UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ

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Whale Shark Movement Ecology Review: Under the Approach of the Organismal Movement Paradigm

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Biología

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Whale Shark Movement Ecology Review: Under the Approach of the Organismal Movement Paradigm

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ABSTRACT

Whale shark (*Rhincodon typus*) movements and distribution have been recorded for over 100 years, and thanks to the latest technological advances of the past 30 years, it has been possible to track their movement patterns and variables associated with them in greater detail. *R. typus* is currently listed as Endangered in the IUCN Red List of Species and its population is in continuous decline. Due to their behavioural and movement ecology, they encounter different including, direct or indirect fishing, collision with boats, climate change and even microplastics. This study is a systematic literature review of the movement ecology of the whale sharks based on the unifying organismal movement ecology paradigm, in order to evaluate what is known about the mechanistic components underlying their movement and distribution patterns. Whale sharks use a rage of auditory, olfactory, electro-magnetic cues to guide their navigation and the possibility of a phylogenetic memory. Sea surface temperature, food availability and bathymetry, have shown to be the main external influential factors leading their movements, despite the individual variation present in their movements, which highly correlates with the sex and size. The understanding the causes, mechanisms, and spatiotemporal patterns of their movement and their interrelation, can help to develop better conservation strategies as well as identify the knowledge gaps related to their movement ecology that need further investment.

Key words: Whale shark, *Rhincodon typus*, movement ecology, motion capacity, navigation capacity, migration, threats.

RESUMEN

Los movimientos y distribución del tiburón ballena (*Rhincodon typus*) se han registrado durante más de 100 años, y gracias a los últimos avances tecnológicos de los últimos 30 años, ha sido posible rastrear sus patrones de movimiento y las variables asociadas con ellos con mayor detalle. *R. typus* figura actualmente como En peligro de extinción en la Lista Roja de Especies de la UICN y su población está en continuo declive. Debido a su ecología de comportamiento y movimiento, se encuentran con diferentes, incluida la pesca directa o indirecta, la colisión con barcos, el cambio climático e incluso los microplásticos. Este estudio es una revisión sistemática de la literatura de la ecología del movimiento de los tiburones ballena basada en el paradigma de la ecología del movimiento del organismo unificador, con el fin de evaluar lo que se conoce sobre los componentes mecanicistas que subyacen a sus patrones de movimiento y distribución. Los tiburones ballena utilizan una serie de señales auditivas, olfativas y electromagnéticas para guiar su navegación y la posibilidad de una memoria filogenética. La temperatura de la superficie del mar, la disponibilidad de alimentos y la batimetría, han demostrado ser los principales factores externos que influyen en sus movimientos, a pesar de la variación individual presente en sus movimientos, la cual se correlaciona altamente con el sexo y el tamaño. La comprensión de las causas, los mecanismos y los patrones espacio-temporales de su movimiento y su interrelación puede ayudar a desarrollar mejores estrategias de conservación, así como a identificar las lagunas de conocimiento relacionadas con la ecología de su movimiento que necesitan una mayor inversión.

Palabras clave: Tiburón ballena, *Rhincodon typus,* ecología del movimiento, capacidad motora, capacidad de navegación, migración, amenazas.

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INTRODUCTION

Spatial ecology and the understanding of the leading causes for movement in marine organisms has been one of the main fields to study in the past decades, as these organisms undertake not just horizontal but also vertical movement patterns and live in a medium with a variety of biotic and abiotic factors influencing them (Bres, 1993; Martin, 2007; Schlaff et al., 2014). As a way to elucidate and understand the leading causes, mechanisms and spatiotemporal patterns of movement and their role in different ecological and evolutionary processes, Nathan et al. (2008) proposed a unified, cross-taxa, movement ecology paradigm which integrates the previous characteristics into a conceptual framework portraying the interplay of four key components that lead movement in an organism. In the first instance, movement is determined by the individual's internal state: the physiological and neurological factors which work as a multidimensional vector, which underlies the "*why* move?" and motivates movement towards a goal e.g., gaining energy/feeding, reproduction, learning or safety, which might bring fulfillment to the best proximate and ultimate evolutionary payoff. This takes into account the proximity of the goals and life momentum of the individual. The second component underlies the "*how* to move" which examines an individual's biomechanisms or motion capacity to deliver movement, and incorporates the body's abilities and limitations to serve as a transport vector. The next question highlighted in the framework is the "*when* and *where* to move?" addressing the navigation capacities of an organism, which is the ability to take, process and use external information to direct, start and cease movement and orient in space and time. The final component includes external biotic and abiotic factors, which affect the other components as well as the direction of movement itself.

Since its publication, this framework has been applied to study the movement ecology of species across two of the three domains: Bacteria and Eukarya, for instance, in the study of fungal ecology and community assemblage (Bielčik et al., 2019) or the movement ecology of adfluvial bull trout (*Salvelinus confluentus*) (Cooke et al., 2016). To a lesser extent, it has been applied to study specific components of the framework such as navigation capacity in salmons and sea turtles derived from geomagnetic imprinting (Lohmann et al., 2008). Here, we apply this framework to an iconic endangered marine organism for which a rapid increase in scientific publications pertaining to its movement ecology since its most recent general biology review in 2012 (Rowat & Brooks, 2012) merits an in-depth update.

The whale shark (*Rhincodon typus*) (Smith, 1828) is the largest extant fish and one of only three filter-feeding shark species (Bone & Moore, 2008). It has attracted increasing attention in the scientific field since the turn of the century, mainly to study its distribution, behavior and movement ecology, due to its well-documented aggregations, highly mobile nature and hitherto enigmatic life history (Eckert & Stewart, 2001; Schmidt *et al*., 2010). Additionally, there is increasing concern regarding its conservation – after a new review of its population status and threats carried out in 2016, its status was updated from Vulnerable to Endangered on the IUCN Red List (Pierce & Norman, 2016).

Technological advances in the last three decades have delivered the ability to precisely identify individuals based on their spot patterns (Arzoumanian et al., 2005) and, through the use of satellite, telemetry, and acoustic tracking, to further understand its spatial ecology. The first quantitative approach towards understanding whale shark movements through the use of satellite tracking, took place in the Sea of Cortez, Mexico, at the turn of the century (Eckert & Stewart, 2001). Following this, a wave of studies using tracking technology emerged in order to understand the movement patterns and variables influencing its distribution, migration patterns and general behavior. This literature review explores our current understanding of whale shark movements across the different key components of the movement paradigm framework and how they interplay with each other to guide and shape their movement. We also consider how current and emerging threats may influence their movements and distribution.

LITERATURE REVIEW METHODOLOGY

Study selection

This systematic review follows the 2009 PRISMA guidelines (Moher et al., 2009) to identify research articles and studies that elucidate the movement ecology of whale sharks from a multi-thematic point of view. We included studies that reported general movement ecology components, as well as those dealing with motion, navigation, physiology, and abiotic and biotic environmental components. Studies were considered from all over the world.

The following terms were used to identify the papers that discuss whale sharks movement ecology and the paradigm components using SCOPUS as the main search engine: *Rhincodon typus*, whale shark, *Rhineodon typus*, move, movement, motion, habitat use, vertical movement, dive, diving, horizontal movement, swim, locomotion, migration*, aggregate*, distribution. To identify the publications that discuss threats to whale sharks, the following terminology was added to the main species search: bycatch, fishery, marine pollution, plastics, tuna purse-seine, fish aggregation device, FAD, underwater sound pollution. Primary and secondary information sources were included.

Data collection

For every eligible study, general information was collected including author(s), year published, journal and the specific location and ocean basin (if available). The topic regarding the movement ecology paradigm (internal state, motion and navigation capacity, external factor, and movement pattern and distribution) was identified for every publication. The same general information collection process was held for the publications on threats to whale sharks.

PUBLICATION TRENDS

General movement ecology trends

This review examined 145 articles related to whale shark movement ecology and its paradigm components, from 1918 to 2020 (*Fig 1.*). A total of 12 papers included physiological or morphological traits of the whale sharks relevant to their internal state, locomotion and/or navigation capacities. The first publications (Gudger 1918, 1934) gathered earlier reports of whale shark observations to present general distribution. The first publication on juveniles was a description of individuals caught in the purse seine fisheries of the Pacific and Atlantic Oceans (Wolfson 1983). It was not until 1996, when Taylor published a study from Ningaloo Reef, Australia, relating seasonality with the distribution and movement of *Rhincodon typus*, when the publication rate for this species really began to increase.

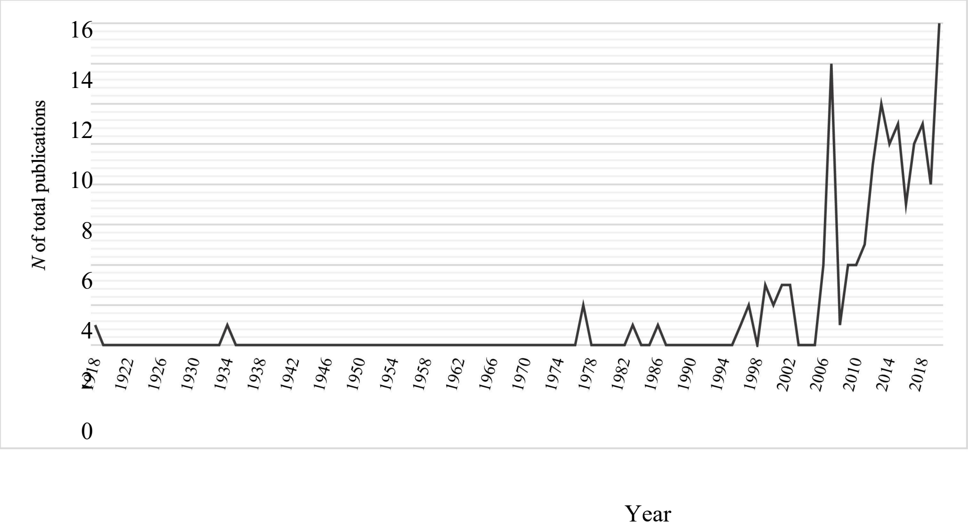
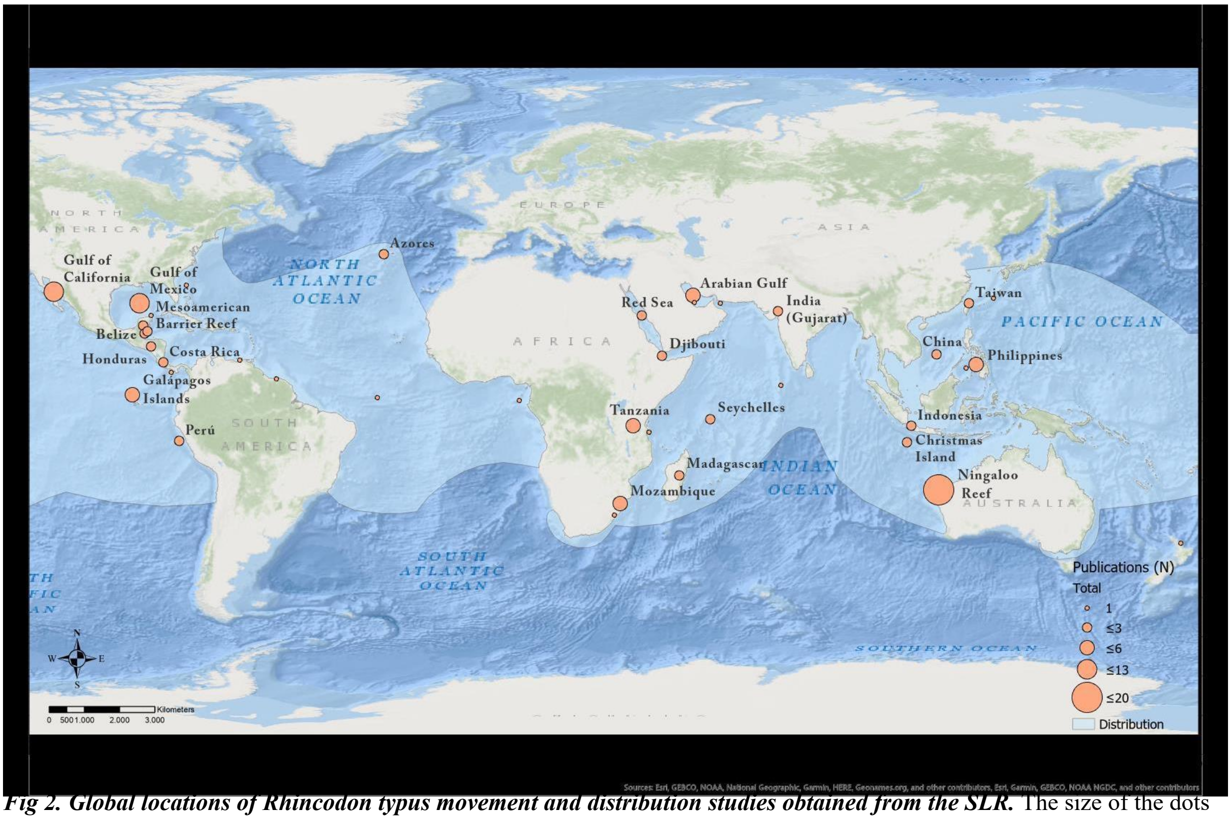


Fig 1. Publication trends of whale shark movement ecology studies since 1918. Total number of studies (n=145).

Geographical distribution

Of the 145 publications of movement ecology and distribution of *Rhincodon typus*, 118 studied location or region specific movement patterns and 14 of them analysed global distributions or general ocean movements. The first location-specific study published was in 1996 at Ningaloo Reef, north-western Australia (Taylor), followed in 1997 at the Gulf of California (Clark & Nelson). Overall, the three locations with the greatest number of publications were, Ningaloo Reef, with the greatest number of publications (n=20), followed by the Gulf of California, north-eastern Pacific Ocean (n=13), which includes the studies done at Baja California and the Sea of Cortez; and finally the Gulf of México, Atlantic Ocean (n=10) (*Fig 2*). Following these sites were Mozambique and the Galápagos Islands, both presenting 6 studies. About 15 locations present just a single study (e.g. Archipelago of São Pedro and São Paulo (ASPSP); Mafia Island; Holbox Island; Quatar; São Tomé, West Africa).



Sources: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org, and other contributors, Esri, Garmin, GEBCO, NOAA NGDC, and other contributors

Fig 2. Global locations of Rhincodon typus movement and distribution studies obtained from the SLR. The size of the dots is relative to the number of publications per location. Publications that present specific geographical locations rather than general ocean or global distribution analyses were included (n=118).

Past 30 years publication trends (1991-2020)

In the last thirty years of publications, a first wave of studies occurred from 1996-2003 (*Fig 3*). 2007 was a particularly productive year (14 publications), but this was followed by a slow period of three years before a relatively steady increasing trend from 2009 to the present day. The years 2020 and 2007 show the highest numbers of publications, 16 and 14 respectively. The study of the overall movement ecology, and how external factors and navigation capacities relate to the patterns observed, are the main topics of research during these periods. Overall, considering three 10-year periods, seven studies were published between 1991-2000, thirty-three form 2001-2010, and nighty-eight in the last 10 years. In the 30 years, this last period from 2011-2020, represents more than the 70% of the total studies.

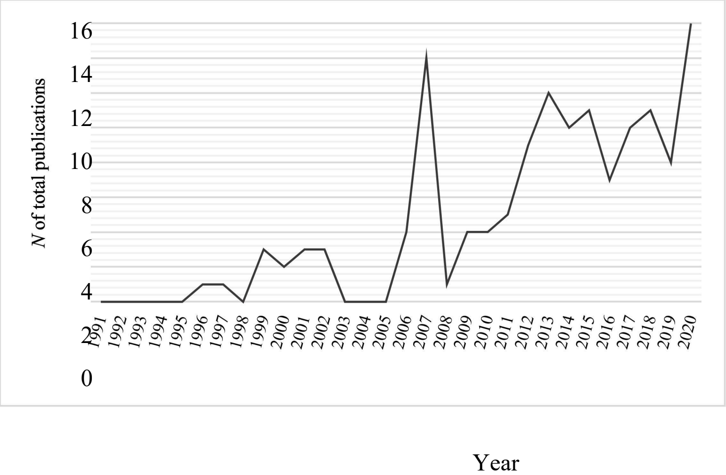


Fig 3. Publication trends of whale shark's (Rhincodon typus) movement ecology since 1990. Total number of studies (n=139).

Geographical distribution

From an ocean basin perspective, almost half of the studies regarding whale shark movement ecology patterns and distribution over the past 30 years took place in the Indian Ocean (43.1%), including those from the Indo-Pacific, which include both basins (*Figure 4*, 0.7%; 1.5%, respectively). Conversely, studies carried out at a worldwide level represent a tenth of the studies (9.5%), and mainly analyse general distribution patterns and the external factor that may be driving them, population genetics, and relationships between ocean basins and migrations of *R. typus*.

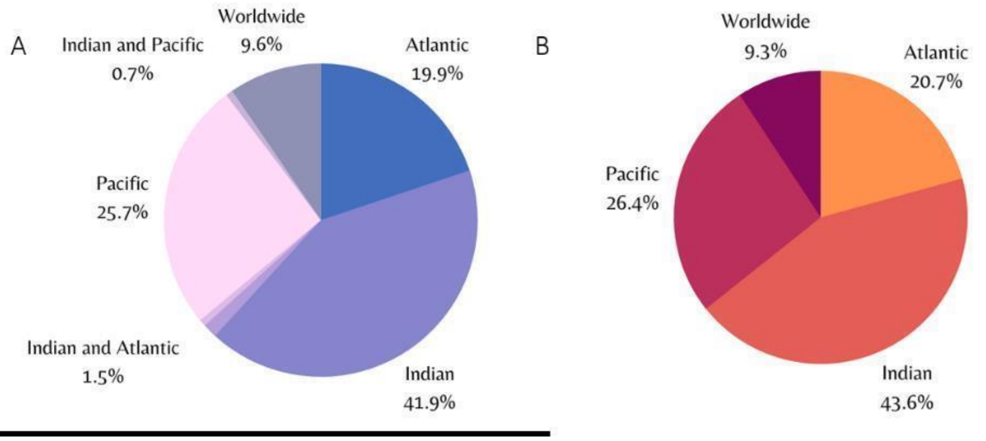


Fig 4. **Geographical distribution of *Rhincodon typus* movement and distribution studies carried out in the past 30 years (1991-2020). D**istribution was considered by ocean region (A) and Ocean basin (B), where the percentages are based on the total number of publications in this period of time (n=136).

Trends in tracking methods

A variety of methods have been used to track whale shark movements over the years. At first, distribution and movement information relied on visual reports, and these continue to be a valuable resource, in combination with more modern tracking technology (Gudger 1918; Gunn et al., 1999; Nelson & Eckert, 2007; Acuña-Marrero et al., 2014). The development of automated photo-identification algorithms for whale sharks based on their unique consistent spot pattern (Arzoumanian et al., 2005), has helped to complement observations, and to determine patterns of sighting or re-visiting of individuals at particular locations around the globe, while also having the benefit of enlisting citizen scientists through an online platform, which allows for a much greater spatio-temporal coverage than would be possible with research teams alone.

Technological advances have also enabled the use of satellite and acoustic tags to track their short and long-term movements. The former records and transmits information from sensors to the Argos satellite system whenever they are near the surface, which can be a problem for large fish that do not spend much time near the sea-surface (Eckert & Stewart, 2001; Márquez-Farias et al., 2006, Sippel, 2009; Hearn et al., 2016). In the case of whale sharks, which are known to spend time at the surface, this involves either a fin-mount tag or a floating tag that is attached to the shark with a cable. These “smart position and temperature” temperature are known as SPOT or SPLASH (if the tags also records depth) tags, and can provide positions with an accuracy of a few kilometres or hundreds of meters. Another kind of satellite tag, known as PSAT, or pop-up archival tags, record depth and light level information, and then detach from the animal and transmit the information from the sea surface. This can be used to infer position based on day length at time-of-year (for latitude) and time of midday in relation to Greenwich Mean Time (for latitude). These tags can have positional errors of 100 km, but there are ways of improving the position based on sea surface temperature records from satellite imagery (Boustany et al., 2001; Sippel, 2009). With this technology, it is possible to follow both vertical and horizontal movements, and environmental profiles of preference (Márquez-Farias et al., 2006). Acoustic tags emit unique high-frequency coded signals, which can be received by underwater or vessel-based hydrophones, thus providing a timed detection log. This can then be used either to build a profile of presence at a given location, of movements between locations where hydrophones are deployed, or to enable real time tracking of diving and movement patterns (Argos, 2011). Furthermore, these tags can be fitted with other types of sensor that provide temperature, direction, speed, and other variables. For instance, accelerometers enable the record of the shark body’s dynamics by recording its orientation, speed, acceleration, precise depth and movement (Gleiss et al., 2009; Whitehead et al., 2020). The simultaneous application of the different monitoring and tracking techniques on individual sharks provides a clearer perspective and better insight into the ecology of their behaviours, movement patterns and distribution.

WHALE SHARK MOVEMENT ECOLOGY

General short-term and long-term movement description.

Vertical movements

Gleiss et al., (2011) recognized five different types of vertical movement dives: bounce or yo-yo dives (Type 1, *Fig 5. a*), two types of V-dives (Type 2 & 3, *Fig 5. b*), which vary in the time spent at the surface between diving events; bottom bounce dives (Type 4, *Fig 5. c*), and U-dives (Type 5, *Fig 5. d*). These diving patterns vary from each other in their energy costs and their geometry, the mean ascent pitch angles being the main difference between dive types. Bounce dives and bottom bounce dives may minimize the costs of vertical movements for travelling, as they present the lowest ascent pitch angles. In contrast, V-dives minimize the costs during vertical movements, mainly as a way to scan deep-water layers in search of food with the minimal energy cost. In the case of large-scale bounce dives (*Type 1*), they may play a dual function for both search and travelling purposes.

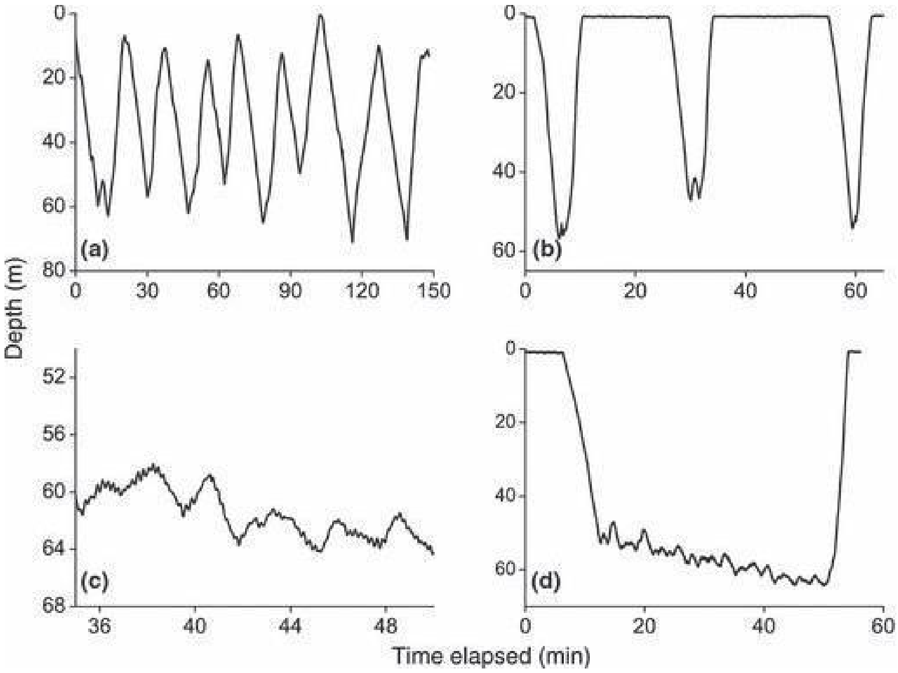


Fig 5. **Whale shark diving patterns determined by Gleiss et al. (2011)**. a) Bounce or yo-yo dives; b) 2 types of V-dives; c) bottom bounce dives; d) U-dives.

Feeding

Observations of feeding aggregations and studies of the diet composition of whale sharks have shown that they mainly feed on copepods, mysids, sergestids (mainly *Lucifer spp., L. faxoni* and *L. hanseni*), decapod larvae and eggs (de la Parra et al., 2011; Rohner et al., 2013, 2015). Specifically, in Belize they feed on snapper spawns and jellyfish (Heyman et al., 2001), on coral spawns at Ningaloo Reef (Norman, 1999) and in México at La Paz and Baja California, on copepod blooms (Clark & Nelson, 1997; Nelson & Eckert, 2007). Their signature fatty acid (FA) composition suggests they may be targeting deep-water zooplankton and fishes, mainly during long-distance movements (Rohner et al., 2013). It has been suggested whale sharks may be following different external cues, such as ocean currents, to reach high prey density areas (Wilson et al., 2001).

Nelson and Eckert (2007), differentiated three main foraging techniques, with particular movements and energetic costs: "active", "vertical" and "passive". Active feeding, otherwise called “dynamic suction” (Ketchum et al., 2014), is performed at the ocean surface, where the whale shark has its mouth wide open, with the upper jaw and its dorsal fin above the sea level, while it performs suction movements. During vertical feeding, they face upwards in a stationary position, with their body in an almost vertical position, and actively sucking water from the surface (Nelson and Eckert, 2007). Passive feeding, commonly known as “ram-filtering” is performed at the sub-surface, while they are travelling at speeds <0.3 ms^{-1} with their mouth partially or completely open (50–75 % of width), passively ram-filtering the plankton from the water column (Nelson and Eckert, 2007; Ketchum et al., 2014). Prey density has been found to determine which of the three feeding techniques is employed, ram-filter feeding being the most commonly observed at aggregation sites with enhanced productivity and the technique that enables the filtering of the greatest biomass abundance (Hoffmayer et al., 2007; Nelson & Eckert, 2007; Motta et al., 2010). For instance, off Cabo

Catoche, at the Yucatán peninsula, plankton densities during this type of filtering were over 4 and 14 times greater during vertical suction feeding and sub-surface passive feeding, respectively (Motta et al., 2010).

Mating

Little is known about whale shark mating behaviour as there is only one known aggregation site, around the mid-Atlantic island of St. Helena, where adults of both sexes are consistently reported in similar proportions and putative mating behaviour has been witnessed (Clingham et al., 2016), although mature individuals of both sexes have also been reported at the Archipelago Sao Pedro and Sao Paulo (ASPSP) (Macena & Hazin, 2016). At both locations, females presented swollen pelvic regions and scars on their pectoral fins. However, a swollen pelvic region may not represent pregnancy, as in-water ultrasounds taken of large females displaying this at the Galapagos Islands did show any signs of pregnancy (Matsumoto et al., in rev.). Large females have been seen or tracked in all the oceanic basins (Eckert & Stewart 2001; Acuña-Marrero et al., 2014; Clingham et al., 2016; Hearn et al., 2016; Macena & Hazin, 2016; Robinson et al., 2016, 2017; Ramírez-Macías et al., 2017; Perry et al., 2020).

Large males, at Seychelles and St. Peter and St. Paul's Rocks, have been recorded rolling over and rotating with their claspers in proximity to boats, and at St. Helena, a male was reported positioning his snout on the caudal fin of the female, these indicating potential pre-copulatory behaviours or post-copulatory behaviours (Macena & Hazin, 2016; Perry et al., 2020). Potential pre-copulatory and post-copulatory wounds in a large female have been reported at St. Helena, where once, two whale sharks where seen coming belly to belly, one swimming below the other on its back, and on a second occasion, two small males going belly to belly, each a time, to a larger female (Clingham et al., 2016; Perry et al., 2020). This is the only potential mating location up to date, which has documented multiple sexual behaviours, highlighting the information gap regarding mating and pupping areas, which are unknown to date.

Large-scale movements

Tracking and identification methods have shown that whale sharks are able to perform long distance movements and migrations. Long distance movements have been recorded in all the ocean basins. In the Pacific Ocean, a whale shark travelled 20,142 km in a period of 841 days, from Panama, passing Hawaii and reaching the Mariana Trench in the Indo-Pacific (Guzman et al., 2018) (*Fig 6c*). In the Galápagos Islands, large female whale sharks regularly perform long-distance movements of several thousand kilometers to Cocos Island (Costa Rica), Malpelo (Colombia), off the shelf break of northern Peru, and into the open ocean west along the South Equatorial Current (SEC) (Hearn et al., 2016). In the Atlantic Ocean, another large female was tracked to travel from the Gulf of Mexico to St. Peter and St. Paul Archipelago in the mid-Atlantic (7,772 km) (*Fig 6a*), and identified back in the Gulf of Mexico, four years later (Hueter et al., 2013). In the Indian Ocean, off the coast of Ningaloo Reed into open ocean (>1,500 km) (Wilson et al., 2006) and off Seychelles into the Indian Ocean whale sharks travel >3000 km showing, in the latter, a prevalent influence of the geostrophic currents during these movements (Rowat & Gore, 2007). A summary of the movements of *R. typus* worldwide can be seen in *Fig 6* (Hearn et al., in press).

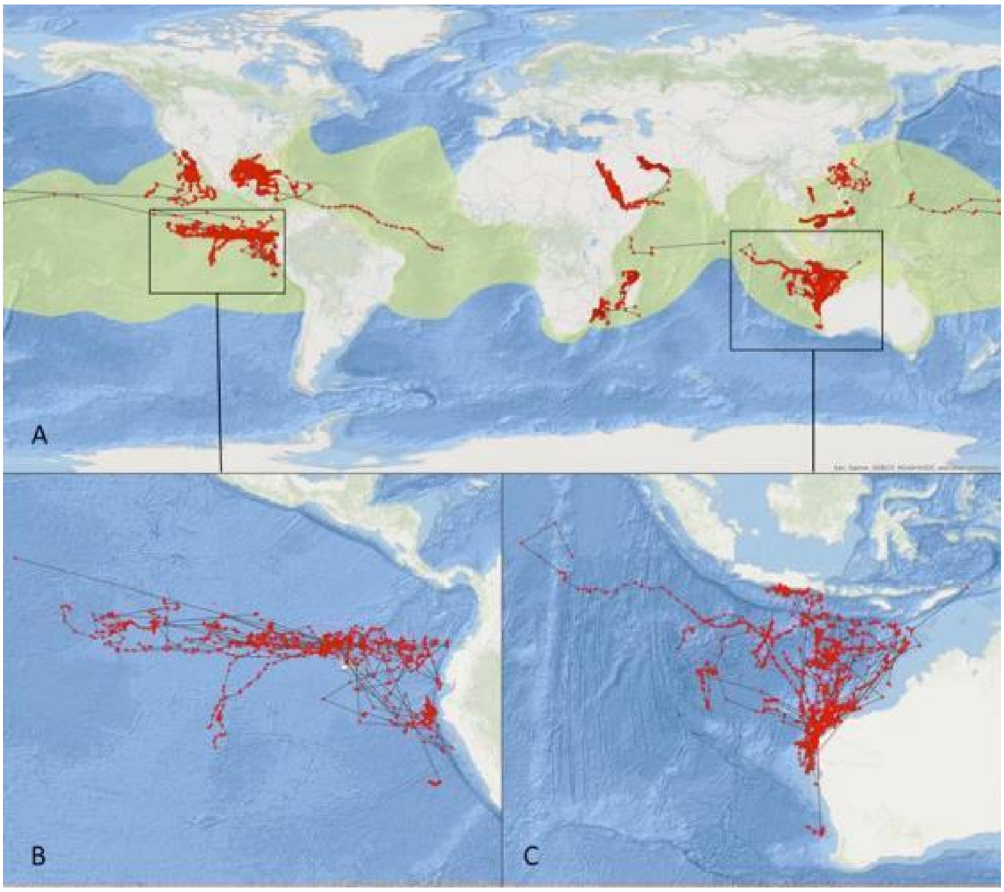


Fig 6. **A) Global summary of whale shark movements based on tracks** (Retrieved from: Hearn et al., in press). Geographical range is shown in green; b) close-up of tracks from Eastern Tropical Pacific; c) close-up of tracks from Western Australia.

Application of the organismal movement ecology framework

Internal State

The internal state of whale sharks comprises the different physiological processes that motivate their horizontal and vertical movements. An important characteristic is their ectothermic physiology – as the rate of metabolic processes scales up with warmer temperatures, they may need to undertake different movement-related behaviours to enable them to meet their thermo-physiological needs (Abram et al., 2016). Indeed, temperature is the main driver of their geographic distribution, which is restricted to tropical and warm temperate waters from 30°N and 35°S, excluding the Mediterranean (Castro et al., 2007).

For instance, the relationship between movements and water temperature has been recorded in the Eastern Gulf of Mexico where whale sharks spent the largest proportion of time in waters ranging 27–30°C and spent less than 1% of the time in water ≤12°C (Tyminski, et al., 2015). In the eastern tropical Pacific 94% of the time was spent in shallow surface waters above the 22°C isotherm (Ryan et al., 2017), at Ningaloo Reef more than 90% of time was spent in waters 23-28°C (Wilson et al., 2006) and at the Galápagos Islands 95% of the time was spent between a sea surface temperature (SST) of 23-25°C (Acuña-Marrero, 2014). However, despite their specific distribution and defined SST range at which they are mainly encountered, their overall temperature tolerance range is wide. Considering vertical and horizontal movements, they are able to tolerate a range of at least 26°C, reaching deep waters as cold as 4°C and surface waters as hot as 34°C (Graham et al., 2006; Berumen et al., 2014). This wide tolerance range indicates that other physiological needs and goals for movement might be playing a higher relative importance than thermoregulation in that moment, for instance energy, safety or reproduction.

The vertical movements of whale sharks have been associated with thermoregulation and foraging (Wilson et al*.,* 2006; Thums, et al., 2013), while horizontal movements have been linked to feeding in high productivity zones (Heyman et al., 2001; Wilson *et al.* 2006) considering energy acquisition as the vector of movement. However, horizontal movements have been also been linked with migrations, which may present different proximate payoffs, or goals that generate directional displacement. Following environmental-seasonal cues (Wilson et al., 2006, Wilson, et al., 2001), mating or reproduction is thought to drive migrations (Ramírez-Macías et al., 2007; Sequeira et al., 2013). These patterns could be part of the evolutionary payoffs integrated as an "instinct" that leads movements, as it has been recognized a level of connection between their metapopulations (Vignaud et al., 2014). The presence of different social structures at the aggregation zones recognized and the limited travelling patterns to specific regions within ocean basin, supports this "instinct" idea. Indeed, Sequeira et al. (2013), suggest that female whale sharks may present a natal philopatry, carrying out long migrations when they are mature to the same locations where they were born, as the longest satellite tracks recorded to date all belong to large females. However, speculation about the reproductive movements of large female whale sharks (Acuña et al., 2014; Eckert & Stewart, 2001; Ketchum et al., 2013; Ramirez et al., 2012, 2017; Robinson et al., 2017; Rowat & Brooks, 2012) must be taken with caution – to date, in-water ultrasounds taken of large female whale sharks in the Galapagos Islands did not result in any evidence of pregnancy (Matsumoto et al., in rev.).

Additionally, the relative importance of the different goals as drivers of movement may vary with an individual's life stage. Juvenile males spend more time near-shore in feeding aggregations, even year-round aggregations (e.g. Ningaloo Reef, Australia; Reynolds *et al.* 2017), while females, especially large adults, tend to display more oceanic movements and do not exhibit strong fidelity to sites, (Hueter et al., 2013; Hearn et al., 2016 Ramírez-Macías et al., 2017). Moreover, Ketchum et al., (2013) suggested that the sex and size segregation present between coastal and ocean basin grounds is not dependent on the oceanographic factors at the southeastern Gulf of California, yet appears to be related to behavioral strategies such as diet preference for juveniles and habitat preference for adults. This idea needs further analysis as different studies have found a direct correlation between oceanographic conditions and movement patterns.

For instance, large females at the Sea of Cortez, in the Pacific Ocean, were recorded filter-feeding near-shore and when moving outside the Sea of Cortez, their distribution seemed to correlate with enhanced productivity zones and showed a preference for SSTs between 28-32°C, with a total temperature range of 20-32°C (Eckert, & Stewart, 2001). However, contrasting this pattern, in the Galapagos Islands the presence of large female whale sharks at Darwin Island is apparently not related to feeding (Acuña-Marrero, et al., 2014, Hearn et al., 2017), and they occupy temperatures between 24–25°C. Interestingly, some whale sharks tagged in Galápagos returned to the islands after prolonged absences. It has been suggested they might be following geostrophic currents such as the westward flowing South Equatorial Current, the Humboldt Current or eastwards flowing North Equatorial Counter Current, which are highly productive (Hearn et al., 2016, Ryan et al., 2017), yet further research needs to be done regarding the main movement driver at this region.

Internal oxygen availability and hypoxic state is a physiological factor to consider when analyzing whale shark movements, as they tend to perform a wide range of deep dives and vertical movements. *Rhincodon typus* has been recorded to reach depths at least as great as 1928m during short V-dives, from the epipelagic to the bathypelagic zone (Tyminski et al., 2015). This movement pattern requires moving into oxygen minimum zones (OMZ) with very low dissolved oxygen concentrations yet high carbon and organic matter flux (Arístegui, et al., 2005). Under the approach of the movement ecology paradigm, which establishes that relative importance of different goals will drive the individual's movement direction (Nathan et al., 2008), deep dives have been related to foraging behaviors below the thermocline in food-scarce environments (Hearn et al., unpublished). This shows that gaining energy is one of the primary drivers for whale shark movements, by crossing the physiological barrier of low oxygen availability by evolving the capacity to tolerate at least short periods within the OMZ in exchange for energy resources.

During deep dives, whale sharks encounter several primary physiological barriers: cold temperatures lower than 5°C (Tyminski et al., 2015), low dissolved oxygen concentrations and high pressure. The mechanisms to cope with these barriers have not been fully studied, yet Nakamura, Matsumoto & Sato (2020), revealed that whale sharks' heat-budget models are lower than any other fish as well as showing that internal heat production does not contribute to changes in muscle temperature, meaning that they can perform these deep dives without high metabolic costs while maintaining a relatively stable body temperatures and withstanding body temperatures as low as 20°C. This ability to perform such short deep dives without harming its internal temperature balance and not requiring additional metabolic costs seems to be an advantage to exploit different niches, mainly of prey that are seeking refuge at depths from their visual predators during the day (Wilson et al., 2006). In this way, the role of gaining energy and its relative importance to promote movement along vertical water columns, which has been previously proposed (Gleiss et al., 2013, Graham et al. 2006), appears to be greater than thermoregulation, as the latter seems not to be such a great constraint. Temperature may not be such an important internal driver for movement as foraging is.

Cooler water has been suggested to decrease gastric evacuation rates and increase assimilation efficiency in different shark and ray species (Schlaff et al., 2014) while warm waters have been suggested to increase metabolism and maximize the foraging efficiency in elasmobranchs. To take advantage of this, they have developed this ‘hunt warm–rest cool’ strategy by modifying their foraging behaviors and digestive physiology to optimize their energy consumption and efficiency (Di Santo & Bennett, 2011). Even though this has not yet been studied directly in *R. typus*; by examining their swimming performance during feeding, Cade et al. (2020), found that the energetic costs of feeding just below the surface and at depth is much less than active surface ram-feeding, due to the increase in drag forces of their open mouth. Yet this energetic cost has been thought to be compensated by the higher prey densities found while performing this feeding behavior, consistently with several observations of whale sharks feeding at surface fish or zooplankton aggregation or dense patches of fish and coral spawns (Gunn et al., 1999; Heyman et al., 2001; de la Parra Venegas et al., 2011).

In terms of horizontal movements and migrations however, it is unclear whether food availability (fish or coral spawns) is the principal driver of movement or whether there are other primary influential factors such as mating. However, to date the only report of possible mating activity is from the mid-Atlantic island of St. Helena (Clingham et al., 2016).

On the other hand, in vertical movement patterns, bounce dives in shallow surface waters have yet been continuously linked to foraging with consistent patterns related to planktonic densities and visual corroboration (Gunn et al., 1999). This reinforces that the leading force of these movements is feeding along with the reduction of energy costs during horizontal movements by taking advantage of their negative buoyancy through their “sink and rise” pattern, gliding to the bottom and actively swimming as they rise (Gleiss et al., 2011). Indeed, a study done by Cade et al. (2020), observed that foraging bouts could last as long as 11 hours in highly productive zones with great conditions, and that the 20% of the total time recorded was spent feeding, on average representing about 2.5 hours per day foraging in dense patches. However, it was noted that surface feeding was performed only during favorable conditions, due to the high energetic costs of surface feeding. The need for whale sharks to make cost efficient movement decisions highlights the relatively high importance role that energy plays among the different movement drivers.

Motion Capacity

The second component of the movement framework is motion capacity, which enables organisms to move in different ways and directions that can be either self-propelled or externally vectored (Nathan, et al., 2008). The body’s morphology and the ways in which its mechanical abilities are used during a movement, is in constant interaction with the individual's physiological state, the energetic costs and outcomes from moving, as well as the environmental factors. For example, the hydrodynamic efficiency found in fish during gliding, is given by a reduced drag coefficient in comparison to the one produced during power locomotion, as in the latter, the body uses wavelike movements creating approximately three times more drag (Weihs, 1974; Gleiss et al., 2001).

Among the different body forms recognized for sharks, whale sharks are within the fast swimming pelagic sharks, characterized by the high aspect ratio of their tail, which in the case of whale sharks provides efficient slower cruising speeds with low center of effort of the tail (Thomson & Simanek, 1977). Their wide dorso-ventrally flattened head as well as the presence of three prominent longitudinal ridges on their upper flanks extending from near the gill region to the caudal peduncle (Thomson & Simanek, 1977; Norman, 2005), are other characteristics that benefit their motion capacity and dynamics. These slower cruising speed rates may represent the most efficient speed for filtering plankton through the unique filtering pads present in them (Motta et al 2010). Additional to the general movement capacities in whale sharks, allometric changes during growth of an individual produces differential propulsive abilities between neonates, juveniles, and adults and thus influences their locomotion performance: a developmental shift, which has also been noted in tiger, bull, blacktip, and nurse sharks (Irschick & Hammerschlag, 2015).

Whale sharks can take advantage of their negative buoyancy by gliding during deep dives, with descents requiring the least mechanical power output, while ascents are characterized by strong locomotion activity requiring the most mechanical power showing steeper pitches >10° (Gleiss, et al., 2011, 2013). As pitch increase, it affects locomotion costs as less lift is produced by the pectoral fins thus more thrust by the caudal fin propulsion is required along with higher energy. Nonetheless, the low angles present during V-diving ascents enable whale sharks to minimize the horizontal cost of locomotion and transportation as well as an efficient searching strategy of a vertical food source (Alexander 1990; Gleiss et al., 2011).

When swimming very slowly near the surface in search of plankton, *R. typus* is close to neutral buoyancy, thus reducing the amount of energy expended (Bone & Moore, 2008). Due to the high-energy demand present in this large shark, it is reasonable to present different motion strategies to minimize locomotion costs and efficient energy consumption depending on the ecological context, the physiological and external factors affecting or guiding movement. This can be noted in the different movement geometry patterns present in the five diving types shown by whale sharks: bounce or yo–yo diving, two types of V-dives, bottom bounce and U-dives (Gleiss et al., 2011). Strategies to reduce the costs during locomotion can be seen in the different feeding methods: surface ram-feeding, active surface feeding, stationary/vertical suction feeding, sub-surface passive feeding and deep feeding (Nelson and Eckert, 2007; Motta et al., 2010).

Navigation Capacity

The sensory mechanisms that lead to navigation and promote directional movement are key elements to understand the way animal travel and deliver movement. In the case of the whale sharks, little research has been done regarding their visual abilities, yet it has been suggested that their small, circular, laterally located eyes, present moderate visual acuity (Martín, 2001), suggesting it is not the primary sensory mechanism they use for navigation. Moreover, this is reinforced by the presence of a relatively reduced mesencephalon, in comparison with other sharks and fish (Yopak & Frank, 2009), region where the optic lobes are located, thus their visual. Furthermore, to aid navigation, their other sensory systems, olfactory, acoustic and electro-magnetic systems, may be of greater importance. Like other sharks, whale sharks possess a specialized electro-magnetic ampullary system, with modified neuromast cells known as ampullae of Lorenzini (Bone & Moore, 2008) which have high sensitivity to very low frequencies or stimuli. Hammerhead sharks (*Sphyrna lewini;* Klimley, 1993), blue sharks (*Prionacea glauca*; Carey & Scharold, 1990) and lemon sharks (*Negaprion brevirostris;* Kalmijn, 1984), appear to be able to perceive movement across the lines of the earth's magnetic fields thanks to the sensitivity of these organs. While this has not been directly tested in *R. typus*, the presence of these magnetic-sensory organs suggests that it may give a navigational aid and ability to navigate across the ocean's magnetic fields. Indeed, Hearn et al. (2010) hypothesize that Darwin Island, in the Galapagos Archipelago, may act as a navigational waypoint with particular magnetic field intensity properties that could be used for orientation during seasonal migrations.

Moreover, little attention has been given to the way chemical cues may play an important role in the navigation capacity of sharks, mainly during open oceanic migrations; further than a mere odor discrimination itself. 'Olfactory spatial' hypothesis presents the olfactory system as a generator of a chemotactic cognitive map for navigation purpose and space orientation, presenting a tight correlation between highly migratory species with the size of their olfactory bulbs (OB) (Jacobs, 2012; Nosal, et al., 2016). Whale sharks present terminal widely separated small nostrils with rudimentary barbells and lack circumnarial folds and grooves (Compagno, 2001; Norman, 2002) (*Fig 7*), yet have very well-developed olfactory lobes and relatively average sized telencephalon (Yopak and Frank, 2009; Dove, 2015). Considering the 'olfactory spatial' hypothesis, it would be expected that they reflect a high adaptive value of tracking a dynamic chemical world and linking locations in olfactory space.

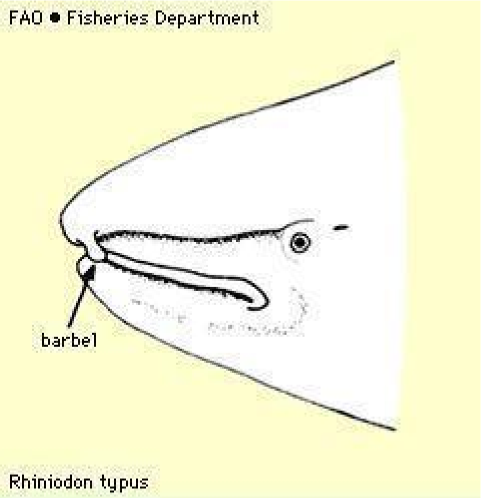


***Fig 7*. Illustration of the lateral view of the head of a whale shark (*Rhincodon typus*, Smith 1828) from the FAO Species Catalogue for Fishery Purpose No.1** (Compagno, 2001).

Dimethyl sulphide (DMS) is a noxious-smelling water-soluble compound released by phytoplankton when grazed upon by zooplankton. It is used as a cue for foraging for seabirds, and has been suggested to serve as navigational and geo-location cue during vertical diel movements for whale sharks (Dacey & Wakeham, 1986: Martín 2007; Rowart & Brooks 2012). Furthermore, whale shark migrations, diving behavior and shifts in vertical movements have been consistently linked to spawning events or food aggregations (Hays, 2003; Sims et al. 2005; Gleiss et al., 2013). Whale sharks use chemosensory cues as a stimulus to detect food sources, which can help direct long-range movements and discrimination of food items, presenting a hierarchical response e.g. direct krill metabolites vs. chemical DMS (Dove, 2015). Yet, the extent at which whale sharks develop a chemotactic cognitive map as navigational media needs to be further studied.

Besides the use of their olfactory sense, whale sharks might be using hearing as a navigational tool to guide their movements. They possess the largest inner ear in the animal kingdom, suggesting a high sensitivity to long wavelengths and low-frequency sounds (Muller, 1999; Myrberg, 2001; Martin, 2007) (*Fig. 8*). Even though the extent at which their hearing capabilities serve as a navigational tool has not been studied yet, there is a high possibility whale sharks use it to guide and/or modify certain movements. It has been suggested that whale sharks locate fish and coral spawning events or high densities of marine zooplankton by following different auditory and olfactory cues. The distinctive sounds of schools of fish generated during spawning-related activities, the bubbles produced and the characteristic sounds of that environment (e.g., snappers drumming), seem to be one of the signals that whale sharks use to direct their navigation and locate their food sources (Heyman et al., 2001). Likewise, Martin (2007) noted that whale sharks dive instantly upon ignition of boat motors, possibly relating it to the low frequency noises it produces.

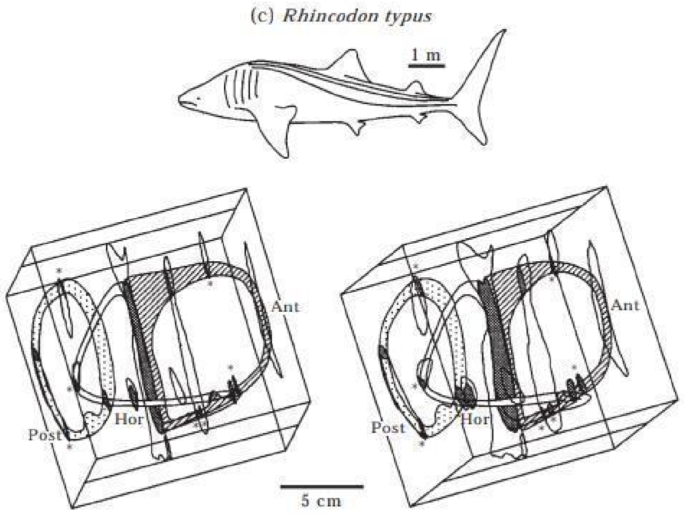


***Fig 8.* Stereographic reconstruction of the whale shark's inner ear** (Retrieved from: Muller, 1999).

As means for navigation, oceanic currents are known to serve as directional movement cues. These navigational cues have been recorded in the Galápagos Islands, where whale sharks associate with the Equatorial Front to move along the South Equatorial Current (SEC) into the open ocean (Hearn, et al., 2016), in the Maldives, Seychelles and off South Africa following monsoonal currents, where in the latter, mainly the warm Agulhas Current (Anderson & Ahmed 1993; Beckley et al. 1997; Wilson et al, 2001). At Seychelles, there is a strong influence of geostrophic currents and boundary currents (Rowat & Gore, 2007). Nonetheless, in Ningaloo Reef, off northern Western Australia, tracking results indicate that whale sharks spend most of the time actively traveling near-surface geostrophic currents yet independently of them despite the additional metabolic costs of this behaviour (Sleeman et al., 2010).

Nathan et al., (2008) suggest the existence of a genetically coded “memory” responding to stored previous experiences. Long distance migrations and horizontal movements have been linked to foraging strategies in search of high primary productive zones and mating or reproduction (Heyman et al., 2001; Wilson et al. 2006; Ramírez-Macías et al., 2007; Sequeira et al., 2013) along with their evolutionary payoffs. The population structures present in the different aggregation locations as well as the connection between meta-populations (Sequeira et al., 2013), emphasizes possible presence of a phylogenetic memory that guides movement and aggregation patterns in whale sharks. Wilson et al. (2001), has suggested the possibility of the existence of a phylogenetic memory in whale shark movements guided by oceanic currents as directional cues. They noted that the strengthening of the southern Leeuwin Current is a temporal and directional signal to initiate southerly movements towards highly productive food sources. Furthermore, due to the lack of stationary cues in open oceanic movement, Nosal et al. (2016), presented the idea that migrations might be facilitated by geomagnetic, chemical and hydrodynamic cues, developing positional and directional information that might act as a 'map-sense' and 'compass-sense' throughout the pelagic navigation. These 'map-senses' could be related to the development of a trans-generational acquired memory that leads to orientation and navigation to *R. typus.*

Although whale sharks are mostly solitary animals, they might actually present a level of social structure though their lives. Whale shark brains exhibit a level of development of the dorsal pallium and a relative enlarged diencephalon and a relatively reduced mesencephalon, which have been associated with social behaviours in other animals that live in complex habitats (Yopak & Frank, 2009). This finding, in addition to the presence of constant specific feeding aggregations at different locations around the globe, suggests the presence of moderate social behaviours in whale sharks. This reinforces the notion of the presence of a phylogenetic memory related to their spatial distribution and thus being a navigational mean for whale sharks.

The most recent genetic analysis results demonstrate the presence of a genetic differentiation between Indo-Pacific and Atlantic populations, as well as a level of genetic distinction between Indian and the Eastern Pacific oceans (Yagishita et al., 2020). These results highlight the previous notion of global-scale high site fidelity among individuals mainly at an ocean-basin scale (Norman et al., 2017), at least between the Atlantic and Indo-Pacific populations. The most recent genetic results have even determined some level of genetic differentiation between the Indian Ocean and Eastern Pacific, as migrations mainly occur in the western North Pacific between the north and south direction and in an east-west direction at the North Pacific. These results have even suggested a level of possible mixing between Indo-Western Pacific populations by showing an unimodal distribution under the population expansion model (Yagishita et al., 2020), reinforced by the latest recording of potentially the longest trans-Pacific migration from Coiba Island (Panama) to the Mariana Trench in the western Indo-Pacific, travelling over 20,000 km (Guzman et al. (2018). These results reinforce the possible existence of an evolutionary genetic "memory" which is basin-dependent, elucidating the need to better understand the way oceanographic and environmental characteristics that represent each ocean basin, leads to the observed movement paths.

External Factors

At a global scale, coastal aggregations of whale sharks are influenced by seabed features (especially seamounts), which indirectly influence upwelling and chlorophyll-a levels, meaning higher primary productivity (Afonso et al., 2014; Gonzales-Pestana, 2020). A recent study in northern Peru by Gonzales-Pestana (2020), determined that depth was the most important variable for spatial distribution prediction, followed by chl-a, and less importantly, SST. Nonetheless, at the Azores islands (mid-northern Atlantic), the thermal boundary seems to play a fundamental role for whale shark detections and their occurrence in the region is associated with the position of the seasonal 22°C isotherm (Afonso et al., 2014). On the other hand, chl-a and seasonal plankton productivity levels as well as fish and invertebrate spawning events, have shown to be the strongest forces to drive distribution patterns and aggregation locations as well as changes in swimming behaviours (Clark &

Nelson, 1997; Eckert & Stewart, 2001; Martin, 2007; Rowat & Brooks, 2012; Gonzales-Pestana et al., 2020). However, in terms of offshore distributions or migration patterns, these external factors may not be the main influences that determine them.

As mentioned previously, oceanic and geostrophic currents are one of the main external factors that influence the distribution and movement of whale sharks in particular in offshore movements (Wilson et al., 2013). For instance, whale sharks at Galápagos moved west along the South Equatorial Current (SEC) and the Equatorial Front upwelling zones coinciding with the greatest observation periods (July-December), following as well the Peru-Humbolt upwelling systems (Palacios, 2004; Ryan et al., 2017). At, Ningaloo Reef where La Niña y El Niño events fluctuations in the Southern Oscillation Index (SOI) play a huge role in the abundance of aggregations of whale sharks, there was a positive correlation between the size of these aggregation and the SOI, strength of the Leeuwin Current, and La Niña events (Wilson et al., 2001).

Photoperiod and light intensity are possible key cues to drive shifts in movement and guide swimming patterns in whale sharks worldwide. Whale sharks present a clear variation in swimming patterns between day and night, and in most aggregation locations sunset and sunrise have shown to be the primary key signals for these changes (Graham et al., 2006; Wilson et al., 2006; Gleiss et al*.,* 2013). Interestingly, Graham et al. (2006), determined that lunar-modulated snapper-spawning events guided the deep diving excursions, showing that there is an interrelation between productivity and photoperiodicity or time of the day, that drive movement, instead of being just a single leading force.

Considering other external factors, influencing movement ecology, are the oxygen minimum zones (OMZ), which the whale sharks encounter during their deep dives into the bathypelagic zone. Schlaff et al. (2014), highlights the ability to penetrate hypoxic environments by hammerhead sharks, as an evolutionary advantage over other predators that do not have this ability due to physiological barriers. However, in contrast with hammerhead sharks, this characteristic of being the being the deepest-diving fish of whale sharks has been linked to searching mechanism of feeding opportunities of zooplankton in the deep-water column in the presence of low periods of surface food availability (Wilson et al., 2006). This physiological adaptation to penetrate OMZ deep in the bathypelagic layer has been seen as well as for whale sharks as a way to reduce competition for resources and feed opportunistically in deeper prey (Taylor 2007; Brunnschweiler & Sims 2011; Ketchum et al., 2013; Rohner et al., 2013).

Deep diving may be related to predator avoidance, although this seems unlikely. The blue shark (*Prionace glauca*) makes deep dives above 1000m (Stevens et al., 2010), orcas (*Orcinus orca*) have average maximum depths above 200m (Wright et al., 2017) and the white shark (*Carcharodon carcharias*) can dive down to 1150m (Skomal et al., 2017). Although they have shown to be predators of neonates (Schmidt et al., 2010), they do not seem to be major predators of adults, suggesting that this evolutionary advantage may not be for predatory evasion, but serve as a foraging mechanism. Moreover, Schlaff et al. (2004), suggest, this capacity to withstand low oxygen availability may have of greater importance as a driver of movement for species that use comparatively lower oxygen habitats.

Movement Patterns

To understand movement paths and patterns, it is important to consider the different factors that motivate each individual, as these factors may vary seasonally, temporally, geographically and even within sex and life stage. The different patterns result from interplay between external factors and internal state, mainly food availability, bathymetry, and temperatures being the greatest drivers of migrations and aggregation (Meyers et al., 2020). However, it cannot be generalized that for instance, foraging is the ultimate driver of vertical or horizontal movements, yet a combination with the other factors that may be influencing the movement direction in a secondary importance category (e.g. ocean currents, oxygen availability and the individual's life stage). The difference between the individual's records may be due to changes in the level of importance of the proximate goals linked to their stage (e.g. feeding, reproduction, behavioral thermoregulation and even "random search"). Additionally, the intrinsic variability of the external factors that affect the movement directions must be considered, as they may vary seasonally and spatially.

Whale sharks display a huge range of vertical movements, with the greatest depth recorded of 1928m (Tyminski et al., 2015) as well as impressive trans-oceanic horizontal movements of 12,620 km (Eckert & Stewart, 2001) over a three-year period, with the greatest distance recorded of 20,142 km over a period of 841 days (Guzman *et al.* 2018). Additionally, whale sharks often segregate by size and sex. This may prevent adult whale sharks from competing for food with juvenile conspecifics in certain coastal aggregation areas (Martín, 2007), or may simply reflect different dietary requirements based on size and sex. Feeding aggregation patterns have been well recognized to be coastal for juveniles and offshore for larger individuals (Graham & Roberts, 2007; Ramírez-Macías et al., 2017), shifting their diet as they grow, and thus it is expected that they would occupy different habitats based on their life stage (Borrell et al., 2011; Rohner et al., 2013). For instance, in the Gulf of California, juveniles occur mostly in the northern parts of the Gulf while adults, greater than 8m long, are present mostly in the southern parts (Eckert & Stewart, 2001).

Associating behaviors at cooler and warmer temperatures with the physiological processes in ectothermic organisms, can help understand preferences along the water column and understand their interaction with the organisms' life stage and sex, as well as other external factors such as oceanic currents and bathymetry. For instance, deep dives seem to be a mechanism to acquire energy, i.e. foraging (Thums et al., 2012; Meekan et al., 2015) yet minimizing the energy consumption during these dives. A study done by Cade et al. (2020)

revealed that, ram feeding requires more energy than sub-surface or deep dive feeding, strengthening the belief that the reason for these deep dives might be to maximize energy budget and reduce energy consumption while exploiting these new range of resources. Whale sharks seem to compensate the higher energy cost during ram-feeding by locating dense zooplankton patches or spawning events.

Additionally, Nakamura, Matsumoto & Sato (2020), found that during deep dives, whale shark body temperature barely changed, and their internal heat does not provide the energy to keep their body temperature. Whale sharks tolerate temperatures as low as 2.2°C (Rowat & Brooks, 2012). The high thermal inertia present in the whale sharks allows them to reach the bathypelagic zone, which exhibits really cold waters. This zone presents other physiological barriers, such as its relative hypoxic environment, which accounts for less than 6-8 times the respiration rates than the mesopelagic zone (Arístegui et al., 2005); high atmospheric pressures encountered at such depths, as well as high amount of organic matter flux. Indeed, whale sharks have been recorded at depths greater than 1900m, which account for almost 200 atmospheres of pressure (Tyminski et al., 2015). Furthermore, it can be noticed how internal states interplay at leading movements in whale sharks and the role of adaptation to a range of physical, chemical, oceanographic, and even anthropogenic pressures.

Viewed from the movement ecological model perspective, it seem that whale shark vertical movements follow different principal goals and the level of impact of the external factors vary among individuals and locations. On one hand, coastal swimming patterns commonly present a diel vertical migration (DVM) pattern, spending most of the time at the epipelagic zone, where the greatest part of their time is spent at the surface waters column above the 15m (Graham et al*.,* 2006; Wilson et al., 2006; Motta et al. 2010). At coastal areas, average daytime depths are greater than at night whether at the latter, occasional deeper dives are carried out. On the other hand, at oceanic waters whale sharks present a reversed DVM pattern. There, most of the time is spent at the mixed surface layer with the presence of abrupt changes in swimming patterns with deep dives during sunset and sunrise to the meso- and bathypelagic zones, deeper than 1,000m (Graham et al., 2006; Brunnschweiler et al., 2009; Gleiss et al., 2013; Tyminski et al., 2015).

Different locations have shown that movement patterns correlate with the bathymetric constraints presenting changings in the swimming patterns from coastal to free-ranging oceanic waters, as well as responding to oceanographic features and variations of water temperature. In the Ningaloo Reef, the retreat of the warm isotherm and the recirculation patterns of the Leeuwin Current/Ningaloo Current (Wilson et al., 2001, 2006) and in the Galápagos Islands at the Equatorial Front in the Pacific (Hearn et al*.,* 2016; Ryan et al*.,* 2017) or at the Indian Ocean where 90% of sightings occur between 26.5–30°C, showing a high correlation with spatial variation in sea surface temperature.

It has been assumed that reverse DVM patterns in oceanic waters may be to target mesopelagic prey and take advantage to feed on organisms of the deep scattering layer such as euphausiids, myctophids, squid, jellyfish, etc. (Wilson et al., 2006; Brierley 2014). Vertical migration patterns show a high influence of seasonality as shallower dives and swimming patterns are mainly observed during prey spawning periods, indicating that whale sharks might be following this as predictable food pulses (Graham et al., 2016). The daily shifts in vertical habitat use of planktivores is thought to be a direct response to the DVM of its prey (Sims et al., 2005). Additionally, thermo-biological frontal zones in the open ocean may be very important and a very effective way to concentrate food sources, whether high seasonal coastal productivity may be the strongest influence at coastal feeding aggregations (Ryan et al., 2017). Variation in vertical migratory patterns occurs as well as a mean of behavioral thermoregulation as whale sharks have shown the ability to tolerate a wide range of temperatures conserving their body heat (Tyminski et al., 2015, Nakamura et al., 2020).

As suggested previously, bottom bounce dives are one of the strategies used by whale sharks to reduce energy consumption by taking advantage of the cooler waters to reduce their metabolic rate (Gleiss et al., 2011; Thums et al., 2013). They act as well as a “survey behavior” in search of food along the water column to assist in moments of lower prey densities in the surface or subsurface layer in a cost efficient way (Cade et al., 2020). Meanwhile, deep V-dives have been considered to be a deep bottom foraging strategy as well as behavioral thermoregulation (Thums et al., 2013; Tyminski et al., 2015), furthermore being more efficient for horizontal traveling and to reduce transportation costs (Hearn et al., in press). Bottom bounce dives and V-dives are often related to offshore locations in oceanic waters where they are not restricted to bottom topology or bathymetry (Wilson et al., 2006; Brunnschweiler et al., 2009; Brunnschweiler & Sims, 2012).

In relation to whale shark horizontal movements, a variety of sighting patterns, records and peaks of occurrences in the different locations and aggregation areas have been gathered. Their distribution has shown to be mainly seasonal or periodical, whereas some locations present all-year round occurrences meanwhile others low residency and low re-sighting patterns. Seasonal occurrences are well known at the Galápagos Islands (Acuña-Marrero et al., 2014; Hearn et al., 2016), in Perú (Pajuelo et al., 2020), at the Ningaloo Reef, Western Australia (Wilson et al., 2001), in Azores, at the mid-Northern Atlantic (Afonso et al., 2014), at St. Helena Island (Clingham et al 2016), The Gulf of Tadjoura (Boldrocchi et al 2020), and in the Mafia Islands in the rainy season from Oct-May (Rohner et al., 2016). Furthermore, Sequeira et al., (2013) suggests the presence of a synchronous occurrence peaks at a global scale which can be seen in January, occurring at KwaZulu-Natal (South Africa), Djibouti and the Christmas Island (Australia). Moreover, from March to May in Gladden Spit (Belize), Gujarat (India), Ningaloo (Australia) and around the Philippines, and finally from August to October in Portugal (around the Azores), Mozambique, Seychelles and

Gulf of California, Mexico. These seasonal and periodical peaks of occurrences and aggregations have shown to be guided by oceanic, atmospheric, thermal or bathymetric conditions (e.g. monsoons, the isotherm, strengthening or changing oceanic current, etc.) or synchronized with different coral and fish spawning or upwelling events related to high primary productivity levels (e.g. Northern Perú (Gonzalez-Pestana et al., 2019), Ningaloo Reef (Wilson 2006), Belize (Heyman et al., 2001), yet re-sighting patterns depend on location.

Furthermore, other locations have reported several months to year-round occurrences of *R. typus.* This can be seen at Saint Peter and Saint Paul Archipelago, in the mid-Atlantic (Hazin et al., 2008), Cenderawasih Bay (Indonesia) (Meyers *et al. in press*), Maldives, Thailand, the Red Sea, Mozambique and Honduras (Norman *et al.* 2017). Additionally to mere occurrences, Tanzania has a unique pattern of long-term residency on such a small geographical area (Rohner et al., 2020), as well as the Maldives Maldives where whale sharks seem to present one of the highest re-sighting rates relative to other nearby locations. They usually remain closely to the area with periodical west to east movements to different regions of India and then back to the Maldives (Riley *et al*., 2010). In contrast, other regions present low re-sighting and short-term residency rates for instance, at the Darwin Island, in the Galapagos Marine Reserve (Acuña-Marrero 2014; Hearn et al., 2016) where female whale sharks seem to present a mean residence time of 2.09 ± 0.51 (mean ±SE) days as well as pretty low re-sighting patterns (Acuña-Marrero 2014).

Additionally, Andrzejaczek et al. (2016), analyzing the ecological connectivity in the Indian Ocean, they presented that overall, nearly two-thirds of whale sharks were observed in only 1 year at each site, with the remainder (35%) re-sighted at least once, Mozambique presenting the lowest re-sighting rate. Interestingly, from all the locations analyzed, it showed the highest proportion of female whale sharks (13.6%); whereas the Maldives with high residency and re-sighting rates, presents the lowest proportion of female whale sharks (3.3%). However, cryptic residency could be more common than previously thought, as when using visual identification, satellite and acoustic data, locations that were previously thought to present temporal occurrences, demonstrate to have longer rates and even year-round residency (Cagua et al., 2015; Andrzejaczek et al., 2016). These patterns clearly highlight the multidimensional characteristic of an individual's state as movement drivers, and for whale sharks, the high variability within the relative importance of different goals. This variability seems dependent on the individual's lifetime and/or sex, interplaying with the different external and physiological factors that vary geographically.

Coastal aggregations have been recorded around the globe consisting mainly of juvenile males or of both sexes, which has been noticed at Belize, Ningaloo Reef (Taylor, 1996; Wilson et al., 2002, 2006; Marcus et al., 2010), Sea of Cortez (Eckert & Stewart, 2001), Seychelles, Kenya, at the Gulf of Mexico (Tyminski et al., 2015), Gulf of California (Ketchum et al., 2013; Ramírez-Macías et al., 2017; Petatán-Ramírez et al., 2020), India (Borell et al., 2011), KwaZulu-Natal (REF),St. Helena (Clingham et al., 2016), northern Perú (Gonzalez-Pestana et al., 2019) Mozambique, the Maldives and at the Christmas Island (Andrzejaczek et al., 2016). Meanwhile, adults have been recorded at oceanic locations such as the Galapagos Islands (Acuña-Marrero et al., 2014; Hearn et al., 2016), Baja California Sur (Ramírez-Macías et al., 2017), Azores (Afonso et al., 2014), St. Helena Island (Clingham et al., 2016) and the Archipelagos de São Pedro and São Paulo (Macena & Hazin, 2016). Sexual and size segregation has been recorded in several locations, despite most of the tracks recorded to date have been of immature juvenile males. Nonetheless, locations like Al Shaheen in the Arabian Gulf of Oman (Robinson et al., 2016) and St Helena (Clingham et al., 2016) have presented aggregations of mature males and females and juvenile as well. However, sexually mature males as well as mating and pupping zones are still rare globally.

Moreover, large females with distended abdomens (suggested by some researchers to be pregnant), have been recorded at Galapagos Islands (Acuna et al., 2014; Hearn et al*.,* 2014; Norman et al., 2017), in the mid-Atlantic at the Gulf of Mexico and the St. Peter and St. Paul Archipelago (Hueter et al*.,* 2013; Macena, & Hazin, 2016), in Mozambique (Brunnschweiler et al. 2009), at St. Helena Island (Clingham et al., 2016), the Gulf of California (Ramírez-Macías et al., 2007), at the Sea of Cortez in the eastern Pacific (Eckertand & Stewart, 2001) and at Al Shaheen, Qatar (Robinson et al., 2016; Robinson et al. 2017). Neonates are rarely reported and most of them have been by incidental catch in purse seine and gill-net fisheries in the eastern Pacific, Atlantic (Wolfson, 1983; Pajuelo et al., 2020) and Indian Ocean (Rowat et al., 2008). There has been just one observation of free-swimming neonates at Sorgoson, Philippines (Aca & Schmidt, 2011), which has been suggested to be a possible nursery ground of the Indo-Pacific Ocean (Sequeira et al., 2013). Juveniles and neonate were also recently reported as by-catch from gill-net fisheries in northern Peru (Pajuelo et al., 2020). Satellite telemetry records of presumably pregnant females moving from the Galápagos Island to areas off the Peruvian northern shelf break (Hearn et al., 2013, 2016), suggest the possibility of the latter being a pupping ground (Pajuelo et al., 2020). The physiological state of the female whale sharks may play an important role to drive the directional movement towards this region as well as demonstrating an important connectivity in the eastern Pacific.

In this way, it can be seen how whale shark movement paths are a clear result from a dynamic interplay of the four basic components as leaders of movement – its internal state, motion and navigation capacities and the external factors influencing its movement. It can be noted as well, the way in which the level of importance of the main goal as leader of movement is dependent on the individual's life stage, as migratory and aggregation distributions patterns show a level of variation between individuals from the same tagging locations as well as between sexes and sizes (Sequeira et al., 2013; Hearn et al., 2016).

MAIN THREATS

The environmental changes led by various anthropogenic activities may present threats to the whale sharks movement ecology patterns, and directly or indirectly the different basic components that underlie them. This interference may consequently affect the ecological and evolutionary processes at which whale sharks are involved. Concerns of the effect they have on the different marine species have arisen due to the increasing amount of contaminants found in water resulting from bad wastewater treatments, and the amount of plastics disposed directly into the ocean on a yearly basis. Even though microplastics and ecotoxicological studies in top predator shark species are new fields, a varied number of them have been assessed in this matter in the blue shark (*Prionace glauca*), the pelagic thresher (*Alopias pelagicus*), the blacktip reef shark (*Carcharhinus melanopterus*) and the oceanic whitetip shark (*Carcharhinus longimanus*) (Lee et al., 2015). Nevertheless, little is known about toxic trace elements and microplastics ingestion in the filter-feeding whale sharks directly and indirectly via biomagnification due to the environmental contamination or via bioaccumulation by feeding. A recent study done in Djibouti of the elemental and organic contaminant loads in whale sharks' skin biopsies found that 62% of all the individuals tested exceeded the maximum residue limit for DDTs and for PCBs in fish set by U.S. EPA and by the EU regulation (Boldrocchi et al., 2020). These chemicals have been found to be harmful to the nervous and immune system, reproductive organs, the thyroid and kidney in its detoxification mechanism due to trace elements accumulation (Escobar-Sánchez et al., 2011; Boldrocchi et al., 2020). Whale sharks, due to their filter-feeding biology, tend to exhibit lower mercury concentrations with respect to carnivorous sharks (Pancaldi et al., 2019), it has being found that the organochlorine compounds (OCs) levels are comparable to those reported for predatory shark species Boldrocchi et al. (2020). These results highlight the need of further studies of the main sources of contamination of these compounds as well as the adverse health effects they might bring to whale sharks.

Moreover, an assessment of microplastic abundance at whale sharks and manta rays' feeding grounds and potential plastic ingestion rates in three different locations in Indonesia revealed that the greatest plastic ingestion of whale sharks is in Java with around 137 pieces per hour (Germanov et al., 2019). Even though these results use a theoretical estimated filter-feeding volume of 326 m^3 per hour (Motta et al., 2010), they give an idea of the magnitude of the potential risk that microplastics pose to whale sharks and other filter-feeding species. Plastic ingestion has also been recorded at Brazil, Thailand, Philippines, Malaysia and at the Sea of Cortez (Germanov et al., 2019). Modern investigations should focus on understanding the levels at which pollutants and plastics may influence the ecology of whale shark behavioral movements. Whether they might affect at a cognitive level, interfering with their navigation mechanism and internal state homeostasis and thus affecting movement-related decisions, or act as external factors driving changes in movement direction.

On the other hand, one of the main anthropogenic threats, which can be considered as an external factor influencing movement patterns and movement itself, is tuna purse-seine fisheries in which whale sharks are usually caught as by-catch. Whale sharks can enter as by-catch from either in non-targeted fishing strategies such as other mega-fauna associated sets (e.g. whale associated or dolphin associated sets), from free swimming school sets or artificial fish aggregate devices sets (FADs) and to a lesser extent from targeted "whale-shark association sets" (Escalle et al., 2016a; Escalle et al., 2017). Whale sharks have been long used as "free living FADs" for tuna fisheries and other highly targeted fish species by fisheries, have shown to aggregate near them, possibly explained by the "meeting point hypothesis" as an evolutionary advantage of schooling to reduce predation, higher food allocation and increase information transfer (Fontes et al., 2020). This fishing method encircles whale sharks with the associated tuna schools, which increase fishing efficiency, yet post-release long-term mortality has not been assessed. In a study done to evaluate immediate morality from whale-shark associated sets has been shown to be very low, at the Indian and Atlantic Oceans (1.38%) (Capietto et al., 2014; Escalle, 2017), and there have been no signs of unusual behavioral post-release effect in the short-term (Escalle et al., 2016b).

Even though it has been suggested that adult whale sharks have a good chance of post-release survival with the correct methodology for release operations detailed by Escalle et al. (2016b), there has not been a specific assessment on the impact for juveniles nor neonates as they might be more sensitive to these operations. In addition, there should be high concerns with neonates remarking the fact that most of their records come from purse seine and gill-net by-catch (Wolfson, 1983; Rowat et al., 2008; Pajuelo et al., 2020) and nursery grounds nor pupping stations have been firmly established. It is important to highlight that only one pregnant female reported so far was caught in Taiwan in 1995 carrying 300 embryos (Joung *et al.,* 1996), with several reports of large females with distended abdomens suggesting to be pregnant (Ramirez-Macias et al. 2012; Hearn et al., 2016). Nevertheless, a step forward on assessing the pregnancy state of whale sharks have been done at the Galápagos Islands, where the team of the Galapagos Whale Shark Project (GWSP), have completed the first underwater ultrasounds on free-swimming whale shark, as well as taken blood samples to confirm the ultrasound results (Gillespie, 2017). The lack of information about the impact and life history of the whale sharks, apart from their low reproduction rates and long gestation periods, represents high concerns at population characterization and risk assessment as well as in the development of conservation strategies to protect these species and their reproductive zones.

Furthermore, regarding fishing, it has been reported by skippers that whale sharks are often not detected before setting, leading to involuntary encirclement (Capietto et al. 2014).

Indeed, FADs have been found to present the highest rates of bycatch diversity, abundance (87-73%) compared to free school sets (41-32%), and whale shark sets (57-67%) (Escalle et al., 2019). In comparison to other type of sets, FADs and whale sharks sets seem to catch mainly juvenile yellowfin (*Thunnus albacares*) and bigeye tuna (*T. obesus*), and incidentally catch much larger bycatch (Escalle et al., 2016a). This results that these fishing methods not only threat whale sharks, but other fish populations as well. Thus, the identification of the main goals, influences and pressures underlying whale sharks' movements may be a very useful tool to develop conservation strategies that reduce risk pressures during fishing activities. For instance, it has been shown that at the seasonal aggregation hotspot in the Atlantic Ocean in the eastern Gulf of Guinea and in the Mozambique Channel in the Indian Ocean, whale sharks sightings and interactions match with fisheries hotspots concentrated areas (Capietto et al., 2014).

These hotspots presented high rates of incidental whale shark capture yet low apparent mortality. However, it is essential to determine long-term post-release behavioral side effects, such as modifications in the re-visiting patterns, feeding behaviours, vertical and horizontal movement patterns and possible displacement of feeding aggregation sites or even reproduction, as well as to estimate the possible hotspots of interaction between fisheries and whale sharks, based on environmental patterns and movement probabilities. This integrative analysis may be useful to establish a novel way to develop conservation strategies for this and other bycatch megafauna.

As it has been discussed previously, *R. typus* may direct their navigation towards spawning events or high densities of marine zooplankton following different auditory and olfactory cues (Heyman et al., 2001). As hearing capacity is a source of navigation for these animals, it is important to study the way in which the underwater noise produced in an anthropogenic way, mainly by vessels on the high seas, could be affecting the routes and migratory behaviours of this species. Many studies on the impact of underwater acoustics and noise on *R. typus* have focused on ecotourism and its impacts in coastal aggregation zones. For example, at Ningaloo Reef it was observed that the sound of tourists' boats caused some individuals to dive to great depths as an evasive behavior of these sounds and to avoid encounters (Martin, 2007). On the other hand, studies assessing the impact of this type of tourism on general behaviors of whale sharks showed an increase in stress levels and a reduction in feeding periods after encounters with boats and tourists (Montero-Quintana, et al., 2018). Despite this, no studies have evaluated nor measured the impact on oceanic areas derived from marine noise pollution from large fleets on the high seas and how this may be affecting migratory routes and behaviors during them.

During migrations, individuals perform both horizontal and vertical movements along the body of water, so it is important to evaluate the impact on these two dimensions of movement. Since in oceanic waters *R. typus* does not present impediments due to bathymetry, it has deeper vertical movements and even takes advantage of feeding on prey in the depths. Due to this diving character for feeding *R. typus*, it is important to evaluate to what extent the presence of high seas fleet's influences vertical feeding patterns, and whether these patterns are derived from environmental noise or are common diving patterns. However, the scarce information about the high seas movements of this species, mainly of adult males, as well as the breeding and reproduction areas, is a limitation.

CONCLUSIONS

In general, some primary movement categories and the relationship of them with different factors have been identified. For instance, at the Cenderawasih Bay, within and near bay, at adjacent coastal area, and offshore at deeper oceanic waters (Meyers at al., 2020) or at at Kilindoni Bay (Rohner et al., 2020), where primary production and food availability at coastal areas seems to be the primary driver for this distribution; which has been noticed as a general pattern at different global coastal aggregations as summarized in *Table 1* below. Despite this, individual variability within studies suggests that despite food availability, and other factors such as bathymetry and temperature, as the primary leaders of these movements, they may not fully explain whale shark's spatial distribution. Results over time suggests as well that not only there may be other factors driving movement, but that they might be location-dependent, further than following general patterns by sex or life stage.

Table 1. **Summary of the coastal aggregation sites that have linked as main driver for these patterns primary productivity and food availability.** This table provides the names and locations of the studies with the sourced where the information has been retrieved.

Aggregation location	**Sources**
Baja California Norte, Mexico	Nelson & Eckert (2007)
Belize	Heyman et al. (2001)
Cabo Catoche, Mexico	de la Parra Venegas et al. (2011)
Cenderawasih Bay, Indonesia	Rohner et al., 2020
Christmas Island	Hobbs, et al. (2009)
Costa Rica	Pachecho-Polanco et al. (2015)
Gulf of California, Mexico	Ramírez-Macías et al. (2012), Ketchum et al. (2013) and Petatán-Ramírez et al. (2020)
Gulf of Mexico, Mexico	Tyminski et al. (2015)
India	Borell et al. (2011)
Kilindoni Bay, Tanzania	Rohner et al., 2020
Madagascar	Jonahson & Harding (2007)
Mafia Island, Tanzania	Rohner et al. (2015)
Mozambique	Roner et al. (2013) and Roner et al. (2018)
Western Australia	Taylor (1996), Wilson et al. (2002), Wilson et al. (2006), Marcus et al. (2010) and Norman et al. (2016)

A long history of observations, records, tracking, and more recently, DNA analysis have elucidated the complexity of *Rhincodon typus* movement ecology. Even though association between temperature, life-stage, primary production, distribution with whale sharks' movements has been examined, often these parameters have been studied independently from each other, or some have not been assessed at all. To deepen the understanding of the movement ecology of these migratory giants, the relative importance of the different physiological factors as leaders of movement in each moment needs to be explored under a cohesive integrative model with the other paradigm components.

There is certain lack of knowledge of some distributions and understanding of the main purpose of movements such as of pregnant females, neonates, oceanic male adults, matting and pupping zones, additionally to the intrinsic complexities tracking them in a long-term. Yet, determining the relative proximate goals associated with movement patterns is key for understanding the way whale sharks take advantage and move along the different environmental oceanic characteristics and might respond to variations in it. Therefore, developing an integrative study model that quantifies the magnitude of force of the physiological, biomechanical and environmental factors, and the way in which relative importance of the different goals change along life stages, will serve as a tool to better understand the movement pattern despite the great variability present between individuals. If we understand why they move to certain places, their motion and navigation advantages and limitations, in the presence of an anthropogenic or environmental disturbance, for instance climate change, it might be easier to predict their movement directions and behaviors and therefore know in which way we can approach in the development of conservation strategies.

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