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Decoding fishery survival rates and use of space of smooth hounds (*Mustelus mustelus* and *Mustelus punctulatus*) and spiny dogfish (*Squalus acanthias*) with a sentinel acoustic array in the northern Adriatic Sea

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Abstract

Sharks, rays and skates have been declining worldwide, particularly in heavily exploited basins such as the Mediterranean Sea. Overfishing and bycatch are the major reasons, taking advantage of these animals' innately sensitive life-history characteristics. Various management measures have the capacity to reduce the impact of such threats but require ample scientific data. This study utilized acoustic telemetry tools to study fishing survival and use of space of commercially important demersal shark species (*Mustelus mustelus*, *Mustelus punctulatus*, and *Squalus acanthias*) in the northern Adriatic Sea. Tagged with the help of chartered fishing vessels, 46 out of 85 individuals were detected over a sentinel array of acoustic receivers. Evidence of tag detachment was found in at least two individuals. Those released in better health conditions were detected in higher proportions and had high (61-100%) estimated survival ratios. It took longer than the expected period of recovery time (2-14 days) to detect animals, especially for the more mobile *S. acanthias*. Differences in use of space between and within species were observed, with residency being higher for smooth hounds (*M. mustelus* and *M. punctulatus*), and adult *M. mustelus* visiting more stations than their juvenile counterparts. Site fidelity was evident in one *M. mustelus* female. Temperature and refuge from fishing activities are proposed as important drivers of shark movement, which has implications for local fishing regulations, though more research is needed before defining strategies such as MPAs.

1.0 Introduction

1.1 Biodiversity and vulnerability of sharks

Sharks, rays, and skates – collectively making up the Elasmobranchii subclass of Chondrichthyes (also known as cartilaginous fish) – have an evolutionary history that predates many other extant megafauna, estimated to have appeared over 350 million years ago in the Devonian (Frey et al. 2019). Today, there exists around 1200 species of elasmobranchs, varied in terms of shapes, size and habitat. Elasmobranch diversity is particularly evident in sharks, which range in length from 19-meter planktivorous whale sharks (*Rhincodon typus*) to 20-centimeter bioluminescent dwarf lanternsharks (*Etmopterus luciferus*). Such a variety allows species to occupy different niches and perform herbivorous, predatory, omnivorous or scavenging roles (Fowler et al. 2005). Regardless of size or trophic level, elasmobranchs often play important ecological roles, shaping communities around them via diverse diets and top-down regulation effects that create complex environmental networks (Bornatowski et al. 2014; Ferretti et al. 2010). Like many ocean predators, they have experienced an important decline in biomass since pre-industrial times (Myers & Worm 2003). According to the International Union for Conservation of Nature (IUCN), over a third of Chondrichthyes are considered vulnerable, endangered, or threatened with extinction (IUCN 2023). Their life history characteristics, meaning their relatively slower growth, later maturation age, and longer gestation times, coupled with lower fecundity in comparison to bony fish, are what make them particularly vulnerable (Myers & Worm 2005). This is especially true for species of commercial importance, those that use unique habitats, and applies to smaller species as well, not just large-bodied predators (García et al. 2008).

1.2 Anthropogenic activities as stressors

Exposure to habitat loss, degradation, events such as oil spills (Romo-Curiel et al. 2022), and the impacts of climate change are important threats to shark species, particularly in coastal waters near the equator (Dulvy et al. 2021). But while part of the drastic decline in elasmobranch biodiversity can be explained by these factors (Barausse et al. 2014), the consensus in the scientific community is that overfishing by target and unintentional (i.e.: bycatch) fisheries are the primary causes (Dulvy et al. 2021). Aside from the fact that sharks are often sought-after for their fins in Asian markets, the more general demand for shark meat globally and high bycatch rates are equally concerning. Unfortunately, the true extent of fisheries exploitation is difficult to measure due to poor stock data, illegal catches, and un or under-reporting; however, researchers estimate that it results in the death of anywhere between 63 and 273 million sharks per year (Worm et al. 2013). Due to their innate vulnerability, it is said that recovery from even light fishing pressure is difficult (Ferretti et al. 2010; Worm et al. 2013). Indeed, elasmobranchs are often born at larger sizes than most bony fish (Freedman & Noakes 2002), and since fisheries select for larger individuals, they are inherently at risk of bycatch. This means that sexually mature elasmobranch females, which contribute to their species' cohort and recruitment, will be disproportionately caught, regardless of whether they are relatively small for their species or if they are older and bigger (Big Old Fat Fecund Female Fish, BOFFFFs; Hixon et al. 2014).

Additionally, it has been shown that many elasmobranch species will perform capture and stress-induced parturition, a phenomenon where young are aborted by females, even prematurely, under stressful conditions such as being caught in nets and handled (Adams et al. 2018). Finally, even if subsequently released, individual survival is often unknown or greatly variable, depending on species, sex, size, and capture technique (Ellis et al. 2017; Musyl & Gilman 2019). Not to mention that secondary and tertiary effects of stress, such as homeostatic disruptions (e.g. ionic and osmotic balance) and eventual changes to growth rates, reproductive output, and disease resistance, are still largely unknown or understudied (Skomal & Mandelman 2012). Thus, the resulting picture is that fisheries of all kinds pose an important threat to sharks.

1.3 Current measures to protect sharks

Regarding management of commercial elasmobranch species, measures such as catch limits (called quotas), or gear restrictions are employed in certain fisheries to maintain population sizes and be as sustainable as possible (DFO 2018; NOAA 2024). The European Union publishes a report each year for fisheries within Union waters, with recent versions promoting being as conservative as possible in Total Allowable Catches (TACs) of elasmobranchs, as their population stock size is often poor or unknown. They also call for the immediate release of certain bycatch species and prohibit the catch of certain ones, like deep-water sharks (EU 2023). Other protection measures for commercial elasmobranchs include temporal or size restrictions, ensuring that young in nurseries or pregnant females are not caught during pupping season (Australian Fisheries Management Authority 2015; Ministry of Fisheries 2008). Of course, every measure has its benefits and downfalls, with implementation being one of the most difficult hurdles to overcome, often because of socio-economic barriers (Booth et al. 2019). Area-based protections are a solution that have been at the forefront of recent biodiversity conservation talks, and various goals for the upcoming decades have been established (e.g.: at least 10% of coastal and marine areas effectively conserved by 2020, or more recently, 30% of the planet by 2030; CBD 2010; IUCN 2022).

According to the National Oceanographic Atmospheric Administration of the United States of America, a Marine Protected Area, or MPA, is a specific marine region that is managed in such a way to protect its resources – this includes species, habitats, and ecosystems – in the long-term (NOAA 2019). Though the designation of MPAs has increased exponentially in the last decades (Worm 2017; Lubchenco & Grorud-Colvert 2015), there exists different types of MPAs, all offering different levels of protection. And while governing bodies often use different naming systems and definitions, "no-take" or "fully protected" areas are the strictest of all (Marine Conservation Institute 2024). In 2022, in response to the lack of inclusion of sharks into identification of important sites for biodiversity, a set of four criteria were laid out, dubbed the Important Shark and Ray Area (ISRA), to pin-point three-dimensional regions for Chondrichthyes protection. The four criteria focus on vulnerable and range-restricted species, as well as areas critical for specific life-history functions and with distinctive, unique attributes (Hyde et al. 2022). But while researchers and decision-makers can now more easily determine which regions are of higher priority for elasmobranch conservation, this requires ample scientific data a priori. In particular, it requires specific knowledge of where animals are, where they are coming from, where they are going, and what they are doing while in the area. The same can be said for fishing restrictions.

1.4 Shark movement ecology

Animals move through their environment for an array of reasons, though mainly to take advantage of resources and find shelter, food, and mates. When their movement is persistent and directional, disrupting regular behaviour, it can be considered a migration (Dingle & Drake 2007). Migrations play an important role in species' population ecology, influencing births and deaths. However, it is important to note that there are different types of migrations (e.g. annual, round-trip, partial, …) and that inter-individual variability is significant, meaning not all individuals of a species will display the same movement patterns. This is true across taxa (Dingle & Drake 2007). Yet, in one way or another, migrations have been observed in elasmobranchs worldwide. The Convention on Migratory Species' (CMS) Memorandum of Understanding on the Conservation of Migratory Sharks (called the Sharks MOU) outlies a list of migratory shark, ray, and skate species that must be appropriately managed by Signatories across the world. This list includes twenty species of rays, large pelagic species like basking sharks, whale sharks, and white sharks, and even smaller species such as spiny dogfish (IUCN 2021). The tiger shark (*Galeocerdo cuvier*) is a compelling example of elasmobranch migration, as research shows that individuals can cover several thousands of kilometers over the northwest Atlantic Ocean when undergoing their round-trip annual migration, supposedly for foraging. In general, migrations can align with the seasons, meaning a change in temperature or irradiance, for instance, can trigger long-range movement, or rather with an internal physiological cue, such as achieving sexual maturity (Bauer et al. 2011). Sometimes, large aggregations of individuals will take place, motivated by social facilitation, mating, or parturition, a behaviour identified in various oceanic elasmobranchs (Chapman et al. 2015).

Additionally, many species are known to preferentially return to their site of birth, a phenomenon known as philopatry; specifically, natal philopatry if the individual returns to its exact birthplace, or regional philopatry if it returns to the general region of its birth (Chapman et al. 2015). Similarly, the term site fidelity is used to describe animals returning to an area they previously resided in after long periods away. Both site fidelity and philopatry have been documented in sharks: for instance, blacktip reef shark (*Carcharinus melanopterus*) females around French Polynesia traverse long distances to reach parturition sites that genetic studies indicate are linked to their own natal sites (Mourier & Planes 2012). Evidence shows that even long-range, wandering species such as blue sharks show philopatry (Fontes et al. 2024). While philopatry is not ubiquitous in the natural world, in theory, it might incur some benefits for animals, such as buffering against the unpredictability of resources (Fontes et al. 2024) and maintaining genetically distinct groups, potentially increasing a species' overall genetic diversity (Elizondo-Sancho et al. 2022). Nevertheless, these behaviours can also increase sharks' vulnerability, as individuals risk returning to an area that has since been degraded and is not suitable for foraging anymore, may lack the gene flow between populations to adapt to changing conditions (Elizondo-Sancho et al. 2022), and can be increasingly targeted by fisheries at their known aggregation sites (Chapman et al. 2015). Protecting marine migratory species is thus especially tricky, as animals can easily cross international boundaries and encounter different levels of anthropogenic threats, requiring cooperation from different States (Lascelles et al. 2014). To better support efforts like the CMS Shark MOU, extensive research on their movements and use of space must be conducted, something that is dependent on our ability to use the right tools and technology.

1.5 Acoustic telemetry as a tool

Acoustic telemetry is considered a useful tool in aquatic animal studies to determine use of space patterns and set up areas of protection and can also be used to solve a variety of other problems, including but not limited to illegal poaching, response to changing conditions, and habitat restoration (Alós et al. 2022). Essentially, this methodology consists of equipping animals (either internally or externally) with tags that have unique identifying codes and emit low-frequency sounds at a consistent rate. Using an array of listening devices, receivers, we can register these when the animal comes within a specific range (Heupel et al. 2006). The tags and receivers themselves can also be equipped with other sensors, such as temperature, depth, and salinity sensors, to provide further site and time-specific information. As opposed to pop-up archival satellite tags (SAT tags), which have a low resolution and can only be retrieved once the tag floats to the surface and communicates its position via satellite, acoustic telemetry can, depending on the receiver array set-up, show fine-scale patterns of animal movement. This is also different from smart position or temperature transmission tags (SPOT tags), which require the animal to come to the surface to transmit data to a satellite and is thus not useful for all species (Hammerschlag et al. 2011). Like any methodology, it has its particularities (number of receivers needed, receivers' placement, tag loss, and more; Heupel et al. 2006), but the main specificities are that the individual must be near the receivers to be detected in the first place, and that the water conditions are suitable (i.e.: low biotic and abiotic noise) for detections to occur. Nonetheless, acoustic telemetry is particularly useful for behavioural studies of animals that are not always readily available for observation, and researchers are using it to study and inform management of elasmobranch species worldwide (Martínez-Ramírez et al. 2024; van Zinnicq Bergmann et al. 2022; Edwards et al. 2022).

1.6 Northern Adriatic species

According to the IUCN, 40% of the evaluated elasmobranch species in European waters are listed as threatened, while approximately 20% are considered data deficient (Nieto et al. 2015). The Adriatic Sea is a heavily exploited basin of the Mediterranean with a long history of coastal change and exploitation, and where large predators, including sharks and rays but also cetaceans and pinnipeds, have been strongly depleted since Roman times (Lotze et al. 2011). Historical data analysis and ecosystem models show that a variety of large-sized pelagic sharks were found and fished in the northern Adriatic up until the mid-20th century, but that the occurrences of the largest species, such as hammerhead, mackerel, thresher, and blue sharks, have seen steep declines of 96-99% in the last century (Lotze et al. 2011), such that they are virtually lost today. While fishing in the Adriatic developed unevenly between the western and eastern sides, with the eastern Croatian coast being slightly less degraded, studies suggest that there have occurred changes in community composition throughout the entire northern Adriatic in response to the historically targeted species' weak recovery potential and excessive fishing (Ferretti et al. 2013). This general decrease in elasmobranch diversity and abundance (Barausse et al. 2014) results in a remaining community that is composed of mostly smaller-bodied demersal species like catsharks, brown skates, and smooth hounds remain, even in the lesser exploited eastern Croatian coast of the Adriatic (Ferretti et al. 2013). However, temporary increases in these species resulting from competitor or predator releases do not indicate a recovering ecosystem, as the shifting baseline syndrome might indicate (i.e. phenomenon where a gradually changing environment only gets studied and compared to an earlier, but not pristine, ecosystem; Pauly 1995). In fact, studies have found that mesopredator elasmobranch populations are also struggling. Long-term time-series of fish market landings and surveys show that the Catch Per Unit Effort of even the smaller catsharks, skates, and shark species in general are unstable and have been declining in the northern Adriatic since the 1940's, or, in the case of spiny dogfish, since the last decade (Barausse et al. 2014; Bargione et al. 2019). The reality is that protection of both target and by-catch Chondrichthyan species is challenging in the Adriatic, considering there are several different countries with varying and sometimes inconsistent policies and regulations sharing the same resources (Giovos et al. 2024).

Located in the northern Adriatic at the base of the productive Venice lagoon, the Chioggia port accounts for most of the seafood weight traded in the Veneto region of Italy (~ 14,035 tonnes in 2012) and is home to the region's major fishing fleet, containing vessels heavier than the national average (Semrau 2012). These vessels deploy a variety of fishing gears, including longlines, purse seines, bottom otter trawls, and hydraulic dredges, and they fish a variety of vertebrate and invertebrate animals. Over 60% of the elasmobranch landings at the Chioggia fish market between 2006 to 2013, which included 14 species of sharks, rays, and skates, was composed of two smooth-hound species: the common smooth-hound *Mustelus mustelus* and the blackspotted smooth-hound *Mustelus punctulatus*. The two are small (35-160 cm for *M. mustelus*, 38-190 cm for *M. punctulatus*) placental viviparous sharks found across the Eastern Atlantic that occupy similar sandy or muddy coastal habitats, up to 200 meters deep (Serena 2005). Considered vulnerable species by the IUCN, they are both often caught in gillnets and bottom trawls as bycatch and give birth from April-May (Riginella et al. 2020). A similarly sized species also found at the Chioggia market is the spiny dogfish *Squalus acanthias*. These ovoviviparous sharks are slightly smaller than the *Mustelus* spp. (25-105 cm) and tend to live on soft bottoms anywhere from 10-700 meters deep (Serena 2005; Capapé & Reynaud 2011). Considered endangered by the IUCN in the Mediterranean but found throughout the Atlantic and Indo-Pacific as well, spiny dogfish are suggested to be more migratory. They have a later summer reproductive season, though their life-history traits in the region might deviate a bit from what is found elsewhere in their range (Bargione et al. 2019). Despite these slight differences, both species of smooth-hound overlap in time and space with spiny dogfish, being caught incidentally in the northern Adriatic in summer at similar depths (Bonanomi et al. 2018). Since life-history traits, habitat use, and vulnerability to anthropogenic activities are intrinsically related, it is important for us to better understand these three demersal species’ movement through the same area; whether they have certain unique preferences or behaviours, and how exactly they are affected by fishery pressure.

1.7 Goals of the study

The goal of this study was to provide scientific support for decision-makers and Fisheries Management to better protect demersal shark species, such as *M. mustelus*, *M. punctulatus*, and *S. acanthias* in the northern Adriatic.

Specifically, this work aims to:

1) quantify post-tagging survival to understand if the release of by-caught individuals following capture stress may provide an effective protection measure
2) explore use of space in terms of movement and residency to characterize inter and intra-specific behaviour and environmental preferences, informing future management measures

2.0 Materials and Methods

2.1 Study area

The northern Adriatic Sea is a narrow sub-basin of the Mediterranean Sea, limited by Italy, Croatia, and Slovenia. It is characterized by shallow depths (on average 30 meters and up to 100 meters at its southernmost end), nutrient and freshwater inputs, and intense human use (Barausse et al. 2011; Lotze et al. 2011). The northernmost region of this sub-basin is considered eutrophic, experiencing frequent algal blooms, including toxin-producing diatoms and dinoflagellates (Tsikoti & Genistaris 2021). On the Italian side, this basin is bordered by the agricultural hotspots of Friuli Venezia Giulia, Veneto, and Emilia Romagna regions, and is watered by the Po River and other minor rivers, all emptying in the Po Delta near the Venice lagoon. Thus, a gradient of primary productivity as well as benthos sediment is visible in the northern Adriatic – starting from highly productive, sandy and muddy waters in the north-east of the basin, to less productive and rocky deeper waters eastwards. Interseasonal temperature, salinity, and circulation variations are apparent, with water temperatures varying nearly 20 degrees between summer and winter, and hydrology being greatly impacted by climatology and wind cycles (Russo & Artegiani 1996). All of these combined lead to water column stratification from April to October and mixing in the following winter months (Giani et al. 2012).

2.2 Receiver array

Our hydrophones were set up as a sort of sentinel array (also called 'fisheries' format, or non-positional design), meaning the acoustic receivers' detection ranges did not overlap, thus creating presence/absence data when an animal was detected, rather than exact positions (Heupel et al. 2006; Kessel et al. 2013). The sentinel array consisted of 15 Innovasea VR2Tx hydrophones deployed between ~3 and ~30 km from the coast near Venice and Chioggia-Sottomarina (Figure 1). The placement of the receivers was, in some way, opportunistic, choosing locations where they were least likely to become detached, lost, or tampered with due to fishing activities. All receivers were located 15 to 27 meters deep (average depth 22.3 meters). Receivers were deployed and recovered at different times due to challenging field conditions (Table 1). Receivers 5.1 and 8.1 were changed to different locations after some time: 5.1 was changed due to the high risk of detachment at its original station, and 8.1 was changed because of the reactivation of a close by, busy gas platform. The former became receiver number 5.2, and the latter was used to study hydrophone detection ranges under different conditions. Receivers 3 and 5.2 were lost sometime after being last recovered in June 2023. All receivers were deployed and recovered in accordance with Innovasea's user guidelines, secured with cable ties and nylon rope, and covered in sheer tights and tape to facilitate handling.

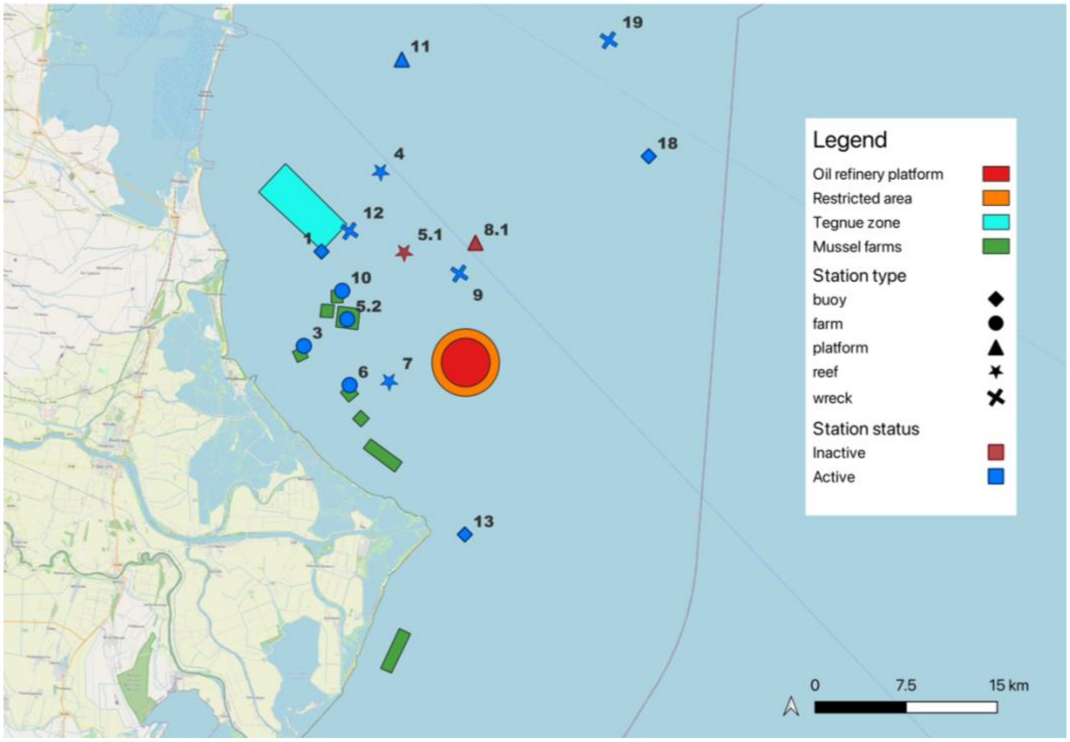


Figure 1 Map of study area (northern Adriatic Sea, between the Venice lagoon Po Delta) with receivers' locations (called "stations"), coloured by type and status, and surrounding marine activity areas

Table 1 Receivers' location, information, and deployment/last retrieval dates. Inactive receivers are greyed out; asteria indicate receivers excluded from some Residency Index calculations (see formulae 1.2 and 2 below)

Receiver (station number)	Latitude, Longitude	Depth (m)	Distance from coast (km)	Type	Deployed	Retrieved
1	45°10.2023, 12°25.8150	23.3	7.8	Buoy	2022-05-13	2024-06-03
3	45°05.9833, 12°24.8961	20.3	5	Mussel farm	2022-06-03	2023-06-08
4	45°13.8192, 12°29.3715	21.5	14.6	Rocky reef	2022-05-13	2024-06-04
5.1*	45°10.2711, 12°31.0037	25	14.6	Rocky reef	2022-05-13	2022-10-28
5.2	45°07.2309, 12°27.5631	23	10.1	Mussel farm	2022-10-30	2023-06-07
6	45°04.3107, 12°27.8463	23.8	5.8	Mussel farm	2022-06-03	2023-06-08
7	45°04.5196, 12°30.3149	26	8.3	Rocky reef	2022-06-03	2023-06-08
8.1*	45°10.808, 12°35.473	24.7	20.5	Platform	2022-06-03	2022-12-08
9	45°09.4112, 12°34.5193	24.7	19.5	Wreck	2022-06-03	2024-06-05
10	45°08.4874, 12°27.1937	22.3	9.9	Mussel farm	2022-06-03	2024-06-05
11	45°18.8513, 12°30.4902	16	14	Platform	2022-10-30	2023-07-08
12*	45°11.1499, 12°27.5333	15	10.2	Wreck	2023-04-22	2024-06-03
13*	44°57.8290, 12°35.3500	19.5	2.8	Buoy	2023-07-11	2024-06-06
18*	45°14.8666, 12°46.2148	27.4	29.6	Buoy	2023-07-08	2024-06-04
19*	45°19.9718, 12°43.4937	21.4	19.7	Wreck	2023-07-08	2024-06-04

Three separate tests were performed to determine the receivers' detection range in the study area; the first two prior to the start of shark tagging, the third at the same time as the other receivers' deployment. The first test consisted of placing four acoustic receivers in a line at different distances (50m, 100m, 300m, and 400m) from the two types of tags used in the study (V13-1x and V9-2x 69kHz Innovasea tags) to find their

50% detection range. The latter is defined by the manufacturer as the distance at which half of the emitted signals are recorded by a receiver (see https://support.fishtracking.innovasea.com). Results from the first test showed that most signals were recorded by our receivers at a range between 360-400 meters (Annex Figure A1; Mazzoldi unpub. data). The second test had the same setup but compared how receivers would detect emissions from tags covered with a non-toxic antifouling dye and tags without dye, as the manufacturer provides them. This was important to study, since biofouling on external tags can create drag, negatively affecting the animal and tag retention over time (Dicken et al. 2006). Results from this second test showed that, in estuarine waters, tags covered by the dye had a signal transmission on the lower end of the detection range (~360 meters; Annex Figure A2). For the third and last test, two receivers were deployed (one at approximately 200m and the other at the 50% detection range) from April to July 2024, to determine the long-term detection range and study the effect of varying environmental conditions. Overall, there were no significant changes in detection rate with temperature over time (Annex Figure A3). For these three tests, the tags were set up to emit a long-lasting transmission, every 10 seconds. Performing further tests was outside the scope of our thesis.

2.3 Tagging sharks

105 individuals (*M. mustelus* n = 38, *M. punctulatus* n = 23, *S. acanthias* n = 44) were caught by local fishers as bycatch using otter trawls (n = 22) or as target species using 60 mm gill nets (n = 71), or trammel nets (n = 12). Sharks' sex was identified, and individuals' total length was measured in centimeters. Sharks were

tagged externally with either a V13-1x or a V9-2x 69kHz Innovasea tag (hereafter called a V13 or V9 tag, respectively), depending on their size. Tags were covered with a non-toxic antifouling dye prior to attachment. V13 tags (30.5 mm long) were used for individuals that were deemed near-fully grown, and V9 tags (27.5 mm long) were used on smaller individuals (i.e. total length below ~70 cm for *M. punctulatus* and *S. acanthias*, or ~74 cm for *M. mustelus*) who could still grow significantly, to try to minimize negative tagging effects (Jepsen et al. 2015). Generally, *M. mustelus* are considered adult at 108.1 cm for males and 121.2 cm for females, *M. punctulatus* at 91.3 cm for males and 109.9 cm for females, and *S. acanthias* at 57.5 cm and 65.9 cm, respectively (Riginella et al. 2020; Bargione et al. 2019). Methodology to attach the tags was adapted from Jepsen et al. (2015). Both tags were attached using fishing line to the base of the shark's dorsal fin – V13 tags used two anchor points ~3 cm apart, while the smaller V9 tags used a single anchor point, thicker fishing line, and disks to minimize friction with the skin (Figure 2). Threads were knotted on the other side of the suture entry points and secured with a small metal clasp. The methodology for attaching V9 tags in 2022 was different and deemed less effective, so these individuals (n = 20) were discarded from our data analysis later. The V13 and V9 tags had estimated battery lives of 633 and 354 days, respectively, and emitted a unique signal every 2 nominal minutes (range of 90-150 seconds). The random nature of these signal emissions was to, as much as possible, avoid signal collisions and thus the creation of false signal IDs. All animals were also tagged with a conventional spaghetti tag below the dorsal fin along the mid-body. Upon release, individuals were given a number from 1 (highest/best) to 4 (lowest/worst) as a "vitality score", as seen in Ellis et al. (2017): 1

meant “Excellent” (vigorous body movements, movement of spiracles/gills), 2 meant “Good/fair” (weak body movements, poor spiracle/gill movement), 3 meant “Poor” (no body movements, limited spiracle/gill movement), and 4 meant “Moribund/Dead” (absence of body and spiracle/gill movement). When in doubt, a worse health state was assumed, and the lower vitality score was assigned. Note that we tagged individuals that were caught, and then released, in proximity of the receivers’ array and during normal fishery procedures, so additional precautions or methods related to the use of fishing gear in the area were out of our control.

Figure 2 Example tagging procedures of a V13 tag (top) and V9 tag (bottom). Conventional spaghetti tag visible in yellow; disks to minimize friction visible by V9 tag. All procedures followed ethics permits regulations

2.4 Ethics statement

All individuals were tagged and handled following the regulations on animal ethics in experiments– the required permit (prot. n 20247, date 07/02/2022) was obtained from University of Padova OPBA.

2.5 Data cleaning and checks

Once offloaded, data from the receivers were manually checked to, first, remove detections of the receivers' internal sync tags (which serve as a confirmation that the receiver is functioning as expected), and second, remove any detections not corresponding to the sharks that we tagged in this study. We refer to a "detection" as a singular signal transmission (made up of 8-10 pings, according to the manufacturer) associated to a specific tag ID and recorded at a receiver with a date and time in UTC. Receivers' temperature and noise data, recorded every hour once a receiver is deployed, was extracted as well. The latter was used to perform a check on ambient noise at each receiver (hereafter named "station"), where any noise beyond 650 mV was considered "high" and would make detection data unreliable (see https://support.fishtracking.innovasea.com). A second round of data cleaning was performed on detections using the 'false_detections' function from R package 'glatos' (Holbrook et al. 2024) to remove false detections (i.e. two or more detections from the same tag recorded at time intervals shorter than the set threshold, or 30 times the tag's emission rate; Pincock 2012).

At this point, detections from individuals tagged with a V9 tag in 2022 were excluded from further analyses, as explained in section 2.3. Abacus plots were then created for every remaining individual in the study to closely inspect movement patterns and try to identify potential tag shedding/death. Patterns were analysed with the help of Martínez-Ramirez et al.'s (2024) and Villega-Ríos et al.'s (2020) findings on individual fate inference from acoustic telemetry. Study length from release (interval between release and last detection), number of detection events (number of occasions on which an individual was detected multiple times within a day at a specific station), and average detection event length were calculated to help single out individuals with patterns resembling tag detachment. Abacus plots with a long detection event at a single station, followed by no more detections for the rest of the study (e.g. Annex Figure A4), were our best identifier of potential detached tags. All analyses were run both including and excluding individuals who were believed to exhibit tag detachment to determine whether results varied.

Individuals detected were plotted by species, age, and maturity for better visualization. Chi square tests were performed to ensure that the number of 'detected' versus 'undetected' individuals across species, vitality scores, and per species (for males/females and adults/juveniles) showed no discrepancies with the amount that should have been detected given the number of individuals tagged in each category (Annex Table A2).

2.6 Data analysis

2.6.1 Survival estimates

The proportion of individuals detected by species and vitality score were plotted at the end of the study (Figure 4) and over time (Figure 5) to determine if there was a particular time by which mortality events would occur, or by when individuals likely recovered from the stress of being caught, tagged, and released and resumed normal movement around the sentinel array.

For all three species, survival ratios were calculated for individuals with vitality scores 2 and 3 to determine their relative survival compared to individuals with vitality score 1, as per Hueter et al. (2006). According to the authors, if all individuals fully recover after a given period of time, tagging affects individuals equally, and all vitality scores have the same "catchability" coefficient (or, in our case, detection probability), we can find the proportion of individuals that will survive in relation to those released in "ideal" conditions. These ratios were calculated by dividing the ratio of detected individuals (e.g. D_2/D_1) by that of tagged individuals (e.g. T_2/T_1) for each vitality score, as in the following formula:

$$\frac{D_2}{D_1} / \frac{T_2}{T_1} = R_2$$

Where, for a given species, R_2 is the survival ratio of individuals with vitality score 2, and R_3 is the survival ratio for those with vitality score 3 (Table 3). 95% confidence intervals of these values were also calculated.

2.6.2 Use of space

We used the number of unique stations visited by individuals as proxies of their movement and use of space, meaning a greater number of stations visited indicates a more active individual that moves more throughout the study area. These values were then averaged per species, sex, and maturity and plotted (Figure 6). Since our data failed to meet the normality assumptions of ANOVA, non-parametric tests on the average number of stations visited were performed to compare values across groups (Table 3). A Kruskal-Wallis test (equivalent to a one-way ANOVA) was performed to compare values across the three species, and Scheirer-Ray-Hare tests (equivalent to a two-way ANOVA) were performed to evaluate how the interactions between species, sex, and maturity influence these values. If significance was found for any group or interaction, a pairwise Wilcox test was performed to determine which pair showed statistically significant differences between their average number of stations visited.

Three different Residency Indices were then calculated for each species using the following formulas from Kraft et al. (2023):

1.1) $I_R = D_d/D_i$

1.2) $I_R = D_d/D_t$

2) Weighted Residency Index: $I_{WR} = \frac{D_d}{D_t} \times \frac{D_d}{D_i}$

Where D_d is the total number of days an individual was detected, D_i is the detection interval, or the number of days between an individual's first and last detection, and D_t is the study interval, meaning the number of days in the study (time between tagging date and last monitoring day). The first and last monitoring days for D_t calculation were determined to be October 22nd, 2022, and June 30th, 2023, respectively, as this was the period for which most of the receivers had a continuous deployment. The values of I_R and I_{WR} can only be between 0 (no residency) and 1 (full residency). The three formulas were used, as they have their own considerations; formula 1.1 represents a maximal residency index but can overestimate residency if the first and last detection days are close to each other, while formula 1.2 and formula 2 are more conservative, taking into consideration the study interval. 95% confidence intervals of these values were also calculated. Lastly, to visualize the animals' movement in the study area throughout the study period and support Residency Indices findings, an abacus plot of all detections was created (Figure 7).

2.6.3 Environmental preferences

Bubble maps of detections, individuals, and release locations per species (Figure 8), as well as graphs of individuals detected per station type, weighted by deployment time (Figure 9), were created to determine whether individuals had any apparent preferences for specific stations/environments. To link our findings with known shark behaviour, abacus plots of the male and female individuals from each species with the most detections and number of stations visited (11034, 11044, 11055, 1693, 1697, and 62020) were superimposed with temperature data from the stations at which they were detected (Figure 10). Any individuals that were deemed to not follow regular or expected movement patterns (e.g. 11052) were further analyzed with abacus plots (Figure 11).

2.7 R script

The above methods were implemented using R studio (version 4.3.2; Posit team 2024) and utilized the following packages: ‘ggplot2’ (Wickham 2016) and ‘patchwork’ (Pedersen 2022) for plotting, ‘dplyr’ (Wickham et al. 2023) for data manipulation, and ‘stats’ (R Core Team 2023) and ‘rcompanion’ (Mangiafico 2023) for statistical analyses. The ‘glatos’ (Holbrook et al. 2024) package was also used to find detection events when understanding individuals’ movement patterns. All code can be found on https://github.com/valenceba/benthic_sharks.

3.0 Results

3.1 Preliminary noise checks

Graphs of average, maximal, and minimal noise throughout the study area revealed that no station remained at ambient noise levels higher than 650mV for prolonged periods (Annex Figure A5). Thus, all stations' detections were deemed reliable, and none were excluded from the analyses based on this criterion.

3.2 Individuals tagged and detected

Excluding those tagged in 2022 with V9 tags (n = 20), we tagged a total of 85 individuals: 34 *M. mustelus*, 21 *M. punctulatus*, and 30 *S. acanthias*. Most individuals were caught using passive gear (gill or trammel nets; n = 67). Note the different numbers of males (n = 34) versus females (n = 51) and adults (n = 40) versus juveniles (n = 45) caught, as well as individuals that were assigned vitality scores 1 (n = 38), 2 (n = 38), and 3 (n = 9) upon release. No *M. punctulatus* were assigned a vitality score of 3 upon release (Table 2).

Table 2 Tagged individuals of *M. mustelus* (MM), *M. punctulatus* (MP), and *S. acanthias* (SA) divided by sex (Male and Female), maturity (Adult and Juvenile), and vitality score (1, 2, or 3); values including the individuals tagged with a V9 tag in 2022 (n = 20) are on the right

	Excluding 2022 V9		Including 2022 V9	
Species	**Sex**	**Number**	**Sex**	**Number**
MM	Male Female	18 16	Male Female	20 18
MP	Male Female	4 17	Male Female	4 19
SA	Male Female	12 18	Male Female	22 22
	Maturity	**Number**	**Maturity**	**Number**
MM	Adult Juvenile	9 25	Adult Juvenile	9 29
MP	Adult Juvenile	4 17	Adult Juvenile	4 19
SA	Adult Juvenile	27 3	Adult Juvenile	39 5
	Vitality	**Number**	**Vitality**	**Number**
MM	1 2 3	16 15 3	1 2 3	16 18 4
MP	1 2 3	10 11 -	1 2 3	12 11 -
SA	1 2 3	12 12 6	1 2 3	14 21 9

Of those 85 individuals, 46 were detected at least once during the study, meaning our study had a ~54% “recapture” rate (Annex Table A1). The detected individuals were composed of 21 *M. mustelus*, 10 *M. punctulatus*, and 15 *S. acanthias,* with varying amounts of males/females and adults/juveniles each throughout the study (Figure 3). Most detected individuals had been originally assigned a vitality score of 1, followed by 2, then 3 (Annex Table A1). Two individuals were suspected of tag detachment, 11037 and 11038, due to the timing of detections at a singular station

(Annex Figure A6). Excluding them from analyses only slightly changed the survival ratios and statistical significance of stations visited (see below) because of lower sample sizes – thus, all following results include these individuals.

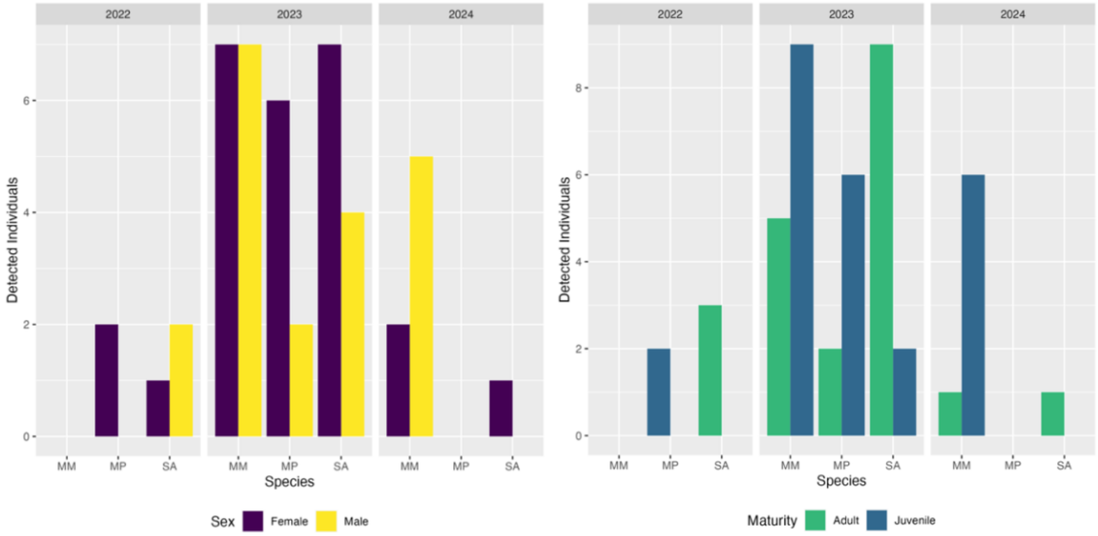


Figure 3 Females versus males (left) and adults versus juveniles (right) detected by year for *M. mustelus* (MM), *M. punctulatus* (MP), and *S. acanthias* (SA)

The Chi-square tests' results showed that there were no discrepancies in the proportions of detected versus not detected individuals, both across species and vitality scores, and within species regarding the different sexes and maturities (Annex Table A2).

3.3 Survival estimates

At the end of the study, a higher proportion of *Mustelus* vitality score 1 individuals had been detected compared to vitality score 2 individuals (60% versus 53% for MM; 60% versus 36% for MP). This was not true for *S. acanthias*, which had a detection proportion of 50% across all three vitality scores by the end of the study

(Figure 4). It took a little over 40 days for these final detection proportions to be reached for *M. mustelus*, followed by approximately 60 days for *M. punctulatus,* and over 200 days for *S. acanthias* (Figure 5).

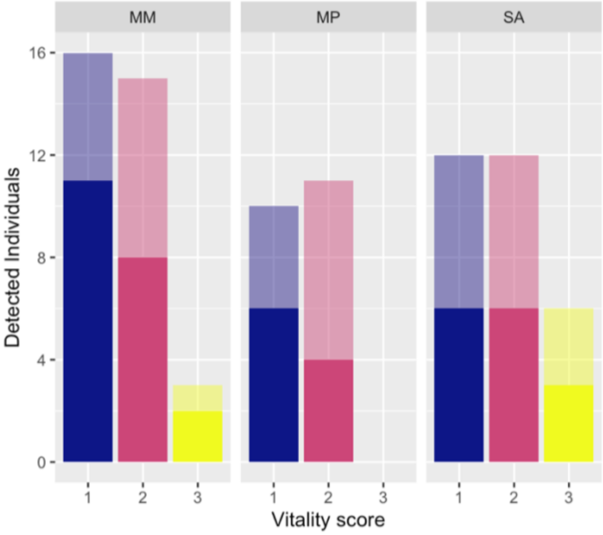


Figure 4 Proportion of *M. mustelus* (MM), *M. punctulatus* (MP), and *S. acanthias* (SA) individuals that were detected by vitality score 1 (blue), 2 (pink), and 3 (yellow)

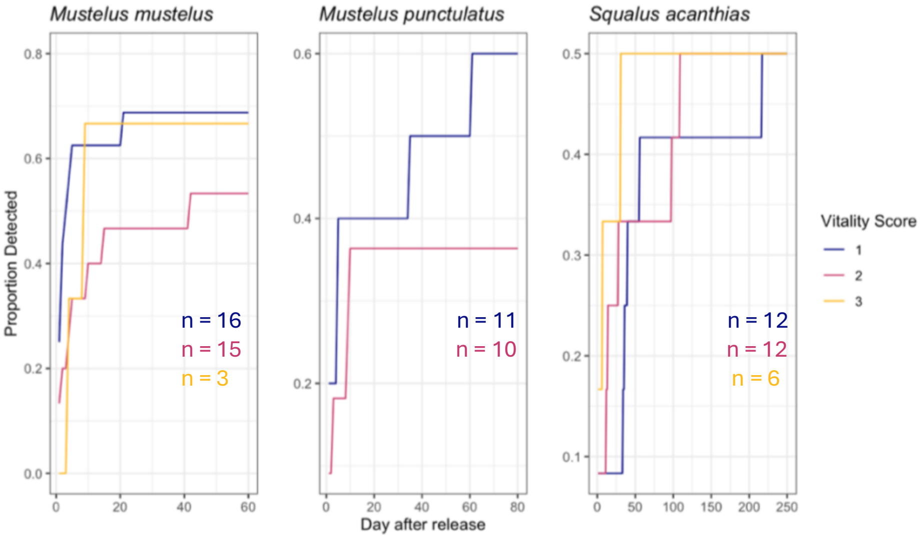


Figure 5 Proportion of individuals by species detected over time, after tagging and release, for vitality scores 1 (blue), 2 (pink), and 3 (yellow). Note the different x- and y-axes for each species. Sample sizes are included for each group

The percentage of vitality score 2 sharks that survived tagging (relative to vitality score 1 sharks of the same species) was ~78% for *M. mustelus*, ~61% for *M. punctulatus*, and 100% for *S. acanthias*. Due to the low sample size, this percentage was ~97% and 100% for vitality score 3 *M. mustelus* and *S. acanthias* sharks, respectively. Note that the 95% confidence intervals are wider for vitality score 3 sharks compared to vitality score 2 sharks because of this low sample size (Table 3). When the two individuals suspected of tag detachment were excluded, *M. mustelus* vitality score 3 sharks had a lower survival ratio (~48%), and *M. punctulatus* vitality score 2 sharks a higher one (~73%). Values above 1 indicate a higher relative survival (i.e. individuals were more likely to survive than those with vitality score 1).

Table 3 Survival ratio and corresponding 95% confidence interval of vitality score 2 and 3 individuals (relative to vitality score 1) all three species; values were calculated using detected and tagged individuals of each category as in Hueter et al. 2006 (see formula in section 2.6.1)

	M. mustelus			*M. punctulatus*			*S. acanthias*		
Vitality	1	2	3	1	2	3	1	2	3
Detected	11 (D_1)	8 (D_2)	2 (D_3)	6 (D_1)	4 (D_2)	-	6 (D_1)	6 (D_2)	3 (D_3)
Tagged	16 (T_1)	15 (T_2)	3 (T_3)	10 (T_1)	11 (T_2)	-	12 (T_1)	12 (T_2)	6 (T_3)
Survival ratio		0.776	0.970		0.606	-		1	1
95% C.I.		[0.561, 1.781]	[0.421, 2.377]		[0.394, 2.538]			[0.449, 2.226]	[0.375, 2.664]

3.4 Use of space

On average, the three species visited a similar number of stations (~2), as did the males and females within all three species – this lack of significant differences was confirmed by Kruskal-Wallis and Scheirer-Ray-Hare tests. However, there appears to be a difference for adults and juveniles (Figure 6). The Scheirer-Ray-Hare test shows that there is a significant interaction between species and maturity (p-value = 0.026749), and the post-hoc pairwise Wilcox test confirms that the difference is significant for *M. mustelus*, with adults visiting more stations than juveniles (~4.67 versus 2, p-value = 0.022), and between *M. mustelus* and *S. acanthias* adults (respectively, ~4.67 versus 2, p-value = 0.022; Table 4).

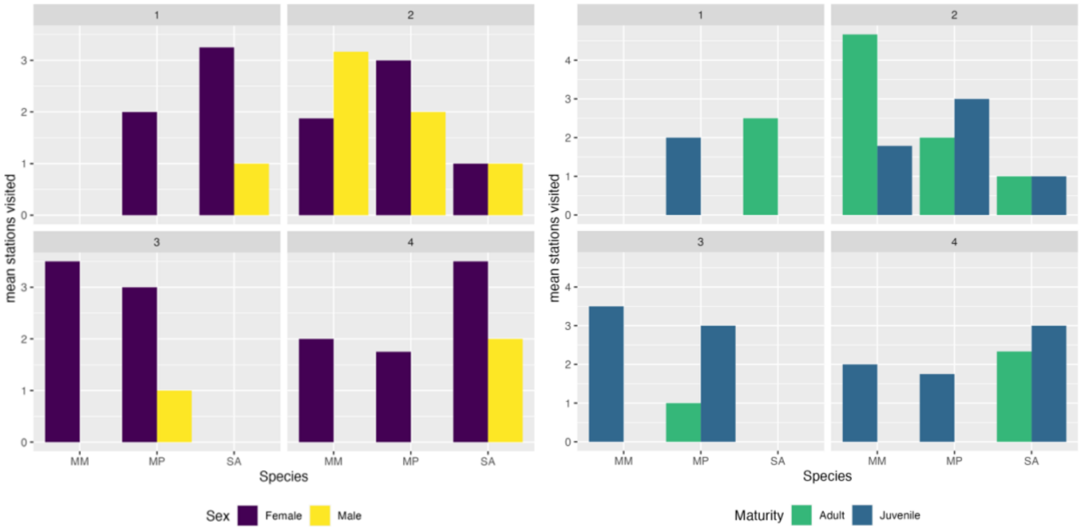


Figure 6 Mean number of stations visited by males and females (left) and adults and juveniles (right) of *M. mustelus* (MM), *M. punctulatus* (MP), and *S. acanthias* (SA) for trimesters 1 (Jan-Mar), 2 (Apr-Jun), 3 (Jul-Sep), and 4 (Oct-Dec)

Table 4 Statistical differences in stations visited according to the a) Scheirer-Ray-Hare test (three variables: species, maturity, and species-maturity) and b) p-values of the post-hoc pairwise Wilcox test for *M. mustelus* (MM), *M. punctulatus* (MP), and *S. acanthias* (SA) adults (A) and juveniles (J). Asteria indicate significance

a)	Df	Sum Sq.	H	p-value
Species	2	1320.2	4.5641	0.102077
Maturity	1	975.9	3.3738	0.066241
Species:Maturity	2	2094.9	7.2425	0.026749 *
Residuals	55	13824.5		

b)	MM (A)	MM (J)	MP (A)	MP (J)	SA (A)
MM (J)	0.022 *	-	-	-	-
MP (A)	0.169	1.000	-	-	-
MP (J)	0.121	0.607	0.800	-	-
SA (A)	0.022 *	1.000	1.000	0.607	-
SA (J)	0.373	1.000	1.000	1.000	1.000

Residency Indices vary across and within species, depending on the formula used, but the results from all three formulas agree that *M. punctulatus* has the highest overall value, followed by *M. mustelus*, and lastly *S. acanthias*. The formula 1.1 results in the highest values (Table 5). Formulas disagree on which sex and which maturity of each species exhibit higher residency, except for *M. punctulatus*.

Table 5 Residency Indices for all three shark species by species, sex, and maturity according to formulas from Kraft et al. 2023 (1.1, 1.2, and 2); corresponding 95% confidence intervals are included for the species

	Mustelus mustelus		*Mustelus punctulatus*		*Squalus acanthias*	
1.1	0.50 [0.24, 0.67]		0.52 [0.20, 0.85]		0.41 [0, 1]	
	Males	Females	Males	Females	Males	Females
	0.43	0.60	0.48	0.53	0.41	0.40
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
	0.39	0.55	0.79	0.45	0.37	0.63
1.2	0.15 [0.07, 0.22]		0.30 [0, 0.63]		0.017 [0.016, 0.019]	
	Males	Females	Males	Females	Males	Females
	0.21	0.07	0.13	0.32	0.016	0.018
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
	0.25	0.08	0.52	0.19	0.017	0.018
2	0.09 [0.03, 0.15]		0.26 [0, 0.60]		0.002 [0, 0.004]	
	Males	Females	Males	Females	Males	Females
	0.13	0.05	0.04	0.29	0.0026	0.0018
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
	0.16	0.05	0.49	0.14	0.003	0.0003

M. mustelus individuals seem to be present in the study area mostly during spring and summer, with some individuals being detected into autumn as well. *M. punctulatus* individuals follow the same pattern, except for a single individual (11052) which had multiple detections into the winter as well. *S. acanthias* individuals were mostly present in autumn and winter, with a few individuals being detected in spring, and none in summer (Figure 7). Most individuals were only detected shortly after being tagged before disappearing from the study area. Some exceptions to this pattern include individuals 11044 (MM) and 62020 (SA), the former of which was seen returning to station 9 a year after originally being detected there (Figure 7).

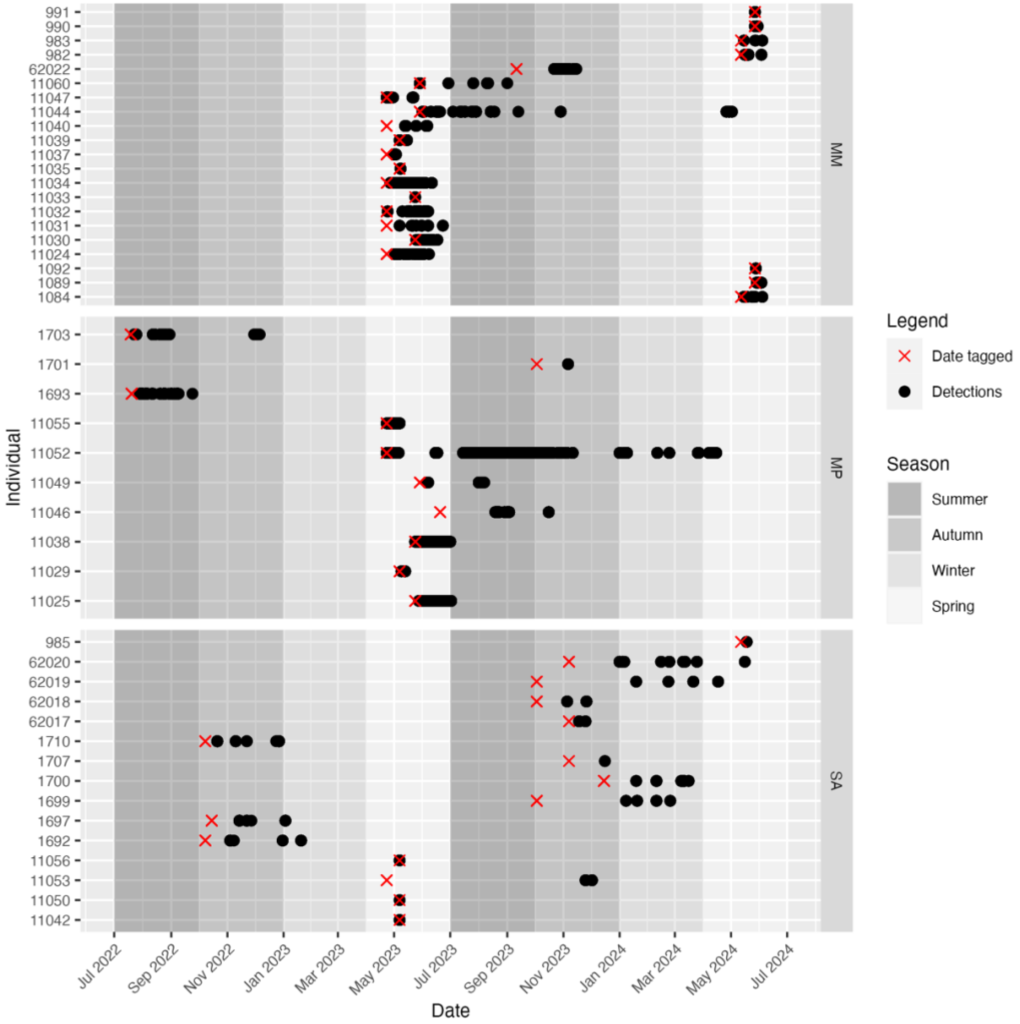


Figure 7 Abacus plot of individuals' detections grouped into *M. mustelus* (MM), *M. punctulatus* (MP), and *S. acanthias* (SA). Individual IDs on y-axis; red crosses indicate individuals' tagging date; shading indicates season of detection

3.5 Environmental preferences

Across species, stations 10 and 5.2 (mussel farms), as well as station 9 (shipwreck) to some extent, seemed to be hotspots for both overall detections and individuals detected. Bubble maps suggest that the stations closest to the coast (i.e. left side of the map) attracted the highest number of individuals compared to the ones further offshore, particularly for *Mustelus* species. Most releases occurred between stations 9 and 13, at least for *M. mustelus* and *S. acanthias* (Figure 8). When the number of individuals detected by type of station was normalized (weighted by the time each station type was deployed), it was found that platforms were the ones that attracted the most *M. punctulatus* individuals (Figure 9).

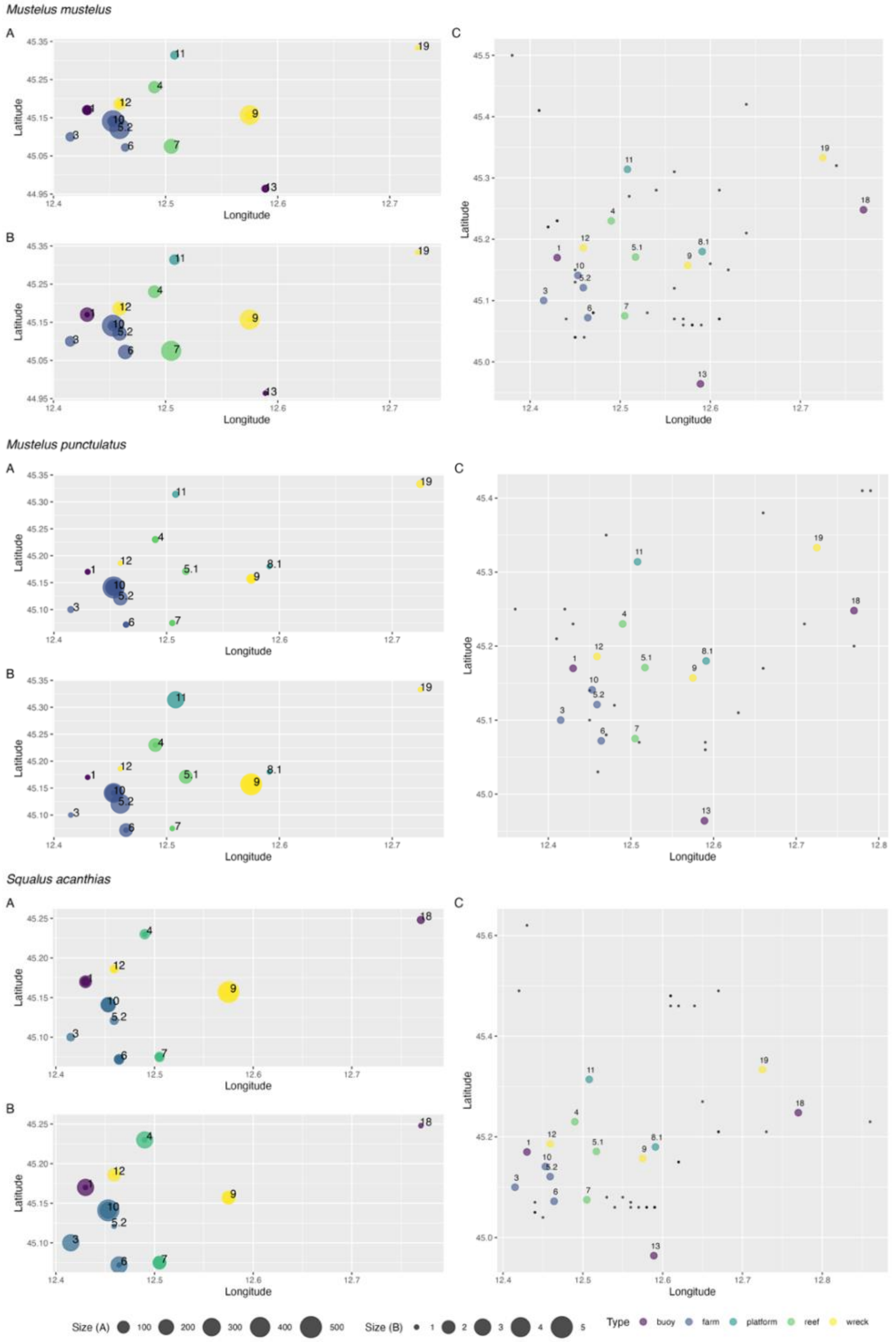


Figure 8 Overall detections (A), number of individuals detected (B), and releases (C) at each station throughout the study for all three species. Size of dots indicates number of detections or individuals, respectively; colour indicates station type (free buoy, mussel farm, artificial platform, rocky reef, or shipwreck)

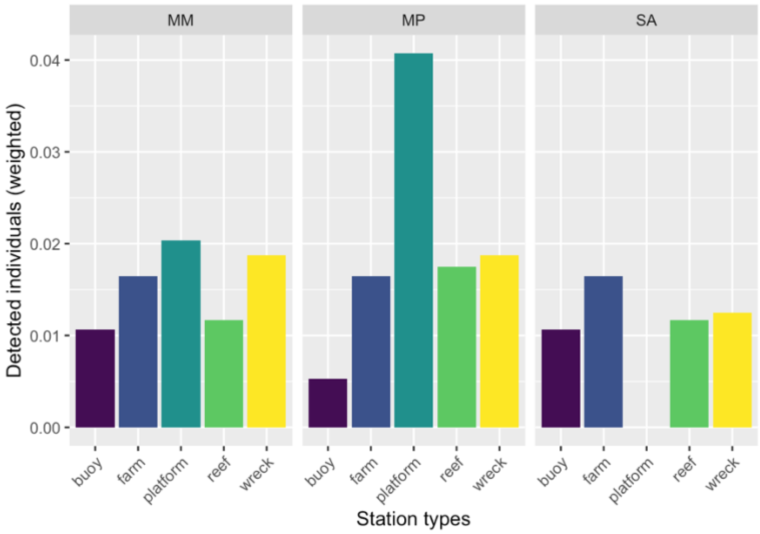
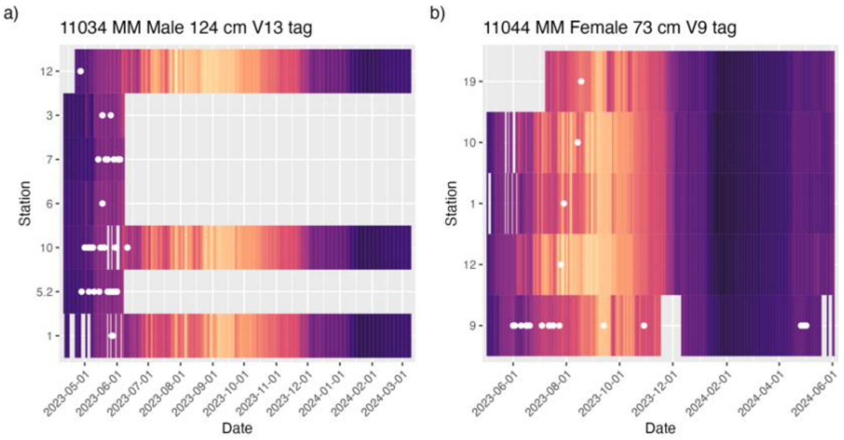


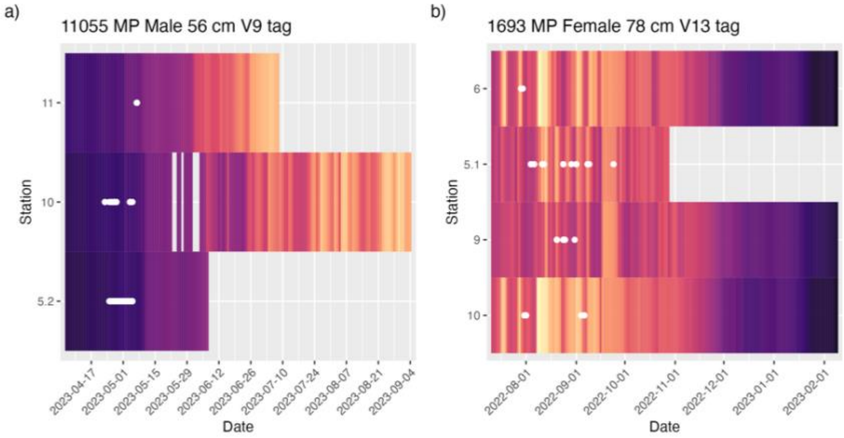
Figure 9 Individuals of *M. mustelus* (MM), *M. punctulatus* (MP), and *S. acanthias* (SA) detected at each station type (free buoy, mussel farm, platform, rocky reef, or wreck), normalized by deployment time, in weeks, of each station type

Despite the varying receiver pick up dates, a trend was visible in the abacus plots, where individuals from both *Mustelus* species were detected during periods of warmer temperatures (approximately 14-23 °C) compared to *S. acanthias* individuals (approximately 10-17 °C; Figure 10). The individuals with the most detections best exemplifying these differences in detection temperatures were individuals 11044 and 62020. Individual 11044 is a *M. mustelus* female that was tagged with a V9 tag in the summer of 2023 at 73 cm and was detected multiple times throughout the study area during spring and summer, but not winter. Individual 62020 is a *S. acanthias* female that was tagged with a V9 tag in late 2023 at 67 cm. She was first detected during the winter of 2024 and into the spring, but not seen in the summer. Additionally, males of both *Mustelus* species seemed to be detected at temperatures slightly lower (approximately 14-17 °C) than their female counterparts (Figure 10).

Mustelus mustelus



Mustelus punctulatus



Squalus acanthias

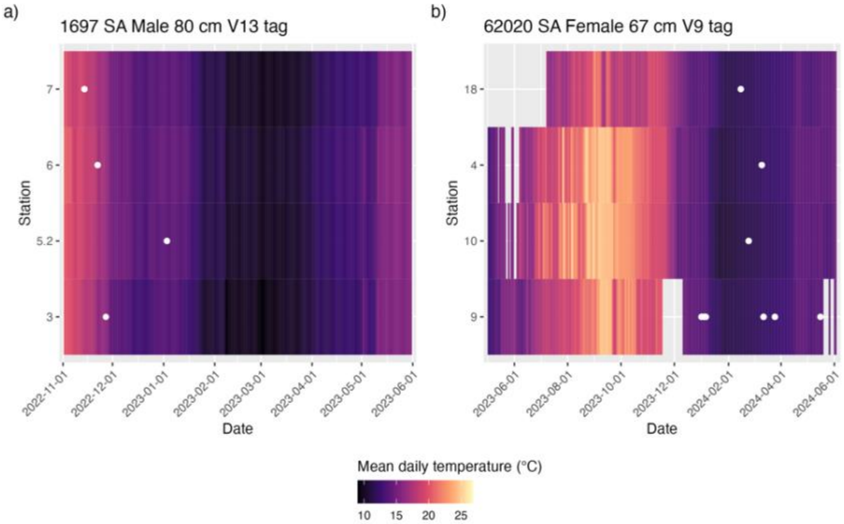


Figure 10 Abacus plots of detections and temperatures over time at the specific stations where a) male and b) female individuals of each species were detected. Missing data indicates when a receiver at its corresponding station was picked up

One exception to the trend of *Mustelus* being present only during the warmer months is individual 11052, a *M. punctulatus* female that was tagged with a V9 tag at 60 cm in the spring of 2023. Detection patterns for this animal were normal until August 2023, when a long and uninterrupted detection event occurred (similar to a pattern for tag detachment). This event continues throughout the winter; however, detections then alternate between two stations, 10 and 9, during spring (Figure 11).

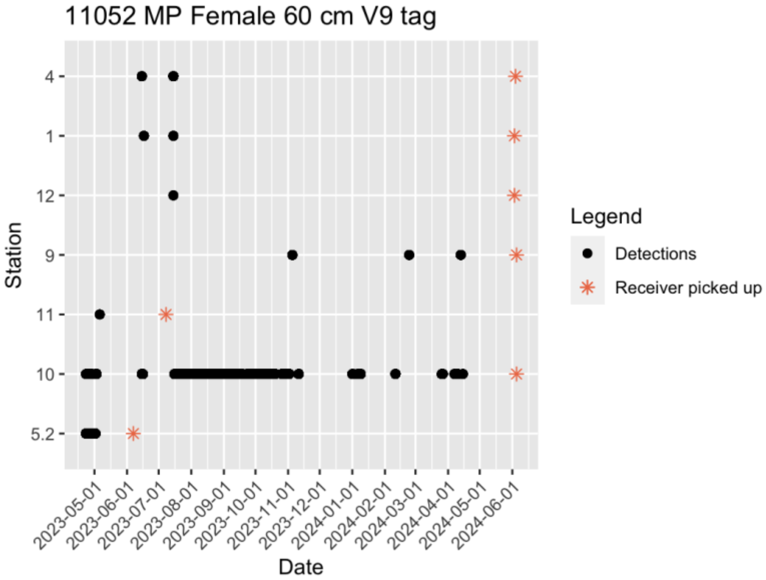


Figure 11 Abacus plot of detections by station for individual 11052 (*M. punctulatus* female tagged with a V9 tag at 60 cm); orange asteria indicate the last time the receiver at the corresponding station was picked up

4.0 Discussion

4.1 General findings

Our study represents the first attempt to understand the post-tagging survival and use of space of commercially important benthic sharks in the area. Survival analyses found that vitality score was a good indicator of "recapture" rate, at least for individuals of both *Mustelus* species. Use of space analyses revealed that the three species behave markedly differently, as do individuals within a species, perhaps in relation to maturity. Sharks' use of space was also linked to certain environmental conditions and habitat types. In the following sections, a deeper dive into these findings – the exact results and previous works that support survival, use of space, and environmental preferences analyses – will be followed by caveats to keep in mind regarding our study, as well as future directions for fisheries management and elasmobranch conservation.

4.2 Connections to literature

4.2.1 Survival estimates

The proportion of tagged animals on which we have data, our "recapture" rate (~54%, or 46 out of 85), is reasonable given the constraints encountered throughout our study. Compared to other acoustic telemetry studies, it is slightly lower; for example, Da Silva et al. (2013) "recaptured" over 63% of smooth hounds tagged in South Africa, with multiple individuals providing at least a year's worth of data each, while Francis (2013) and Espinoza et al. (2011) detected the totality of smooth hounds they tagged (in a New Zealand and California estuary, respectively). However, compared to conventional mark-recapture or tags equipped with float jackets for retrieval, our value is much higher (e.g. Griffiths et al. 2020 saw a 1.3% and 14.4% return rate, respectively, when studying a related smooth hound species in UK waters). Given that our receiver array is non-overlapping, as opposed to the three former studies on smooth hounds, the amount of data recovered in this study is quite satisfactory. When going over the following sections, it must be remembered that our results do not offer precise survival estimates or determine individuals' exact fate, but represent instead species' relative survival.

The proportions of individuals detected by vitality score was, for *Mustelus* individuals, higher if the individual was released in a better health condition (i.e. vitality score 1). We indeed expected animals that exhibited very few to no signs of stress to recover more quickly from the catch-tag-release event and be found alive in the area shortly after, at least compared to individuals released in a poorer health condition. This was not true for *S. acanthias*, which may be due to a variety of reasons, mainly physiological. For one, the different energy requirements of ram ventilators, fish that must keep swimming to passively move water over their gills and breathe, and buccal pumpers, which rely on muscle contractions to draw water into their gills, can affect survival (Carlson & Parsons 2001). Research is divided on the subject, with some suggesting that demersal species with buccal pump ventilation are more resistant to stress (Ellis et al. 2017), and others finding that ram ventilation can enhance recuperation post-release (Brooks et al. 2011). Note that individuals can be obligate ram ventilators or buccal pumpers, or use a combination of the two mechanisms

(Carlson & Parsons 2001). *S. acanthias* are preferentially ram ventilators but are still capable of buccal pumping (Kelly et al. 2020), while smooth hounds species seem to do the opposite. In a study on metabolic rate changes of *Mustelus antarcticus* caught by gill nets, it was found that individuals perform buccal pumping when at rest but can rely on ram ventilation under stressful situations (Molina et al. 2020). It is important to remember that many other variables come into play when studying metabolism and energy requirements under stressful biotic (e.g. lowered immune system, pregnancy, etc.) and abiotic (e.g. poor water oxygenation, inadequate temperature, etc.) conditions. Additionally, body size plays an important role, with larger individuals being more resistant to stress than smaller ones, as demonstrated by the *M. antarcticus* study (Molina et al. 2020). Depending on which breathing mechanism an individual uses to recover post-release, its mobility may change, in turn affecting detections in a given study area. It is thus difficult to explain our results of spiny dogfish detection proportions, but since they are generally smaller than the smooth hounds, this may have played a role in the lowered detection of individuals released in a good health condition. As for the time it took to reach these final detection proportions, this may have been greatly influenced by our study's receiver array design. Typically, post-release recovery takes up to 14 days for elasmobranchs (Alonso-Fernández et al. 2022), with most mortality events occurring very shortly afterwards (~2 days; Martínez-Ramírez et al. 2024). Due to our non-overlapping receiver array, we could not state that every individual which was not detected after two weeks had died, seeing as they were most likely in the area but had simply gone undetected by receivers.

In fact, since detecting all tagged individuals seemed highly unlikely given our receivers' non-overlapping detection ranges, the formula from Hueter et al. (2006) was used to define more precisely their relative survival. Survival ratios indicated that, compared to those assigned a vitality score of 1, 61 to 78% of vitality score 2 *Mustelus* individuals in our study likely survived. These values are in line with research on elasmobranch bycatch discard in Florida (66-81%; Hueter et al. 2006) and Spain (66-100%; Alonso-Fernández et al. 2022) and post-capture survival in Tasmania (63-100%; Bell & Lyle 2016). Minor differences in percentages between studies can be attributed to the distinct study species and areas, as well as the fishing gear and techniques used. Particularly, a shorter soak time, defined as the time between setting and hauling of fishing gear (Carruthers et al. 2011), was found to reduce damage to specimens and greatly increase survival (Alonso-Fernández et al. 2022; Bell & Lyle 2016). In this case, it is important to recall the three assumptions underlying Hueter et al.'s (2006) survival ratio formula: 1) negative effects from the tags themselves are equal across health conditions, 2) all individuals can be caught at the same rate, and 3) individuals will all experience regular, natural mortality rates following the catch-tag-release event. The first two assumptions are accounted for in our study, thanks to the precautions taken during the tagging procedure and Chi-square tests results which indicate no discrepancies in catchability between vitality scores. However, the third assumption – that individuals will experience the same long-term effects and mortality following the event regardless of their vitality score – cannot be easily confirmed, as internal changes that continue long after an initial stress recovery period are difficult to study in situ. Survival ratios for *S. acanthias* indicated that 100% of the individuals, regardless of their vitality score, survived the event compared to vitality score 1 individuals. While this could be true, we must also consider the low sample size for some groups, as well as the species' inherent mobility that can reduce detections in a non-overlapping receiver array, especially compared to smooth hounds (Serena 2005). This higher mobility may also explain why it took much longer to reach the final proportion of detected spiny dogfish in our array. For instance, individual 1153 (Adult male, vitality score 1) was detected for the first time nearly eight months after being released – if detection within the regular recovery period (2-14 days) had been considered the cutoff for fate determination, this individual would have been erroneously deemed dead.

4.2.2 Use of space

The number of stations visited by individuals in our study revealed some differences between and within species. Results showed evidence of age-based dispersal within *M. mustelus*, with adults exhibiting higher mobility (number of stations visited). This can potentially be explained by ontogenetic shifts; meaning that, as individuals grow, they require more resources, so their ranges expand to meet this demand (Speed et al. 2010). For example, smaller, immature tiger sharks (*Galeocerdo cuvier*) were found to travel shorter distances than adults throughout the Atlantic (i.e. they exhibited reduced migration propensity; Lea et al. 2015). However, the positive relationship between age/size and home range (defined as the area in which an individual performs its normal activities at a given time; Speed et al. 2010) is not universally applicable, as inter-individual variability in movement patterns is important in elasmobranchs. In New Zealand, juvenile rig (*Mustelus lenticulatus*) – a related

Mustelus species that also resides in shallow coastal habitats – exhibited significant diversity in how their nursery sites were utilized by individuals throughout the year (Francis 2013). One could also expect to observe sex-based dispersal in our results, as this is a common phenomenon among elasmobranchs (Speed et al. 2010) and has been found in other populations of *S. acanthias* (Dell'Apa et al. 2016). Females have been theorized to travel more compared to males, perhaps due to their typically larger size, or due to their higher reproductive requirements which encourage them to search for optimal conditions (McMillan et al. 2019). This was found to be the case with *Mustelus asterias* females in the Northeast Atlantic, which had longer average distances between release and recapture locations than males (Griffiths et al. 2020). Others suggest the opposite, that males travel more and contribute further to their species' genetic dispersal, as with brown smooth hounds (*Mustelus henlei*) in the Gulf of California (Sandoval-Castillo & Beheregaray 2015). Though none of these phenomena were visible in our findings according to the Scheirer-Ray-Hare tests (no differences in how many stations males and females visited), it should be noted that the detected adult *M. mustelus* were all males. Results also showed that these individuals visited significantly more stations than adult *S. acanthias*, which were composed of a roughly equal number of males and females. We theorize that, due to spiny dogfish's more migratory nature, individuals may have moved away from our study area faster, thus negatively affecting the number of stations they visited. So, while this value suggests that they are less mobile than smooth hounds, it is in fact the opposite. This theory is supported by *S. acanthias*' lower Residency Index (regardless of the formula used) compared to both *Mustelus* species. Regarding the latter, Espinoza et al. (2011) found that gray smooth hounds (*Mustelus californicus*) had a mean Site Fidelity Index of 11-13%, which is equivalent to I_R values of 0.11-0.13 (formula 1.2). This approaches our I_R value of 0.15 for *M. mustelus* (formula 1.2) and fits inside the species' 95% confidence interval for both I_R 1.2 and I_{WR}.

Generally speaking, our Residency Indices and overall detection patterns echo existing research. Various acoustic telemetry studies outline that *Mustelus* species are increasingly detected in the summer months, as adults come to shallow coastal regions to mate and give birth, and then leave their respective area at varying points, with the pups following suit into the fall (Espinoza et al. 2011; Francis 2013; Da Silva et al. 2013; Able et al. 2014). The same can be said when looking at our abacus plot of detections throughout the study. We also found evidence of site fidelity in one individual: 11044, a *M. mustelus* female. Both elasmobranch sexes are known to exhibit site fidelity, though females are unique in that they sometimes exhibit parturition or nursery site fidelity, returning to known sites to release their young (Chapman et al. 2015). Difficult to study, this phenomenon has been observed thanks to genetic analyses in a variety of shark species and depends on reproductive cycle and gestation period length (Chapman et al. 2015). Based on its size at the time of tagging, individual 11044 was determined to be a juvenile (73 cm total length), and would likely not have been sexually mature when it was detected at station 9 one year later (according to growth rate estimates from Boscolo Palo et al. 2022), so it may simply be exhibiting regular site fidelity. Detections across the study period can also explain why the Residency Indices of *M. punctulatus* are higher than those of *M. mustelus*, and are higher for females; this is likely due to individual 11052, a female whose tag was detected in the area throughout winter. Based on our work and existing studies, we could not ascertain whether individual 11052 displayed a novel use of space pattern not yet seen in the species.

4.2.3 Environmental preferences

Our study did not focus on the environmental variables that can affect sharks' use of space beyond water temperature, such as chlorophyll and oxygen concentration, tides, salinity, or bottom composition. Nevertheless, preference for stations could still be ascertained with our acoustic array, and receivers located at mussel farms and platforms attracted the most individuals, independent of release locations and deployment time. Mussel farms in this region are typically areas of high productivity (Semrau 2012) and, just like the platforms in our study area, are usually free of fishing pressure from commercial vessels (due to the possibility of net entanglement). Platforms and other man-made structures can, over time, serve as artificial reefs that attract a high concentration of vertebrate and invertebrate organisms and thus higher trophic level predators such as sharks (Paxton et al. 2020). Modelling predicts that catches of *S. acanthias* females in the northeastern United States are correlated with indicators of high primary productivity, such as increased chlorophyll content (Dell'Apa et al. 2016). It has also been shown that refuge from fishing activity, particularly from commercial trawling, can accurately predict elasmobranch occurrence in and around European MPAs (Dureuil et al. 2018). Other studies' models on *Mustelus* have indicated that luminosity (time of day), moon phase, and depth are important variables for predicting their presence, commonly documenting diel-vertical migrations (Francis 2013; Drymon et al. 2020; Griffiths et al. 2020). *S. acanthias* females were also found to prefer shallower waters, potentially to avoid aggressive male copulation (Dell'Apa et al. 2016). However, the effect of depth could not be evaluated in our study, considering the low depth profile of our study area (i.e. offshore stations are only a couple meters deeper than the rest, and individuals swimming at the surface could still be detected by our receivers).

Our results do highlight the importance of temperature as a predictor of smooth hound and spiny dogfish presence, pinpointing certain ranges that were preferred by *Mustelus* (~ 20 °C) and *S. acanthias* (~15 °C). *Mustelus* females also seemed to be present during periods of higher water temperature than males. Da Silva et al. (2021) found that *M. mustelus* in south Africa avoid temperatures below 15 °C in the winter and prefer temperatures between 17-20 °C in the summer, or up to 24 °C for females. These slight differences between sexes can be explained by thermoregulatory needs. According to the thermal-niche hypothesis, individuals such as pregnant females may incur physiological benefits from residing in areas with slightly elevated temperatures for certain periods of time (e.g. shorter gestation times and larger sizes at births; Jirik & Lowe 2012; McMillan et al. 2019). In the northern Adriatic, there is evidence of sex-based dispersal in relation to the reproductive period of *S. acanthias*: while their catches peak in January and males are caught almost year-round, pregnant females carrying nearly full-term embryos are caught primarily in summer, when temperatures are the highest (Bargione et al. 2019). Models of female *S. acanthias* occurrence in the northeastern United States also showed a positive correlation with warmer waters (Dell'Apa et al. 2016). Thermoregulation, however, is not exclusive to pregnant females – it is a physiological and behavioural phenomenon useful for all individuals, particularly during periods of high temperatures near the physiological maximum or of intense energy exertion (Haesemeyer 2020). To reduce metabolic losses and increase foraging efficiency, blue sharks studied using satellite tags were found performing diel vertical migrations, thus benefitting from thermoregulation in cooler waters (Campana et al. 2011). A similar mechanism may be at play in *M. asterias* in the Northeast Atlantic (Griffiths et al. 2020), indicating that temperature and temperature changes play a key role in elasmobranch's use of space.

4.3 Assumptions and caveats

Some details must be taken into consideration when evaluating our study's results, mostly related to the nature of setting up acoustic telemetry experiments, which presents many challenges. First, due to its opportunistic design, our sentinel receiver array did not allow for the fine-scale tracking of animals. This means that instead of precise triangulations and auto-correlated data, we have a lot of "gaps" or "zeroes" in our data because of the non-overlapping receiver ranges. In our dataset, a lack of detections does not necessarily mean the animal was not present in the area, and detections themselves are approximated to a 400-meter radius around the station that recorded their tag ID. This was why the number of stations an individual visited was taken as a proxy of mobility instead of, say, kilometers traveled. It also did not allow us to use other tools commonly discussed in acoustic telemetry studies, such as Time Local Convex Hull (T-LoCoH), State-Space models, or autocorrelated kernel density estimations (AKDEs), and made the use of Brownian Bridges and Home Range estimations more difficult (Kraft et al. 2023). Second, the fact that the V13 and V9 tags used on sharks were external, rather than internal (i.e. inserted into an animal's abdominal cavity), may have increased the occurrence of tag detachment. Many of the individuals that were not detected at the end of our study might not have left the study area or died, but simply lost their tag. Short-term individual fate is, essentially, difficult to infer with our study's setup, and differentiating between tagging mortality, natural mortality, fishing mortality, tag shedding, or dispersal into other areas is always challenging in acoustic telemetry research (Martínez-Ramírez et al. 2024; Villega-Ríos et al. 2020). For instance, it is unclear whether individual 11052 is an example of tag detachment, or if it simply exhibits a different behaviour compared to its conspecifics. If it is the former, then data from this individual could be inadvertently affecting the results for *M. punctulatus*. Individual 11037 was deemed to be a case of tag detachment even though it looked different to our clear example of this phenomenon (Annex Figure A4) because, when looking closely, its detections appeared nearly-perfectly timed with tide movements – nevertheless, depending on the resolution at which detection data is analyzed, such a pattern is difficult to identify. Both these caveats could thus be behind our lower amount of detection data compared to other acoustic telemetry studies on related species that used overlapping receivers and internal tags (i.e. Da Silva et al. 2013, Francis 2013, and Espinoza et al. 2011).

While detections were thoroughly filtered and the risk of there being any false detections in the final dataset is minimal, there was significant fouling on the receivers observed during their retrieval, which has been shown to decrease a receiver's performance over time (Heupel et al. 2008). This could mean some datapoints were potentially missed, which could affect the results of both the survival analysis (i.e. lower proportion of individuals detected for a given vitality score) and use of space analysis (i.e. less stations visited and lower Residency Indices). Thus, one could say that our findings are quite conservative. Our results' large uncertainty may stem from the non-overlapping receiver array, the fact that individuals were tagged and released at varying times throughout the study, and the fact that receivers vary in their deployment time. Though the latter two variables are accounted for in how the Residency Indices were calculated, these factors culminate in a partial view of the study area over time. It should also be noted that there may be some hidden biases in our data due to sampling. For example, the gill nets used by commercial fishers in the area are size-selective, meaning they may affect the maturity count – and to some extent, the sex count, since female elasmobranchs are typically larger – of species. Additional methodologies related to gear that may have affected a priori the health conditions and vitality scores of caught individuals (e.g. soak time, on-board handling, etc.) were not totally in our control, given the necessary collaboration with commercial fishing vessels. Nonetheless, we sampled individuals at different points over the study period, covering all seasons (albeit not evenly, due to the different occurrence of the species throughout the year), and throughout the study area, as evident in the release maps, since captures and releases occur shortly after one another. Thus, biased sampling is potentially reduced for size/maturity, as is any potential sex bias, given the assumption that males, females, adults, and juveniles use the space differently. Moreover, individuals with different vitality scores were tagged.

This being said, our study still offers useful insight into smooth hounds' and spiny dogfish's general use of space, and particularly into their tagging survival. Indeed, sentinel, non-overlapping array designs are said to be helpful in defining long-term survivorship (Heupel et al. 2006; Kessel et al. 2013). Our findings are also meaningful in terms of informing management in the region and open the door to conversations regarding best practices to ensure the future of elasmobranch species and fisheries in the northern Adriatic.

4.4 Future directions

Many sharks in the Mediterranean Sea serve as mid- to high-level predators, eating a variety of taxa and transferring energy up the food-chain, acting as links between humans and lower trophic levels (Nuez et al. 2024). Protecting them is therefore a question of protecting the entire ecosystem and affects local people and businesses as much as it does the marine environment. Further monitoring fisheries and providing new regulations appears as pathways to sustainability. Though our work did not touch on the effect of gear on individuals' survival, we did find a link between vitality score (i.e. health condition of the animal when brought on board) and survival once tagged and released. This has implications for elasmobranch bycatch; indeed, research on longline fishing shows that if target catch landings do not increase as a function of soak time, then limiting it would benefit bycaught species without causing economic losses for fishers (Carruthers et al. 2011). Though the long-term effects of stress from being caught and brought onboard (e.g. changes to homeostasis, growth, reproduction, etc.) are still to be thoroughly understood, release of bycaught individuals, particularly those in a good health condition, presents itself as a practical alternative to increase species' outcome in the northern Adriatic. This approach seems promising and is supported by our results, given the high proportion of vitality 2 individuals that were detected, and therefore survived, compared to vitality 1 individuals. Our work also underlines potential differences in survival between species, indicating that the intrinsic characteristics of some individuals, such as mobility and size, may further expose them to anthropogenic risks. The smaller sizes and higher fecundity of *M. punctulatus* compared to *M. mustelus* could indicate a higher vulnerability to fishing pressure for the latter, considering the two species co-occur in a heavily exploited region and are caught by the same fishing gears (Riginella et al. 2020). Limiting catches for *M. mustelus*, especially females (as they are mainly responsible for the reproductive potential of the species), seems like another viable option, but comes with some issues – namely the fact that the two species are at times difficult to differentiate (Marino et al. 2017). We know that freeing elasmobranch species from overfishing pressure can, over time, allow populations to bounce back, enough to support sustainable fisheries again. Such is the case in the western Atlantic, where strong management enforcement was found to offset fishing pressure for species such as white sharks, great hammerheads, and Atlantic blacktip sharks (Pacoureau 2023). In our study region, the main fish markets recorded increases in mid-sized elasmobranch landings after periods of reduced fishing efforts (e.g. during the two World Wars; Ferretti et al. 2013), evidence that smooth hounds and spiny dogfish may benefit from these protection measures.

Another appealing option to protect these commercially important benthic sharks would be to implement MPAs. Key to MPA design is knowledge on the protected species' use of space; meaning, where and when are animals most likely present, and how are they utilizing the area? This link between species' use of space and MPA effectiveness is evident in the South African Langebaan Lagoon – a pupping and nursery area for *M. mustelus* exhibiting high residency in the summer – where the established no-take MPA was determined to enhance protection during peak fishing periods (Da Silva et al. 2013). Based on our study of smooth hound and spiny dogfish use of space and environmental preferences, the importance of areas for shark conservation that have high productivity and are free from fishing pressure cannot be ignored. Establishing radii around manmade and artificial structures (e.g. mussel farms, shipwrecks, oil platforms, etc.) could thus offer some respite for elasmobranchs and benefit the surrounding ecosystems, increasing nearby catches over time thanks to the "spillover" effect (the movement of animals within a reserve beyond its limits and into fishable grounds; Roberts et al. 2005). Though appropriate MPA size is a debated topic (Burns et al. 2023), some have found it to be positively correlated with elasmobranch abundance within its boundaries (Dureuil et al. 2018). However, research shows that while the effectiveness of an MPA is somewhat dependent on its design, its performance is mainly linked to its management plan (i.e. investment into monitoring and assessment, education and communication, and community engagement; Álvarez-Fernández et al. 2024). The efficiency of any conservation measure, but particularly area-based ones such as these, is often contingent on how binding and legally enforceable they are for states (Giovos et al. 2024). This is crucial to keep in mind when considering that recent research shows trawling efforts inside MPAs in the European Union sometimes at higher rates than outside their boundaries (Dureuil et al. 2018).

In the Mediterranean and Adriatic seas, threatened species of sharks, rays, and skates coincide with bottom trawling, gillnet, and longline activity, creating focal points for conservation and prompting efforts to better protect these animals (European Commission 2023). Determining the best practices for fisheries in the region to eliminate excessive harm to elasmobranch species, however, requires extensive research on the species themselves. A review of the horizontal gaps and inconsistencies amongst marine management in the Mediterranean showed that a common issue for states was the availability (i.e. findability, accessibility, interoperability, and reusability) of fisheries data (Giovos et al. 2024). Our study provides an initial decoding of smooth hound and spiny dogfish tagging survival, as well as their use of space in the northern Adriatic, but it could be useful to explore other techniques and methodologies in the future. For instance, modelling probability of presence for individuals and species using variables such as sex, maturity, temperature, tides, and habitat type deserves consideration, as our work and previous findings suggest these are key in explaining movement. Additionally, without overlapping acoustic receiver arrays or internal tags to maximise detections and minimize tag detachment, eDNA metabarcoding could be a valuable additional tool. Indeed, eDNA can be used to indirectly monitor mobile and elusive shark species, identify hotspots of biodiversity and abundance, and potentially improve conservation strategies (Bakker et al. 2017). So perhaps the most obvious next step to further protect sharks in the northern Adriatic and beyond is to continue with research efforts. Our findings serve as a reminder of how much is still required to clearly characterize the vulnerable smooth hounds and spiny dogfish. Applicable to any shared basin or migratory species which crosses international boundaries, additional information on the survival and use of space of threatened elasmobranchs brings us one step closer to sustainable fisheries that respect and benefit from healthy ecosystems and shark populations.

References

Able, K. W., Grothues, T. M., Turnure, J. T., Malone, M. A., & Henkes, G. A. (2014). Dynamics of residency and egress in selected estuarine fishes: Evidence from acoustic telemetry. *Environmental Biology of Fishes*, *97*(1), 91–102. https://doi.org/10.1007/s10641-013-0126-6

Adams, K. R., Fetterplace, L. C., Davis, A. R., Taylor, M. D., & Knott, N. A. (2018). Sharks, rays and abortion: The prevalence of capture-induced parturition in elasmobranchs. *Biological Conservation*, *217*, 11–27. https://doi.org/10.1016/j.biocon.2017.10.010

Alonso-Fernández, A., Mucientes, G., & Villegas-Ríos, D. (2022). Discard survival of coastal elasmobranchs in a small-scale fishery using acoustic telemetry and recapture data. *Estuarine, Coastal and Shelf Science*, 276. https://doi.org/10.1016/j.ecss.2022.108037

Alós, J., Aarestrup, K., Abecasis, D., Afonso, P., Alonso-Fernandez, A., Aspillaga, E., Barcelo-Serra, M., Bolland, J., Cabanellas-Reboredo, M., Lennox, R., McGill, R., Özgül, A., Reubens, J., & Villegas-Ríos, D. (2022). Toward a decade of ocean science for sustainable development through acoustic animal tracking. *Global Change Biology*, 28, 5630–5653. https://doi.org/10.1111/gcb.16343

Álvarez-Fernández, I., Sánchez-Carnero, N., & Freire, J. (2024). Governance, not design, rules European Atlantic MPA performance. *Regional Studies in Marine Science*, *71*, 103419. https://doi.org/10.1016/j.rsma.2024.103419

Australian Fisheries Management Authority. (2015). *School Shark Rebuilding Strategy*. Retrieved June 9, 2024, from: https://www.afma.gov.au/sites/default/files/2023-02/School-Shark-Rebuilding-Strategy.pdf

Bakker, J., Wangensteen, O. S., Chapman, D. D., Boussarie, G., Buddo, D., Guttridge, T. L., Hertler, H., Mouillot, D., Vigliola, L., & Mariani, S. (2017). Environmental DNA reveals tropical shark diversity in contrasting levels of anthropogenic impact. *Scientific Reports*, *7*(1), 16886. https://doi.org/10.1038/s41598-017-17150-2

Barausse, A., Correale, V., Curkovic, A., Finotto, L., Riginella, E., Visentin, E., & Mazzoldi, C. (2014). The role of fisheries and the environment in driving the decline of elasmobranchs in the northern Adriatic Sea. *ICES Journal of Marine Science*, *71*(7), 1593–1603. https://doi.org/10.1093/icesjms/fst222

Barausse, A., Michieli, A., Riginella, E., Palmeri, L., & Mazzoldi, C. (2011). Long-term changes in community composition and life-history traits in a highly exploited basin (northern Adriatic Sea): The role of environment and anthropogenic pressures. *Journal of Fish Biology*, *79*, 1453–1486. https://doi.org/10.1111/j.1095-8649.2011.03139.x

Bargione, G., Donato, F., La Mesa, M., Mazzoldi, C., Riginella, E., Vasapollo, C., Virgili, M., & Lucchetti, A. (2019). Life-history traits of the spiny dogfish *Squalus acanthias* in the Adriatic Sea. *Scientific Reports*, *9*(1), 14317. https://doi.org/10.1038/s41598-019-50883-w

Bauer, S., Nolet, B., Giske, J., Chapman, J., Akesson, S., Hedenström, A., Fryxell, J. (2011). Cues and decision rules in animal migration. Animal Migration: Oxford University Press. pp. 68-87. 10.1093/acprof:oso/9780199568994.003.0006.

Bell, J. D., & Lyle, J. M. (2016). Post-capture survival and implications for by-catch in a multi-species coastal gillnet fishery. *PLOS ONE*, *11*(11), e0166632. https://doi.org/10.1371/journal.pone.0166632

Bonanomi, S., Pulcinella, J., Fortuna, C. M., Moro, F., & Sala, A. (2018). Elasmobranch bycatch in the Italian Adriatic pelagic trawl fishery. *PLOS ONE*, *13*(1), e0191647. https://doi.org/10.1371/journal.pone.0191647

Booth, H., Squires, D., & Milner-Gulland, E. J. (2019). The neglected complexities of shark fisheries, and priorities for holistic risk-based management. *Ocean & Coastal Management*, *182*, 104994. https://doi.org/10.1016/j.ocecoaman.2019.104994

Bornatowski, H., Navia, A. F., Braga, R. R., Abilhoa, V., & Corrêa, M. F. M. (2014). Ecological importance of sharks and rays in a structural foodweb analysis in southern Brazil. *ICES Journal of Marine Science*, *71*(7), 1586–1592. https://doi.org/10.1093/icesjms/fsu025

Boscolo Palo, G., Di Lorenzo, M., Gancitano, S., Ragonese, S., Mazzoldi, C., & Colloca, F. (2022). Sharks do not always grow slowly: Tagging data reveal a different pattern of growth, longevity and maturity for threatened smooth-hounds in the central Mediterranean Sea. *Journal of Marine Science and Engineering*, *10*(11). https://doi.org/10.3390/jmse10111647

Brooks, E.J., Sloman, K.A., Liss, S., Hassan-Hassanein, L., Danylchuk, A.J., Cooke, S.J., Mandelman, J.W., Skomal, G. B., Sims, D. W., & Suski, C.D. (2011). The stress physiology of extended duration tonic immobility in the juvenile lemon shark, *Negaprion brevirostris* (Poey 1868). *Journal of Experimental Marine Biology and Ecology*, doi:10.1016/j.jembe.2011.09.017

Burns, E. S., Lopazanski, C., Flower, J., Thomas, L. R., Bradley, D., & Lester, S. E. (2023). Finding harmony in Marine Protected Area design guidelines. *Conservation Science and Practice*, *5*(6), e12946. https://doi.org/10.1111/csp2.12946

Campana, S., Dorey, A., Fowler, G. M., Joyce, W., Wang, Z., Wright, D., & Yashayaev, I. (2011). Migration pathways, behavioural thermoregulation and overwintering grounds of blue sharks in the northwest Atlantic. *PloS one, 6*. e16854. 10.1371/journal.pone.0016854

Capapé, C., & Reynaud, C. (2011). Maturity, reproductive cycle and fecundity of the spiny dogfish *Squalus acanthias* (Chondrichthyes: Squalidae) off the Languedocian coast (southern France, northern Mediterranean). *Journal of the Marine Biological Association of the United Kingdom*, *91*(8), 1627–1635. https://doi.org/10.1017/S0025315411000270

Carlson, J. K., & Parsons, G. R. (2001). The effects of hypoxia on three sympatric shark species: Physiological and behavioral responses. *Environmental Biology of Fishes*, *61*(4), 427–433. https://doi.org/10.1023/A:1011641302048

Carruthers, E. H., Neilson, J. D., & Smith, S. C. (2011). Overlooked bycatch mitigation opportunities in pelagic longline fisheries: Soak time and temperature effects on swordfish (*Xiphias gladius*) and blue shark (*Prionace glauca*) catch. *Fisheries Research, 108*(1). https://doi.org/10.1016/j.fishres.2010.12.008

Chapman, D. D., Feldheim, K. A., Papastamatiou, Y. P., & Hueter, R. E. (2015). There and back again: A review of residency and return migrations in sharks, with implications for population structure and management. In *Annual Review of Marine Science, 7*, 547–570. https://doi.org/10.1146/annurev-marine-010814-015730

Convention on Biological Diversity [CBD] (2010). *CBD/COP/DEC/X/2 2010, decision adopted by the conference of the parties to the Convention on Biological Diversity at its tenth meeting, Nagoya, Japan, 18–29 October 2010*. In: The Strategic Plan for Biodiversity 2011–2020 and the Aichi biodiversity targets. Retrieved on May 22, 2024, from: https://www.cbd.int/doc/decisions/cop-10/cop-10-dec-02-en.pdf

Da Silva, C., Kerwath, S., Attwood, C., Thorstad, E., Cowley, P., Økland, F., Wilke, C., & Næsje, T. (2013). Quantifying the degree of protection afforded by a no-take marine reserve on an exploited shark. *African Journal of Marine Science*, *35*(1), 57–66. https://doi.org/10.2989/1814232X.2013.769911

Da Silva, C., Kerwath, S., Winker, H., Lamberth, S., Attwood, C., Wilke, C., & Næsje, T. (2021). Testing the waters to find the 'goldilocks' zone: Fine-scale movement of *Mustelus mustelus* in relation to environmental cues. *Marine and Freshwater Research, 73*. 10.1071/MF20369

Dell'Apa, A., Maria Grazia, P., & Bonzek, C. (2016). Modeling the habitat distribution of spiny dogfish (*Squalus acanthias*), by sex, in coastal waters of the northeastern United States. *Fishery Bulletin*, *115*(1), 89–100. https://doi.org/10.7755/FB.115.1.8

Fisheries and Oceans Canada [DFO]. (2018). *Skates*. Retrieved on June 9, 2024, from: https://www.dfo-mpo.gc.ca/species-especes/skates/info/index-eng.html#fisheries

Dicken, M. L., Booth, A. J., & Smale, M. J. (2006). Preliminary observations of tag shedding, tag reporting, tag wounds, and tag biofouling for raggedtooth sharks (*Carcharias taurus*) tagged off the east coast of South Africa. *ICES Journal of Marine Science*, 63(9), 1640–1648. https://doi.org/10.1016/j.icesjms.2006.06.009

Dingle, H., & Drake, V.A. (2007). What is migration?. *BioScience*, 57(2), 113–121. https://doi.org/10.1641/B570206

Drymon, J. M., Dedman, S., Froeschke, J. T., Seubert, E. A., Jefferson, A. E., Kroetz, A. M., Mareska, J. F., & Powers, S. P. (2020). Defining sex-specific habitat suitability for a northern Gulf of Mexico shark assemblage. *Frontiers in Marine Science*, *7*, 35. https://doi.org/10.3389/fmars.2020.00035

Dulvy, N. K., Pacoureau, N., Rigby, C. L., Pollom, R. A., Jabado, R. W., Ebert, D. A., Finucci, B., Pollock, C. M., Cheok, J., Derrick, D. H., Herman, K. B., Sherman, C. S., VanderWright, W. J., Lawson, J. M., Walls, R. H. L., Carlson, J. K., Charvet, P., Bineesh, K. K., Fernando, D., … & Simpfendorfer, C. A. (2021). Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Current Biology*, *31*(21), 4773–4787.e8. https://doi.org/10.1016/j.cub.2021.08.062

Dureuil. M., Boerder, K., Burnett K. A., Froese, R., & Worm, B. (2018). Elevated trawling inside protected areas undermines conservation outcomes in a global fishing hot spot. *Science, 362*, 1403-1407. DOI:10.1126/science.aau0561

Edwards, J. E., Hedges, K. J., Kessel, S. T., & Hussey, N. E. (2022). Multi-year acoustic tracking reveals transient movements, recurring hotspots, and apparent seasonality in the coastal-offshore presence of Greenland sharks (*Somniosus microcephalus*). *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.902854

Elizondo-Sancho, M., Rodríguez-Arriatti, Y., Albertazzi, F. J., Bonilla-Salazar, A., Arauz-Naranjo, D., Arauz, R., Areano, E., Avalos-Castillo, C. G., Brenes, Ó., Chávez, E. J., Dominici-Arosemena, A., Espinoza, M., Heidemeyer, M., Tavares, R., & Hernández, S. (2022). Population structure and genetic connectivity of the scalloped hammerhead shark (*Sphyrna lewini*) across nursery grounds from the Eastern Tropical Pacific: Implications for management and conservation. *PLOS ONE*, *17*(12), e0264879. https://doi.org/10.1371/journal.pone.0264879

Ellis, J. R., McCully Phillips, S. R., & Poisson, F. (2017). A review of capture and post-release mortality of elasmobranchs. *Journal Of Fish Biology, 90*(3), 653–722. https://doi.org/10.1111/jfb.13197

Espinoza, M., Farrugia, T. J., & Lowe, C. G. (2011). Habitat use, movements and site fidelity of the gray smooth-hound shark (*Mustelus californicus* Gill 1863) in a newly restored southern California estuary. *Journal of Experimental Marine Biology and Ecology*, *401*(1–2), 63–74. https://doi.org/10.1016/j.jembe.2011.03.001

European Commission. (2023). *LIFE ELIFE (Elasmobranchs Low-Impact Fishing Experience).* Retrieved on April 2, 2024, from: https://webgate.ec.europa.eu/life/publicWebsite/project/LIFE18-NAT-IT-000846/life-elife-elasmobranchs-low-impact-fishing-experience

European Union [EU]. (2023). *Council Regulation (EU) 2023/194 of 30 January 2023 fixing for 2023 the fishing opportunities for certain fish stocks, applicable in Union waters and, for Union fishing vessels, in certain non-Union waters, as well as fixing for 2023 and 2024 such fishing opportunities for certain deep-sea fish stocks*. Retrieved on June 9, 2024, from: https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A32021R0092

Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R., & Lotze, H.K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, *13*, 1055–1071. https://doi.org/10.1111/j.1461-0248.2010.01489.x

Ferretti, F., Osio, G. C., Jenkins, C. J., Rosenberg, A. A., & Lotze, H. K. (2013). Long-term change in a meso-predator community in response to prolonged and heterogeneous human impact. *Scientific Reports*, *3*(1), 1057. https://doi.org/10.1038/srep01057

Fontes, J., Schouten, M., Afonso, P., & Macena, B. (2024). The return of Scarface: Philopatry in an ocean wandering shark? *Ecology 105*(3), e4234. https://doi.org/10.1002/ecy.4234

Fowler, S. L., Cavanagh, R. D., Camhi, M., Burgess, G. H., Callitet, G. M., Forham, S. V., Simpfendorfer, C., & Musick, J. (2005). Sharks, rays and chimaeras: the status of the Chondrichthyan fishes. Status survey. Gland: IUCN/SSC Shark Specialist Group. 189 p.

Francis, M.P. (2013). Temporal and spatial patterns of habitat use by juveniles of a small coastal shark (*Mustelus lenticulatus*) in an estuarine nursery. *PLOS ONE, 8*(2), e57021. https://doi.org/10.1371/journal.pone.0057021

Freedman, J. & Noakes, D. (2002). Why are there no really big bony fishes? A point-of-view on maximum body size in teleosts and elasmobranchs. *Reviews in Fish Biology and Fisheries*, *12*. 403-416. https://doi.org/10.1023/A:1025365210414

Frey, L., Coates, M., Ginter, M., Hairapetian, V., Rücklin, M., Jerjen, I., & Klug, C. (2019). The early elasmobranch Phoebodus: Phylogenetic relationships, ecomorphology and a new time-scale for shark evolution. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1912), 20191336. https://doi.org/10.1098/rspb.2019.1336

García, V. B., Lucifora, L. O., & Myers, R. A. (2008). The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1630), 83–89. https://doi.org/10.1098/rspb.2007.1295

Giani, M., Djakovac, T., Degobbis, D., Cozzi, S., Solidoro, C., & Umani, S. F. (2012). Recent changes in the marine ecosystems of the northern Adriatic Sea. *Estuarine, Coastal and Shelf Science*. https://doi.org/10.1016/j.ecss.2012.08.023

Giovos, I., Pytka, J. M., Barone, M., Koehler, L., Loth, C., Lowther, J., Moutopoulos, D. K., Niedermüller, S., & Mazzoldi, C. (2024). Conservation and management of chondrichthyans in the Mediterranean Sea: Gaps, overlaps, inconsistencies, and the way forward. *Reviews in Fish Biology and Fisheries*. https://doi.org/10.1007/s11160-024-09857-z

Griffiths, C. A., Wright, S. R., Silva, J. F., Ellis, J. R., Righton, D. A., McCully Phillips, S. R. (2020). Horizontal and vertical movements of starry smooth-hound *Mustelus asterias* in the northeast Atlantic. *PLOS ONE, 15*(10): e0239480. https://doi.org/10.1371/journal.pone.0239480

Haesemeyer, M. (2020). Thermoregulation in fish. *Molecular and Cellular Endocrinology*, *518*, 110986. https://doi.org/10.1016/j.mce.2020.110986

Hammerschlag, N., Gallagher, A. J., & Lazarre, D. M. (2011). A review of shark satellite tagging studies. *Journal of Experimental Marine Biology and Ecology*, *398*(1–2). https://doi.org/10.1016/j.jembe.2010.12.012

Hueter, R. E., Manire, C. A., Tyminski, J. P., Hoenig, J. M., & Hepworth, D.A. (2006). Assessing mortality of released or discarded fish using a logistic model of relative survival derived from tagging data. *Transactions of the American Fisheries Society, 135*, 500-508. https://doi.org/10.1577/T05-065.1

Heupel, M., Semmens, J., & Hobday, A. (2006). Automated acoustic tracking of aquatic animals: Scales, design and development of listening station arrays. *Marine and Freshwater Research, 57*. https://doi.org/10.1071/MF05091

Heupel, M., Reiss, K., Yeiser, B., Simpfendorfer, C. (2008). Effects of biofouling on performance of moored data logging acoustic receivers. *Limnology and Oceanography-Methods*, *6*, 327–335. 10.4319/lom.2008.6.327

Hixon, M. A., Johnson, D. W., & Sogard, S. M. (2014). BOFFFFs: On the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science*, *71*(8), 2171–2185. https://doi.org/10.1093/icesjms/fst200

Holbrook, C., Hayden, T., Binder, T., & Pye, J. (2024). _glatos: A package for the Great Lakes Acoustic Telemetry Observation System_. R package version 0.7.2, https://github.com/ocean-tracking-network/glatos

Hyde, C. A., Notarbartolo di Sciara, G., Sorrentino, L., Boyd, C., Finucci, B., Fowler, S. L., Kyne, P. M., Leurs, G., Simpfendorfer, C. A., Tetley, M. J., Womersley, F., & Jabado, R. W. (2022). Putting sharks on the map: A global standard for improving shark area-based conservation. *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.968853

International Union for the Conservation of Nature [IUCN]. (2021). *Convention on Migratory Species Shark MOU and Sharks*. Retrieved on July 14, 2024, from: https://www.iucnssg.org/sharksmou.html

International Union for the Conservation of Nature [IUCN]. (2022). *Post-2020 Global Biodiversity Framework*. Retrieved on May 23, 2024, from: https://www.iucn.org/sites/default/files/2022-11/iucn-issues-brief_post2020_final.pdf

International Union for the Conservation of Nature [IUCN]. (2023). *International Union for Conservation of Nature, Red List of Threatened Species 2023*. Retrieved on April 2, 2024, from: https://www.iucnredlist.org

Jepsen, N., Thorstad, E. B., Havn, T., & Lucas, M. C. (2015). The use of external electronic tags on fish: An evaluation of tag retention and tagging effects. *Animal Biotelemetry*, *3*(1), 49. https://doi.org/10.1186/s40317-015-0086-z

Jirik, K.E., & Lowe, C.G. (2012). An elasmobranch maternity ward: Female round stingrays *Urobatis halleri* use warm, restored estuarine habitat during gestation. *Journal of Fish Biology, 80*, 1227–1245. https://doi.org/10.1111/j.1095-8649.2011.03208.x

Kelly, M. L., Murray, E. R. P., Kerr, C. C., Radford, C. A., Collin, S. P., Lesku, J. A., & Hemmi, J. M. (2020). Diverse activity rhythms in sharks (Elasmobranchii). *Journal of Biological Rhythms, 35*(5), 476–488. https://doi.org/10.1177/0748730420932066

Kessel, S., Cooke, S., Heupel, M., Hussey, N., Simpfendorfer, C., Vagle, S., & Fisk, A. (2013). A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries, 24*. 10.1007/s11160-013-9328-4

Kraft, S., Gandra, M., Lennox, R. J., Mourier, J., Winkler, A. C., & Abecasis, D. (2023). Residency and space use estimation methods based on passive acoustic telemetry data. *Movement Ecology*, *11*(1), 12. https://doi.org/10.1186/s40462-022-00364-z

Lascelles, B., Notarbartolo di Sciara, G., Agardy, T., Cuttelod, A., Eckert, S., Glowka, L., Hoyt, E., Llewellyn, F., Louzao, M., Ridoux, V., & J., T. (2014). Migratory marine species: Their status, threats and conservation management needs. *Aquatic Conservation Marine and Freshwater Ecosystems*, *24*, 111–127. https://doi.org/10.1002/aqc.2512

Lea, J. S. E., Wetherbee, B. M., Queiroz, N., Burnie, N., Aming, C., Sousa, L. L., Mucientes, G. R., Humphries, N. E., Harvey, G. M., Sims, D. W., & Shivji, M. S. (2015). Repeated, long-distance migrations by a philopatric predator targeting highly contrasting ecosystems. *Scientific Reports*, *5*(1), 11202. https://doi.org/10.1038/srep11202

Lotze, H., Coll, M., & Dunne, J. (2011). Historical changes in marine resources, food-web structure and ecosystem functioning in the Adriatic Sea, Mediterranean. *Ecosystems*, *14*, 198–222. https://doi.org/10.1007/s10021-010-9404-8

Lubchenco, J. & Grorud-Colvert, K. (2015). Making waves: The science and politics of ocean protection. *Science, 350*. 10.1126/science.aad5443

Mangiafico, S. S. (2023). rcompanion: Functions to support extension education program evaluation. version 2.4.30. Rutgers Cooperative Extension. New Brunswick, New Jersey. https://CRAN.R-project.org/package=rcompanion

Marine Conservation Institute (2024). *MPA Guide Marine Protection*. Retrieved on June 9, 2024, from: https://mpatlas.org/mpaguide/

Marino, I., Finotto, L., Colloca, F., Di Lorenzo, M., Gristina, M., Farrell, E., Zane, L., & Mazzoldi, C. (2017). Resolving the ambiguities in the identification of two smooth-hound sharks (*Mustelus mustelus* and *Mustelus punctulatus*) using genetics and morphology. *Marine Biodiversity*, *48*. https://doi.org/10.1007/s12526-017-0701-8

Martínez-Ramírez, L., Bentes, L., Dias, A., Erzini, K., Gandra, M., Kraft, S., Winkler, A. C., & Abecasis, D. (2024). Tagging mortality in acoustic telemetry studies: Insights from a multispecies analysis. *Journal of Fish Biology*, 1–11. https://doi.org/10.1111/jfb.15790

McMillan, M. N., Huveneers, C., Semmens, J. M., & Gillanders, B. M. (2019). Partial female migration and cool-water migration pathways in an overfished shark. *ICES Journal of Marine Science*, *76*(4), 1083–1093. https://doi.org/10.1093/icesjms/fsy181

Ministry of Fisheries. (October 2008) *New Zealand national plan of action for the conservation and management of sharks*. Wellington. 90 p.

Molina, J. M., Finotto, L., Walker, T. I., & Reina, R. D. (2020). The effect of gillnet capture on the metabolic rate of two shark species with contrasting lifestyles. *Journal of Experimental Marine Biology and Ecology, 526*. https://doi.org/10.1016/j.jembe.2020.151354

Mourier, J., & Planes, S. (2013). Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia. *Molecular Ecology*, *22*(1), 201–214. https://doi.org/10.1111/mec.12103

Musyl, M. K., & Gilman, E. L. (2019). Meta-analysis of post-release fishing mortality in apex predatory pelagic sharks and white marlin. *Fish and Fisheries*, *20*(3), 466–500. https://doi.org/10.1111/faf.12358

Myers, R., & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, *423*, 280–283. https://doi.org/10.1038/nature01610

Myers, R. A., & Worm, B. (2005). Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1453), 13–20. https://doi.org/10.1098/rstb.2004.1573

Nieto, A., Ralph, G. M., Comeros-Raynal, M. T. Kemp, J., Criado, M. G., Allen, D. J., Dulvy, N. K., Walls, R. H. L., Russell, B., Pollard, D., García, S., Craig, M., Collette, B. B., Pollom, R., Biscoito, M., Chao, N. L., Abella, A., Afonso, P., Álvarez, H., Carpenter, K. E., et al. (2015). European Red List of marine fishes. Publications Office of the European Union, Luxembourg

National Oceanic and Atmospheric Administration [NOAA]. (2019). *What is a marine protected area (MPA)?* Retrieved on June 9, 2024, from: https://oceanexplorer.noaa.gov/facts/mpas.html

National Oceanic and Atmospheric Administration [NOAA]. (2024). *Atlantic sharks commercial minimum sizes and retention limits*. Retrieved on June 9, 2024, from: https://www.fisheries.noaa.gov/action/atlantic-sharks-commercial-minimum-sizes-and-retention-limits

Nuez, I., Gazo, M., Borrell, A., Aguilar, A., Barría, C., Navarro, J., Cardona, L. (2024). Filling the gap: The unique isotopic niche of medium-sized and large sharks in the northwestern Mediterranean Sea. *Estuarine, Coastal and Shelf Science, 299*. https://doi.org/10.1016/j.ecss.2024.108698

Pacoureau, N., Carlson, J. K., Kindsvater, H. K., Rigby, C. L., Winker, H., Simpfendorfer, C. A., Charvet, P., Pollom, R. A., Barreto, R., Sherman, C. S., Talwar, B. S., Skerritt, D. J., Sumaila, U. R., Matsushiba, J. H., VanderWright, W. J., Yan, H. F., & Dulvy, N. K. (2023). Conservation successes and challenges for wide-ranging sharks and rays. *Proceedings of the National Academy of Sciences of the United States of America*, *120*(5), e2216891120. https://doi.org/10.1073/pnas.2216891120

Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology & Evolution*, *10*(10), 430. https://doi.org/10.1016/S0169-5347(00)89171-5

Paxton, A.B., Newton, E.A., Adler, A.M., Van Hoeck, R.V., Iversen, E.S. Jr, Taylor, J.C., Peterson, C.H., & Silliman, B.R. (2020) Artificial habitats host elevated densities of large reef-associated predators. *PLOS ONE, 15*(9). e0237374. https://doi.org/10.1371/journal.pone.0237374

Pedersen, T. (2022). *patchwork: The Composer of Plots*. R package version 1.1.2, https://github.com/thomasp85/patchwork

Pincock, D.G. (2012). False detections: What they are and how to remove them from detection data. Amirix Document DOC-004691 Version 03, Available at: http://vemco.com/wp-content/uploads/2012/11/false_detections.pdf

Posit team (2024). RStudio: Integrated development environment for R. Posit Software, PBC, Boston, MA. URL http://www.posit.co/

R Core Team. (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Riginella E., Correale, V., Marino, I. A. M., Rasotto, M. B., Vrbatovic, A., Zane, L., & Mazzoldi, C. (2020). Contrasting life-history traits of two sympatric smooth-hound species: Implication for vulnerability. *Journal of Fish Biology*, *96*, 853–857. https://doi.org/10.1111/jfb.14262

Roberts, C. M., Hawkins, J. P., & Gell, F. R. (2005). The role of marine reserves in attaining sustainable fisheries. *Philosophical Transactions of the Royal Society B: Biological Sciences, 360*(1453). https://doi.org/10.1098/rstb.2004.1578

Romo-Curiel, A. E., Ramírez-Mendoza, Z., Fajardo-Yamamoto, A., Ramírez-León, M. R., García-Aguilar, M. C., Herzka, S. Z., Pérez-Brunius, P., Saldaña-Ruiz, L. E., Sheinbaum, J., Kotzakoulakis, K., Rodríguez-Outerelo, J., Medrano, F., & Sosa-Nishizaki, O. (2022). Assessing the exposure risk of large pelagic fish to oil spills scenarios in the deep waters of the Gulf of Mexico. *Marine Pollution Bulletin*. https://doi.org/10.1016/j.marpolbul.2022.113434.

Russo, A. & Artegiani, A. (1996). Adriatic Sea hydrography. *Scientia Marina, 60*, 33–43.

Sandoval-Castillo, J., & Beheregaray, L. (2015). Metapopulation structure informs conservation management in a heavily exploited coastal shark (*Mustelus henlei*). *Marine Ecology Progress Series*, *533*, 191–203. https://doi.org/10.3354/meps11395

Semrau, J. (2012). Fisheries in Veneto, Policy Department B: Structural and cohesion policies (Directorate-General for Internal Policies). *European Parliament*. Retrieved on April 2, 2024, from: https://www.europarl.europa.eu

Serena, F. (2005). *Field Identification Guide to the Sharks and Rays of the Mediterranean and Black Sea*.

Skomal, G. B., & Mandelman, J. W. (2012). The physiological response to anthropogenic stressors in marine elasmobranch fishes: A review with a focus on the secondary response. *Select Papers from a Symposium on the Physiological Stress Response in Elasmobranch Fishes*, *162*(2), 146–155. https://doi.org/10.1016/j.cbpa.2011.10.002

Speed, C., Field, I., Meekan, M., & Bradshaw, C. (2010). Complexities of coastal shark movements and their implications for management. *Marine Ecology Progress Series*, *408*, 275–293. https://doi.org/10.3354/meps08581

Tsikoti, C., & Genitsaris, S. (2021). Review of harmful algal blooms in the coastal Mediterranean Sea, with a focus on Greek waters. *Diversity*, *13*(8), 396. https://doi.org/10.3390/d13080396

van Zinnicq Bergmann, M. P. M., Guttridge, T. L., Smukall, M. J., Adams, V. M., Bond, M. E., Burke, P. J., Fuentes, M. M. P. B., Heinrich, D. D. U., Huveneers, C., Gruber, S. H., & Papastamatiou, Y. P. (2022). Using movement models and systematic conservation planning to inform marine protected area design for a multi-species predator community. *Biological Conservation*, *266*. https://doi.org/10.1016/j.biocon.2022.109469

Villegas-Ríos, D., Freitas, C., Moland, E., Thorbjørnsen, S. H., & Olsen, E. M. (2020). Inferring individual fate from aquatic acoustic telemetry data. *Methods in Ecology and Evolution, 11*, 1186–1198. https://doi.org/10.1111/2041-210X.13446

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org

Wickham, H., François, R., Henry, L., Müller, K., Vaughan, D. (2023). dplyr: A grammar of data manipulation. R package version 1.1.4. https://CRAN.R-project.org/package=dplyr

Worm, B., Davis, B., Kettemer, L., Ward-Paige, C. A., Chapman, D., Heithaus, M. R., Kessel, S. T., & Gruber, S. H. (2013). Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy*, *40*, 194–204. https://doi.org/10.1016/j.marpol.2012.12.034.

Worm, B. (2017). Marine conservation: How to heal an ocean. *Nature, 543*. 10.1038/nature21895

Annex

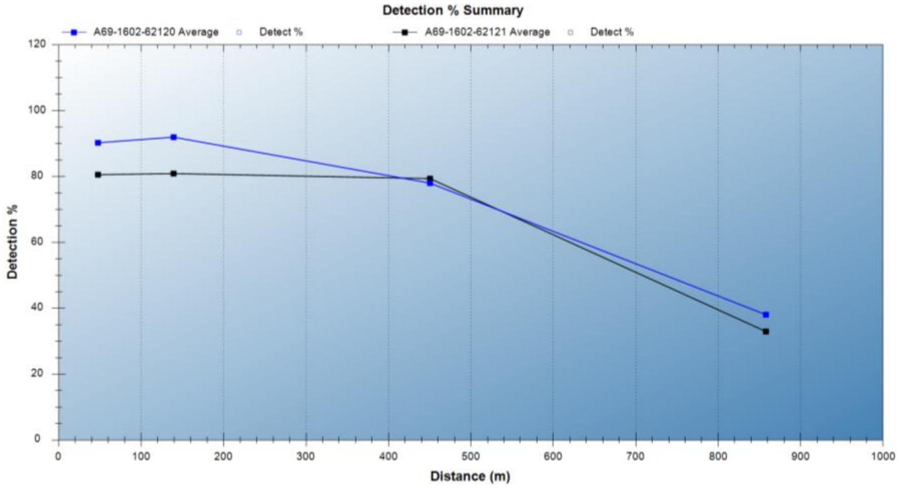


Figure A1 Detection range of Innovasea VR2Tx hydrophones in the study area (separate study; Mazzoldi unpub. data)

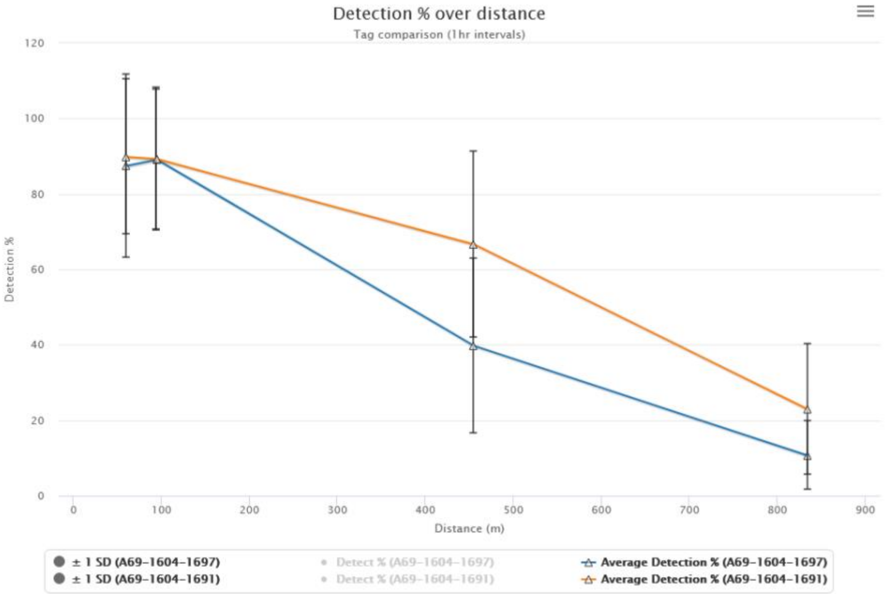


Figure A2 Detection range of Innovasea VR2Tx hydrophones paired to a tag covered with antifouling dye (blue line) versus an uncovered tag (orange line; separate study; Mazzoldi unpub. data)

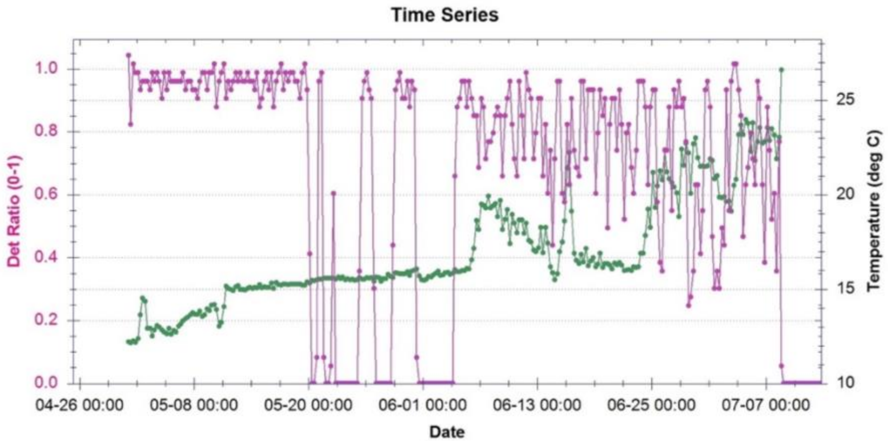


Figure A3 Long-term detection range of Innovasea VR2Tx hydrophones (separate study; Mazzoldi unpub. data)

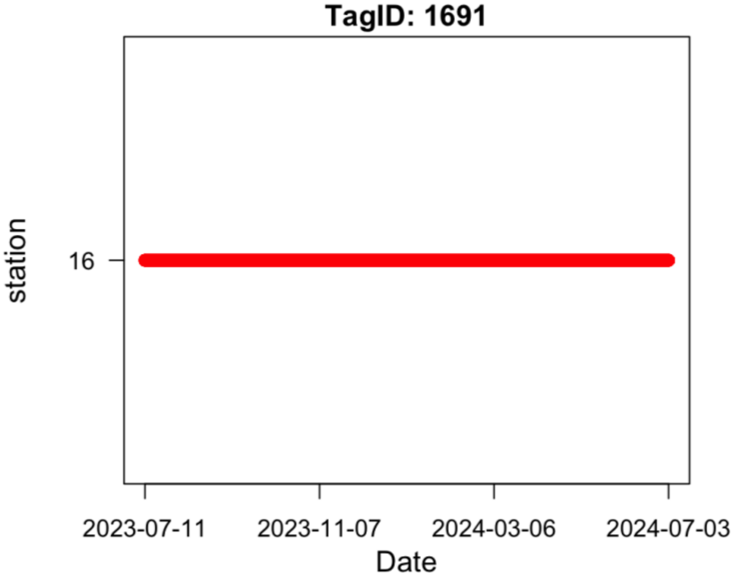


Figure A4 Example abacus plot of a detached tag with over 233 thousand detections at a single station. Data comes from individual 1691 (*S. acanthias* female, tagged with a V13 tag in 2022); not included in our study due to unfinished analyses of new receivers picked up in August, 2024

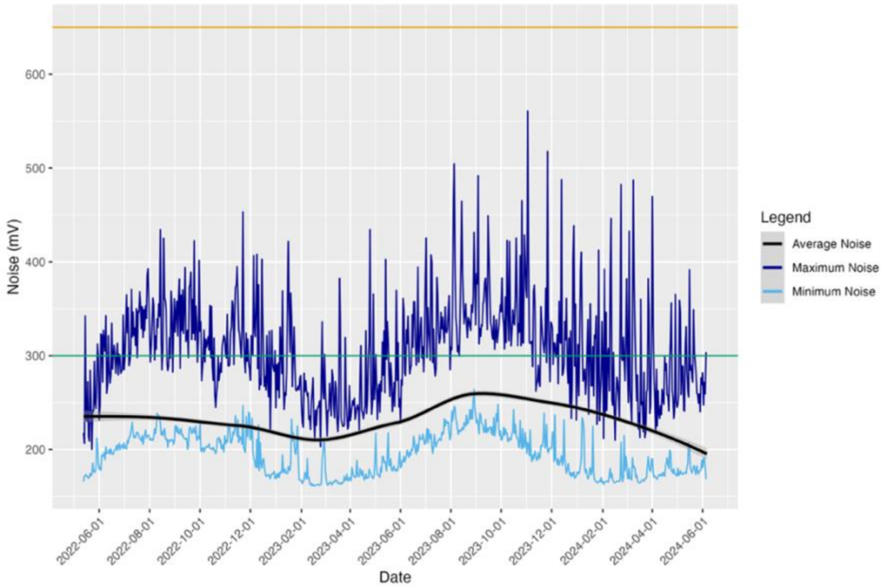


Figure A5 Maximum (dark blue), average (black), and minimum (light blue) ambient noise (mV) of stations throughout deployment; orange line at 650 mV indicates the threshold for excessive noise, green line at 300 mV the threshold for moderate noise

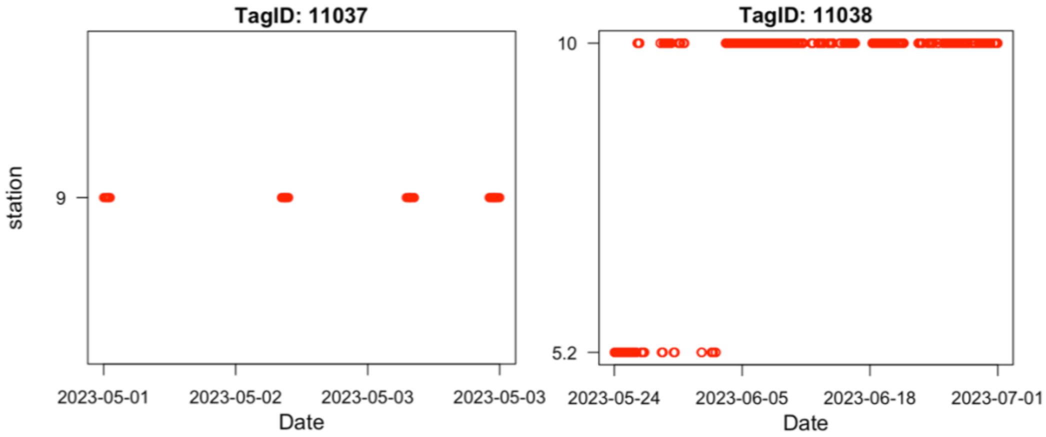


Figure A6 Abacus plots of individuals 11037 (*M. mustelus* female) and 11038 (*M. punctulatus* female) showing detection data suspected to represent detached tags sometime in May and June, 2023, respectively. The timing between individual 11037's detections might be indicative of tidal movement.

Table A1 Detected individuals' tag ID, species, sex, maturity, vitality score, tag type, gear with which they were caught, date caught/released, and number of detections. MM stands for *M. mustelus*, MP for *M. punctulatus*, and SA for *S. acanthias*. Individuals whose tag is believed to have detached during the study are greyed out.

ID	Species	Sex	Maturity	Vitality	Tag type	Gear	Date	N. detections
1084	MM	Female	Juvenile	3	V9	GNS	2024-05-12	535
1089	MM	Male	Juvenile	1	V9	GNS	2024-05-27	151
1092	MM	Female	Juvenile	1	V9	GNS	2024-05-27	16
11024	MM	Male	Adult	2	V13	GTR	2023-04-23	205
11025	MP	Female	Juvenile	1	V13	GNS	2023-05-24	865
11029	MP	Female	Adult	2	V13	GNS	2023-05-07	201
11030	MM	Male	Adult	1	V13	GNS	2023-05-24	220
11031	MM	Male	Juvenile	2	V13	GNS	2023-04-23	181
11032	MM	Male	Adult	2	V13	GNS	2023-04-23	1223
11033	MM	Female	Juvenile	1	V13	GNS	2023-05-24	4
11034	MM	Male	Adult	1	V13	GNS	2023-04-23	1194
11035	MM	Female	Juvenile	1	V13	GNS	2023-05-07	100
11037	MM	Female	Juvenile	3	V13	GNS	2023-04-23	79
11038	MP	Female	Adult	1	V13	GNS	2023-05-24	9804
11039	MM	Female	Juvenile	1	V13	GNS	2023-05-07	94
11040	MM	Male	Adult	1	V13	GNS	2023-04-23	223
11042	SA	Female	Juvenile	1	V9	GNS	2023-05-07	11
11044	MM	Female	Juvenile	1	V9	OTB	2023-05-29	1023
11046	MP	Female	Juvenile	1	V9	OTB	2023-06-20	1161

11047	MM	Male	Juvenile	1	V9	GTR	2023-04-23	318
11049	MP	Male	Juvenile	2	V9	OTB	2023-05-29	328
11050	SA	Male	Adult	3	V9	GNS	2023-05-07	4
11052	MP	Female	Juvenile	1	V9	GTR	2023-04-23	31041
11053	SA	Male	Adult	1	V9	GNS	2023-04-23	51
11055	MP	Male	Juvenile	2	V9	GTR	2023-04-23	2838
11056	SA	Female	Adult	2	V9	GNS	2023-05-07	7
11060	MM	Female	Juvenile	2	V9	OTB	2023-05-29	355
1692	SA	Male	Adult	2	V13	GNS	2022-10-08	65
1693	MP	Female	Juvenile	2	V13	OTB	2022-07-20	662
1697	SA	Male	Adult	3	V13	GNS	2022-10-15	64
1699	SA	Female	Adult	2	V13	GNS	2023-10-03	59
1700	SA	Female	Adult	1	V13	GTR	2023-12-15	210
1701	MP	Female	Juvenile	1	V13	GNS	2023-10-03	12
1703	MP	Female	Juvenile	1	V13	OTB	2022-07-19	848
1707	SA	Male	Adult	1	V13	GTR	2023-11-07	5
1710	SA	Female	Adult	2	V13	GNS	2022-10-08	535
62017	SA	Female	Juvenile	2	V9	GTR	2023-11-07	28
62018	SA	Male	Adult	1	V9	GNS	2023-10-03	99
62019	SA	Female	Adult	2	V9	GNS	2023-10-03	66
62020	SA	Female	Adult	1	V9	GTR	2023-11-07	427
62022	MM	Female	Juvenile	2	V9	OTB	2023-09-11	441

982	MM	Male	Adult	2	V13	GNS	2024-05-12	142
983	MM	Male	Juvenile	2	V13	GNS	2024-05-12	17
985	SA	Female	Adult	3	V13	GNS	2024-05-12	11
990	MM	Male	Juvenile	1	V13	GNS	2024-05-27	220
991	MM	Male	Juvenile	2	V13	GNS	2024-05-27	170

Table A2 Chi-square tests of ‘detected’ versus ‘not detected’ individuals by vitality score, species, and by sex and maturity for each species. A p-value > 0.05 leads us to fail to reject the null hypothesis H_0 (normal proportions of ‘detected’ versus ‘not detected’ individuals)

	Vitality score 1		Vitality score 2		Vitality score 3	
Detected	23		18		5	
Not detected	15		20		4	
X^2	1.333					
df	2					
p-value	0.514					
	Mustelus mustelus		*Mustelus punctulatus*		*Squalus acanthias*	
Detected	21		10		15	
Not detected	13		11		15	
X^2	1.363					
df	2					
p-value	0.506					
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
Detected	6	15	2	8	13	2
Not detected	3	10	2	9	14	1
X^2	0.125		0.0112		0.370	
df	1		1		1	
p-value	0.724		0.916		0.543	
	Males	Females	Males	Females	Males	Females
Detected	12	9	2	8	6	9
Not detected	6	7	2	9	6	9
X^2	0.389		0.0112		0	
df	1		1		1	
p-value	0.533		0.916		1	