^{201}Hg (‰)	Δ^{204}Hg (‰)	Reference
UM-Almadén	4	-0.51 ± 0.06	-0.05 ± 0.04	0.00 ± 0.08	-0.09 ± 0.08	0.00 ± 0.12	This study
	-	-0.57 ± 0.05	-0.02 ± 0.03	0.01 ± 0.03	-0.03 ± 0.03	-0.01 ± 0.05	Blum et al., 2013[1]
ETH-Fluka	4	-1.38 ± 0.06	0.08 ± 0.06	0.03 ± 0.02	0.04 ± 0.10	-0.09 ± 0.18	This study
	-	-1.43 ± 0.12	0.07 ± 0.05	0.01 ± 0.05	0.03 ± 0.07	0.01 ± 0.11	Jiskra et al., 2017[2]
TORT 3	3	-0.02 ± 0.18	0.66 ± 0.02	0.04 ± 0.14	0.50 ± 0.18	-	This study
	-	0.13 ± 0.12	0.69 ± 0.10	-	-	-	Li et al., 2016[3]
BCR 464	4	0.60 ± 0.09	2.27 ± 0.04	0.07 ± 0.08	1.91 ± 0.04	-0.05 ± 0.08	This study
	-	0.69 ± 0.06	2.40 ± 0.06	0.08 ± 0.04	1.97 ± 0.05	-0.10 ± 0.05	Blum et al., 2013[1]

Appendix 4-2 – Parametric t test results comparing females and males for total length (TL), $\delta^{13}C$, $\delta^{15}N$, $\Delta^{199}Hg$, $\Delta^{200}Hg$, $\delta^{202}Hg$ and THg. When normality or equality of variance conditions were not met, its non-parametric equivalent, Wilcoxon test, was applied and noted (*) in the table.

Species	Variable	t student test Wilcoxon test (*)	p-value
Blue shark	TL	15.5 (*)	p > 0.05
	$\delta^{13}C$	28.5 (*)	p > 0.05
	$\delta^{15}N$	2.96	p < 0.05
	$\Delta^{199}Hg$	-0.63	p > 0.05
	$\Delta^{200}Hg$	-0.29	p > 0.05
	$\delta^{202}Hg$	-0.09	p > 0.05
	THg	0.78	p > 0.05
Shortfin mako shark	TL	15 (*)	p > 0.05
	$\delta^{13}C$	9 (*)	p > 0.05
	$\delta^{15}N$	19 (*)	p > 0.05
	$\Delta^{199}Hg$	12 (*)	p > 0.05
	$\Delta^{200}Hg$	0	p > 0.05
	$\delta^{202}Hg$	-1.26	p > 0.05
	THg	-0.74	p > 0.05
Smooth hammerhead shark	TL	-2.17	p > 0.05
	$\delta^{13}C$	28 (*)	p > 0.05
	$\delta^{15}N$	1.55	p > 0.05
	$\Delta^{199}Hg$	-1.27	p > 0.05
	$\Delta^{200}Hg$	-2.65	p < 0.05
	$\delta^{202}Hg$	-1.83	p > 0.05
	THg	-1.66	p > 0.05

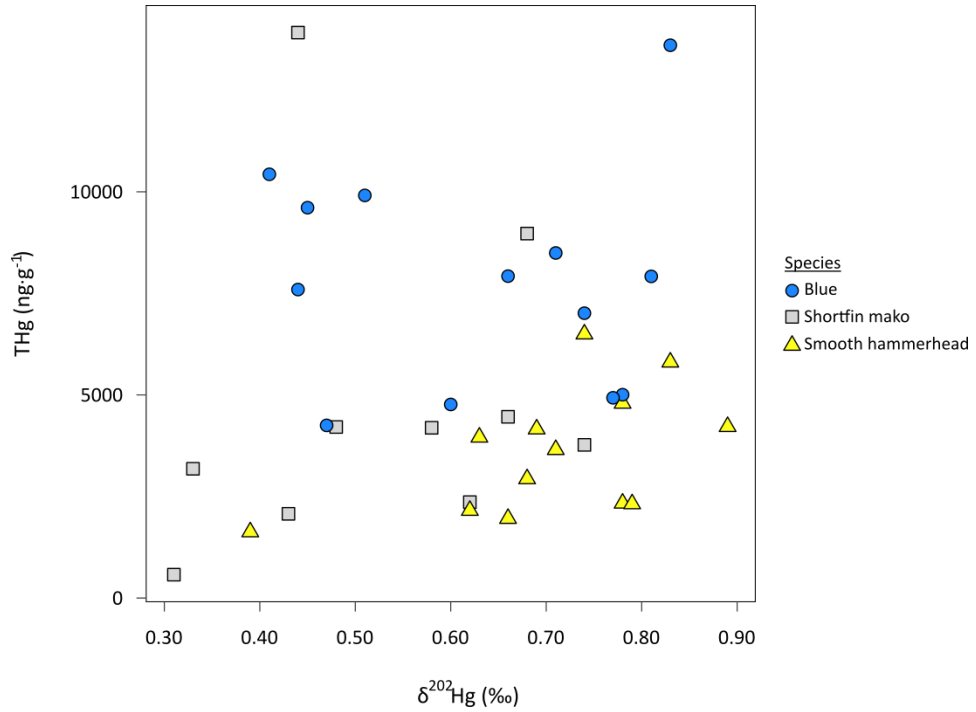


Appendix 4-3 – Relationship between muscle $\Delta^{199}Hg$ and muscle $\delta^{202}Hg$ for all shark species. No significant linear correlations could be established at the inter- or at the intraspecific level between the two isotopic profiles (Pearson, $p > 0.05$).

Appendix 4-4 – Parametric backward stepwise selection of generalized linear models (GLMs) with muscle THg as the response variable (y). Models are ranked by ΔAICc (difference with the best fitting model) and Akaike weights (w_i) with mentions of residual degrees of freedom (R. df), deviance explained and marginal r-squared (R^2_m). The best-fitted model is presented in bold and its coefficients presented in the second table.

Model	R. df	Deviance explained	AICc	ΔAICc	w_i	R^2_m
$y = \alpha + \beta_1*\Delta^{199}Hg + \beta_2*Species + \beta_3*\delta^{202}Hg + \beta_4*\delta^{15}N + \beta_5*Age + \beta_6*\delta^{13}C$	28	60.30	675.33	11.19	0.00	0.60
$y = \alpha + \beta_1*\Delta^{199}Hg + \beta_2*Species + \beta_3*\delta^{202}Hg + \beta_4*\delta^{15}N + \beta_5*Age$	29	60.15	671.88	7.74	0.01	0.60
$y = \alpha + \beta_1*\Delta^{199}Hg + \beta_2*Species + \beta_3*\delta^{202}Hg + \beta_4*\delta^{15}N$	30	59.99	668.70	4.56	0.05	0.60
$y = \alpha + \beta_1*\Delta^{199}Hg + \beta_2*Species + \beta_3*\delta^{202}Hg$	31	59.44	666.08	1.94	0.20	0.59
$y = \alpha + \beta_1*\Delta^{199}Hg + \beta_2*Species$	**32**	**58.35**	**664.14**	**0**	**0.53**	**0.58**
$y = \alpha + \beta_1*\Delta^{199}Hg$	34	49.20	666.04	1.89	0.21	0.49
$y = \alpha$	35	0.00	688.03	23.89	0.00	0.00

	Coefficient	Standard error	t value	p-value
(Intercept)	25320.96	4663.81	5.43	$p < 0.001$
$\Delta^{199}Hg$	-10581.60	2374.61	-4.46	$p < 0.001$
Blue shark	-1058.66	1304.34	-0.81	$p > 0.05$
Smooth hammerhead shark	-2438.34	969.15	-2.52	$p < 0.05$



Appendix 4-5 – Variation of THg concentration with δ^{202}Hg values in the muscle of blue, shortfin mako and smooth hammerhead sharks. No significant correlations could be established at the inter- or at the intraspecific level (Pearson, p>0.05).

Appendix 4-6 – Age estimation (in years) based on previous growth parameters established for blue (Blanco-Parra et al., 2008)[1], shortfin mako (Ribot-Carballal et al., 2005)[2] and smooth hammerhead sharks (Morán Villatoro et al., 2018)[3] in the studied region. Data are means (± standard deviation). Different letters indicate significant differences between species.

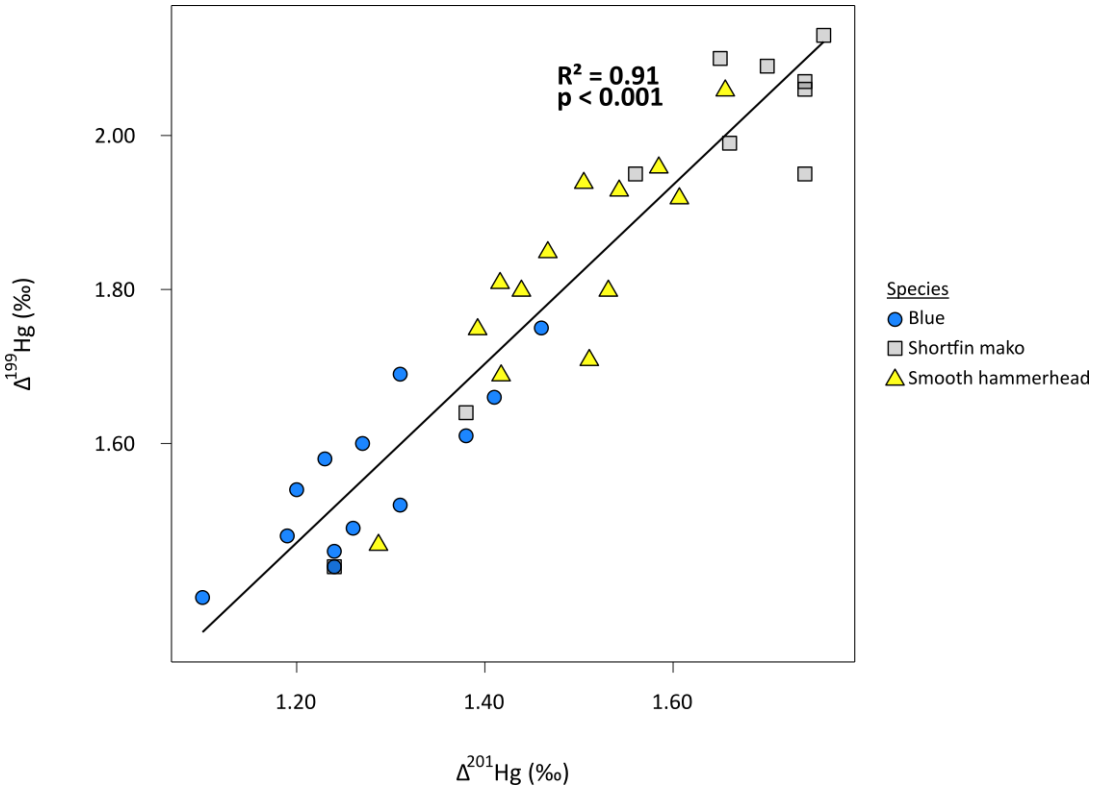
References:

(1) Blanco-Parra, M. del P., Magaña, F.G., Farías, F.M., 2008. Age and growth of the blue shark, Prionace glauca Linnaeus, 1758, in the Northwest coast off Mexico. Rev. Biol. Mar. Oceanogr. 43, 513–520.

(2) Ribot-Carballal, M.C., Galván-Magaña, F., Quiñónez-Velázquez, C., 2005. Age and growth of the shortfin mako shark, Isurus oxyrinchus, from the western coast of Baja California Sur, Mexico. Fish. Res. 76, 14–21. https://doi.org/10.1016/j.fishres.2005.05.004

(3) Morán Villatoro, J.M., Galvan-Magaña, F., Hernández Herrera, A., 2018. Edad y crecimiento del tiburon martillo Sphyrna zygaena (LINNAEUS, 1758) en la costa occidental de baja california sur. (Thesis). Instituto Politécnico Nacional. Centro Interdisciplinario de Ciencias Marinas.

	Blue	**Shortfin mako**	**Smooth hammerhead**
Age estimated	9.6 (± 3.4) ^{A}	4.6 (± 3.6) ^{B}	7.4 (± 1.1) ^{AB}



Appendix 4-7 – Relationship between muscle $\Delta^{199}Hg$ and muscle $\Delta^{201}Hg$ for all shark species. A significant linear correlation was established at the interspecific level between the two isotopic profiles with $\Delta^{199}Hg = 1.16 \times \Delta^{201}Hg + 0.08$.

CHAPTER 5

Appendix 5-1 – Summary (mean ± 2SD) of mercury isotopic ratios measured in certified reference materials (CRM).

CRM	n	δ^{202}Hg (‰)	Δ^{199}Hg (‰)	Δ^{201}Hg (‰)	Reference
UM-Almadén	8	-0.53 ± 0.09	-0.02 ± 0.02	-0.05 ± 0.03	*This study*
	4	-0.51 ± 0.06	-0.05 ± 0.04	-0.09 ± 0.08	Besnard et al., 2021[1]
	13	-0.64 ± 0.16	-0.02 ± 0.08	-	Le Croizier et al., 2020[2]
	-	-0.57 ± 0.05	-0.02 ± 0.03	-0.03 ± 0.03	Blum et al., 2013[3]
ETH-Fluka	8	-1.34 ± 0.03	0.08 ± 0.03	0.02 ± 0.03	*This study*
	4	-1.38 ± 0.06	0.08 ± 0.06	0.04 ± 0.10	Besnard et al., 2021[1]
	12	-1.37 ± 0.18	0.11 ± 0.08	-	Le Croizier et al., 2020[2]
	-	-1.43 ± 0.12	0.07 ± 0.05	0.03 ± 0.07	Jiskra et al., 2017[4]
BCR 464	10	0.81 ± 0.06	2.25 ± 0.04	1.85 ± 0.03	*This study*
	4	0.60 ± 0.09	2.27 ± 0.04	1.91 ± 0.04	Besnard et al., 2021[1]
	4	0.71 ± 0.10	2.28 ± 0.06	-	Le Croizier et al., 2020[2]
	-	0.69 ± 0.06	2.40 ± 0.06	1.97 ± 0.05	Blum et al., 2013[3]

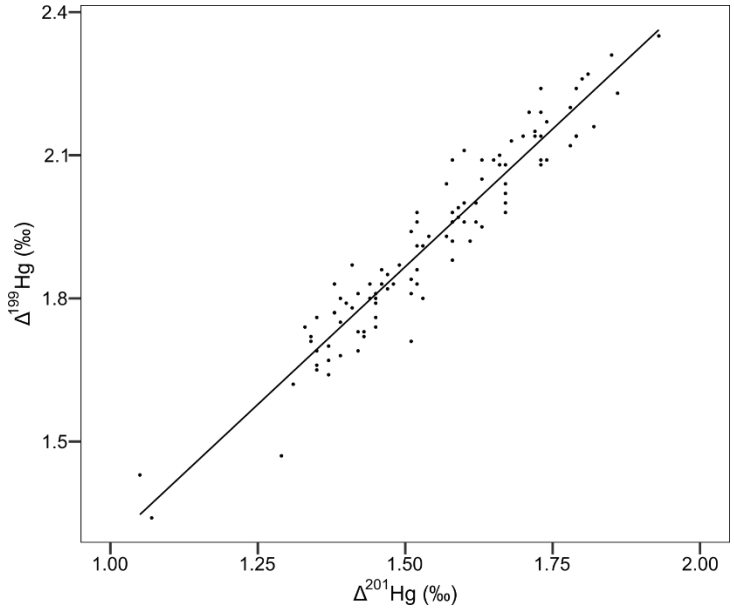
References:

(1) Besnard, L., Le Croizier, G., Galván-Magaña, F., Point, D., Kraffe, E., Ketchum, J., Martinez Rincon, R.O., Schaal, G., 2021. Foraging depth depicts resource partitioning and contamination level in a pelagic shark assemblage: Insights from mercury stable isotopes. Environmental Pollution, 283, 117066. https://doi.org/10.1016/j.envpol.2021.117066

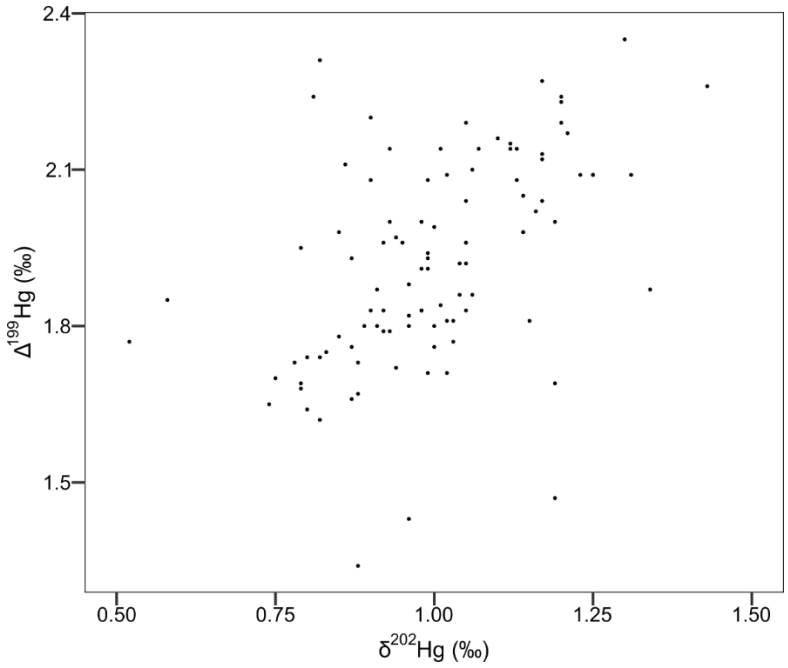
(2) Le Croizier, G., Lorrain, A., Sonke, J. E., Jaquemet, S., Schaal, G., Renedo, M., Besnard, L., Cherel, Y., Point, D., 2020. Mercury isotopes as tracers of ecology and metabolism in two sympatric shark species. Environmental Pollution, 265, 114931, https://doi.org/10.1016/j.envpol.2020.114931

(3) Blum, J.D., Popp, B.N., Drazen, J.C., Anela Choy, C., Johnson, M.W., 2013. Methylmercury production below the mixed layer in the North Pacific Ocean. Nat. Geosci. 6, 879–884. https://doi.org/10.1038/ngeo1918

(4) Jiskra, M., Wiederhold, J.G., Skyllberg, U., Kronberg, R.-M., Kretzschmar, R., 2017. Source tracing of natural organic matter bound mercury in boreal forest runoff with mercury stable isotopes. Environ. Sci. Process. Impacts 19, 1235–1248. https://doi.org/10.1039/C7EM00245A



Appendix 5-2 – Relationship between muscle $\Delta^{199}Hg$ and $\Delta^{201}Hg$ values. A linear regression (R^2=0.92, F=1081, p < 0.001) was applied to describe the increase of $\Delta^{199}Hg$ values with $\Delta^{201}Hg$ values.



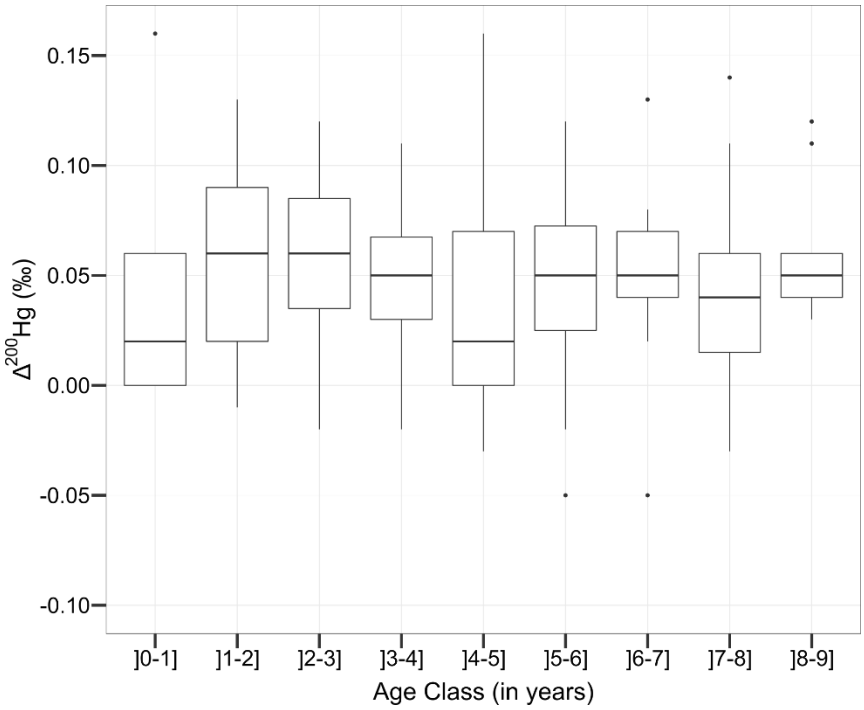
Appendix 5-3 – $\Delta^{199}Hg$ values in relation to $\delta^{202}Hg$ values in the muscle of juvenile smooth hammerhead sharks.

Appendix 5-4 – Equation used to estimate smooth hammerhead shark age based on their total length (Morán-Villatoro et al., 2018[1]). Error estimates for each parameters were not available from the study. TL_t is the total length of the organism at a given time (t), TL_∞ is the theoretical maximum total length of smooth hammerhead sharks in the region and k is the growth coefficient. These parameters were TL_∞=338.5 cm, k=0.18 year^{-1}, ∞=7.8, for females and TL_∞=349.5 cm, k=0.16 year^{-1}, ∞=8.0, for males.

$$TL_t = \frac{TL_\infty}{1 + e^{-k(t-\infty)}}$$

References:

(1) Morán-Villatoro, J.M., Galvan-Magaña, F., Hernández Herrera, A., 2018. Edad y crecimiento del tiburon martillo Sphyrna zygaena (LINNAEUS, 1758) en la costa occidental de baja california sur. Instituto Politécnico Nacional. Centro Interdisciplinario de Ciencias Marinas.



Appendix 5-5 – Boxplots of Δ^{200}Hg values in the muscle of smooth hammerhead sharks. No significant differences were observed between the mean Δ^{200}Hg values of each age class.

Both Δ^{199}Hg and δ^{202}Hg values are affected by photochemical transformation and vary vertically (Blum et al., 2013[1]). However, δ^{202}Hg is also subjected to fractionation via other biogeochemical processes (e.g., volatilization), internal metabolic reactions such as demethylation, and present inconstant discrimination factors from prey to

consumers (Kwon et al., 2016[2]; Le Croizier et al., 2020[3]; Zheng et al., 2007[4]). Due to both trophic and physiological variations, $\delta^{202}Hg$ values were not used in this study. In some regions, coastal areas are more influenced by atmospheric gaseous Hg(0) (with slightly negative $\Delta^{200}Hg$ values) introduced via riverine and terrestrial runoff, while pelagic ecosystems are characterized by equal contribution of Hg(0) and inorganic Hg(II) (positive $\Delta^{200}Hg$ values) delivered by precipitation (Chen et al., 2012[5]; Meng et al., 2020[6]). Given the absence of ontogenetic variability in muscle $\Delta^{200}Hg$ values of smooth hammerhead sharks (Appendix 5-5), isotopic clocks were parametrized using muscle $\Delta^{199}Hg$ values only.

References:

(1) Blum, J.D., Popp, B.N., Drazen, J.C., Anela Choy, C., Johnson, M.W., 2013. Methylmercury production below the mixed layer in the North Pacific Ocean. Nat. Geosci. 6, 879–884. https://doi.org/10.1038/ngeo1918

(2) Kwon, S. Y., Blum, J. D., Madigan, D. J., Block, B. A., & Popp, B. N. (2016). Quantifying mercury isotope dynamics in captive Pacific bluefin tuna (Thunnus orientalis). Elem Sci Anth, 4(0), 000088. https://doi.org/10.12952/journal.elementa.000088

(3) Le Croizier, G., Lorrain, A., Sonke, J. E., Jaquemet, S., Schaal, G., Renedo, M., Besnard, L., Cherel, Y., & Point, D. (2020). Mercury isotopes as tracers of ecology and metabolism in two sympatric shark species. Environmental Pollution, 265, 114931. https://doi.org/10.1016/j.envpol.2020.114931

(4) Zheng, W., Foucher, D., & Hintelmann, H. (2007). Mercury isotope fractionation during volatilization of Hg(0) from solution into the gas phase. Journal of Analytical Atomic Spectrometry, 22(9), 1097–1104. https://doi.org/10.1039/B705677J

(5) Chen, J., Hintelmann, H., Feng, X., & Dimock, B. (2012). Unusual fractionation of both odd and even mercury isotopes in precipitation from Peterborough, ON, Canada. Geochimica et Cosmochimica Acta, 90, 33–46. https://doi.org/10.1016/j.gca.2012.05.005

(6) Meng, M., Sun, R., Liu, H., Yu, B., Yin, Y., Hu, L., Chen, J., Shi, J., & Jiang, G. (2020). Mercury isotope variations within the marine food web of Chinese Bohai Sea: Implications for mercury sources and biogeochemical cycling. Journal of Hazardous Materials, 384, 121379. https://doi.org/10.1016/j.jhazmat.2019.121379

Appendix 5-6 – Coefficients of the ordinary least squares linear regression used to describe the relationship between median t_i and total length.

	Estimate	Standard error	*t* value	Pr(>|t|)
Intercept	41.99	38.15	1.10	0.27
Total length	1.65	0.31	5.38	$p < 0.001$

Appendix 5-7 – Parameters of the nonlinear least square method used to fit the Michaelis-Menten model to the normalized t_i data.

	Estimate	Standard error	*t* value	Pr(>|t|)
a	0.85	0.10	8.80	p < 0.001
b	784.43	262.07	2.99	p < 0.01

Appendix 5-8 – Outputs from the isotopic clock and Michaelis-Menten models separately run between female (n=31) and male (n=56) smooth hammerhead sharks. For median t_i estimates (i.e., mean minimum/maximum of the medians and the overall mean of the medians), 95% confidence intervals are written in italic. Michaelis-Menten model constants and their associated standard error are reported as well as $Age_{50\%}$ estimation. Owning to a and b standard error estimations, $Age_{50\%}$ of males varied between 1017 and 1161 days and $Age_{50\%}$ of females varied between -467 days and 692 days.

	Median t_i estimates after rejection sampling procedure (in days)			**Michaelis-Menten model constants estimation**	**$Age_{50\%}$ (in days)**
	min	**mean**	**max**		
Female	110 (*107 – 113*)	252 (*226 – 279*)	427 (*423 – 431*)	a = 0.65 ± 0.09 b = 138.66 ± 195.70	458
Male	90 (*87 – 93*)	236 (*217 – 256*)	430 (*426 – 435*)	a = 1.05 ± 0.15 b = 1210.99 ± 411.71	1109

CHAPTER 6

Appendix 6-1 – References used to classify elasmobranch species as pelagic, neritic and coastal. When possible, references are adapted to the species range of total length (TL) sampled and to the study area. Species classified as pelagic are all highly mobile and might occasionally forage in neritic ecosystems over continental shelfs and slopes. Some species classified as neritic also present one or numerous pelagic phases in their life cycles like for the tope (G. galeus), the scalloped hammerhead (S. lewini) and the smooth hammerhead (S. zygaena) sharks. These changes in habitats are ontogenetic and occur most of the time around sexual maturity. Here, tope sharks ranged between 78 and 92 cm (TL), scalloped hammerhead sharks between 79 and 98 cm (TL) and smooth hammerhead sharks between 79 and 107 cm (TL) corresponding to juvenile stages in all species. Therefore, we considered them as neritic, foraging between coastal and continental slope habitats.

Species	Habitat	TL (in cm)	References
Alopias pelagicus	Pelagic sharks	200-300	Calle-Morán & Galván-Magaña[1]; Páez-Rosa et al., 2018[2]; Rigby et al., 2019[3]
Alopias vulpinus		254-340	Cartamil et al., 2010[4]; Cortés et al., 2010[5]; Rosas-Luis et al., 2017[6]
Carcharhinus falciformis		167-220	Cabrera-Chávez-Costa et al., 2010[7]; Lopez et al., 2020[8]; Musyl et al., 2011[9]
Isurus oxyrinchus		109-163	Abascal et al., 2011[10]; Musyl et al., 2011[9]; Sepulveda et al., 2004[11]; Vaudo et al., 2016[12]
Prionace glauca		68-135	Madigan et al., 2021[13]; Musyl et al., 2011[9]; Queiroz et al., 2010[14]; Stevens et al., 2010[15]
Galeorhinus galeus	Neritic sharks	78-92	Lucifora et al., 2006[16]; Nosal et al., 2021[17]; Ramírez-Amaro et al., 2013[18]; Walker et al., 2020 [19]
Mustelus californicus		81-110	Espinoza et al., 2011[20]; Freedman et al., 2015[21]; Pérez-Jiménez et al., 2015[22]
Mustelus henlei		52-98	Campos et al., 2009[23]; Pérez-Jiménez et al., 2016[24]; Smith et al., 2009[25]
Rhizoprionodon longurio		96-106	Alatorre-Ramirez et al., 2013[26]; Márquez-Farías et al., 2005[27]; Pollom et al., 2019[28]

Sphyrna lewini		79-98	Estupiñán-Montaño et al., 2021[29]; Hoyos-Padilla et al., 2014[30]; Hussey et al., 2011[31]; Rosende-Pereiro et al., 2018[32]
Sphyrna zygaena		79-107	Diemer et al., 2011[33]; Francis, 2016[34] ; Gallagher and Klimley, 2018[35]; Logan et al., 2020[36]
Gymnura marmorata	Coastal rays	27-78	Pollom et al., 2020[37]
Myliobatis californica		22-170	Bezerra et al., 2021[38]; Murillo-Cisneros et al., 2019[39]
Pseudobatos productus		55-92	Márquez Farías et al., 2007[40]; Murillo-Cisneros et al., 2019[39]

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Appendix 6-2 – Mean (± 2SD) of mercury isotopic ratios measured in certified reference materials (CRM).

CRM	References	δ^{202}Hg (‰)	Δ^{199}Hg (‰)	Δ^{200}Hg (‰)	Δ^{201}Hg (‰)	Δ^{204}Hg (‰)
UM-Almadén	Blum et al., 2013[1]	-0.57 (0.05)	-0.02 (0.03)	0.01 (0.03)	-0.03 (0.03)	-0.01 (0.05)
	This study (*n=10*)	-0.54 (0.11)	-0.01 (0.15)	-0.02 (0.12)	-0.05 (0.19)	-0.03 (0.16)
ETH-Fluka	Jiskra et al., 2017[2]	-1.43 (0.12)	0.07 (0.05)	0.01 (0.05)	0.03 (0.07)	0.01 (0.11)
	This study (*n=14*)	-1.43 (0.20)	0.10 (0.13)	0.04 (0.10)	0.04 (0.10)	-0.05 (0.17)
BCR-464	Blum et al., 2013[1]	0.69 (0.06)	2.40 (0.06)	0.08 (0.04)	1.97 (0.05)	-0.10 (0.05)
	This study (*n=10*)	0.75 (0.10)	2.34 (0.11)	0.08 (0.09)	1.92 (0.14)	-0.08 (0.24)

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Appendix 6-3 – Mean ± standard deviation of stable isotope values in ‰ for each sampled species at each location. Number of sampled individuals (N) is presented as well as total length (TL) measured in cm.

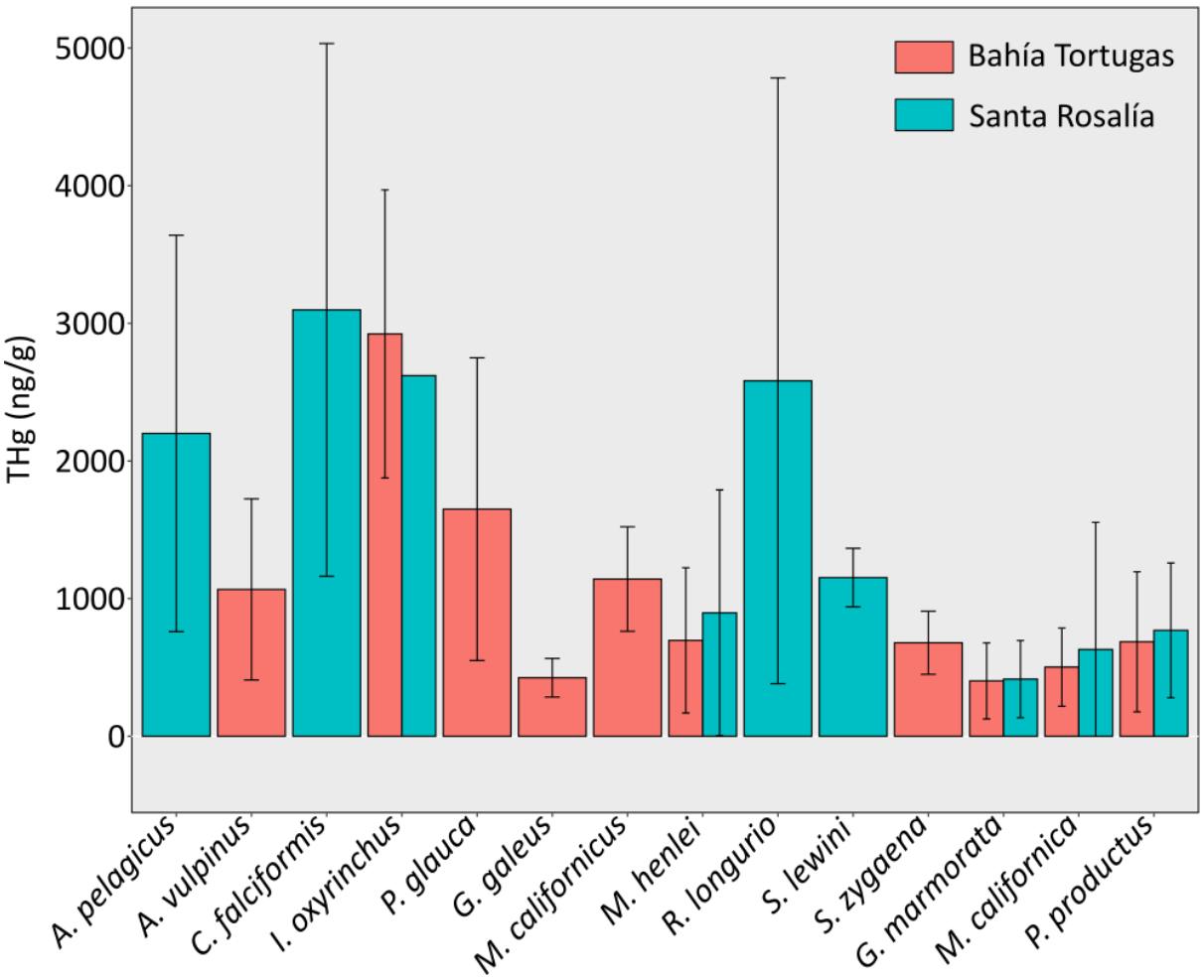
Species	Location	N	Habitat	TL (min-max)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\Delta^{199}Hg$ (‰)	$\delta^{202}Hg$ (‰)	$\Delta^{200}Hg$ (‰)
Alopias pelagicus	Gulf of California	10	Pelagic sharks	200 - 300	-15.79 ± 0.28	19.99 ± 0.85	1.64 ± 0.14	0.82 ± 0.24	0.06 ± 0.04
Alopias vulpinus	Pacific Ocean	8		254 - 340	-16.37 ± 0.41	18.92 ± 0.56	2.08 ± 0.12	0.71 ± 0.15	0.03 ± 0.05
Carcharhinus falciformis	Gulf of California	8		167 - 220	-16.10 ± 0.41	18.38 ± 0.59	1.98 ± 0.21	0.91 ± 0.16	0.06 ± 0.05
Isurus oxyrinchus	Pacific Ocean	9		109 - 163	-16.69 ± 0.32	19.37 ± 1.10	2.10 ± 0.12	0.72 ± 0.09	0.04 ± 0.05
	Gulf of California	1		160	-15.38	21.23	1.54	0.79	0.11
Prionace glauca	Pacific Ocean	10		68 - 135	-17.78 ± 0.38	16.26 ± 0.66	1.63 ± 0.09	0.32 ± 0.16	0.04 ± 0.05
Galeorhinus galeus	Pacific Ocean	8	Neritic sharks	78 - 92	-16.79 ± 0.21	19.58 ± 0.54	1.89 ± 0.15	0.37 ± 0.24	0.02 ± 0.05
Mustelus californicus	Pacific Ocean	10		81 - 110	-16.23 ± 0.37	17.49 ± 0.73	1.55 ± 0.09	0.48 ± 0.14	0.04 ± 0.03
Mustelus henlei	Pacific Ocean	8		70 - 98	-17.01 ± 0.56	17.63 ± 0.63	1.79 ± 0.08	0.46 ± 0.20	0.07 ± 0.08
	Gulf of California	10		52 - 76	-15.36 ± 0.23	20.96 ± 0.38	1.18 ± 0.09	0.68 ± 0.14	0.03 ± 0.03
Rhizoprionodon longurio	Gulf of California	10		96 - 106	-15.07 ± 0.29	22.74 ± 0.20	1.00 ± 0.14	0.21 ± 0.22	0.04 ± 0.06
Sphyrna lewini	Gulf of California	10		79 - 98	-14.35 ± 0.32	22.82 ± 0.38	1.04 ± 0.14	-0.10 ± 0.22	0.03 ± 0.05
Sphyrna zygaena	Pacific Ocean	10		79 - 107	-15.81 ± 0.57	17.19 ± 1.26	2.14 ± 0.11	1.17 ± 0.36	0.05 ± 0.04
Gymnura marmorata	Pacific Ocean	9	Coastal rays	27 - 78	-15.16 ± 0.73	18.24 ± 1.24	1.82 ± 0.20	0.31 ± 0.28	0.03 ± 0.03
	Gulf of California	10		39 - 68	-14.42 ± 0.65	20.36 ± 0.59	1.05 ± 0.22	0.07 ± 0.32	0.03 ± 0.04
Myliobatis californica	Pacific Ocean	10		22 - 118	-15.99 ± 0.76	16.27 ± 0.87	1.20 ± 0.30	0.23 ± 0.36	0.04 ± 0.06
	Gulf of California	9		48 - 170	-14.00 ± 0.50	18.54 ± 1.00	0.61 ± 0.08	-0.03 ± 0.24	0.05 ± 0.04
Pseudobatos productus	Pacific Ocean	9		76 - 118	-16.59 ± 0.74	17.50 ± 0.74	1.60 ± 0.22	0.44 ± 0.12	0.06 ± 0.06
	Gulf of California	10		55 - 92	-15.14 ± 0.54	19.80 ± 0.38	0.71 ± 0.18	0.18 ± 0.32	0.05 ± 0.03

Appendix 6-4 – Comparison between the accuracy and the kappa statistics of single classification tree and random forest iterations using elasmobranch habitats (i.e., pelagic shark, neritic shark and coastal ray) as the response variable.

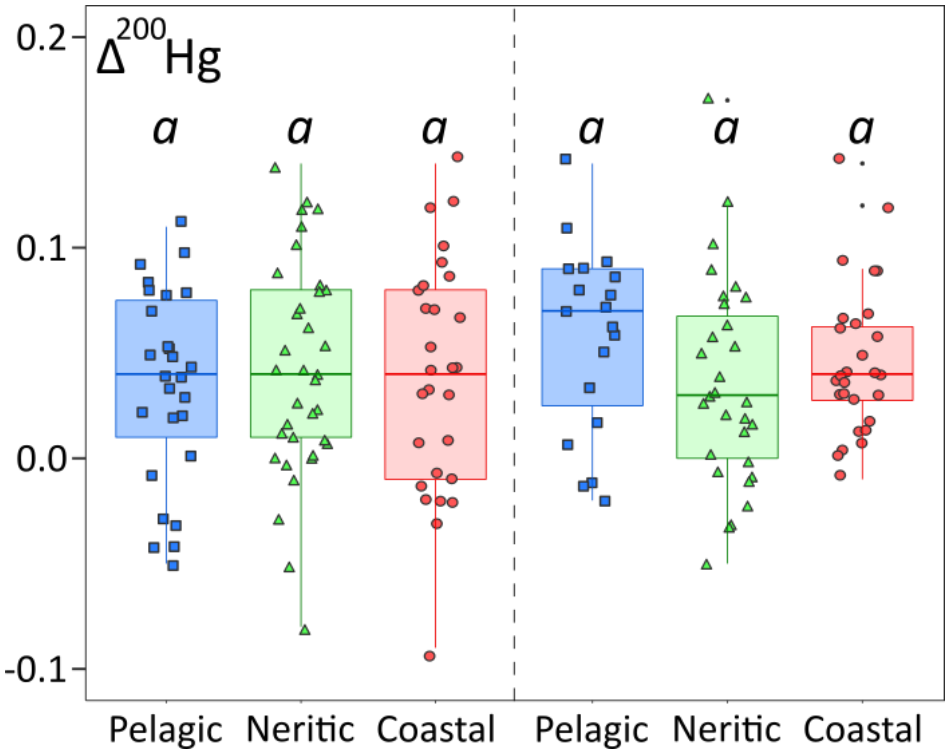
Predictor variables	**Location**	**Classification tree**		**Random forest**	
		Accuracy	**Kappa**	**Accuracy**	**Kappa**
~ $\delta^{13}C + \delta^{15}N$	Pacific Ocean	0.70	0.55	0.56	0.33
	Gulf of California	0.88	0.82	0.86	0.79
~ $\delta^{13}C + \delta^{15}N + \Delta^{199}Hg + \delta^{202}Hg$	Pacific Ocean	0.80	0.70	0.69	0.54
	Gulf of California	0.97	0.96	0.94	0.90

Appendix 6-5 – Inter-specific differences in $\Delta^{199}Hg/\delta^{202}Hg$ slopes at both sampled locations. R^2 and associated p-value of linear regressions are reported.

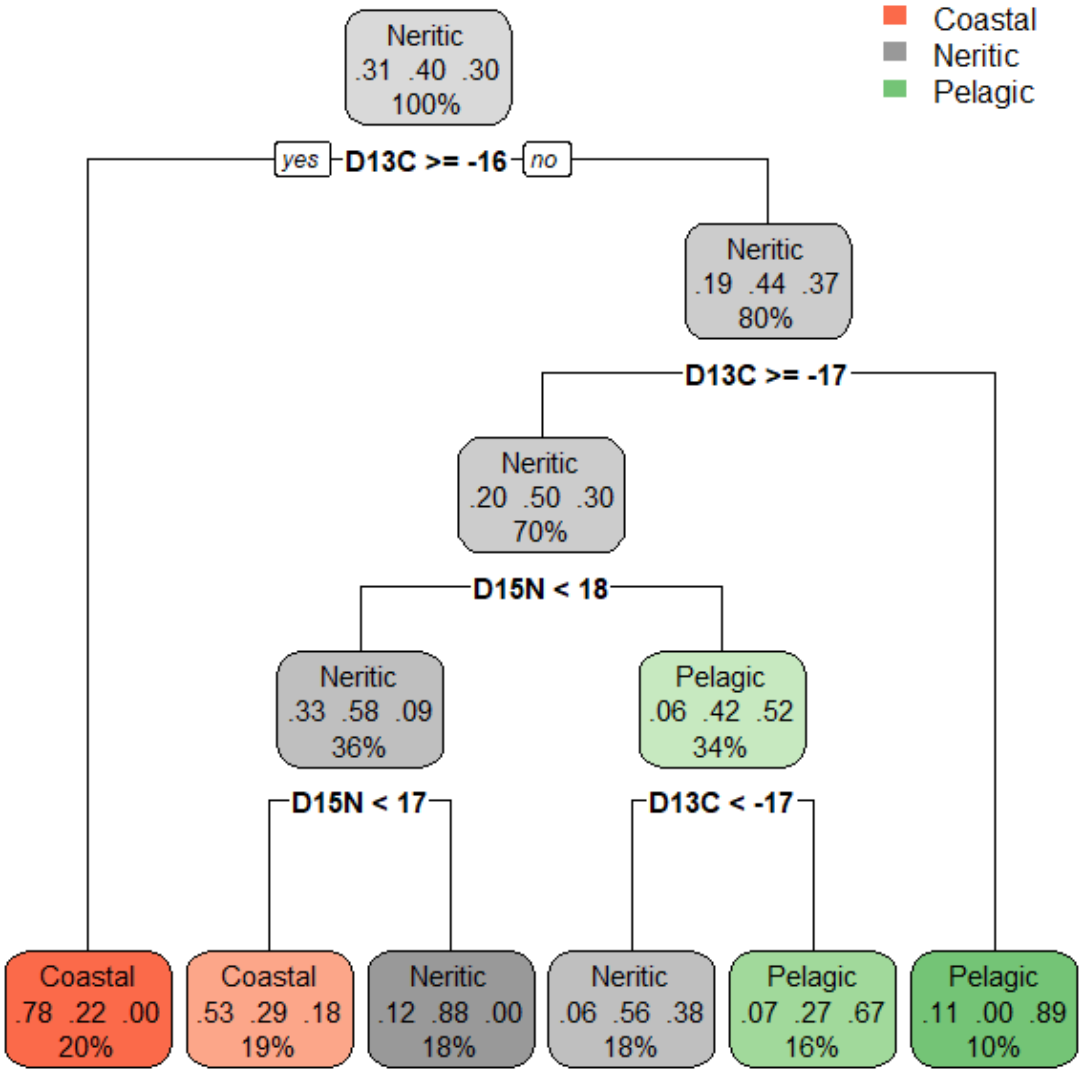
Location	**Species**	**$\Delta^{199}Hg/\delta^{202}Hg$ slope**	***R^2***	***p-value***
Pacific Ocean	*A. vulpinus*	0.51	0.48	p>0.05
	I. oxyrinchus	0.61	0.23	p>0.05
	P. glauca	0.36	0.43	**p<0.05**
	G. galeus	0.43	0.46	p>0.05
	M. californicus	0.40	0.38	p>0.05
	M. henlei	0.09	0.06	p>0.05
	S. zygaena	0.48	0.39	p>0.05
	G. marmorata	0.20	0.06	p>0.05
	M. californica	0.74	0.80	**p<0.001**
	P. productus	1.74	0.82	**p<0.001**
Gulf of California	*A. pelagicus*	0.31	0.27	p>0.05
	C. falciformis	0.62	0.22	p>0.05
	M. henlei	0.19	0.10	p>0.05
	R. longurio	0.35	0.32	p>0.05
	S. lewini	0.13	0.04	p>0.05
	G. marmorata	0.35	0.19	p>0.05
	M. californica	0.01	0.00	p>0.05
	P. productus	0.40	0.54	**p<0.05**



Appendix 6-6 – Histogram of the total mercury concentration (THg) in dry muscle of elasmobranch species in Bahía Tortugas (Pacific Ocean) and Santa Rosalía (Gulf of California). Error bars represent standard deviation estimates.

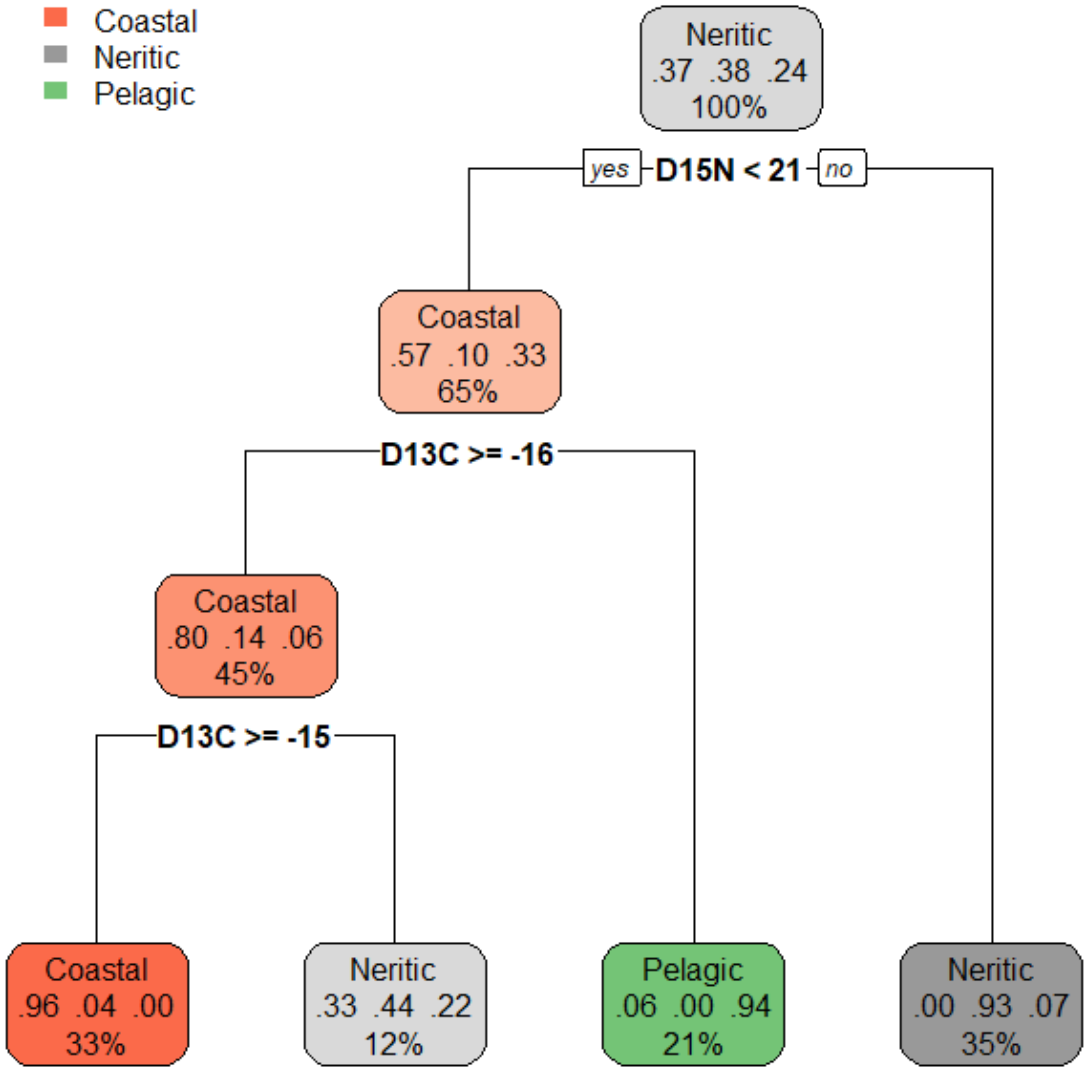


Appendix 6-7 – Boxplots of muscle $\Delta^{200}Hg$ values (in ‰) for each theoretical trophic habitat of elasmobranch species in the Pacific Ocean (on the left) and in the Gulf of California (on the right).



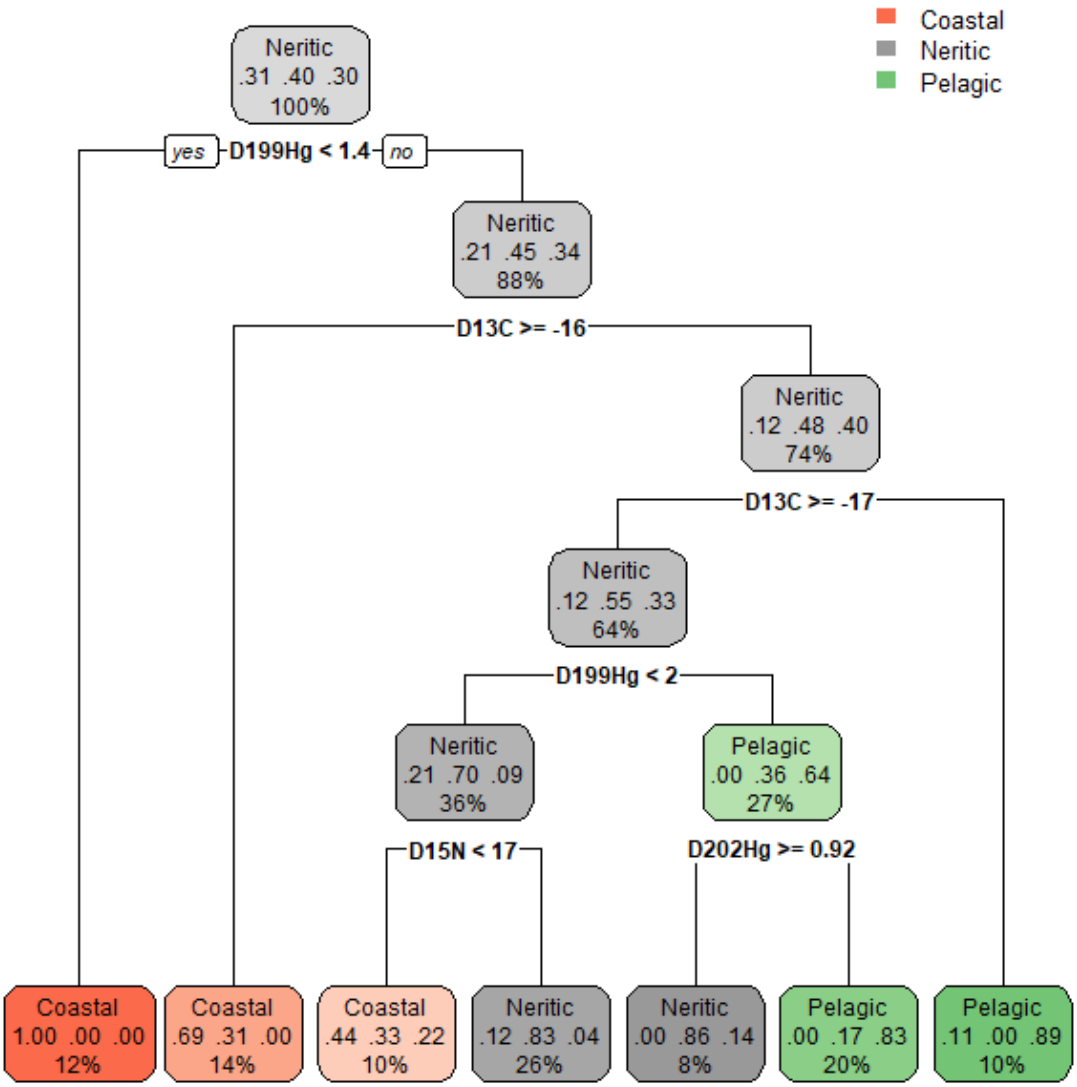
		Predicted		
		Coastal	**Neritic**	**Pelagic**
Observed	**Coastal**	23	3	2
	Neritic	9	23	4
	Pelagic	3	6	18

Appendix 6-8 – Classification tree using elasmobranch habitats (i.e., pelagic shark, neritic shark and coastal ray) as the response variable and $\delta^{13}C$ (D13C in the Figure), $\delta^{15}N$ (D15N in the Figure) as predictor variables and its associated correlation matric in the Pacific Ocean.



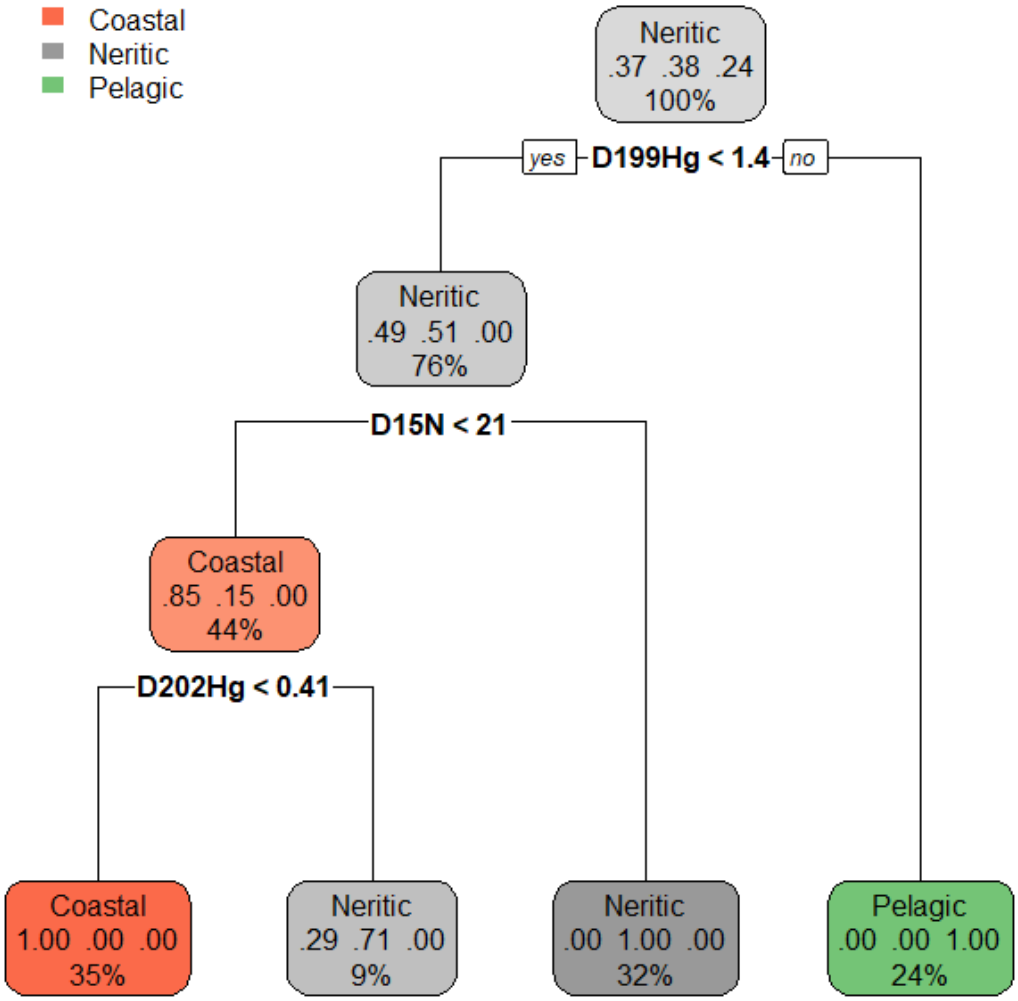
		Predicted		
		Coastal	**Neritic**	**Pelagic**
Observed	**Coastal**	25	3	1
	Neritic	1	29	0
	Pelagic	0	4	15

Appendix 6-9 – Classification tree using elasmobranch habitats (i.e., pelagic shark, neritic shark and coastal ray) as the response variable and $\delta^{13}C$ (D13C in the Figure), $\delta^{15}N$ (D15N in the Figure) as predictor variables and its associated correlation matric in the Gulf of California.



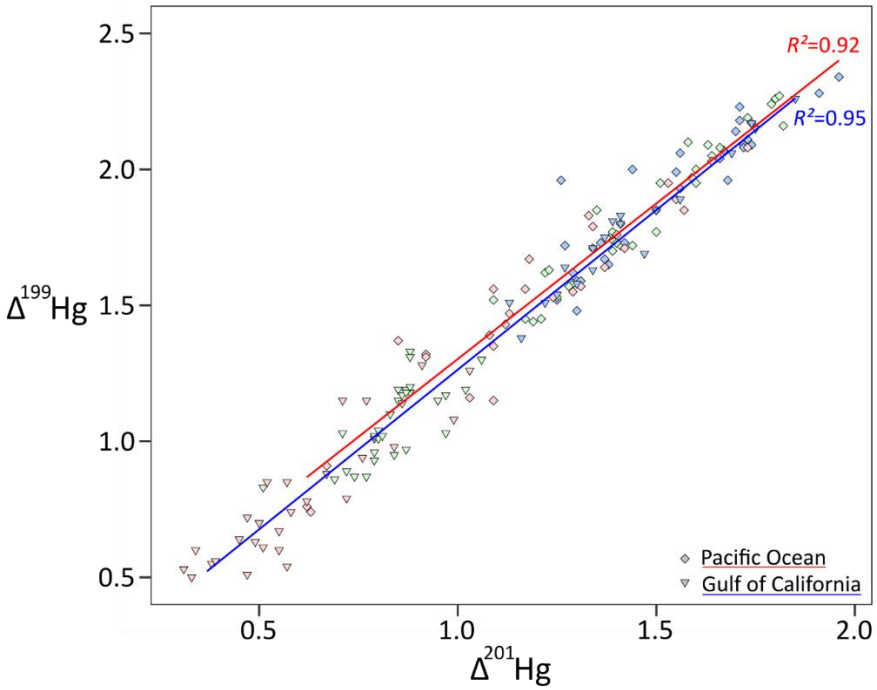
		Predicted		
		Coastal	**Neritic**	**Pelagic**
Observed	**Coastal**	24	3	1
	Neritic	7	26	3
	Pelagic	2	2	23

Appendix 6-10 – Classification tree using elasmobranch habitats (i.e., pelagic shark, neritic shark and coastal ray) as the response variable and $\delta^{13}C$ (D13C in the Figure), $\delta^{15}N$ (D15N in the Figure), $\Delta^{199}Hg$ (D199Hg in the Figure), $\delta^{202}Hg$ (D202Hg in the Figure) as predictor variables and its associated correlation matric in the Pacific Ocean.



		Predicted		
		Coastal	**Neritic**	**Pelagic**
Observed	**Coastal**	27	2	0
	Neritic	0	30	0
	Pelagic	0	0	19

Appendix 6-10 – Classification tree using elasmobranch habitats (i.e., pelagic shark, neritic shark and coastal ray) as the response variable and $\delta^{13}C$ (D13C in the Figure), $\delta^{15}N$ (D15N in the Figure), $\Delta^{199}Hg$ (D199Hg in the Figure), $\delta^{202}hg$ (D202Hg in the Figure) as predictor variables and its associated correlation matric in the Gulf of California.



Appendix 6-11 – Δ^{199}Hg values (‰) in relation to Δ^{201}Hg values (‰) in the muscle of shark and ray species. Blue points correspond to pelagic shark species, green points to neritic shark species and red points to coastal ray species. Linear regressions were applied to describe the increase of Δ^{199}Hg with Δ^{201}Hg with associated R^2 reported on the Figure. An analysis of covariance (ANCOVA) established that there was no statistical difference between slopes (F=0.4, p > 0.0

DOCTORAT SCIENCES BRETAGNE DE LA MER LOIRE ET DU LITTORAL

UBO Université de Bretagne Occidentale

Titre : Écologie trophique des requins de Basse Californie du Sud, Mexique : répartition de la ressource, changements ontogéniques et perspectives de conservation

Mots clés : Réseaux trophiques, Requins marteaux, Isotopes stables, Mercure, Mouvement, Pêcherie artisanale

Résumé : Décrire la niche trophique occupée par les requins est fondamental dans la compréhension du contrôle trophique qu'ils exercent sur les communautés associées et des potentielles conséquences de leur surpêche sur le milieu marin. Dans cette thèse, l'habitat alimentaire de différentes espèces de requins a été étudié le long des côtes de Basse Californie du Sud (Mexique), une région où la pression de pêche sur ces prédateurs est forte. D'un point de vue écologique, l'idée directrice était de décrire l'importance de la répartition de la ressource dans la définition des niches trophiques à l'échelle intra- et inter-spécifique. Pour cela, plusieurs outils ont été utilisés tels que les isotopes stables du carbone, de l'azote et du mercure, ainsi que la composition en acides gras permettant la description verticale et horizontale des habitats alimentaires. À l'échelle intra-spécifique, la répartition de la ressource chez les requins marteaux juvéniles est liée à l'utilisation d'écosystèmes et de proies distincts au cours de la croissance. À l'échelle inter-spécifique, elle s'exprime par des différences de profondeur d'alimentation au sein des assemblages pélagiques, mais dépend aussi des conditions environnementales telles que la présence d'upwelling. Ce travail a également conduit à une meilleure caractérisation du cycle de vie du requin marteau commun (*Sphyrna zygaena*), démontrant ainsi une vulnérabilité accrue aux pressions de pêche liée à une résidence prolongée en milieu côtier. Finalement, la complémentarité des marqueurs trophiques utilisés offre de prometteuses perspectives quant à l'étude des réseaux alimentaires.

Title: Trophic ecology of sharks around Baja California Sur, Mexico: resource partitioning, ontogenetic shifts and conservation perspectives

Keywords: Food webs, Hammerhead sharks, Stable isotopes, Mercury, Movement, Artisanal fisheries

Abstract: Characterizing the trophic ecology of sharks is fundamental to understand the potential cascading effects of their current decline in marine ecosystems. This thesis investigates the trophic niches of shark species in coastal and offshore ecosystems around Baja California Sur (Mexico) in both the Pacific Ocean and the Gulf of California, a region characterized by a strong pressure from artisanal fisheries. Ecologically, the guiding thread was to elucidate the importance of resource partitioning in shaping shark realized trophic niches, at both the intra- and inter-specific level. To achieve this objective, multiple trophic biomarkers were used, such as carbon, nitrogen and mercury stable isotopes, and fatty acid compositions, to describe the vertical and horizontal dimensions of shark foraging habits. At the intra-specific level, resource partitioning was supported by the use of distinct ecosystems for juvenile hammerhead sharks due to ontogenetic shifts in habitat and prey. Inter-specific resource partitioning seems to be driven by foraging at different depth within pelagic assemblages, but could also depend on local environmental conditions, such as upwelling activity. This work also characterized the life cycle of a poorly studied hammerhead species, the smooth hammerhead shark (*Sphyrna zygaena*). The prolonged coastal residency of this species through ontogeny suggests significant vulnerability to local artisanal fisheries. Finally, the demonstrated complementarity of trophic markers provides a promising insight to unravel food web structure and ecological mechanisms.