JOFFREY HENRI PIERRE BAEYAERT

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A comparison study with preliminary personality traits observed in mesocosms.

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Trabalho efectuado sob a orientação de:

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Bimini Biological Field Station

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Dissertation submitted in fulfillment of the requirements for the Degree of Master of Science in Marine Biology

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“Nothing in Biology Makes Sense Except in the Light of Evolution”

Theodosius Dobzhansky, 1973.

To my very own heroes of war & in loving memory of Jean.

Á mes deux héros de guerre & en memoire de Jean.

Juvenile lemon sharks, *Negaprion brevirostris*, caught in a gillnet in a nursery area, Bimini Islands, Bahamas. Late May 2016. Credits: Charlotte Sams, Bimini Biological Field Station

ABSTRACT

Unevenness within a population is challenging to explain. It appears hazardous to interpret inter-individual dissimilarities in behavior, mainly due to a lack of information about the underlying mechanisms responsible for such expression. The key component of this study was the focus on the relationship between an intrinsic decision-making mechanism and the expression of individual movements. The uniqueness of this research laid in the study of *how* personality in juvenile lemon sharks, *Negaprion brevirostris* (Poey, 1868), may influence their natural behavior, providing a correlative analysis between personality and movement ecology. Twelve individuals were preliminarily exposed to a novel open field test to quantify a personality trait. Afterwards, the sharks were fitted with acoustic transmitters and monitored inside their nursery area, using an array of fifteen acoustic receivers, over an eight-month period. Movement patterns were assessed using active tracking. Home range and core area were measured using Minimum Convex Polygon (MCP) and Kernel Utilization Density (KUD). Although the two analyses produced different outputs, both revealed high individual differences in term of location and size. The results suggested an extensive use of the mangrove by the juveniles. The home range varied from 568.52m^2 to 1296.01 m^2 whilst using MCP approach, and ranged from 770.10 m^2 to 1474.51 m^2 based on the kernel-bivariate analysis. Similarly, core area estimates ranged from 85.88 m^2 to 323.67 m^2 (KUD). The estimation of the distance from the nearest shore captured a similar pattern and ranged from 38.16 m to 155.38 m. These inter-individual differences persisted even after effects of body size, sex or monitoring features were removed. However, multiple correlations revealed a strong relationship between personality traits and the spatial metrics (home range, Rs = 0.71; core area, Rs = 0.84; distance from the shore, Rs = 0.69). The results uncovered the likelihood of an influence of personality on the movement ecology of juvenile lemon sharks. Identifying mechanisms driving the expression of movement patterns provided crucial insight into decision-making processes at an individual level. Such observation should encourage further investigations to consider individual-based analyses for conservation purposes and advocate for the integration of behavioral ecology and movement ecology into a common framework to enhance the understanding of evolutionary and ecological processes.

Keywords: Personality; Movement Ecology; *Negaprion brevirostris*; Acoustic Telemetry; Nursery Ground; Home Range

RESUMO

É difícil explicar a ausência de uniformidade em populações. Pode ser arriscado interpretar diferenças comportamentais entre indivíduos, principalmente devido à falta de informação sobre os mecanismos subjacentes responsáveis pela expressão destes comportamentos. O principal foco deste estudo foi a relação entre o mecanismo intrínseco de tomada de decisão e a expressão dos movimentos individuais. A originalidade deste trabalho baseia-se no estudo de como a personalidade na tubarões jovens, Negaprion brevirostris (Poey, 1868), pode influenciar o seu comportamento natural, criando uma análise de correlação entre a personalidade e a ecologia do movimento. Doze indivíduos foram previamente expostos a um teste novo para quantificar traços de personalidade. Seguidamente, os tubarões foram equipados com transmissores acústicos e monitorados dentro de sua área de maternidade, usando um conjunto de quinze receptores acústicos, ao longo de um período de oito meses. Os padrões de movimento foram avaliados através de um seguimento activo. A extensão da área habitada e a área central foram medidas usando Minimum Convex Polygon (MCP) e Kernel Utilization Density (KUD). Embora as duas análises tenham tido resultados diferentes, ambas revelaram grandes diferenças individuais em termos de localização e tamanho. Os resultados sugerem um uso intensivo de mangais pelos juvenis. Utilizando a abordagem MCP, a extensão da área habitada variou entre 568.52m^2 e 1 296.01 m^2. Utilizando a análise bivariada de kernel, a variação foi entre 770.10 m^2 e 1 474.51 m^2. Da mesma forma, as estimativas da área central variaram entre 85.88 m^2 e 323.67 m^2 (KUD). A estimativa da distância à costa mais próxima evidenciou um padrão semelhante, com uma variação de 38.16 a 155.38 m. Estas diferenças inter-individuais persistiram mesmo depois de removidos os efeitos do tamanho, sexo e características de monitorização. No entanto, várias correlações revelaram uma relação forte entre traços de personalidade e as métricas espaciais (área habitada, Rs = 0.71; área central, Rs = 0.84; distância à costa, Rs = 0.69). Os resultados revelaram a possibilidade da personalidade influenciar a ecologia do movimento de tubarões-limão jovens. A identificação de mecanismos que impulsionam a expressão de padrões de movimento forneceu percepção crucial sobre os processos de tomada de decisão a nível individual. Estas observações devem servir de incentivo a novas investigações, para que considerem análises individuais para fins de conservação, e insistir na integração da ecologia comportamental e ecologia do movimento num plano de trabalhos comum, com o fim de melhorar a compreensão dos processos evolutivos e ecológicos.

Palavras-chave: Personalidade; Ecologia do Movimento; *Negaprion brevirostris*; Telemetria Acústica; Área de Maternidade; Área de Vida

SUMMARY

Noticeable individual differences in spatial ecology (e.g. movement patterns, habitat use, home range) have been detected within the same population by various studies over the last decades, mostly reported via the use of tracking methodologies. Most of these investigations failed to elucidate the underlying cause(s) leading to the expression of such heterogeneous patterns. Identifying the source of individual dissimilarities raised an interest in behavioral research, focusing on the consistency, across time and context, of these behavioral differences. It is under this context that there has been increasing interest in the personality field of research over the past decades. An extensive literature provides remarkable insights on the capture of personality traits in laboratory experiments. However, very few studies attempted to investigate such heterogeneity within populations in natural conditions. This emerging topic appears of considerable relevance regarding the ecological and evolutionary implications personality traits might have. The importance of investigating such distinctive characteristics in order to provide better understanding of the relationship between the individual, its environment and natural selection is widely recognized and of a particular significance for protection and conservation purposes. This study considers novel areas rarely explored, focusing on the link between individual spatial ecology in natural conditions and personality traits in juveniles of a top-predator species of elasmobranch. One of the main interests lay in the prospect of providing a fertile ground between behavioral ecology and movement ecology to uncover the underlying processes driving decision-making mechanisms leading to the expression of a spatial pattern in a species of shark. The lemon shark, *Negaprion brevirostris*, is a coastal tropical shark species form the Carcharhinidae family. It is mainly found in the subtropical areas of the Atlantic and Pacific coasts of North and South America, but also in the western African coast and in the Pacific islands. In 2009, the lemon shark was listed by the World Conservation Union as a near-threatened species. For many years this shark has been the center of interest of the research at the Bimini Biological Field Station, in the Bahamas. Extensive literature designates the lemon shark as an interesting model, hardy in captivity. Also, two main nursery areas have been identified within the shallow waters of Bimini and presented a great advantage for the current project. Exploring the causes of individual variations and understanding behavior within the nursery area of populations would provide suitable insight to develop adequate measures for conservation and protection of elasmobranchs. Preliminary research on lemon shark's personality has been carried out in mesocosms in Bimini Islands for the past few years. Personality traits experiments on sharks were carried out in mesocosms in 2015 and consisted in exposing the juveniles to a novel open field test. The sharks were tested in pens constructed in the nursery area, the North Sound. Recently, this method has been acknowledged as an efficient way to quantify personality in lemon sharks. Such testing allowed assessing each individual behaviour by providing exploratory scores. As expected, the first inferences revealed evidence of repeatability (i.e. consistency in individual differences). The next phase was to determine whether personality features could be reflected by the expression of natural spatial ecology and movement patterns. Therefore, after the personality trial, a total of twelve individuals were fitted with a 14-months acoustic transmitter (Sonotronics ®) and released in their respective nursery area, the capture location. The post-release movement ecology of the individuals was monitored over an eight months period, between August 2015 and April 2016 using a network of fifteen passive receivers. Information on real-time movement patterns was obtained from active acoustic tracking. An investigation of the detection range of the receivers revealed a reduced probability of detection on the western flank of the North Sound, which is undergoing dramatic anthropogenic disturbances. Unusual detection features were also uncovered, contradicting the commonly accepted idea that the closest the tag is to a receiver, the higher is the probability of detection. The heterogeneity of the landscape and challenging environment (i.e. shallow waters with patches of seagrass meadows, sponges) might play an important role in the underwater sound propagation; thereby further investigations are currently being undertaken.

The interest of the study focused on the assessment of home range and core area, as well as the distance from the shore. Minimum Convex Polygon (MCP) and Kernel Utilization Distribution (KUD) methods were evaluated to determine the formers while the later was calculated using a straightforward arithmetic. The results allowed corroborating 25 years of research on the lemon shark in the North Sound, indicating that juveniles are resident of the area for months to years after birth. Likewise, an examination of the spatial occupation confirmed the ecological importance of the mangrove fringe of the nursery, currently identified as the preferred habitat of most individuals. Such observation raised concerns on the impact of anthropogenic disturbances on populations of juvenile lemon sharks in Bimini. Furthermore, both analyses provided intriguing results, revealing high inter-individual differences in spatial ecology of juveniles lemon sharks. The home range and core area sizes varied greatly amongst individual, as well as the distance from the shore. The typical factors potentially held responsible for such dissimilarities in most of the literature, such as gender, body size or even monitoring design, failed to explain the captured patterns. However, the investigation of the relationship between the personality traits and the spatial metrics revealed strong relationships. Multiple correlations were identified between home range and personality, core area and personality as well as with the distance from the shore (i.e. distance from the Mangrove). Personality was identified as an intrinsic factor potentially responsible for the expression of variable patterns within the same population. This observation underlined the likelihood of an influence of personality trait, as a driving mechanism, on the movement ecology of juvenile lemon sharks. Such perspective provided crucial insight into the processes influencing movement patterns, encouraging further investigations to consider individual-based analyses for conservation purposes.

SUMÁRIO

Vários estudos detectaram consideráveis diferenças individuais a nível de ecologia espacial (e.g. padrões de movimento, uso de habitat e área de vida) dentro da mesma população ao longo das últimas décadas, a maioria das quais identificada através do uso de metodologias de monitoramento. Grande parte destas investigações falhou em encontrar a causa subjacente à expressão de tais padrões heterogéneos. Tal levou a um interesse em identificar a(s) fonte(s) responsável por tais diferenças individuais e, consequentemente, em pesquisa comportamental, com foco na consistência, no tempo e no contexto das mesmas. É neste contexto que tem havido um crescente interesse neste campo de investigação ao longo das últimas décadas. Uma extensa literatura oferece conhecimento relativamente à captura de traços de personalidade em experiências laboratoriais. Porém, poucos estudos visam investigar a heterogeneidade destas populações em condições naturais. Este tópico emergente aparenta ser relevante no que diz respeito a implicações ecológicas e evolutivas que os traços de personalidade possam ter. É amplamente reconhecido que uma investigação que conduza a uma melhor compreensão da relação entre o indivíduo, o seu ambiente e a seleção natural é particularmente importante no que diz respeito a propósitos de protecção e conservação. O presente estudo considera novas áreas infrequentemente exploradas, focando-se na ligação entre ecologia espacial em condições naturais e traços de personalidade em juvenis de uma espécie de predador de topo de elasmobrânquio. Um dos principais interesses reside em fornecer um elo entre ecologia comportamental e ecologia do movimento, de modo a desvendar os processos subjacentes aos mecanismos do processo de decisão que leva à expressão de um padrão espacial numa espécie de tubarão. O tubarão limão, *Negaprion brevirostris*, é uma espécie de tubarão costeiro e tropical da família Carcharhinidae. Esta espécie pode ser encontrada tanto nas áreas subtropicais atlânticas e pacíficas das costas norte e sul americanas como na costa oeste de África e ilhas do Pacífico. Em 2009 o tubarão limão foi registado pela União Internacional para a Conservação da Natureza como uma espécie quase ameaçada. Durante muitos anos este tubarão tem sido o foco de pesquisa da Estação Biológica de Bimini nas Bahamas. Extensa literatura indica o tubarão limão como um modelo interessante e resistente em cativeiro. Duas principais áreas de maternidade foram já identificadas nas águas pouco profundas de Bimini e representaram uma grande vantagem no decorrer deste

projecto. A descoberta das causas de variações individuais e a compreensão do comportamento em áreas de maternidade fornecerá um conhecimento mais aprofundado importante para o desenvolvimento de medidas adequadas para a conservação e protecção dos elasmobrânquios. Pesquisa preliminar relativamente à personalidade do tubarão limão tem sido realizada nos últimos anos em mesocosmos nas ilhas Bimini. Experiências de traços de personalidade foram realizadas em mesocosmos em 2015 consistindo em expor juvenis a um novo teste em ambiente aberto. Os tubarões foram testados em baías construídas na área de maternidade, o North Sound. Recentemente este método tem sido reconhecido como uma forma eficiente de quantificar a personalidade em tubarões limão. Como tal este método permitiu avaliar cada comportamento individual ao oferecer notas exploratórias. Como esperado, as primeiras inferências revelaram repetibilidade (i.e. consistência em diferenças individuais). A fase seguinte consistiu em determinar se características de personalidade poderiam ser refletidas pela expressão de ecologia espacial natural e por padrões de movimento. Assim, após estes julgamentos de personalidade, um total de doze indivíduos foram equipados com um transmissor acústico de 14 meses (Sonotronics ®) e libertados na sua respectiva área de maternidade, o local de captura. O movimento ecológico pós-libertação foi controlado durante um período de oito meses, entre agosto de 2015 e abril de 2016, usando uma rede de quinze receptores passivos. A informação em tempo real dos padrões de movimento foi obtida através de rastreamento acústico activo. Investigação relativa ao alcance de deteção dos receptores demonstrou uma probabilidade reduzida de detecção no flanco ocidental do North Sound, local no qual se podem verificar dramáticas perturbações antrópicas. Recursos de detecção incomuns foram também descobertos, contrariando a ideia geralmente aceite de que quanto mais próximo da tag está um receptor, maior é a probabilidade de detecção. A heterogeneidade do ambiente e as suas características desafiantes (águas rasas ou seja, com manchas de pradarias marinhas, esponjas) pode desempenhar um papel importante na propagação do som subaquático; assim, novas investigações estão a atualmente ser desenvolvidas atualmente. O interesse deste estudo incidiu sobre a avaliação da área de vida e área central, assim como a distância até à costa. Os métodos de Kernel Utilization Distribution (KUD) foram calculadas usando uma aritmética simples e então utilizados para determinar o Minimum Convex Polygon (MCP). Os resultados permitiram corroborar 25 anos de pesquisa sobre o tubarão limão no North Sound, indicando que os juvenis são residentes desta área por

meses ou anos após nascimento. Da mesma forma, a análise da ocupação espacial confirmou a importância ecológica da franja de mangal da área de maternidade, actualmente identificado como o habitat preferido da maioria dos indivíduos. Esta observação levantou preocupações relativamente ao impacto das perturbações antrópicas nas populações de juvenis de tubarões limão em Bimini. Ademais, ambas análises resultaram em interessantes resultados, que revelam grandes diferenças inter-individuais na ecologia espacial de tubarões limão juvenis. O tamanho das áreas de vida e central variaram muito entre indivíduos, bem como a distância até à costa. Na maior parte da literatura os factores potencialmente responsabilizados por estas diferenças, tal como sexo, tamanho do corpo ou até mesmo design de monitoramento, falharam em explicar os padrões detectados. No entanto, a investigação da relação entre os traços de personalidade e as métricas espaciais revelou relacionamentos fortes. Foram identificadas várias correlações entre a área de vida e personalidade, área central e personalidade, bem como com a distância à costa (ou seja, distância até ao mangal). A personalidade foi identificada como um factor intrínseco potencialmente responsável pela expressão de padrões variáveis dentro da mesma população. Esta observação realça a probabilidade da influência de traços de personalidade, como mecanismos condutores da ecologia do movimento de tubarões limão juvenis. Esta perspectiva fornece uma percepção crucial relativamente aos processos que influenciam os padrões de movimento, encorajando novas investigações que considerem análises individuais para fins de conservação.

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LIST OF ABBREVIATION & SYMBOLS

Ar$_i$: Absolute residency index
BBFS: Bimini Biological Field Station – Shark Lab (South Bimini Islands, Bahamas)
COA: Center of activity
CT (acoustic tag): Coded transmitters
CVh: Cross Validation
DfS: Distance from the shore
DNA: Deoxyribonucleic acid
FL: Fork length (cm)
GLMM: Generalized linear mixed model
GPS: Global Positioning System
ID: Identification
LED: Light-emitting diode
KUD: Kernel Utilization Density
MCP: Minimum Convex Polygon
MPA: Marine protected area
NS: North Sound (North Bimini Island, Bahamas)
PCL: Precaudal length (cm)
PIT: Passive integrated transponder (Destron Fearing Corp. ®)
PVC: Polyvinyl chloride
ROM: Rate of Movement
Rr$_i$: Relative residency index
SUR: Submersible Ultrasonic Receivers (Sonotronics Inc. ®)
TL: Total length (cm)
USA: United States of America
USR: Ultrasonic Receiver (for active tracking; Sonotronics Inc. ®)
VIF: Variance Inflating Factor

Δ: Delta (difference operator)
σ: Sigma (variance)
τ max: Theoretical maximum

Ø: Diameter

I. GENERAL INTRODUCTION

I.1. Background

Personality traits in Hominidae have been widely described and well documented with the rise of psychological and neurological sciences over the past decades (Dollard & Miller, 1950; Ebstein *et al.*, 1996; King & Figueredo, 1997; Pervin & John, 1999; Weiss *et al.*, 2000; Dingemanse & Réale, 2005; Dingemanse *et al.*, 2010). Lately, the discipline has been expanding, and personality features in non-primate organisms have been recently tackled and described (Gosling, 2001; Sih *et al.*, 2004a; Sih *et al.*, 2004b). Although the basic framework behind the "animal personality" concept refers to the consistency in individual behavior across situations and time, a variety of terms, such as "coping styles", "temperament", "behavioral syndrome" can be found in the literature (Koolhaas *et al.*, 1999; Dall *et al.*, 2004; Sih *et al.*, 2004a; Sih *et al.*, 2004b; Réale *et al.*, 2007; Groothuis & Trillmich, 2011). These two first terms tend to encompass different approaches of the notion, whereas "behavioral syndromes" conveys a divergent idea suggesting a correlation among traits (Sih *et al.*, 2004a; Sih *et al.*, 2004b; Biro & Stamps, 2008; Wolf & Weissing, 2012). From the confusion around the vocabulary use emerges the complexity and ambiguity behind the concept of personality.

Individual behavioral traits have been determined to have a role in biological adaptations, and have been suggested to influence natural selection (Wilson *et al.*, 1993; Sih *et al.*, 2004a; Réale *et al.*, 2007; Wolf & McNamara, 2012; Mittelbach *et al.*, 2014). Already Wilson *et al.* (1993) pointed out the lack of randomness in the behavioral variations between individuals and led behavioral ecologists to turn towards an evolutionary approach, raising awareness on the relevance of personality traits in regards to natural selection. Although the question remains open, Wolf and McNamara (2012) interpreted the diversity of personality traits within a population as an evolutionary adaptive response to a complex environment. Personality can be approached from an ecological point of view, related to the lifetime of the individual. The current research focus is mostly centered on the investigation of repeatability in the nature of the reaction, across different contexts. Specific traits are examined, described in Mittelbach *et al.* (2014) and Réale *et al.* (2007), such as boldness-shyness, exploration-avoidance, aggression levels and activity patterns but also sociability (Sih *et al.*, 2004a; Sih *et al.*, 2004b; Laskowski & Pruitt, 2014).

It appears undeniable that personality has an impact on various variables such as food supply, dispersion, “anti-predator” behavior, sociability, reproduction and spawning (Biro & Stamps, 2008). It presumably influences both the survival and the fitness of individuals. Wolf and Weissing (2012) recently underscored the relationships between personality and life-history traits, revealing a lack of data and research on this matter. Correlations between individual traits and biological features have been identified. Several studies on the Chinook salmon, *Oncorhynchus tshawytscha* as well as in the rainbow trout, *Oncorhynchus mykiss*, suggested a relationship between physiology, behavior and cognition (Taylor, 1990; DiBattista *et al.*, 2005; Schjolden *et al.*, 2005; Schjolden *et al.*, 2006). A recent study demonstrated that less explorative individuals tend to exhibit a lower level of aggressiveness but manifest a faster growth rate than conspecifics expressing antagonistic behavior (Adriaenssens & Johnsson, 2010). A first approach on the influence of environmental factors on personality has been reported in a study of the effect of temperature variation. The results indicated that abiotic variables might alter the level of expression of personality traits (Biro *et al.*, 2010). Extended knowledge is required to explore the relationship between environmental factors and behavior.

More recently, another domain of the discipline, involving sociability, has been explored, indicating an evidence of population cohesion (Bell, 2007; Bergmüller & Taborsky, 2010; Conrad *et al.*, 2011; Jacoby *et al.*, 2014). In this perspective, Bergmüller and Taborsky (2010) intended to relate ecological and social niches to personality, identifying an influence of the former on the development of personality.

An interesting example is the study case of the social spider, *Stegodyphus mimosarum*, where social interactions have been recognized to strengthen personality traits (Laskowski & Pruitt, 2014).

The importance of focusing future research on the understanding of the consistency in individual behavior across situations and time in an evolutionary and ecological context is well recognized (Réale *et al.*, 2007). Fish appear to be an efficient model in related investigations and have been used for preliminary studies in behavioral characterization, introducing a first overview of the consistency of reactions across contexts, in two species, the anadromous three-spined stickleback, *Gasterosteus aculeatus* (Huntingford, 1976; Huntingford, 1982) and the freshwater bluegill sunfish, *Lepomis macrochirus* (Ehlinger & Wilson, 1988; Wilson *et al.*, 1993; Wilson *et al.*, 1994), mainly focusing on degrees of aggression (i.e. boldness-shyness). In recent years knowledge on fish behavioral traits and consistent individual differences in behavior has been expanding, with several fields of research benefiting from these investigations. Different studies approach personality from a neurobiological angle (Øverli *et al.*, 2007). A comparative study on behavioral and physiological traits in the rainbow trout, *Oncorhynchus mykiss*, allowed an insight into gene transcription related to neurogenesis (Johansen *et al.*, 2012). Huntingford and Adams (2005) analyzed risk-taking and aggressiveness in farmed salmonids while exposed to limited resources and manifested some concerns regarding the welfare in aquaculture facilities.

Although over the past decade animal personality is investigated to a greater extent, various ecological and evolutionary aspects of individual behavioral traits remain to uncover, leading to the interest of this research project, focusing on the relationship existing between personality and **movement ecology** in natural conditions.

I.2. Quantification of movements and spatial use in the wild: concepts, history & development of techniques

Movement ecology is a field of research associated with ecology investigating the dynamics of animal movement, that is to say the patterns, mechanisms, drivers and consequences of movements, where movement is –presently- interpreted as a motion resulting in a shift from a spatial location to another over a given time span. Likewise, the notion of movement embraces the three-dimensional displacements an individual exhibits whilst accessing resources that are necessary to survive and reproduce. Besides, spatial ecology can be considered as a branch of movement ecology focusing on the relationships existing between organisms and their environment, including both abiotic and biotic features, with a particular emphasis on the spatial component of these interactions.

Movement patterns and space utilization can vary spatially and temporally according to diverse reasons, mainly related to the biological needs of the organism and its life-history events (Abecasis & Erzini, 2008; Abecasis *et al.*, 2009; Afonso *et al.*, 2009; Abecasis *et al.*, 2013). Consequently, it clearly appears that movement and spatial

ecology analyses encompass various concepts depending on the breadth of the study.
Thus, as –partly- interpreted as the investigation of the relationships between an individual and its surroundings under the scope of a four-dimensional continuum (i.e. the three-dimensional spatial distribution as well as the temporal attribute), movement ecology includes the identification and characterization of site fidelity, habitat use, **home range** and centers of activity (i.e. core areas) of an individual.

Bearing in mind this multi-dimensional magnitude of movements, under a broad scope, site fidelity and residency can be interpreted as the aptitude of an animal to remain within a particular area – principally integrating the home range - over an extended period of time (i.e. during a season or a distinct life stage). In this case, the site attachment can be related to a sedentary pattern.

Shifting to a more restricted extent, the habitat use of an animal includes the biotic communities and the physico-chemical structures (i.e. substrate, topography, morphology, microclimate) the individual interacts with on a recurrent and usual basis. Conjointly, habitat use typically contains the home range of an organism, which designates the sufficient area an individual requires to meet its daily basic needs (Burt 1943) (i.e. feeding, resting, socializing, mating).

While moving forward to a finer scale spectrum, it emerges that animals tend to concentrate their elementary movements and activities around particular areas, evincing the establishment of centers of activity within their home range (Simpfendorfer *et al.*, 2002). Whilst progressing at an even finer scale, centers of activity can additionally enable the capture of diel patterns and regular changes in spatial use, while the individual frequents the feeding or meeting ground for instance.

The dynamic of movement features therefore requires an adequate experimental design as well as an efficient technology that would enable scientists to capture a significant time frame within the life stage of the species of interest and seize its related daily activities.

At the onset of the discipline, research on movement ecology of free-ranging organisms emerged from indirect appreciation of spatial use and dispersal of specimen through the use of conventional tagging methodologies, originally initiated to study population dynamics (e.g. survival rate, growth rate) (Robson & Regier, 1964; Kareiva, 1983; Pradel, 1996). For instance, mark-recapture studies produced information on general migration patterns in several fish (MacDonald & Smith, 1980;

McClellan & Cummings, 1997; Thompson *et al.*, 1999). These more or less non-invasive methods are reliable and cost-effective, manifesting low mortality rates (Krebs, 1989), however, they do not allow the capture of fine scale movements nor do they provide a pertinent insight into the drivers and consequences of the observed patterns. Data are limited to the date and location of capture-release and recapture, and are related to the fishing effort per location, which potentially includes a methodological bias.

Quantifying movement patterns at fine multi-scales required more advanced techniques, possible with the recent development of remote sensing technologies such as **telemetry**. The term "telemetry" originates from the Greek "*tele*" which stands for "far", and "*metron*" meaning "measure" (Chatzisavvas, 2005). Conceptually, it refers to a one-way direction information transmission, from the sensor towards the data logger – receiver-. In biological sciences, telemetry mainly consists of an omnidirectionnal wireless data transfer allowing remote measurement and monitoring of multi-scale information; most commonly employed in movement ecology to provide spatio-temporal data. The assessment of the distant animal operates via different means, such as satellite transmission (i.e., geographical positional fixes obtained using orbiting satellites that detect the signals), radiographic signals (viz. involving very high frequency radio tracking) or ultrasonic acoustic signals. The latter technology, widely involved in marine organism tracking, implies the propagation of information through high frequency sound waves (from 30 kHz to 300 kHz). Compared to radio waves, it has a better efficiency in salt water and covers greater distances (Baggeroer, 1984).

Acoustic –ultrasonic- telemetry systems include three main components: the transmitter (1), an acoustic tag, fitted to the animal, which emits the signal via a series of acoustic pings –or sound pulses-, at a determined frequency, and at a regular pace; the hydrophone (2), which detects and converts the signal and the receiver (3), which records the signal from a tagged individual passing within its detection range. The choice of each element depends on a wide range of parameters such as the aim of the investigation, the size of the study area, the size of the organisms, the time required for the study, the type of signal. Nevertheless, an ethical rule requires that the size of the tag should not exceed more than 1.5% to 2% of the body weight of the animal out of the water (Kilfoyle & Baggeroer, 2000).

Acoustic surveys became a sophisticated technique allowing the assessment of wild behavior, evaluating spatial ecology, movement in free-living animals within their natural environment. The first application of **acoustic telemetry** to the marine environment was initiated in 1956 by the U.S. Bureau of Commercial Fisheries and the Minneapolis-Honeywell Regulator Corporation (Hockersmith & Beeman, 2012).

Since then, this tool experienced a significant use and has been employed in aquaculture as an intelligent system for monitoring the feeding activity and health status of the fish, but also to monitor the activity pattern (Baras & Lagardère, 1995; Cooke *et al.*, 2000). In fisheries science, telemetry has been used to determine home range and habitat use of organisms, to lead bioenergetics studies and for population dynamics (e.g. to estimate mortality rates) (Heisey & Fuller, 1985; Weimerskirch *et al.*, 1997; Arnold & Dewar, 2001). It can be applied to study diverse physiological changes in the organisms (Laming and Savage 1980; Lucas, et al. 1993) but also to assess the anthropogenic impacts on fish (Chateau & Wantiez, 2008).

In movement ecology field of research, telemetry encompassed a wide breadth of applications, contributing to a more detailed quantification of movements and spatial metrics in wild populations (Abecasis & Erzini, 2008; Abecasis *et al.*, 2009; Abecasis *et al.*, 2013). It provided essential information on the daily movements of an organism (Lino *et al.*, 2011), the activity pattern of tracked species (Abecasis & Erzini, 2008; Abecasis *et al.*, 2009), contributed to the characterization of habitat use (Hatase *et al.*, 2002; Aarts *et al.*, 2008), provided insight into population dynamic (Heisey & Fuller, 1985; Weimerskirch *et al.*, 1997), and additionally supported connectivity studies (Webster *et al.*, 2002).

The important asset behind such a wide spread use lies in the fact the technical design is relatively simple but also because it is sub-divided into a passive and active component. Passive and active telemetry are employed according to different objectives. Active telemetry is a labor-intensive short-term tracking process (e.g. 24 hours), which can be conducted from a boat or a kayak (Guttridge *et al.*, 2015), during which the purpose is to obtain very detailed metrics on the movements of a particular individual (i.e. real-time location) (Burnham *et al.*, 1988; Lino *et al.*, 2011).

Passive telemetry provides broader information on the spatial use of organisms. It is used for long-term studies, when several to many tagged fish remain in the study area (Abecasis & Erzini, 2008; Abecasis *et al.*, 2009). A network of passive listening stations – receivers - is deployed in the study site and enables an automatic recording of the information the tag of a fitted individual swimming within the detection range emits. It is a valuable tool preventing any bias resulting from the presence of an observer, potentially influencing the natural behavior of the animals (i.e. occurring while snorkeling, scuba diving).

The difficulties of observing and capturing the expression of individual behavior in the wild remain a current reality. However, in recent years, significant advances in remote sensing technologies allowed progress in behavioral ecology (Hussey *et al.*, 2015). For instance, the quantification of social behavior in free ranging juvenile lemon sharks became possible due to the development of proximity detectors fitted to the sharks (Guttridge *et al.*, 2010).

Over the past years, the extensive use and development of experimental remote sensing devices resulted in remarkable technological advances, providing a better resolution and more details not only about the movement metrics of the tracked organisms but also about their biology and physiology (Kilfoyle & Baggeroer, 2000; Hussey *et al.*, 2015). Along with it came a better treatment of the data, producing sophisticated models and algorithms enabling a deeper perception and appreciation of the spatial and movement features of animals (Krejcar, 2011; Bastille-Rousseau *et al.*, 2016). The recognition of acoustic telemetry as powerful and valuable tool justified its use in the present study and has been acknowledged to provide efficient and relevant data allowing the capture of movement metrics in the shallow waters of the Bahamas. Furthermore, an insightful review of behavioral studies involving acoustic telemetry in the lemon shark not only supports the main methodology currently employed but also endorse the use of lemon shark as a model (Sundström *et al.*, 2001). Indeed, to comprehensively apprehend and seize the complexity of animal personality, various aspects need to be (re)considered, including the species of focus/interest. An examination of the literature revealed a considerable lack of knowledge about large marine organisms’ personality. Therefore, another peculiarity of the present research lies in the use of an elasmobranch species as model, the lemon shark, ***Negaprion brevirostris***.

I.3. Biology of the lemon shark, *Negaprion brevirostris*

In recent years strong evidence of an increasing rate of biodiversity decline has come to light (Díaz *et al.*, 2006; Worm *et al.*, 2006; Cardinale *et al.*, 2012). Dramatic declines were reported in large pelagic marine organisms, including coastal and pelagic elasmobranchs (Dulvy *et al.*, 2008; Dulvy & Forrest, 2010) . Human pressure and considerable anthropogenic impacts have been identified as the main causes (Díaz *et al.*, 2006; Jennings *et al.*, 2008). Sharks have a long story of exploitation (Stevens *et al.*, 2000), yet their status remains largely disregarded in most areas of the world (Dulvy *et al.*, 2008; Dulvy & Forrest, 2010). In the Caribbean, an absence of sharks underlined the crucial need for management, protection and conservation of elasmobranchs (Ward-Paige *et al.*, 2010). In an effort of participative preservation, the *Bahamas Acts to Protect Sharks* proclaimed the region a “shark sanctuary” (Techera, 2012). Nevertheless, information on the driving features of their movement ecology is very scarce. Gaps in knowledge about the mechanisms behind the movements and spatial use of large predators may induce the prospect to be at risk of focusing the conservation efforts in the wrong places. These considerations raised a particular interest in a team of shark biologists at the Bimini Biological Field Station, Bahamas, adopting the lemon shark as a model species for behavioral and ecological studies.

The lemon shark, *N. brevirostris* (Poey, 1868) (**Fig. 1**), is a coastal tropical shark species form the Carcharhinidae family, mainly found in the subtropical areas of the Atlantic and Pacific coasts of North and South America, as well as in the western African coast and in the Pacific islands (Compagno, 2001). They are commonly found in shallow waters, around mangrove fringe coastlines, coral reefs, inhabiting sounds and bays. In 2009, the Lemon shark was listed by the World Conservation Union as a near-threatened species (Sundström, 2015).

The vernacular name of the species finds its origin in the pale yellow-brown coloring of their skin, a particular asset to camouflage when cruising over sandy areas. The lemon shark possesses an anatomical particularity in that it has two dorsal fins of comparable size. The shark is also recognizable due to its flat head and rounded short snout.

The species reaches its maturity at 11-13 years for a size comprised between 225 cm and 240 cm (Brown & Gruber, 1988), for a maximum recorded size reaching 350cm. In 2005, the growth rate of the lemon shark was reported to approximate 5.0 ± 0.3 cm per year in the **nursery area** of interest (Barker *et al.*, 2005).

The biology of the lemon shark is well documented and its life history traits were thoroughly described thanks to the life work of Dr. Samuel Gruber (cf. Literature). The species was characterized as philopatric, that is to say mature females, after a gestation period of 10-12 months, return to their shallow nursery ground of origin to pup, between April and September (Feldheim *et al.*, 2014). The species is placentally viviparous, giving birth to free-swimming neonates, measuring between 50 and 60 cm (Feldheim *et al.*, 2002). Afterwards, the pups remain in the nursery area for several years (Morrissey & Gruber, 1993b; Dibattista *et al.*, 2007).

The feeding behavior of the species is characterized by a high degree of preferences in prey items under favorable environmental conditions. Its diet consists mainly of teleosts (about 80%) but may also include crustaceans and mollusks (Wetherbee *et al.*, 1990; Newman *et al.*, 2010). Cannibalism has also bee reported, larger conspecifics predating on juvenile lemon sharks (Guttridge *et al.*, 2011b).

The species represents a relevant model for large marine predators, able to survive in captivity (Brown & Gruber, 1988; Cortés & Gruber, 1990; Feldheim *et al.*, 2001; Sundström *et al.*, 2001; Feldheim *et al.*, 2002; Guttridge, 2009). This particularity emanates from the ability of the sharks to enhance oxygen uptake due to the high oxygen affinity characteristics of their blood, allowing the juveniles to inhabit areas with low oxygen contents such as mangroves roots. Gruber *et al.* (1988) identified a restricted activity space and a home-ranging pattern in lemon sharks in Bimini Islands, Bahamas. The species appears to be site-attached, enabling the delineation of well-defined home ranges and habitat use, a valuable statement for the present study (Morrissey & Gruber, 1993a, b; Chapman *et al.*, 2009). The authors noticed that space requirement tend to increase with the development of the shark. Their observations suggested neither aggression nor territoriality and they reported a grouping behavior while simultaneously tracking two individuals.

Fig 1. A juvenile lemon shark, *Negaprion brevirostris*, caught in a gillnet in its nursery area in May 2015, Bimini Islands, Bahamas (credits: Charlotte Sams Photography, Bimini Biological Field Station). Notice the peculiar skin pigmentation behind the vernacular name of the species, allowing an efficient camouflage in sandy-bottom areas.

The doctoral thesis of Dr. Tristan Guttridge brings a complementary insight into the behavior of the juvenile lemon sharks (Guttridge, 2009) and provides crucial information. Guttridge *et al.* (2009) focused on the social behavior of the species and found that juveniles (2 – 3 years; 55.4 +/- 7.6 cm) are social animals, exhibiting a conspecific preference to form groups. The authors assumed the grouping behavior to be a possible key to the survival and development of the juveniles. This study led them to presume that shark active association might induce cooperation between individuals, implying possible population cohesion. Moreover, a subsequent study consisted in the analysis of group composition of juveniles in natural conditions (Guttridge et al., 2011a). They determined body length as a group structure and observed a non-random association, with sharks showing persistent pair-wise patterns. They noticed leadership from larger (older) individuals, which were followed by smaller ones. Their hypothesis behind such observation is based on the supposition that larger individuals had accumulated more information regarding their environment (i.e. on habitats, prey abundance, possible predators). They interpreted this social behavior as a possible transfer of information – collaboration – between individuals.

Pioneer research on lemon shark personality has been carried out in mesocosms around Bimini Islands. The primary conclusions reported in 2013 by Finger (2013) and his team revealed evidence of consistent differences in behavior in this species. Finger *et al.* (2016), supporting the initial observation previously conveyed, conducted a more elaborate study, establishing an appropriate method to capture personality traits. Hence, the uniqueness and importance of this research project lies in the study of how personality observed in captivity in juveniles – assessed following the methodology described in after Finger *et al.* (2016) - influences their natural spatial use and movement ecology, providing a comparative analysis in a top predator species.

I.4. Context of the study

The present study is part of a doctoral project, which intends to provide significant advances in animal personality. Its originality lies in the different approaches tackled that were until now globally neglected. This investigation considers novel areas rarely explored, focusing on the individual variations in behavior across context and time of juvenile lemon sharks in natural conditions, around Bimini Island, in the Bahamas.

Understanding between-individual variations in behavior across contexts and time is of considerable relevance regarding the ecological and evolutionary implications personality traits might have for organisms and populations (Biro & Stamps, 2008; Wolf & Weissing, 2012). The importance of investigating the personality of organisms in order to provide better insight into the relationship between the individual, its environment and natural selection is widely recognized.

Although the number of publications related to fish personality has been increasing (Toms *et al.*, 2010; Conrad *et al.*, 2011; Mittelbach *et al.*, 2014), several aspects have not been addressed. Indeed, for the past decades, personality and individual temperament raised a particular interest in various organisms. Yet, for practical purposes, most research has tended to involve small-sized species of relatively short life history traits, usually captive bred, or convenient domestic organisms (i.e. pig;

Spoolder *et al.* (1996)), eluding the ultimate causes and consequences of personality. This consideration justifies the need for further investigation and investments.

The present study intends to extend the knowledge and attempt to fill some gaps by proposing new perspectives in approaching the investigation of personality in wild marine species. Firstly, the majority of the published literature considers freshwater species such as trout and other teleosts (e.g. *Oncorhynchus tshawytscha*, *Lepomis gibbosus*) (Taylor, 1990; Wilson *et al.*, 1993; Huntingford & Adams, 2005; Adriaenssens & Johnsson, 2010). Less interest has been held on marine organisms. Secondly, although their ecological importance in the marine environment is recognized (Heithaus *et al.*, 2008), little concern has been directed to predators' personality. Thirdly, in regards to the evolutionary process, individual behavioral variations remain misunderstood and the influence personality on movement ecology in natural conditions has so far been largely disregarded.

A few pioneering studies addressed the question of individual variations in sharks under a renewed approach. Jacoby *et al.* (2014) focused on the repeatability of shark social networks across different habitats. The authors successfully identified consistency in the network position of individuals in the small spotted catshark, *Scyliorhinus canicula*. However, this paper, as well as most of the literature in this domain, presents a major limitation. Conclusions tend to be drawn from idealistic and controlled experimental conditions (i.e. laboratory or mesocosms). In this perspective, in recent years, tracking technologies captured interesting patterns of between-individual variability, at large spatial scale, using satellite telemetry but also at a smaller scale –over a restricted period of time-, using ultrasonic telemetry (Dagorn *et al.*, 2000; Vaudo *et al.*, 2014). The key components of the findings reported by Vaudo *et al.* (2014) resides in their failure to associate the observed differences in movements with biotic or abiotic factors. They provided an interesting insight into the existing variability between tiger shark individuals. However, this research, as well as Dagorn *et al.* (2000), solely considered the "physical" expression of movements. Vaudo *et al.* (2014) formulated various hypotheses to explain the variability in diving patterns but neglected the intra-individual components and their possible influence on the observed patterns. Another study emphasized ontogenic niche shifts in habitat use in juvenile bull sharks (Matich & Heithaus, 2015). Using acoustic telemetry, the team followed the natural movement patterns and habitats use of the individuals. They reported a microhabitat shift correlated with increased energetic requirements and body conditions. They also underlined the pressure of intrinsic factors, such as individual variability, to explain the differences in habitat use within age-classes. Some aspects of this research inspired the current project.

Nevertheless, these investigations embody the limit of tracking studies in analyzing individual differences, as it appears challenging to distinguish the expression of personality from the response to external factors (i.e. environmental variables). It is, therefore, crucial to complement the assessment of movements and spatial use with adequate experiments enabling the identification of personality traits.

A global framework for animal movement research was recently proposed by Nathan *et al.* (2008), identifying 4 main mechanisms underlying movements – and spatial use to some extent-: the intrinsic features proper to the individual (1), the motion capacity (2), the moving ability (3) and the external factors (4) (i.e. environmental parameters). The first component is where personality studies should be integrated. Although a very large amount of publications and researches undertaken so far thoroughly considered the 3 last mechanisms, the internal origin of movement and spatial use at an individual scale have been widely neglected.

Yet, overcoming this gap in the knowledge is at the center of the future directions in movement ecology. Recent debates pointed out the need of inter-disciplinary approaches to study animal movement, emphasizing the benefits a consortium of different fields of research would provide (Nathan, 2008; Nathan *et al.*, 2008). Movement ecology is, in part, the appreciation of the external expression of a behavior. The study of the drivers, as they are the intrinsic causes of the external expression of movement, requires collaboration between behavioral ecologists and movement ecologists. Although scarce, some recent studies embody this step forward (Chapman *et al.*, 2011; Harrison *et al.*, 2015). For instance, an original study successfully captured personality dependent spatial ecology in the burbot, *Lota lota*, using an acoustic monitoring array (Harrison *et al.*, 2015).

An avant-garde study on the exploratory behavior in great tits revealed consistent inter-individual differences. The authors conducted a novel open field test in captivity with wild individuals. This innovative initiative inaugurated the pathway for the scientific consortium previously mentioned and addressed future directions in behavioral ecology research (Dingemanse *et al.*, 2002). Nevertheless, this investigation did not proceed to an assessment of the movement patterns in natural conditions after release of the birds. It is in this perspective that a novel open field test was adapted and applied to juvenile lemon sharks (Finger *et al.*, 2016), in order to provide a powerful experiment enabling the determination of individual behavioral attributes beforehand. The authors developed an accurate and efficient method to quantify personality traits in semi-captivity. They documented consistent individual differences in juvenile lemon sharks over a repetition of trials. The design employed during the indicated study is at the center of the preliminary personality traits analyses performed during the present project.

Consequently, the current investigation took place under this recent standpoint, providing the first insight into the presumed influence of personality on wild movements and spatial use of juvenile lemon sharks. The urge to understand the driving mechanisms of the movement ecology of marine animals has led to new perspective, suggesting the association of observations limited in time and space (i.e. in mesocosms) with free-ranging observations. This study embodies a step-forward in animal ecology in the sense that it integrates behavioral experiments, movement ecology and spatial use analyses into a common framework, initiating the cross-disciplinary efforts advocated by Nathan (2008) & Nathan *et al.* (2008). This project intends to enhance the understanding of animal movement by providing a fertile ground between personality traits measured in semi-captivity and spatial metrics captured in the natural environment. The innovation of this project thereby resides in the investigation of the relationship between personality traits and movement ecology, as it is the first to propose such insight into the driving mechanisms of movements in an elasmobranch species.

The current research addresses complementary questions under a novel approach, attempting to depict the influence of lemon shark personality on movement ecology in natural conditions.

I.5. Aim of the study, objectives & hypothesis

I.5.1. Aims

The major aim of this study is to provide an insight into predator's personality and contribute to the development of a fertile ground between behavioral ecology and movement ecology. A step forward in animal ecology lies in the consideration of personality as a driving mechanism partly responsible for the expression of movement patterns and spatial use in an individual. This research places the individual at the center of the focus to interpret movement and spatial use in the wild and considers the intrinsic decision-making driving mechanisms, setting aside the biochemical and physiological characteristics components.

Over the last couple of years, more interest has been focused on animal personality, mainly introducing new theoretical & analytical directions. An increased literature participates to the debate, allowing a wide description of the main framework and future guidelines. Thereby, this project intends to contribute to improving the knowledge.

I.5.2. Objectives and hypotheses

The study has three main objectives. The first purpose is to substantiate over 20 years of research on the spatial ecology and movement patterns of juvenile lemon sharks in Bimini Islands **(1)**. Secondly, this project intends to determine whether there is a link between the individual behavior observed in captivity through preliminary experiments and the study of movement patterns in juvenile lemon sharks in natural conditions **(2)**. Such assessment would lead to reveal *how* personality may influence the relationship between the individual and its environment by establishing a putative correlation between movement patterns and personality traits **(3)**. Sharks exhibiting high scores after being exposed to a Novel Open Field test are expected to manifest an extended home range, being more active and exhibiting exploratory movements – away from the core area and home range -, certainly spending less time in camouflaged areas (mangroves) than other individuals. Sharks with a lower score would exhibit a more restricted home range, and a less exploratory movement pattern.

A positive correlation between personality and spatial ecology might be expected. Finally, an inherent goal is to enable a clarification of observed differences in movement patterns and spatial use existing between individuals of a same population. Personality might elucidate the individual variability in Movement Ecology reported by several studies.

II. MATERIAL & METHODS

II.1. Study site

Bimini, Bahamas, is a subtropical island cluster (25°44’0.9”N, -79°16’23.0”W), located approximately 86 km east of Miami, Florida (U.S.A) and situated on the north-western edge of the platform of the Great Bahama Bank (25°42’N, -79°17’W). It encompasses the islands of South Bimini (hosting the Bimini Biological Field Station “BBFS”, aka Shark Lab) & North Bimini (Morrissey & Gruber, 1993a). The surrounding waters are described as the largest tropical shallow area in the Western Atlantic (Buchan, 2000). The Gulf Stream, flowing roughly one nautical mile west of the islands, is recognized to influence the sub-tropical climate as well as the biological communities of Bimini (Edrén & Gruber, 2005) (**Fig. 2**).

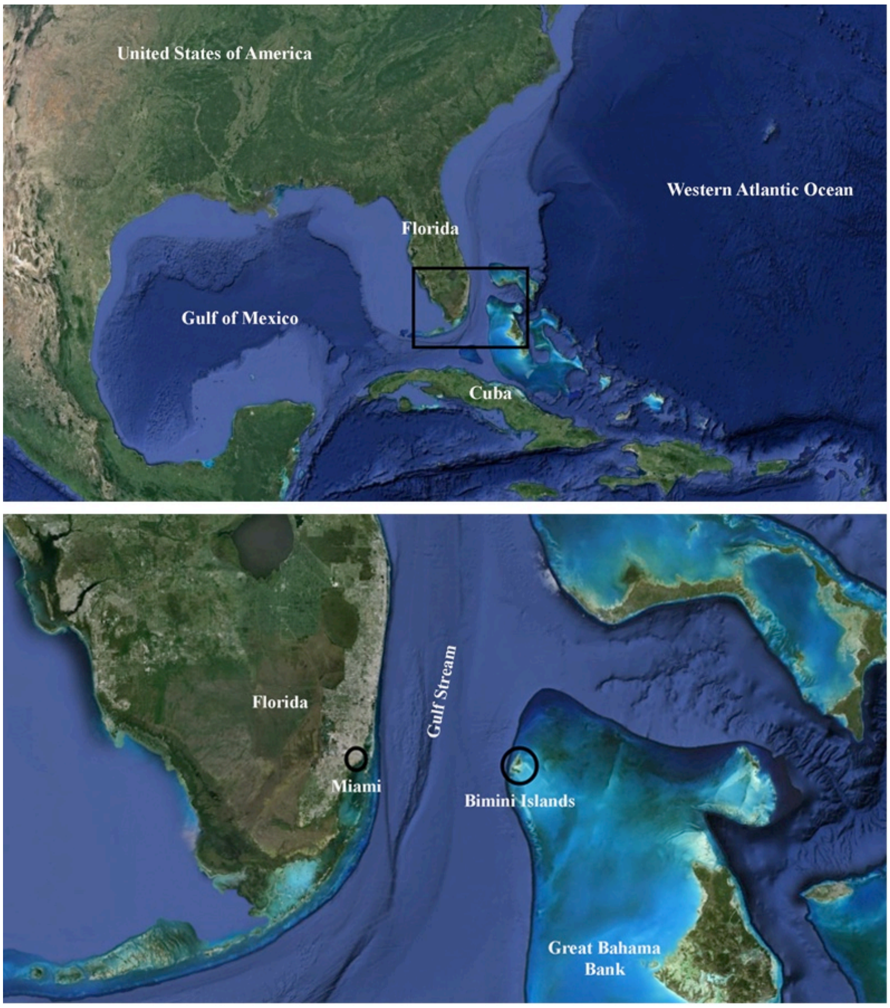


Fig. 2. Regional context and satellite maps of the Bahamian archipelago (source: Google Earth, accessed in April 2016).

The study was conducted in one of the primary nursery ground for lemon sharks in Bimini, a semi-enclosed sandy bottom area, covering 3km^2, known as the “North Sound” (25º75′N 79º26′W; NS, **Fig. 3**), sitting between the western and eastern arms of the island of North Bimini (Morrissey & Gruber, 1993a; Franks, 2007). This mangrove fringe inlet has been depicted as a suitable habitat for almost 250 juvenile and sub-adult lemon sharks every year (DiBattista *et al.*, 2009). A dense red mangrove canopy (*Rhizophora mangle*) borders the eastern side of the NS, which substrate is stabilized by sparse turtle seagrass meadows (*Thalassia testudinum*) (Edrén & Gruber, 2005; Franks, 2007).

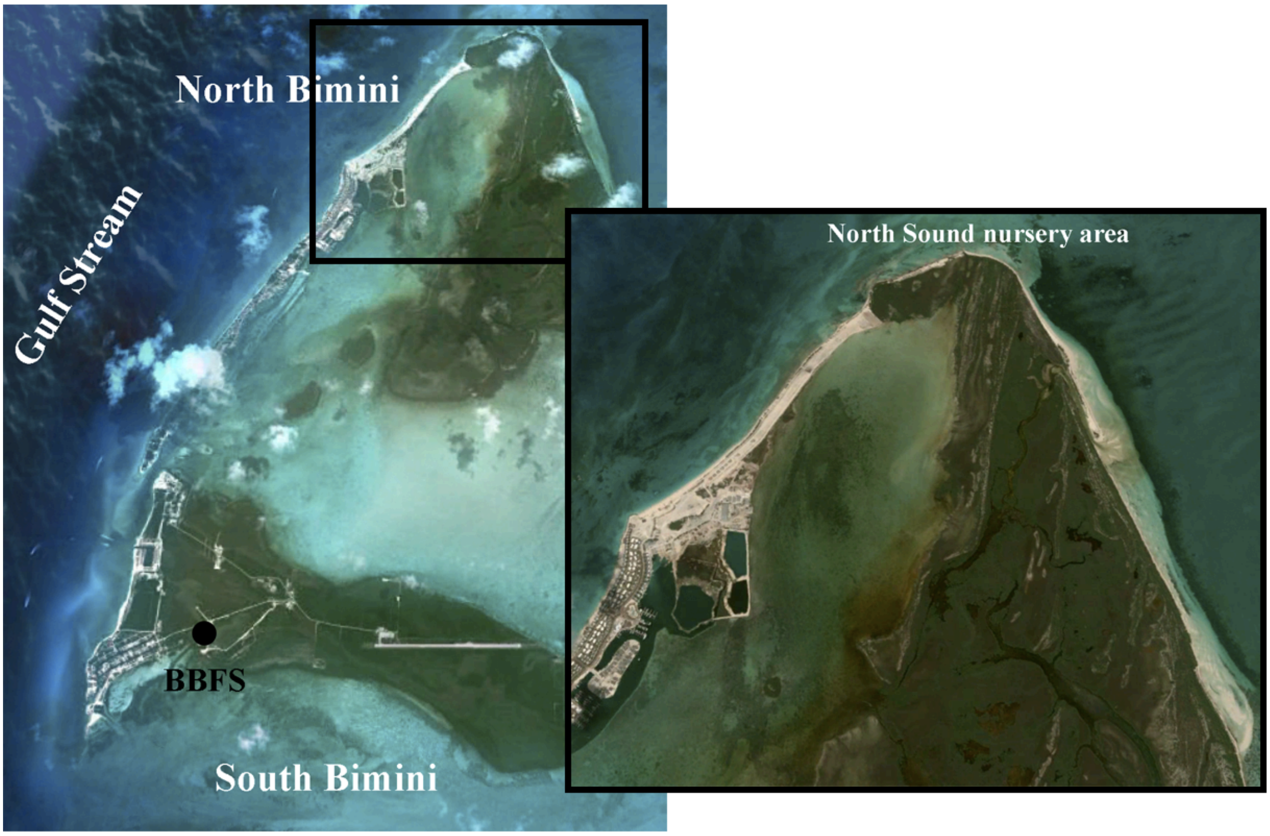


Fig. 3. Satellite maps of the study area. North & South Islands of Bimini, Bahamas (left panel) and the North Sound, nursery ground for juvenile lemon sharks, *Negaprion brevirostris* (right panel).

Abiotic components are highly influenced by the enclosed aspect of the NS and can be subjected to wide and rapid fluctuations, depending on the tidal phases, seasons and local microclimate. Due to its narrow opening to the south, the area is mostly affected by southward winds and exhibits specific hydrological features, characterized by limited tidal amplitude. The reported depth range during the investigation varied from a minimum of 0 m at the edges to a maximum of 170 m in the middle part, respectively measured at low and high tide. Consequently, much of the banks were exposed at low tide. The restricted tidal flow also induces relatively high temperatures and salinity gradients (recorded temperatures varied from 20.9ºC in February 2016 to 31ºC in late May 2016 and observed salinity ranged between 38.9 & 42.5 ppt).

During the present study period, the western coastline, already affected by a decade of anthropogenic influence (DiBattista *et al.*, 2011), was subject to acute tourism development and constructions. As a result, the majority of the shoreline has been distorted and the mangroves wiped out. Therefore, in March 2016 a new assessment of the western coastal line of the NS was conducted. A 6 meters shallow skiff was used to follow the shoreline while excessive depth prevented from walking, and GPS (Global Positioning System; accuracy < 10 m) waypoints were recorded every 10 to 20 meters. However, the construction dynamics remaining unknown to the "Shark lab", the teams leading fieldwork in the NS between March and May 2016 were able to witness a continuous re-shaping of the western banks. Resources restraints (i.e. gas supply, skiff and volunteers' availability) and overall schedule of the research station hindered from renewing the operation.

Moreover, from late November 2015 onward, construction disturbances contributed to a deterioration of the water quality, increasing the turbidity, particularly along the south-western flank, which tended to receive larger quantities of silt due to dredging efforts (pers. obs.). Therefore, although the receivers were subjected to a thorough detection range testing in two similar environments in 2013 – including one within the current study area - (van Zinnicq Bergmann, 2013), the worsening of the conditions in the study area led to the agreement that a new test was necessary. This experiment is developed in **section 2.4.3.** of the present dissertation.

II.2. Shark capture

Sharks were captured between the 7th & 8th of June 2015, in the NS, using 25 lb monofilament gill nets (180 m x 150 cm), with 10 cm stretch meshes, as part of the 2015-"PIT" campaign of the Shark lab. "PIT" is an annual mark-depletion-recapture experiment and population genetics sampling program initiated in 1995 by Dr. Gruber at the Shark Lab, named after the tags implanted in all captured individuals (Passive Integrated Transponder "PIT", Destron Fearing Corp. ®, South St. Paul, Minnesota).

It consists in an intense gillnetting of juvenile lemon sharks in the two main nursery grounds of Bimini, the NS and Sharkland, between mid-May and mid-June, after pupping by females. During 12 nights (i.e. 6 per nursery), three nets are tied to the mangrove roots, deployed perpendicular to the shore and checked every 15 minutes over a period of 12 hours. Every year, approximately 99% of the neonate and juveniles present in the area are caught (Gruber *et al.*, 2001; DiBattista *et al.*, 2009). Upon capture, sharks are removed from the net; time, location and gill-net section in which the individual is caught are recorded (from A to D, A corresponding to the section the closest to the mangrove; D, the furthest away from it). The individuals are then brought aboard a skiff, sexed, weighed, DNA is sampled (from the dorsal fin) as is blood, and a set of length measurements is taken to the millimeter (precaudal length (PCL), fork length (FL), total length (TL) and pectoral girth (PG); **Fig. 4**).

Fig. 4. Left panel: A juvenile lemon shark, *Negaprion brevirostris*, caught in Sharkland nursery area in late May 2016 during the annual PIT campaign, Bimini Islands, Bahamas (credits: Charlotte Sams; Bimini Biological Field Station). Right panel: A juvenile lemon shark, *Negaprion brevirostris*, caught in a gillnet during 2016-PIT campaign, placed in tonic immobility prior to blood sample and morphometrics measurements, Bimini Islands, Bahamas (late May 2016, credits: Patrick Duong).

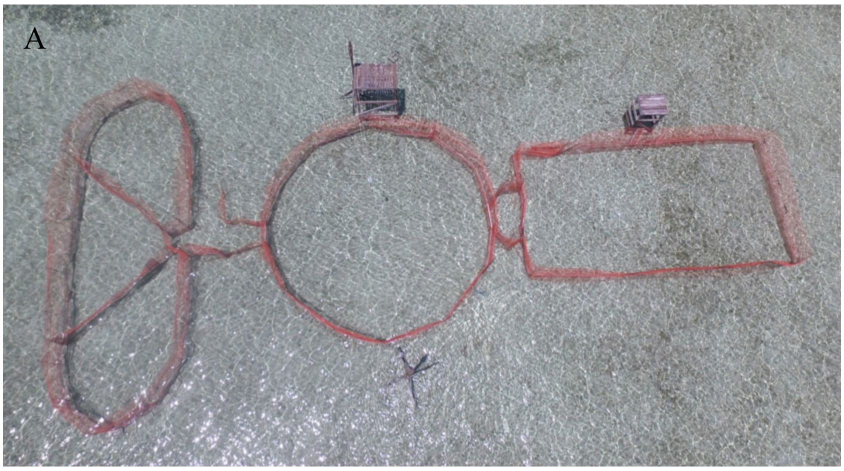
If no PIT ID number is detected during the work-up, a tag is inserted in the musculature beneath the dorsal fin. Finally, the juveniles are transported to a close-by holding pen made of flexible polyvinyl chloride fencing mesh, constructed in the nursery area.

As a consequence of the effectiveness and the yearly occurrence of the campaign, some of the individuals involved in the current investigation have been previously captured (June 2014), worked-up (i.e. size measurements taken), processed following the behavioral experiment described in the section below, released and recaptured in June 2015.

II.3. Preliminary behavioral experiments

The present study is part of two ongoing PhD studies on lemon shark behavior and personality traits and focuses on the influence of personality on the wild movement ecology of juveniles. As a component of these doctoral research studies, two series of preliminary captive behavioral experiments have been conducted after first capture of the sharks, in June 2014 and June 2015, in order to determine personality traits in the individuals (Finger *et al.*, 2016).

Within a month following the capture during PIT and after an adaptation period to captivity, the sharks were exposed to a novel open field test (**Fig. 5-A&B**), as detailed in Finger *et al.* (2016). Each individual was subjected to an unknown rectangular pen separated into 18 sections for 10 minutes during which the total number of sector visited was counted. Environmental variables (depth, visibility, wind speed) were recorded for each experiment.



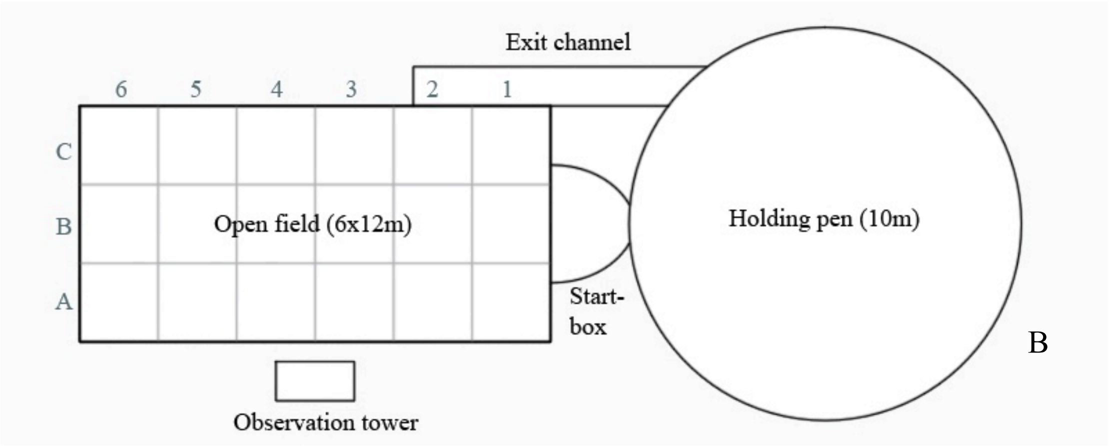


Fig. 5. A & B. Novel Open Field experimental design involved in the preliminary study for personality traits as developed by Félicie Dhellemmes and Jean-Sebastien Finger. A: Aerial view of the set-up for trials (credits: Jack Massuger, Bimini Biological Field Station). B: Diagram of the experiment extracted from Finger *et al.* (2016).

The sharks captured in 2014 were part of the first series of trials and released after the experiments. All juveniles implicated in the acoustic monitoring depicted in the following section were tested beforehand.

II.4. Experimental design & acoustic telemetry equipment

Data collection occurred between May 2015 & May 2016. The research was carried out at the Shark Lab with the help of the staff members and volunteers at the time.

The four following sections intend to cover the acoustic monitoring methodology involved during this investigation. Both active tracking and passive acoustic telemetry surveys were conducted using the equipment developed by Sonotronics Inc.® (Tucson, Arizona). A detailed methodology of Submersible Ultrasonic Receivers “SUR” manipulation and maintenance is given in **Appendix I**.

II.4.1. Tagging procedure

Subsequently to the series of preliminary personality experiments, in July 2015, a total of 12 processed sharks were selected (PCL comprised between 50 cm & 55 cm) to be surgically implanted with internal Sonotronics ® acoustic coded transmitters

CT-82-2-I. Preliminary study showed that personality was correlated to PCL, therefore, in order to prevent the introduction of noises due to size, sharks were selected within a size-class not exceeding 5 cm of difference between individuals (Finger *et al.*, 2016). As well, PCL might be related to home range size and could include bias into the further comparison with personality traits (Gruber *et al.*, 1988; Morrissey & Gruber, 1993b).

Five to ten minutes before beginning of the procedure, the sharks were placed into tonic immobility, an intrinsic response in elasmobranchs, characterized by a state of immobility and lethargy, comparable to hypnosis (Watsky & Gruber, 1990).

Then, the tag was inserted into the peritoneal cavity through a 3-4 cm incision, anterior to the left pelvic fin, using sterilized instruments (**Fig. 6**). The incision was stitched with sterile polydioxanone monofilament absorbable sutures (75cm x 24mm; CP Medical ® Portland, Oregon, U.S.A.). Afterwards, the juveniles were placed back into the pen and monitored daily for 7 days. The sharks were released in their nursery area (capture location) on the eighth day posterior to surgery.

The implanted electronic tags measured 53 mm in length and 15.6 mm in diameter and weighed 9.5g in the water (**Fig. 6**). The expected battery life of the tags predicted by the manufacturer was 14 months if used continuously. It was ensured that the size did not exceed the threshold of 2% of the body weight of the fitted organisms out of the water advocated by Kilfoyle and Baggeroer (2000).

Each transmitter emitted an individually coded acoustic signal at a predefined frequency (70 kHz to 79 kHz). The combination of a specific sequence of pulses repeated at regular interval of time in milliseconds, transmitted at a particular frequency, allowed the identification of the individuals (**Table 1**). A network of acoustic receivers was set to decode such signals and is described in the paragraphs below.

Fig. 6. Surgical procedure and transmitter implantation performed by Félicie Dhellemmes on a juvenile lemon shark, *Negaprion brevirostris*, while in tonic immobility (left panel) and Sonotronics ® CT acoustic tag (Code #4648) similar to the ones fitted to the sharks (right panel) (53 mm x 15.6 mm Ø, 9.5g in water).

II.4.2. Passive acoustic array

A fixed array of 15 multi-channels scanning, omnidirectional Submersible Ultrasonic Receivers (SUR-3, Sonotronics Inc., Tucson, Arizona, U.S.A.) was deployed, between approximately 500 m and 700 m from each other, to monitor the movements of the juvenile lemon sharks within their nursery ground (**Fig. 7**). The network was designed to ensure the maximum coverage of the area achievable considering the available means. Three main array of receivers were delineated: 5 SURs were positioned on the west side, 3 in the middle, and 6 on the east side. An extra receiver was intermittently placed at the entrance of "Sharkland", an adjacent nursery area, as a control for possible migration between nurseries. However, this receiver was severely damaged by the propeller of a vessel in March 2016, resulting in an absence of coverage of this area from this time on.

Due to the shallow features of the NS, the receivers were oriented upward and contained inside PVC housings (43-45 cm l x 60 mm Ø) embedded in a concrete base (36 cm x 36 cm x 6 cm), set right on the sea bottom (see **Appendix I**. for technical details). A slot in the top lid allowed the transducer to protrude, reducing the impediment for the signals detection. The transducer is the receiving unit of the SUR and necessitates being submerged to detect a signal (**Fig. 8**). Thereby, during low tides falling below a threshold of 45 centimeters of water (size of the SUR inside a PVC housing), the receivers were not able to detect a close-by individual.

The receivers were retrieved from the field on a monthly basis, cleaned, inspected for possible anomalies and the data downloaded over a two-day period in order to minimize the pending period.

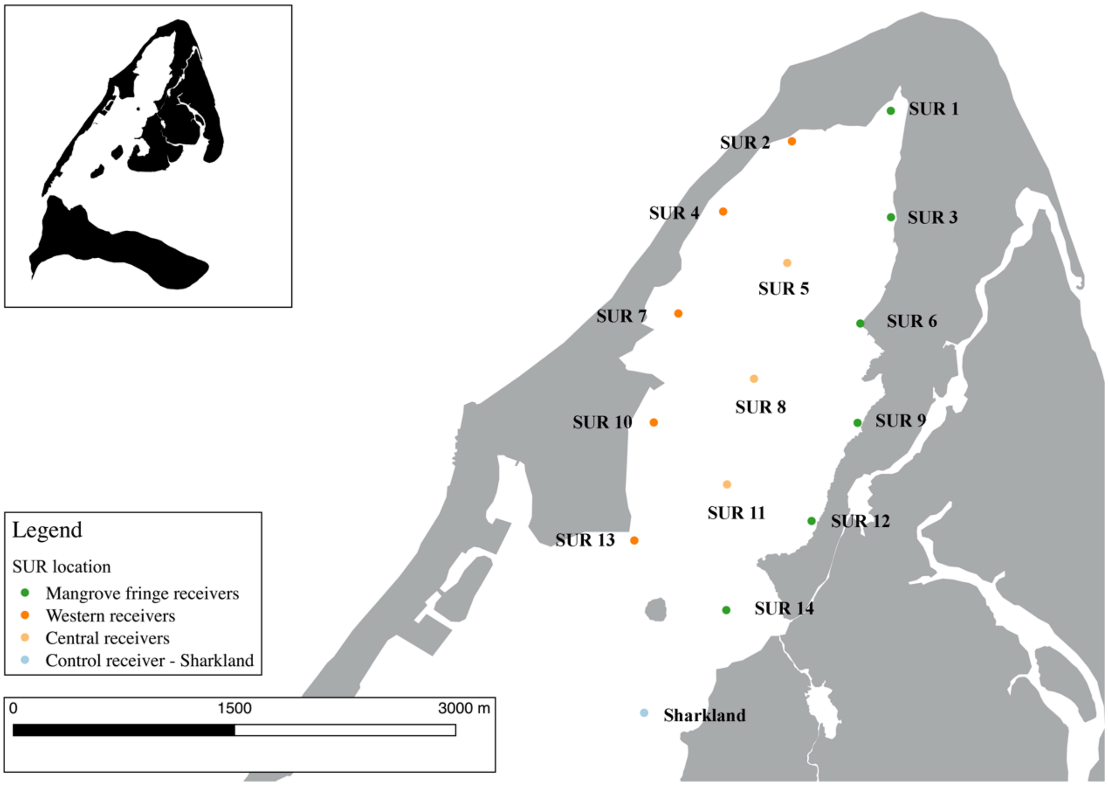


Fig. 7. Map of the network of 15 passive acoustic listening stations deployed in August 2015 within the study area, North Sound, Bimini Islands, Bahamas.

These receivers are able to scan multiple frequencies simultaneously, which reduce the probability for two signals emitted at a similar frequency to collapse (cf. **II.5.3.a**) (Heupel *et al.*, 2006; Singh *et al.*, 2009). The SURs are positively buoyant equipment, measuring 38 cm (from the top of the transducer to the bottom lid) for a diameter of 60mm and a weight of 1 kg (**Fig. 8**). The internal memory (2 MB) enables the saving of over 100 000 detections. Each SUR recorded time, date (mm/dd/yy), hour (hh:mm:ss), frequency (kHz) and nominal interval period between successive pulses (in ms) emitted by the tag fitted to a shark that swam within its detection range.

II.4.3. Detection Range testing design

Remote sensing technologies are widely used in movement ecology research. Detection range testing has been advocated to be an integrated part of all investigations using passive acoustic telemetry (Kessel *et al.*, 2014).

This process allows determining the ability of a receiver to detect and record the information emitted by a transmitter at various distances and under diverse environmental conditions. In the present investigation, detection range is defined as the relationship between detection probability and the distance between the receiver and the tag (Topping & Szedlmayer, 2011).

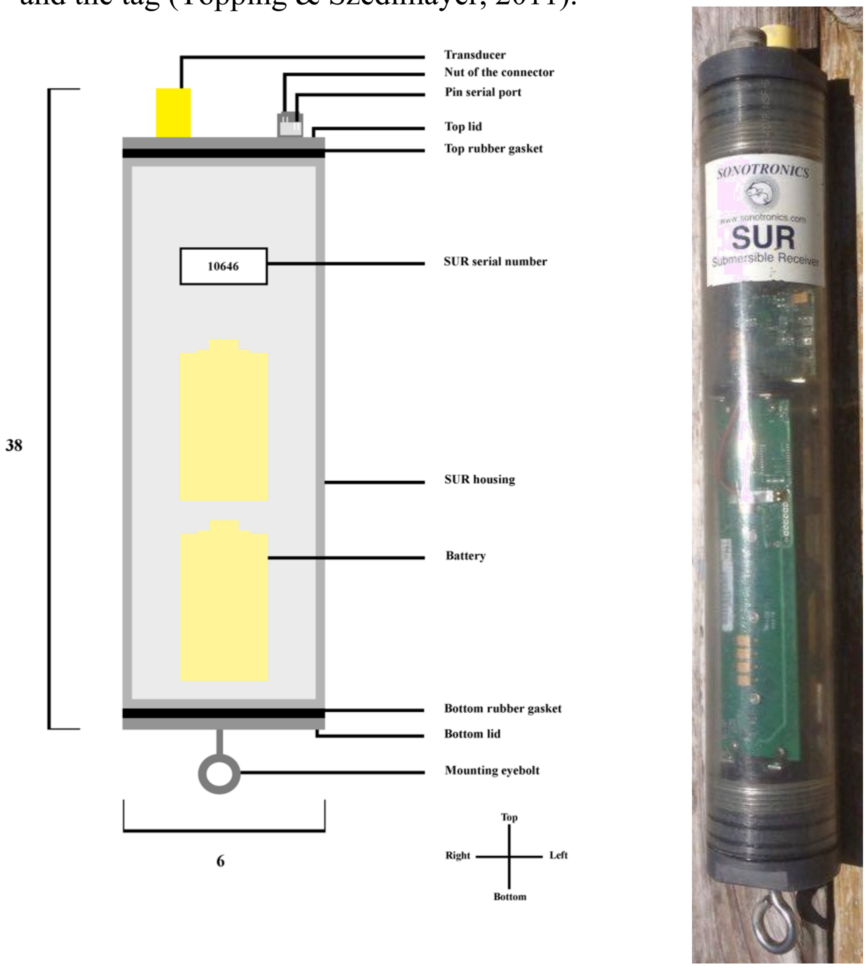


Fig 8. Diagram (left panel) and picture (right panel) of a Submersible Ultrasonic Receiver (SUR) Sonotronics ®.

Due to the physical characteristics of underwater sound propagation, it is understandable that many biotic and abiotic variables might impact the spreading of the acoustic signal within the water column. These factors affecting acoustic conditions, and thereby detection range, can differ significantly from one location to another and with time at a particular location (Kessel *et al.*, 2014). Range testing is therefore crucial to understand detection performance but also to clarify the inferences likely to be applied to the extracted data. Indeed, it is possible only to determine the position of an individual when the tagged animal swims within the detection range of the array or of at least one receiver.

In 2013, the deployed receivers were subjected to a thorough detection range testing, involving a similar CT acoustic tag (van Zinnicq Bergmann, 2013). The trials were performed in two representative habitat types of Bimini, a sandy bottom area with sparse seagrass as well as a red mangrove fringe with dense seagrass coverage. Nevertheless, the deterioration of the conditions in the western side of the nursery area stressed the necessity to renew the experiments. The two main concerns in this study were to understand if the circumstances implied a greatly reduced range, which would suggest that a tagged individual could be in close proximity with the receiver without being detected (Udyawer *et al.*, 2013) as well as elucidating the likelihood of an overlapping of the detection range. Therefore, in May 2016, a protocol similar to the one established by van Zinnicq Bergmann (2013) was set up and trials were conducted.

A straight line of 13 receivers was deployed at two locations, selected as the most representative of the whole array: (1) at the location of a western receiver (SUR-7), experiencing silt discharge due to intense dredging occurring southward and (2) in the center of the area, the deepest part of the NS (SUR-8 location), circa 500m east of SUR-7 (**Fig. 9**).

Prior to deployment, the internal clock of the receivers was synchronized, the number of channels to scan set to 2 (78kHz and 79kHz; frequencies of the tags) and the channel and scan delay set to 1s, the default value.

In situ, the SURs were oriented vertically on a straight line, 0.5 m away from each other and set-up on the sea bottom using lead weight attached to their eyebolt. Two sets of six rebars were deployed, parallel to one another (1 m apart), at increasing distances from the receivers, starting at 10m, 50m, then 100m and every 100m until a maximum of 400m.

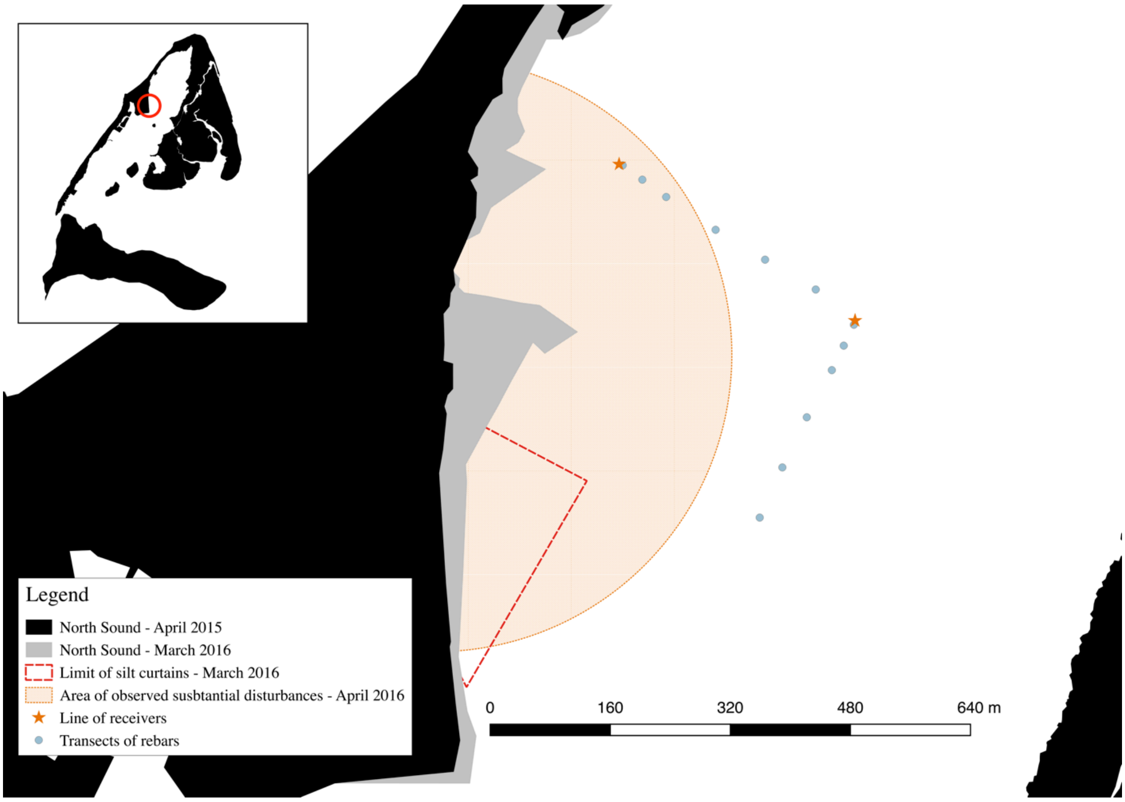


Fig. 9. Context of the detection range testing performed within the study area in May 2016, North Sound, Bimini Islands, Bahamas.

Two CT transmitters similar to the ones fitted in the juveniles were used as the acoustic source (identical power output). The tags were housed inside a plastic tube (length, approx. 15cm), attached to a hollow PVC pole (length, 170cm), 0.5 m above the sea bottom, to ensure that they were positioned at a consistent depth replicating the activity of juvenile lemon sharks–foraging, resting and swimming- (Guttridge, 2009). A detailed illustration of the setup is depicted in **Fig. 10**.

Trials were conducted over slack high & low tide and mid-tide to test the acoustic range at varying depths and conditions. The time of the tidal phases was determined using the online tide-table available for South Bimini (https://www.windfinder.com/forecast/south_bimini_south_beach), considering the 1½ hour delay in high tide and a 2 ½ hour delay in low tide from South Bimini (Newman, 2003). Trials were operated upon forecast checking, and days were selected according to the wind prediction (max. 10 knots) and rain probability (0%; no equipment was available to quantify rainfall). Trials were held within a 1-hour window on either side of slack low and high tide and during mid-tide, enabling a complete coverage of the transect during each tidal phase (2 hours).

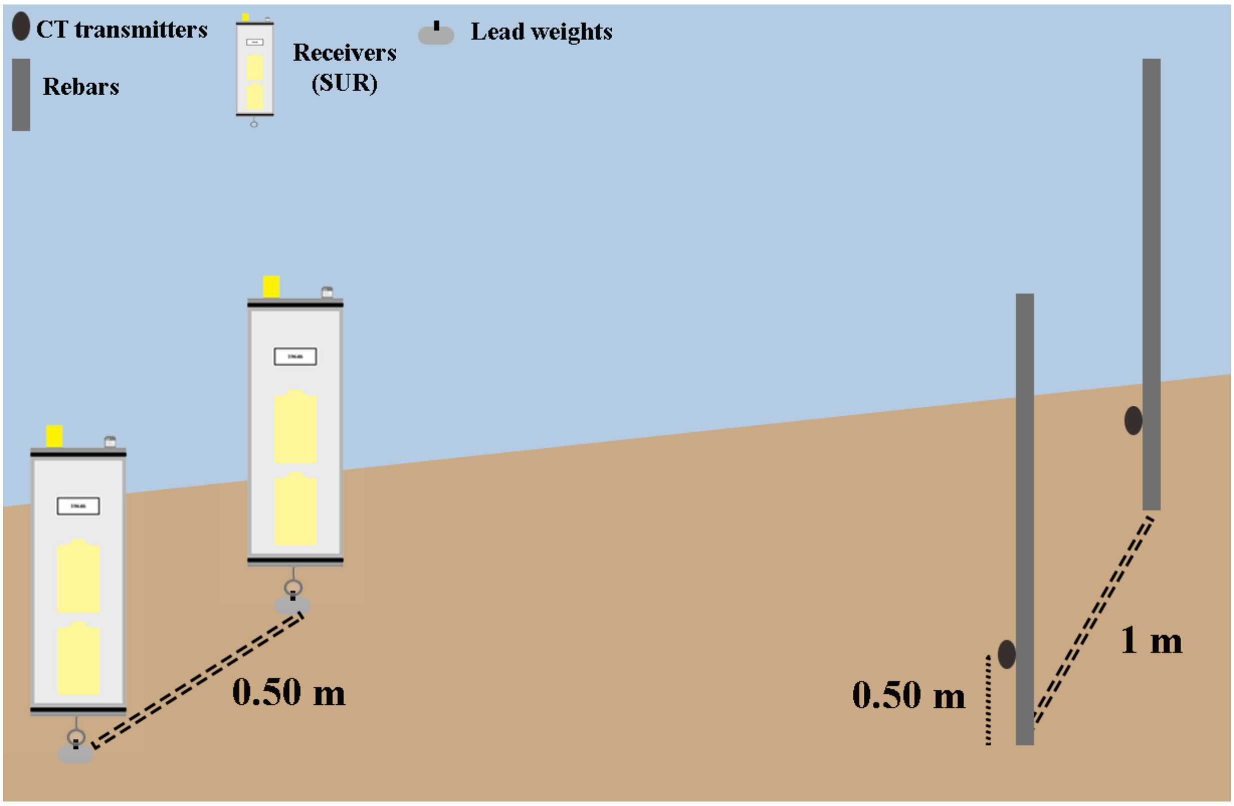


Fig. 10. Diagram of the experimental design set-up for range testing trials using Sonotronics ® passive Submersible Ultrasonic Receivers (SUR). The brown area represents the sea bottom while the blue patch corresponds to the water column.

During the trials, the PVC pole was slid on the rebar and each recording lasted for 10 minutes (estimated time to emit a significant number of signals whilst using two tags, Dr. Guttridge pers. comm.). It was ensured that the engine of the skiff was turned off during the listening period and that the boat was not obstructing the acoustic signal propagation between the receivers and the tags.

A complete transect corresponded to the testing of the 6 distances over the total period of a tidal phase. At the beginning and end of each trial, flow and wind velocity were measured (cm/sec; mechanical flowmeter, General Oceanics Inc. ®, Florida, U.S.A. & mph; anemometer, model: EA63010U, La crosse technology, Ltd. ®, Colorado, U.S.A.). Depth (ft) and temperature (F) at the position of the SURs were automatically recorded every 5-min throughout the duration of the trial, using a Temperature Depth Recorder (TDR) device (Sensus Ultra, ReefNet Inc. ®, model: U-04123; accuracy of ± 1 ft & ± 0.02F). A water sample was taken at the beginning of each trial, at 10m and 50m from the SURs for turbidity analysis.

II.4.4. Active tracking

Active tracking allows a more detailed approach of the spatial use of an individual and complements passive acoustic data. It is a labor-intensive fieldwork that enables the capture of real-time movement and position of the sharks, providing fine scale information.

In order to proceed, a transect constituted of 54 waypoints, allowing the entire coverage of the nursery area (approx. 3 km^2) over a full working day (i.e. 6h to 8h), was determined and active tracking was ideally conducted twice a week (**Fig. 11**). However, the number of sampling days was not evenly spread across the study period as field work was strongly driven by weather (i.e. wind velocity, waves and storms), resources (i.e. boats and volunteers' availability) and overall schedule of the research station.

The tracking day started at the northernmost point and, following each waypoint using a GPS, the trackers navigated their way south aboard a flat-bottomed skiff able to skim waters as shallow as 40 cm. During low tides below this threshold, the boat was towed. The sharks were tracked using a directional hydrophone (DH-4, Sonotronics Inc. ®), which detects and transmits the signal emitted by a tag to the portable receiver (USR-08 Ultrasonic Receiver, Sonotronics Inc. ®), which converts the high frequency signals (70 kHz -79 kHz) into audible pings the tracker could hear. While conducting the active tracking, the hydrophone was mounted onto a PVC pole and immersed into the water column from the bow of the vessel. Once a shark swam within the detection range of the hydrophone and under the condition that the full code was heard and entirely read by the tracker, the distance of the signal, the bearing and the GPS coordinates were taken. The bearing of the shark was established by rotating the hydrophone towards the source of the pings and reading the indication from a compass.

An individual was identified by its unique coded signal, emitted by the transmitters at a nominal frequency. For instance, the transmitter with the code 3-6-5 emitted 3 pulses, a short pause, 6 pulses, a short pause, 5 pulses, a longer pause (corresponding to the interval, in ms, between two consecutive transmitted codes), and then repeated again (**Fig. 12**). The transmissions were continuous therefore the code was reiterated all over until the shark and the hydrophone were too distant for the tracker to read the entire code and/or until the individual swam out of the detection range of the gear.

The sound pulses emitted by an acoustic transmitter were used to estimate the position of the individual in real time. The intensity and loudness of the signal was related to the distance between the boat and the shark. The distance was confidently estimated with an accuracy of ± 10 m.

A training of the trackers as well as a constant detection range testing performed prior to every tracking effort mitigated the inherent bias resulting from this process.

Fig. 11. Map of active tracking transect, designed so that it enables a suitable coverage of the entire nursery area over 6h to 8h. Bimini Islands, Bahamas.

A CT transmitter similar to the ones fitted in the juveniles was used as the acoustic source. The tags were housed inside a tube (length, approx. 15cm), attached to a hollow PVC pole (length, 170cm), 20 cm to 50 cm above the sea bottom, to ensure a depth consistent with the activity of the sharks (Guttridge, 2009). The PVC pole was slid onto a rebar positioned in the middle of the NS. Then, the boat was anchored 50 meters away from the transmitters (maximum determined distance allowing the clear reading of the entire code emitted by the tags at the lowest loudness), and the tracker had to ensure the clear reading of the emitted code. This process favored a "hearing calibration" and allowed an inference of the distance between the shark and the tracker comprised between 0 m and a maximum of 50 m.

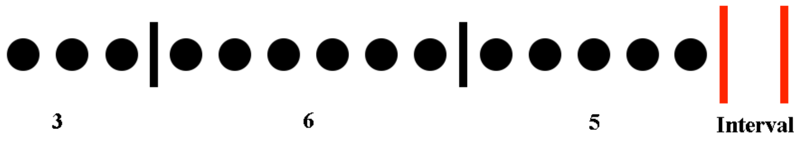


Fig. 12. Example of complete transmission from tag code #365. Each filled dot represent a sound pulse emitted by the transmitter. The black horizontal lines correspond to the short break subsequent to the emission of series of pulse composing the ID number (i.e. code). The two red horizontal lines correspond to the interval in milliseconds before two successive complete emissions.

II.5. Data treatment and analyses

Data treatment and analyses were performed using R software (version 3.2.3; 2015-12-10) and RStudio (version 0.98.1091). The mapping process was carried out with Q.G.I.S. (Quantum Geographic Information System; version 2.14).

II.5.1. Personality analysis

The preliminary analyses of personality traits consisted in the investigation of the rate of movement (R.O.M.) of the sharks in the novel open-field test (i.e. proxy for the swimming speed, obtained from the number of sectors visited in 10 minutes). Data were treated using "*lme4*" and "*lmerTest*" packages following the analyses depicted in Finger *et al.* (2016).

ROMs were obtained as the number of sectors visited per seconds and tested for repeatability, using the following formula (Dingemanse *et al.*, 2002):

$$\text{Individual } \sigma^2 / \text{Individual } \sigma^2 + \text{Residual } \sigma^2$$

where σ^2 stands for the variance. Repeatability enables the assessment the consistency in the responses of the sharks under similar conditions. A likelihood ratio test was applied to evaluate the significance of the individual within the model.

As discussed in Finger *et al.* (2016), the underlying motivation for this analysis is the prediction that the reaction of an individual to the test should covary with the number of exposures. In other words, it assumes the ROM measured during the very first exposure captured the reaction to novelty, that is to say the personality of the individual. Therefore, only the ROM value acquired after first exposure to the trial is considered and included into further analyses.

II.5.2. Detection range analysis

Data management

The first step was to organize environmental and metrics data. Measurements of wind, flow and secchi depth were averaged per tidal phase and remaining data were averaged per 10-min windows and combined to the respective distance.

Detections considered as spurious for passive monitoring analyses were herein preserved and incorporated into further analysis, to investigate the relationship between distance and probability of detection.

Theoretical maximum (τmax) & probability of detection

A probability of detection, as a function of distance, was obtained by a ratio between the number of detections per distance increment and the maximum number of detections a receiver has the ability to record over a defined time span. Thereby, the basis of this proportionality lies in the comparison between an observed number and a theoretical maximum (τmax). Constructive discussions with the designer of the equipment and M. van Zinnicq Bergmann underlined the complexity of the estimation of the latter while employing receivers scanning multiple frequencies. Although by definition a theoretical value cannot be calculated, the intricacy of the technology involved necessitated including a practical weight in the interpretation. Therefore, both a hypothetic and an empirical procedure were operated to evaluate and balance the estimation of τmax value.

Initially, the manufacturer specifies technical particularities of the receivers in an online manual (http://sonotronics.com/wp-content/uploads/2010/07/SURmanual.pdf), providing interesting formulas on the detection ability of the gear. It is explained that each receiver allocates 2 seconds of listening per frequency, then powers down for 1 second – “channel delay” - (a blanking time established as a battery-saving procedure). Once the channel map is completed (i.e. once all frequencies are scanned), the SUR powers down for another second – “scan delay” -. Due to these two processes, a theoretical minimum time span between 2 decoding can be obtained from the following elementary arithmetic:

(2 channels x 2 sec/channel[1]) + (1sec “channel delay” x 2 channels) + 1 sec “scan delay” = a listening window every 7 seconds for each tag

[1]. The SUR were setup to scan 2 frequencies (78 kHz & 79 kHz) during the range testing.

This result implies that the receiver is able to detect a maximum of τmax = 85 signals over 10 minutes. However, in the course of the conversations it appeared this method was simplistic and produced unrealistic estimates regarding the functioning and the performance of the gear. Therefore, detailed calculations have complemented this equation (M. Gregor, designer of the equipment, pers. comm.). The following paragraph refers to exchanges with M. Gregor, advocating for the incorporation of the particularities of the equipment into the estimation.

First of all, the CT tags employed exhibit an end-of-code delay of a few seconds (**Fig. 12**). Secondly, a SUR displays a 1.5 sec of overhead after detecting a tag. This phenomenon is partly related to electronic “tasks” the receiver is performing, such as the blinking of the LED –indicating a detection-, the data storage and auto-verification. Moreover, the SUR has a detection timer of approximately 5-7 seconds to cover the 5-7 seconds of end-of-code delay. Then, an additional overhead is triggered every 52 detections, due to the structural functioning of the internal memory, switching the overhead delay from 1.5 sec to 2 sec. Including these parameters into the calculations provided an estimate of a theoretical maximum of 60 detections during 10 minutes.

In order to corroborate this finding, a laboratory experiment was conducted to estimate the maximum number of detections a receiver can decode over 10 minutes in optimum conditions. Two SURs were disposed on a bench, and a tag was placed 3 cm away from the transducer (M. Gregor. pers. comm.). After a listening period of an hour, the raw data were retrieved and closely inspected. A maximum of 58 detections per 10-minutes-window was assessed, encouraging the use of τmax = 60 detections.

Probability of detection and total number of detections were plotted for each site, as a function of distance, using a linear model, to assess the overlapping attributes of the network of receivers.

Model building & comparison between sites

The second driving feature behind the detection range test conducted in this study was to understand the impact of anthropogenic disturbances on the detection performances of the array. To provide a clear idea of detection ability amongst locations, generalized linear mixed effects models (GLMM) were fitted using "*lme4*" and "*MCMCglmm*" packages.

Preliminary multicollinearity analysis led to the removal of receivers' depth as a fixed effect, the VIF value reported significantly co-varied with the transmitters' depth. A subsequent examination revealed no obscuring correlations among the remaining predictor variables (Variance Inflating Factor threshold of 5; Rogerson (2001)).

The null model (i.e. intercept with & without the fixed effects) as well as the minimum adequate model were fitted, the latter via a backward elimination procedure. A likelihood ratio test was carried out to compare full models (containing the fixed effect of interest) against reduced models (without the fixed effect of interest). The transmitters' depth, average wind speed, flow velocity, turbidity and water temperature were centered and subsequently included into the model as fixed effects. Similarly, the locations and tidal phases were computed as fixed effects. The SUR ID as well as the day of trial were fitted as random effects so that each was assigned a different intercept value. This contributes to the integration of performance disparities between receivers into the model (control for non-independence) and allows controlling for fluctuations due to different trial dates.

II.5.3. Metrics data analysis

The analyses of spatial metrics described in the following sections were performed using active tracking (i.e. real-time locations) as well as passive acoustic data collected between September 2015 and May 2016. Due to battery failure in several stations, the data obtained during the deployment of February were discarded. Detections within one month of the surgical procedure and release were not included in the analysis in order to exclude potential short-term bias in behaviors (Rogers *et al.*, 2007).

II.5.3.a. Passive data processing and purification

Spurious detections

Before analysis, all passive acoustic monitoring data were examined and inspected for spurious and unrealistic detections. The first step consisted in identifying the individuals by matching the analogous interval (ms) with its nominal frequency (**Table 1**). A tolerance of ± 4 ms than the designated individual pulse interval was used to separate valid from spurious decoding (March *et al.*, 2009; van Zinnicq Bergmann, 2013). Then, single detections emitted by a single transmitter over a period of 24 h were considered as spurious and removed.

ID #	PIT #	Freq (kHz)	Interval (ms)
5866	4C3A78136D	79	1230
4447	4C4A70705B	70	1120
365	4C4956480F	71	890
3545	4C4A764B1C	70	1040
4546	4C4A403B08	71	1150
3368	4B7B49697B	73	990
5666	4C49503212	77	1210
5667	4C4B24674D	78	1200
4878	4C4998664F	75	1190
4888	4C4A4B5124	76	1180
4547	4C4B195F42	72	1140
4657	4C4B02774F	74	1160

Table 1. Summary of the characteristics of the Sonotronics ® acoustic transmitters fitted to the juvenile lemon sharks, *Negaprion brevirostris*. Freq is the frequency at which the tag emits the sound waves (kHz). The interval corresponds to the end-of-code break (i.e. pause) in milliseconds. ID # is the code each transmitter emit and corresponds by extension to the ID of the sharks. PIT # is the PIT identification number implanted under the dorsal fin of the juveniles upon capture.

Double detections

Secondly, the data were inspected for double detections. Double detections can appear when the detection range of various receivers overlap, leading to the occurrence of a signal simultaneously decoded by at least two adjacent receivers, producing two detections at a similar time for a single individual. Different systems were developed to estimate the localization of an individual detected by multiple stations using time-at-arrival positioning algorithms (Andrews *et al.*, 2011; Espinoza *et al.*, 2011). However, their utility is quite restricted for the analyses involved in the current investigation. This study mostly focuses on the spatial use of juveniles, requiring a broad spacing between SURs in order to prevent undetected movements beyond the monitored area (Farmer & Ault, 2014). Conserving these paired detections would not only inflate the data but would also overestimate the spatial use of the sharks. Therefore, double detections were discarded.

Swimming behavior filters

Finally, an algorithm was developed to filter all detections according to the natural swimming behavior of the juvenile lemon sharks. For each individual, an average theoretical possible distance covered was calculated between successive detections (Δd) using the following formula:

$$\Delta d = TL \times 0.3 \ bl.s^{-1} \times \Delta t$$

where TL corresponds to the total length of each shark in cm; 0.3 $bl.s^{-1}$, the designated cruising speed of a juvenile, in body length per seconds, as averaged from different sources (Gruber *et al.*, 1988; Nixon & Gruber, 1988; Bushnell *et al.*, 1989; Edrén & Gruber, 2005); Δt, the difference of time between the two successive detections, in seconds. Subsequently, an additional procedure involving the same algorithm and following a similar process was conducted ($\Delta d'$), using a speed of 1.1 $bl.s^{-1}$, corresponding to a critical swimming speed recorded for a juvenile lemon shark (Graham *et al.*, 1990). The maximum detection range reported during range testing trials was used as a weight and subtracted from the distance observed between two detections (~ 400 m per receivers).

Then, each distance between successive detection was compared with the two theoretical estimations. If the distance observed was greater than both Δd and $\Delta d'$, a close inspection of the data set allowed determining whether the detections were unrealistic or valid. For each case, detection patterns were assessed for detections decoded by two neighboring receivers and potentially reflecting the overall activity of the sharks. Then, if detections occurred on two distant receivers, without the tag being detected by any of the receivers deployed in-between, the detection was considered spurious. Also, if distant detections occurred repetitively over an extended period of time, the pattern would be considered suspicious and the detections would therefore be discarded. Finally, the date and time of each uncertain detection was compared with the last detection of the individual (date, time and location) and with the visual on sharks reported during active tracking.

An unrealistic distance between two successive detections can find its interpretation in two different domains. First of all, it can be technology-related and may be an effect of signals colliding, a phenomenon whereby multiple individual acoustic signals emitted on the same frequency are received simultaneously by a single receiver (Heupel *et al.*, 2006; Singh *et al.*, 2009). As a result of the collapsing, an erroneous detection can be recorded by the receiver and misidentified as a tagged individual.

Secondly, it can have a biological explanation. An improbable covered distance could be the artifact of a predation event, resulting in the predator ingesting the transmitter fitted to a juvenile, leading to a misinterpretation of the detection(s) as an authentic presence of the individual within the array (viz. the predator exhibits a faster swimming speed). Such instance is supported by the repetitive detection of a bull shark, *Carcharhinus leucas*, in the NS, between September 30th and October 13th 2015.

II.5.3.b. Spatial use analyses

The movement and spatial use analyses were performed using solely passive acoustic data extracted from the array of receivers deployed between September 2015 and May 2016, excluding February 2016. The data analysis followed various subsequent steps explained in the section below.

Residency index: a site fidelity indicator

First of all, to quantify the degree of site fidelity of the juveniles within the nursery area, an absolute residency index was calculated for each shark, over the entire acoustic array. This first index was based on the ratio between the total number of days the individual was detected and the total number of days of effective duty of the receivers. A relative residency index was estimated from the number of days with detection between the first and last detections, divided by the interval in days between first and last detection. Residency indexes vary from 0, indicating no residency pattern, to 1, suggesting absolute residency – or "sedentarity" -.

Centers of activity

Secondly, prior to estimate home range and core area, locating the centers of activity (COA) enabled a relevant inference about the horizontal movement patterns and space use of the individuals. Therefore, COA were obtained for each individual, following the analytical method described by Simpfendorfer *et al.* (2002). This mean-position algorithm uses data from multiple receivers, performing a triangulation of the detections, and converting them to position estimates (i.e. relocation) based on weighed means of the number of detections at each receiver over a determined period of time – Δt -. Using the arithmetic approach, a range of Δt was preliminarily tested and the appropriate time interval for COA computation for the juvenile lemon sharks was determined to be 15 minutes. This decision resulted from a close inspection of the data, revealing limited changes in position with greater intervals, the sharks supposedly exhibiting turnings to remain within a certain area (Simpfendorfer *et al.*, 2002).

Minimum convex polygon

Then, a minimum convex polygon (MCP) was assessed for each shark as a proxy for home range and core area. Originally, MCP is the earliest method and most frequently used to delineate home range. It consists in binding all the most external localizations so that it generates a minimum convex that incorporates all other positions. This method is a rough indicator of the dispersion of an individual throughout the monitored area. However, it was subjected to substantial criticisms due to its main inadequacy in the sense that the area of the MCP increases with the number of data, but also owing to the over-estimation of the positions. Therefore, this analysis was not employed to provide a representative appreciation of the movements and spatial occupation of the individual but to quantify the extent of the animal's range (Worton 1987). Nevertheless, to mitigate the major limitation of the method, COA locations were used as data input, enabling an improved perception of the space use and a more reasonably suitable approximation of the distribution of the sharks within their nursery area. The analysis was conducted using the "*adehabitatHR*" package developed for R software (Calenge, 2006). A 95% MCP (i.e. excluding 5% of the most external COA) was used as proxy for the home range and a 50% MCP was established as a surrogate for the core area.

Home range & core area

Finally, a second method was used to assess spatial utilization. The most impartial basis to establish and determinate home range and core area is the use of a probability estimator. The main analytical concept behind home range was settled according to a probabilistic model, the utilization distribution, assuming an individual uses a certain area over a given period of time. It is therefore acknowledged that the home range comprises 95 % of the positions of an individual while the core area encompasses 50% of them (Worton, 1989; Seaman & Powell, 1996).

A formal model, the Kernel Utilization Distribution model (KUD), was applied to the data using "*adehabitatHR*" package, where a 50% KUD was assessed to measure an individual's core activity area and a 95% area as the individual home range. KUD delineations are key components in most spatial ecology studies in the sense that they provide inferences about populations based on restricted sample (Abecasis *et al.*, 2009; Abecasis *et al.*, 2013; Abecasis *et al.*, 2014b; Abecasis *et al.*, 2014a).

This model is a bivariate probability density function used as a proxy for space utilization, outlining a zone corresponding to the putative space utilization of the individuals from (re)location data (i.e. COA). It provides a summary of the space-use in terms of map boundaries over the period of a study. Thereby, for each individual, a Kernel bivariate function was applied to all COA relocations (coordinates "*x*" & "*y*" as longitude and latitude) and the values extracted from these functions were averaged all together. In order to establish rational estimations of the home range and core area size, a complex smoothing factor (*h*) has to be calculated and included in the model, so that a bandwidth is attributed to each relocation. This bandwidth parameter has to be chosen appropriately due to its substantial influence on the output and estimations of the model (**Fig. 13** & **Table 2**). A review of the literature as well as a fruitful discussion with Dr. David Abecasis stressed the importance of a researcher's knowledge about the studied population/individuals, area and equipment (i.e. detection range) in the choice of the bandwidth and underlined the necessity of investigating various options to reach a reasonable *h* value.

The correct choice for the value to compute the *h* parameter has been subject to important discussions and resulted in the development of more or less intricate evaluations (Worton, 1989; Seaman & Powell, 1996; Horne & Garton, 2006). Nevertheless, a main computational analysis is recognized as reference for the determination of the bandwidth, the Cross Validation (CVh; *href* – "*adehabitatHR*"; Calenge (2006)) method. *H* value was therefore initially estimated using this algorithm, integrated into the KUD model and the outputs closely examined. The extracted sizes and graphic representations of the areas (i.e. 95%KUD & 50%KUD) were compared with the ones obtained from the MCP analyses (i.e. 95%MCP & 50%MCP) as well as with the COA locations. After inspection, the *h* value (*href* = 390.8587) was evaluated as significantly over-estimating the home range and core area and therefore discarded.

A second method to calculate *h* was attempted using "*sm*" package. The established value (*h.select* = 186.3386) did not appear applicable, due to exceedingly scattered patterns in home ranges and above all generating an underestimation of the spatial use of the sharks.

At this stage, another process was favored over an individual calculation of *h* smoothing factor in order to conserve the population aspect of the analysis. Therefore, a third approach was intended, inspired by the protocol developed in Kie (2013). The *href* (i.e. Cross Validation *h*) automatically computed by the *KernelUD* function from the package (*href* = 390.8587) was run into an arithmetic computation sequentially reducing *href* value by 0.10 increments (such as 0.9 *href*, 0.8 *href* until 0.1 *href*), inducing an exploration of the optimum value of *h* (*ad hoc h*) starting from a smoothing factor equal to the initial *href*. Then, the *ad hoc h* values were plotted against the corresponding sizes of the home ranges (**Fig. 13**). The home range areas associated with the *href* and *h.select* were examined and respectively used as upper and lower threshold for the determination of the specific *ad hoc h* value so that:

$$(h.select < ad\ hoc\ h < href)$$

A secondary outset was established as a "mediator", using the overall distance at which the 50% probability of detection was reached (i.e. obtained combining detection range analysis performed at both sites), included as a weight to afford a more balanced decision (Dr ~ 100 m) (March *et al.*, 2009). Afterwards, the *ad hoc h* values contained within the *h.select*/*href* interval were computed in the KUD analysis and the outputs were mapped.

A trade-off criteria for *h* value selection was established from Kie (2013) in order to provide an optimum smoothing factor, minimizing both highly scattered and dislocated home ranges (i.e. multiple patches within the studied area) and under- or over-estimation of the areas. The outputs were compared with the literature and knowledge about juvenile lemon sharks within their nursery area (Morrissey & Gruber was used to calibrate and mitigate the observe patterns). After close inspection of the KUD results displayed upon use of these *ad hoc h* values, $h = 0.7href$ (*ad hoc h* = 273.6011) was considered the most reasonable value provided by the described method. This established bandwidth fitted the data more closely and thereby, it appeared more rational to include it into further computations.

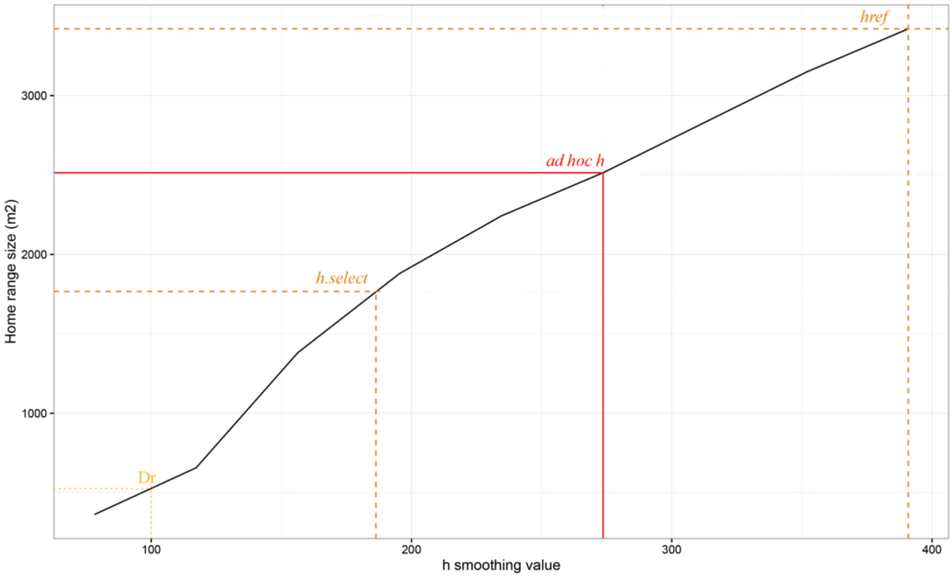


Fig. 13. Graphic representation of the influence of *h* parameter on the home range size of juvenile lemon sharks, *Negaprion brevirostris*. 0.1 *href* has been removed due to the out-of-bound home range value it produced (0.1 *href* = 39.085 & respective home range area = 16 308.1438 m^2), nevertheless the original figure is presented in **Appendix II**.

A boundary function was primarily incorporated into the KUD calculations in order to take into account the presence of dense mangrove fringe edges the sharks were unlikely to penetrate. However, this approach appeared idealistic, constrained by substantial restrictions, producing simple boundary shapes excluding detailed morphological features of the coastlines but above all obscuring the results (Calenge, 2015). For the sake of consistency in the treatment of the data amongst sharks and in order to avoid the creation of noise within the data and possibly corrupt the outputs, the function was eluded.

Increments	*h* parameter value	HR size (m^2)
	ad hoc h	
href	*390.8587*	*3420.1802*
0.9*href*	351.7728	3148.3778
0.8*href*	312.687	2831.2750
0.7*href*	**273.6011**	**2514.1722**
0.6*href*	234.5152	2242.3698
0.5*href*	195.4293	1879.9666
0.4*href*	156.3435	1381.6622
0.3*href*	117.2576	656.8558
0.2*href*	78.17174	362.4032
0.1*href*	39.08587	16308.1438
	h.select	
	186.3386	1766.7156

Table 2. Summary of the output from the *ad hoc* method to choose *h* values for smoothing parameter in kernel home range analysis and respective home range sizes. *h.select* products are also reported. HR stands for home range. The bolded values correspond to the *h* parameter included into the Kernel Utilization Distribution analyses.

Spatial analysis estimator accuracy

In an attempt to examine the relevance of both analytical methods employed during this study, straightforward comparisons were computed between the output from the MCP (50% & 95%) and KUD (50% & 95%) analyses.

Firstly, a percentage of change (Δ C) in core area (50% MCP - 50% KUD) and home range (95% MCP – 95% KUD) sizes was evaluated using the following formula:

$$\Delta C = [(KUD-MCP)/KUD] \times 100$$

where K represents either the 50% KUD or 95% KUD and MCP corresponds to the respective MCP percentage.

Secondly, a Wilcoxon paired test was performed to assess the significance of the difference in area size using the two different methods.

II.5.3.c. Movement analysis

The movement analysis was performed using active tracking data and consisted in evaluating the distance of the individual from the nearest shore. All real-time locations were collected between September 2015 and April 2016.

Data filters

Initially, the data set of real-time locations was filtered for redundancy, that is to say, upon inspection, the number of track location per shark over 30 minute periods was restricted to a maximum of two. This protocol prevents an inflation of the dataset and reduces over-estimation of real-time positions while computing the mean distance from shore. It also contributes to the mitigation of a possible alteration of the natural behavior of the juveniles due to the presence of a skiff, although such manifestation was described as relatively unlikely (Gruber *et al.*, 1988; Morrissey & Gruber, 1993a).

Secondly, a threshold of three days of tracking coupled with an overall minimum of three different real-time locations per shark was applied to the dataset, below which the individual was excluded from further analysis.

Distance from nearest shore

Real-time relocations were calculated using the “x” and “y” coordinates, bearing and distance gathered during active tracking (“*Geosphere*” package). The relocations were afterwards plotted, verified, and removed if considered unrealistic (i.e. relocation localized on land). This visual assessment resulted in the dismissal of a few positions.

Then, using “*rgeos*” package, the distance from the nearest shoreline (DfS) was computed for each relocation. Finally, a mean DfS ± standard error was computed per shark.

II.6. Spatial metrics & personality traits comparison

The first step in the comparison analysis was to determine whether each set of data followed a normal distribution by performing a Shapiro test. Afterwards, the adequate parametric (Pearson correlation test) or non-parametric (Spearman correlation test) analysis was performed to shed light on the link between personality and spatial use in natural conditions.

In addition, a linear regression analysis was performed to investigate and plot the relationship between personality traits and movement ecology metrics. This analysis was conducted in an attempt to model the relationship between two variables by fitting a linear equation to the observed data for it considers one variable to be the explanatory variable (i.e. personality score) and a dependent variable (i.e. the observed spatial patterns). Beforehand, scatterplots were fitted to determine whether or not there is a relationship between the variables of interest.

Pearson and Spearman tests were used to measure the degree of relationship between two commodities while linear regression was performed to explain causal relationship between them.

Therefore, Residency indexes, KUDs (50% & 95%), MCPs (50% & 95%), DfS values as well as the number of COA were investigated and compared to the ROM scores obtained during the first exposure to the novel open-field test using both correlation analysis and linear regression.

III. RESULTS

III.1. Summary

Acoustic equipment considerations

All the SURs of the array were effective from August 2015 to May 2016, and several transmitters were decoded until the day of retrieval, the 07th of May 2016, endorsing a battery life fairly consistent with the predictions of the manufacturer (14 months).

A compromised battery life of the receivers was not noticed in time, leading to an unreliability of the listening stations between February and March 2016. The few detections reported during this period were threfore discarded. In addition, an individual (#4888) was only detected during active tracking, implying a possible technical anomaly of the tag. No spatial use analysis (i.e. involving passive monitoring data) was therefore performed for this shark. Aside from this misstep, no technical failure of the acoustic gear was reported.

The acoustic equipment was reliable and allowed a suitable quantification of the movement and spatial use during the study period.

Sharks monitoring

A total of twelve lemon sharks, *N. brevirostris*, were involved in this study. All sharks were acoustically tagged during July 2015. The overall operation lasted between 02:22 min and 06:33 min. All 5 females and 7 males were juveniles (Barker *et al.*, 2005), from young-of-the-year to circa 2 years old, with a total length (TL) ranging from 65.5 cm to 71 cm and a weight varying from 1.2 kg to 2.1 kg. Post-surgery monitoring indicated all individuals were healthy. Release in the NS (i.e. capture site) occurred a week after the procedure. A summary of the morphometric measurements of the sharks is reported in **Table 3** and illustrated in **Fig. 14.**

After examination of the detection characteristics for singularities (i.e. inspection for a tag uniformly decoded by the same receiver over a relatively extended period of time; Abecasis *et al.* (2009)), it was confirmed that no tag was lost and that the transmitters were successfully implanted.

Despite the gap in the operational duty period of the array in February 2016, between September 2015 and May 2016, eleven out of the twelve individuals fitted with an ultrasonic transmitter were detected either by the network of receivers (**Fig. 15**) or during an active tracking effort. For these sharks, the total monitoring period between first and last detection ranged from 13 to 191 days, although the manufacturer predicted an expected battery life of 14 months. Over the 210 days of acoustic passive monitoring, the eleven sharks were detected by at least 8 different receivers. The total number of detections per individual ranged from 2 179 to 36 887, for an overall total of 228 972 detections. A summary of the data extracted from the passive monitoring array is reported in **Table 4** and individual abacus calendar plots of daily detections are provided in **Fig. 15**.

Table 3. Summary data for juvenile lemon sharks, *Negaprion brevirostris*, captured, subjected to the novel open field trial and tagged in the North Sound nursery area, Bimini Islands, Bahamas. ID # corresponds to the tag ID # and is used to identify each individual; D.cap stands for Day of capture. The PCL (cm) corresponds to the precaudal length at capture. FL (cm) is the fork length. TL (cm) corresponds to the total length. Girth (cm) corresponds to the dorsal girth. Measurements are illustrated in the figure below.

ID #	D.cap	PCL (cm)	FL (cm)	TL (cm)	Girth (cm)	Weight (kg)	Sex	Trial date	Surgery date	Surgery duration (min)
5866	7-Jun-15	52.5	58	67.5	23	1.8	F	Jun-14	16-Jul-15	02:52
4447	8-Jun-15	50.7	56	66	19.5	1.4	F	Jun-15	17-Jul-15	02:38
365	7-Jun-15	50.5	56.2	66.4	21	1.4	M	Jun-14	17-Jul-15	03:29
3545	8-Jun-15	52.7	57.8	67.9	22	1.5	F	Jun-15	17-Jul-15	02:22
4546	7-Jun-15	54	59.8	70.1	21.5	1.5	M	Jun-15	16-Jul-15	03:48
3368	7-Jun-15	53	58.8	69.3	22.5	1.7	M	Mar-14	16-Jul-15	04:10
5666	7-Jun-15	50.9	56.1	65.5	22.5	1.6	M	Jun-15	13-Jul-15	04:32
5667	8-Jun-15	52.6	59.3	69.2	22	1.7	F	Jun-14	14-Jul-15	03:33
4878	7-Jun-15	54.3	60	71	28	2.1	M	Jun-15	14-Jul-15	04:35
4888	7-Jun-15	54	59.6	69.4	23	1.7	M	Jun-15	13-Jul-15	06:33
4547	7-Jun-15	50.5	55.5	66	21	1.2	M	Jun-14	13-Jul-15	06:30
4657	7-Jun-15	52.6	58.4	68.5	23	1.6	F	Jun-14	14-Jul-15	04:00

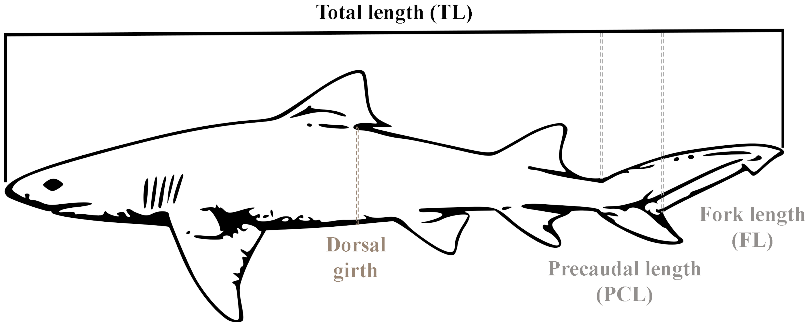


Fig. 14 Morphometric measurements of lemon sharks, *Negaprion brevirostris*.

Overall, both residency indexes indicated that most sharks remained within the nursery area during the period of the study, however, presence was variable among individuals (**Table 4**). A Spearman's rank correlation applied to the Rr_i unveiled that this variability would be attributed to individual size (p-value < 0.05; Rs = -0.6911347), smaller sharks exhibiting greater site fidelity than larger specimen. Specifically, some individuals were detected almost everyday, displaying substantial site attachment, such as shark #4447 (Ar_i & Rr_i = 0.91; **Fig. 15**), while others were nearly absent (#3368; Ar_i = 0.22; Rr_i = 0.38; **Fig. 15**). Intermediate patterns were also disclosed, as demonstrated by the intermittently detected individual #5666 (**Fig. 15**).

Yet, seven juveniles, accounting for approximately 58% of the sharks fitted with a transmitter, spent more than half of the monitoring period within the study area ($Ar_i <$ 0.50; **Table 4** & **Fig. 15**). Five of them were last detected in May 2016 (Ar_i ranging from 0.74 to 0.91), suggesting an almost continuous presence of these individuals within the nursery through the complete period of the study.

Interestingly, the relative residency index indicated an abrupt loss of track of two highly resident individuals.

Indeed after September 2015, shark #4546 (Rr_i = 1; Ar_i = 0.06) did not emit anymore. After investigation of the patterns provided by the swimming speed algorithm (**Material & Method**) no intricate detection feature were reported. The last detection was decoded by SUR5.

However, individual #3545 (Rr_i = 0.96) presented an interesting pattern over the last days of its monitoring. The examination of the swimming speed revealed a relatively fast speed, inconsistent with the normal swimming speeds of a juvenile lemon shark. Detections were spread across areas usually visited occasionally, mostly situated at the southeastern mouth of the NS. SUR14 (**Fig. 21**) was over-represented during these days, but more strikingly, successive detections occurred between distant receivers, with no decoding by the receivers located in-between. Therefore, detections after the 5th of October 2015 were discarded. The last detection occurred on SUR14 on the 8th of October.

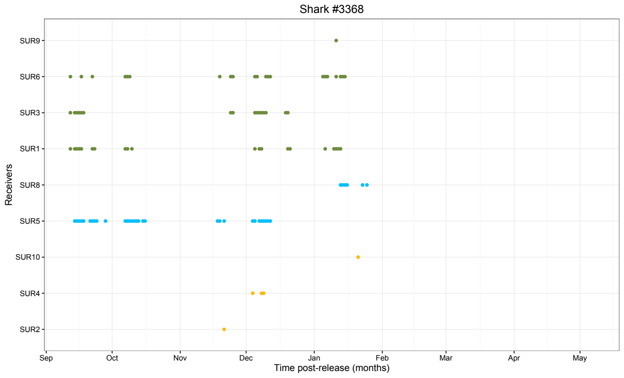
One shark was never detected within the study area, neither by the passive acoustic array, nor during active tracking (#5866).

The control receiver situated at the southernmost margin of the NS, deployed at the junction with the second nursery ground, Sharkland, showed very few detections of only two individuals, subsequently detected by other SURs within the array (#5666 & #4547; cf. **Fig. 15**).

The amount of metrics data gathered along the 9 months of study was appropriate and the overall patterns depicted by the residency analysis indicated the data were suitable to perform further movement and spatial analyses. Spatial ecology and real-time movement analyses revealed high individual variability. The two methods employed to assess home ranges and core areas presented relatively different output. The results from the comparisons conducted between the scores obtained during the novel open field trial and the spatial metrics unveiled significant correlations between personality and movement ecology.

Table 4. Summary of passive acoustic monitoring array for individual juvenile lemon sharks, *Negaprion brevirostris*, in their nursery area, Bimini Islands, Bahamas. ID # corresponds to the ID of the shark; TD is the total number of detections; DD stands for number of days with detection; T Period corresponds to the total period in days between first and last detections, excluding the non effective duty period of the stations; Last Det is the day of last detection of the individual; Ar_i corresponds to the absolute residency index; Rr_i is the relative residency index; Receivers represents the total number of unique receivers at which the shark has been detected. Control receiver has been excluded from the total number of receivers with detection due to a restrained effective duty period.

ID #	TD	DD	T Period	Last Det	Ar_i	Rr_i	Receivers
5866	-	-	-	-	-	-	-
4447	26 659	191	210	07-May-16	0.91	0.91	9
365	18 954	190	210	07-May-16	0.90	0.90	12
3545	15 876	24	25	06-Oct-15	0.11	0.96	14
4546	8 924	13	13	24-Sep-15	0.06	1	11
3368	2 179	47	127	15-Jan-16	0.22	0.38	8
5666	36 887	155	206	03-May-16	0.74	0.75	12
5667	34 681	125	129	18-Jan-16	0.60	0.97	14
4878	32 593	175	210	07-May-16	0.83	0.83	10
4888	-	-	-	-	-	-	-
4547	16 913	190	210	07-May-16	0.90	0.90	12
4657	35 306	129	130	19-Jan-16	0.61	0.99	13
Total	**228972**	-	**210**	-	-	-	**14**



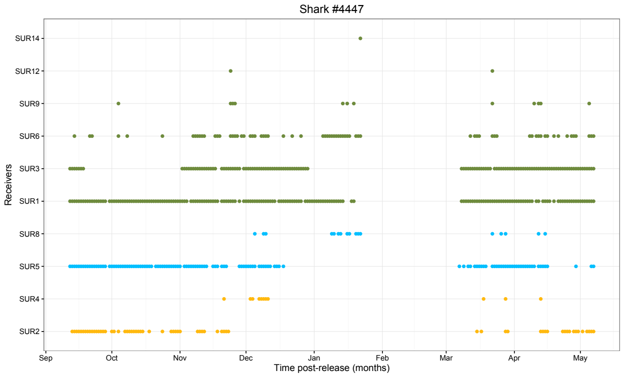


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Fig. 15. Abacus plot of daily detection of juvenile lemon sharks, *Negaprion brevirostris*, fitted with an acoustic transmitter within their nursery area, between September 2015 and May 2016, North Sound, Bimini Islands, Bahamas. The green dots represent detections at mangrove fringe receivers; Blue ones, detections at receivers deployed in the central area; Orange ones, detections reported on the western flank receivers. Note that only sharks with more than 30 days are represented therefore individuals #4546 & #3545 are absent.

III.2. Personality traits

All sharks were part of a broader personality experiment in mesocosms and demonstrated consistent individual differences in R.O.M. values (repeatability = 0.37; restricted likelihood ratio test = 3.0955, n = 63 individuals, p-value < 0.05). Eleven individuals were tested either during summer 2014 or summer 2015. One juvenile was tested in March 2014. The scores, obtained from a ratio of the number of sections visited by seconds, are presented in **Table 5**.

A Pearson correlation test indicated no significant correlation between the size of the individual and the score obtained during first exposure to the novel open field test (p value > 0.05; Rs = 0.510153).

ID #	Size *t*	Score
5866	50.4	0.303
4447	50.7	0.232
365	49.1	0.272
3545	52.7	0.387
4546	54	0.327
3368	47.9	0.233
5666	50.9	0.215
5667	46.7	0.081
4878	54.3	0.288
4888	54	0.292
4547	47.6	0.245
4657	47.8	0.273

Table 5. Summary table of the personality scores obtained by each individual juvenile lemon shark, *Negaprion brevirostris*, after first exposure to the novel open field experiment. Size *t* stands for Size at trial, corresponding to the precaudal length of the shark at the time of the trial.

III.3. Detection Range

The linear models assessing the number of detections as a function of distance, fitted for the range analyses at both locations, were preliminarily tested and found to be significant (Western flank: F(1,60) = 7.68, p-value = 0.00742; Middle: F(1,50) = 29.1, p-value ~ 0). Similarly, the linear models used to investigate the relationship between distance and probability of detection were significant (Western flank: F(1,124) = 48.16, p-value ~ 0; Middle: F(4,159) = 12.13, p-value ~ 0).

Overall, noteworthy disparities were discernable in the detection features between the western flank, undergoing anthropogenic influences, and the middle part of the NS, characterized by a less disturbed ground.

Number of detections & maximum detection range

The number of detections per distance as well as the maximum detection range varied substantially between sites, the central area demonstrating higher values than the western side (**Fig. 16** & **17**). The relative maximum number of detections (i.e. averaged from all receivers and combining all tidal phases) was 40 for the central area and 22 for the western side. A comparison of the generalized linear mixed model with and without the fixed effect of interest (i.e. location) revealed a significant difference in the total number of detections per site ($\chi^2(1) = 9.8312$, p-value < 0.001). Moreover, turbidity significantly reduced the number of detections ($\chi2(2)= 99.254$, $p < 0.001$), the western flank exhibiting higher levels of silt (average FTU ~ 6.00) than the central area (average FTU ~ 1.93).

Interestingly, the area exposing the lowest number of detections and higher degree of anthropogenic influence, presented a maximum detection range of over 400 meters (average for all receivers of 3.55 detections ± 0.72 standard error), longest range recorded for both trials, while the central area of the NS, deeper and less affected, resulted in a maximum detection range comprised between 300 m (average for all receivers of 20.8 detections ± 5.59 standard error) and 400 m (no detections).

A second atypical consideration was the observation, for both locations, of a maximum number of detections recorded at 50 meters instead of an expected theoretical maximum at the closest distance between the transmitters and the receivers (i.e. 10 m). A statistical analysis confirmed the variation between the amount of detections at 10 meters and 50 meters was significant (Western flank, p-value < 0.001; Central area, p-value < 0.001).

Probability of detection

Accordingly, similar features are depicted when considering the probability of detection against distance (**Fig. 18** & **19**).

The probability of detection appeared greater in the middle of the NS than on the western flank (**Fig. 18** & **19**), the former exhibiting a maximum probability of detection of circa 89% whereas the latter displayed a maximum of approximately 52%. Intriguingly, this observation pointed out the underlying singularity that, over the whole experiment, the maximum probability of detection did not reach 100% at any distance. Remarkably, another assertion concordant with the results reported in the previous section, emerged from these two values.

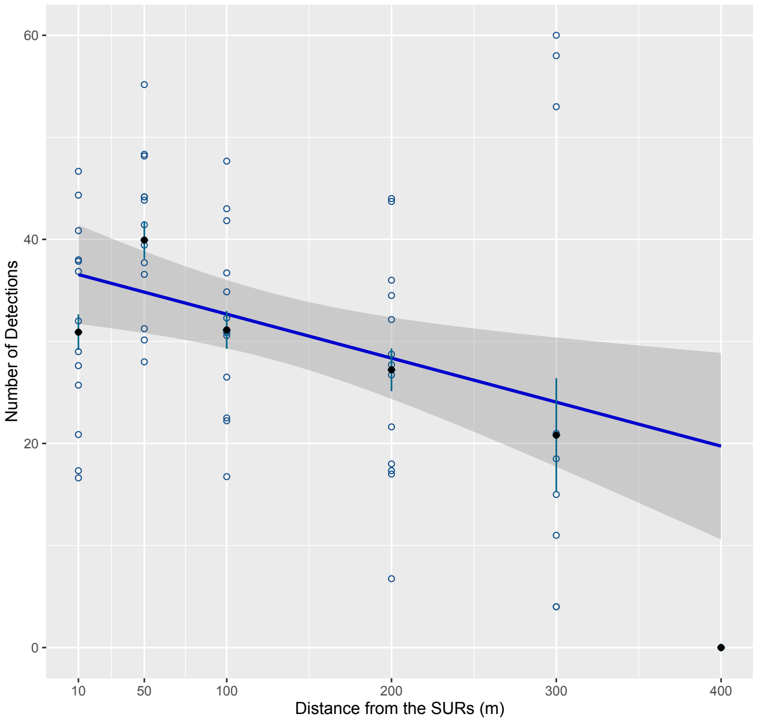


Fig 16. Total number of detections as a function of distance between receivers and transmitters in the central area of the North Sound, Bimini Islands, Bahamas. Hollow dots represent the average of detections per receiver. Filled dots are the overall average values of detections with the corresponding standard error. The gray shade represents the confidence interval.

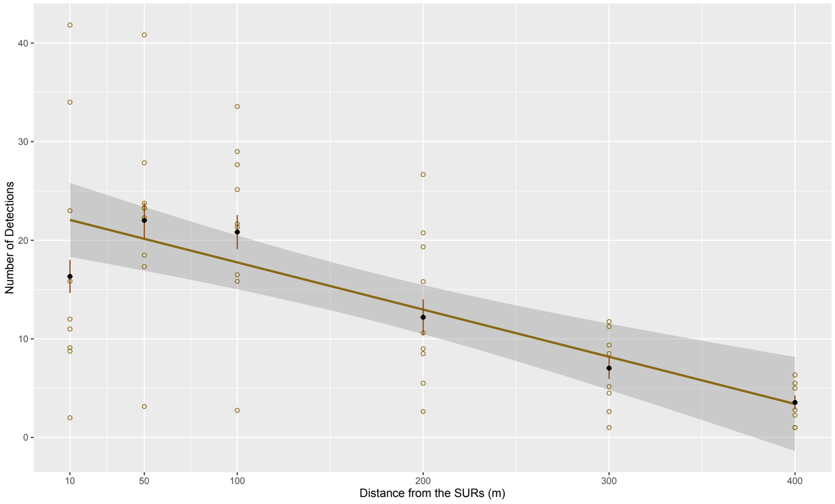


Fig. 17. Total number of detections as a function of distance between receivers and transmitters in the western side of the North Sound, Bimini Islands, Bahamas. Hollow dots represent the average of detections per receiver. Filled dots are the overall average values of detections with the corresponding standard error. The gray shade represents the confidence interval.

The highest probability of detection was recorded at 50 meters (Western side = 52.2%; Middle = 89%) where it would have been expected to be reported at 10 meters (Western side = 39.95%; Middle = 74.49%).

The 50% probability of detection was attained at a distance of almost 200 meters for the central area while this threshold was reached between 50 meters and 100 meters on the western side.

Overall, combining both sides, the 50% probability of detection was reached at 100 m (**Fig. 20**).

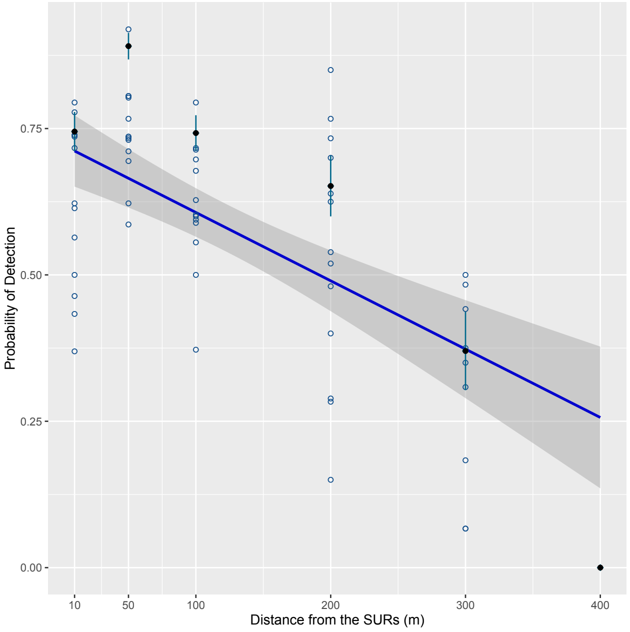


Fig 18. Probability of detections as a function of distance between receivers and transmitters in the central area of the North Sound, Bimini Islands, Bahamas. Hollow dots represent the average values of detections per receiver. Filled dots are the overall average values of probability detections with the corresponding standard error. The gray shade represents the confidence interval.

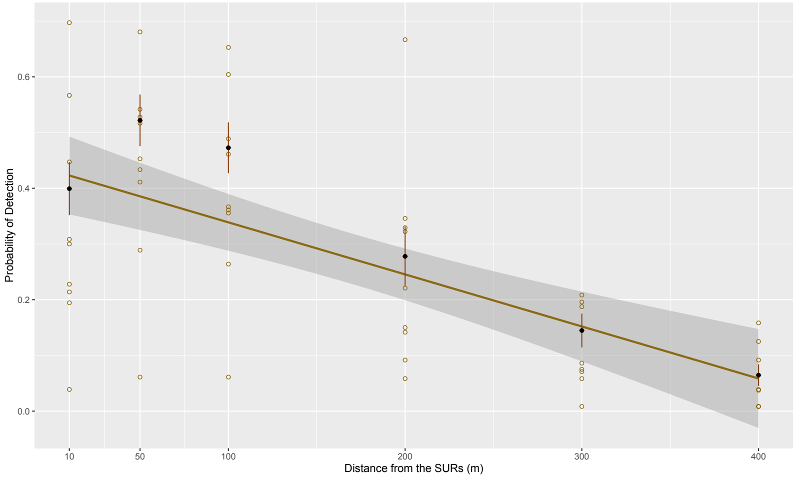


Fig 19. Probability of detections as a function of distance between receivers and transmitters in the western side of the North Sound, Bimini Islands, Bahamas. Hollow dots represent the average values of detections per receiver. Filled dots are the overall average values of probability detections with the corresponding standard error. The gray shade represents the confidence interval.

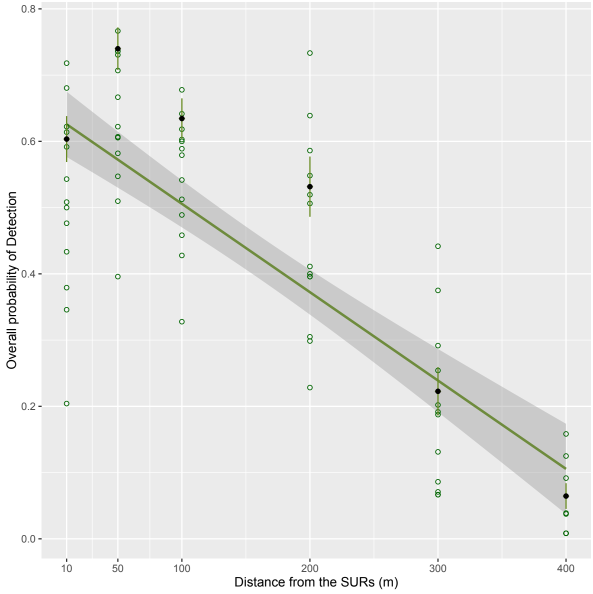


Fig 20. Overall probability of detections as a function of distance between receivers and transmitters in the North Sound, Bimini Islands, Bahamas, estimated from both location of experiments. Hollow dots represent the average values of detections per receiver. Filled dots are the overall average values of probability detections with the corresponding standard error. The gray shade represents the confidence interval.

III.4. Spatial ecology

A broad summary of the sharks' detections within the array of receivers is provided in **Fig. 21 & 22** and revealed a relatively higher number of detections along the eastern mangrove fringe of the NS compared to the central area and the western flank. Globally, the total percentage of cumulative detections for all mangrove fringe stations (i.e. East) reached 54.20% for the overall period of the study whereas the central part comprised 27.90% and the western side only attained 17.88%.

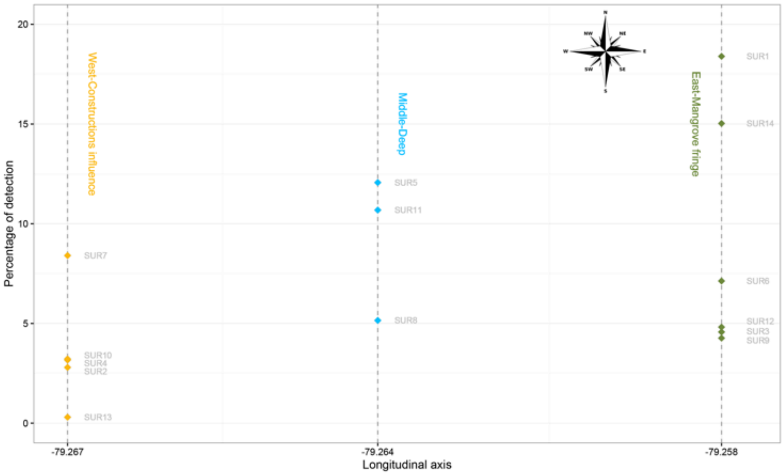


Fig. 21. Detection distribution within the network of receivers of juvenile lemon sharks, *Negaprion brevirostris*, North Sound (NS), Bimini Islands, Bahamas. The left panel presents the proportion of detection per receiver, organized by category (i.e. Western – undergoing anthropogenic influence, Yellow; Central area – deepest part of the NS, Blue; Eastern mangrove fringe, Green), Sharkland control receiver was excluded due to a fairly poor percentage (~ 0%).

At an individual scale, the movement patterns and spatial utilization of the nursery area were relatively different for each shark, both in term of number of stations visited and localization (**Table 4**, **Fig. 15** & **22**).

The individual abacus plots of daily detections per receiver tended to reflect the heterogeneity of space use existing among the juveniles. For instance, most sharks appeared to distribute their activities between the deepest part and the mangroves (i.e. #5666, #4878, #4547), yet, despite the construction influence, some individuals seemed more inclined to remain ar the western side (i.e. #5667). Some individuals also exhibit intermediary patterns, such as #4657 and #3368.

III.4.1. Spatial metrics

MCP and KUD assessments were only estimated for the ten sharks detected by the passive array and reported by at least two receivers.

Centers of activity, home range sizes (95% KUD & 95% MCP), core areas (50% MCP & 50% KUD), are presented in **Table 6**, while the individual spatial attributes are plotted in **Fig. 22**. Individual COA and MCP maps are reported in **Appendix II**.

Centers of activity

Overall, a total of 36 515 centers of activity was estimated for the ten sharks monitored within the passive array. The number of relocations varied greatly amongst individuals, and ranged from 482 (#3368; 127 days of monitoring) to 6 508 (#4878; 210 days of monitoring).

After examination, no correlation was found between the PCL of the sharks and the number of centers of activity exhibited ($p\text{-value} > 0.05$, $Rs = -0.1496488$). The number of days with detection was found to significantly influence the amount of COAs ($Rs = 0.6643244$, $p\text{-value} < 0.01$). The analysis between the number of days between first and last detection and the number of COAs revealed an absence of significant correlation ($Rs = 0.5252565$, $p\text{-value} > 0.05$).

Minimum convex polygon

The main result from MCP analyses was the difference in area estimates between sharks (**Table 6**). Both 50% & 95% MCP size estimations varied widely amongst juveniles, the former ranging from 36.33 m^2 (#3368) to 453.55 m^2 (#4447) (i.e. over a ten times difference), the latter, spanning from 568.51m^2 (#4878) to 1296.01 m^2 (#3545). Interestingly, sharks exhibiting the smallest and the highest 50% MCP areas were not the sharks respectively displaying the smallest and highest 95% MCP areas.

No relationship was found between the PCL (cm) and the 50% & 95% MCP areas (m^2) (respectively: p-value > 0.05, Rs = 0.018; p-value > 0.05, Rs = - 0.03658605). Similarly, neither the investigation of the correlation between the two MCP estimations and the number of days between first and last detection (50% MCP: p-value > 0.05, Rs = -0.112555; 95% MCP: p-value > 0.05, Rs = -0.5127504) nor the evaluation of the relationship between the number of days with detections and both MCP areas proved to be significant (50% MCP: p-value > 0.05, Rs = -0.01823717; 95% MCP: p-value > 0.05, Rs = -0.443771).

No significant interaction was found between gender and 50% MCP (p-value > 0.05) or 95% MCP (p-value > 0.05).

Home range & core area

The most striking result was the large individual variations in spatial occupation and area ranges existing between sharks (**Table 6** & **Fig. 22**). Home range sizes varied substantially amongst individuals. The core area estimations (50% KUD) spanned between 85.88 m^2 (#5666) and 323.67 m^2 (#3545), representing an almost four-fold difference, while the home range sizes assessment (95% KUD) varied from 745.83 m^2 (#4878) to 1474.51 m^2 (#3545).

There was no significant correlation between the number of days each shark was monitored and their 50% KUD (Rs = -0.5299915; p-value > 0.05) or 95% KUD (Rs = -0.5377626; p-value > 0.05). Similarly, no significant relationship was determined between the number of days with detection and the 50% KUD (Rs = -0.570122; p-value > 0.05) or 95% KUD (Rs = -0.4316129; p-value > 0.05).

Furthermore, no correlation was established between the size of the individual (PCL, cm) and the 50% KUD or 95% KUD (respectively: Rs = 0.5504613, p-value > 0.05; Rs = -0.03048837, p-value > 0.05).

The number of relocations per individual was found to have no significant impact on the size of both KUD estimations (50% KUD: Rs = -0.3647433, p-value > 0.05; 95% KUD: Rs = -0.4909091, p-value > 0.05).

No correlation between gender and 50% KUD (p-value > 0.05) or 95% KUD (p-value > 0.05) was reported.

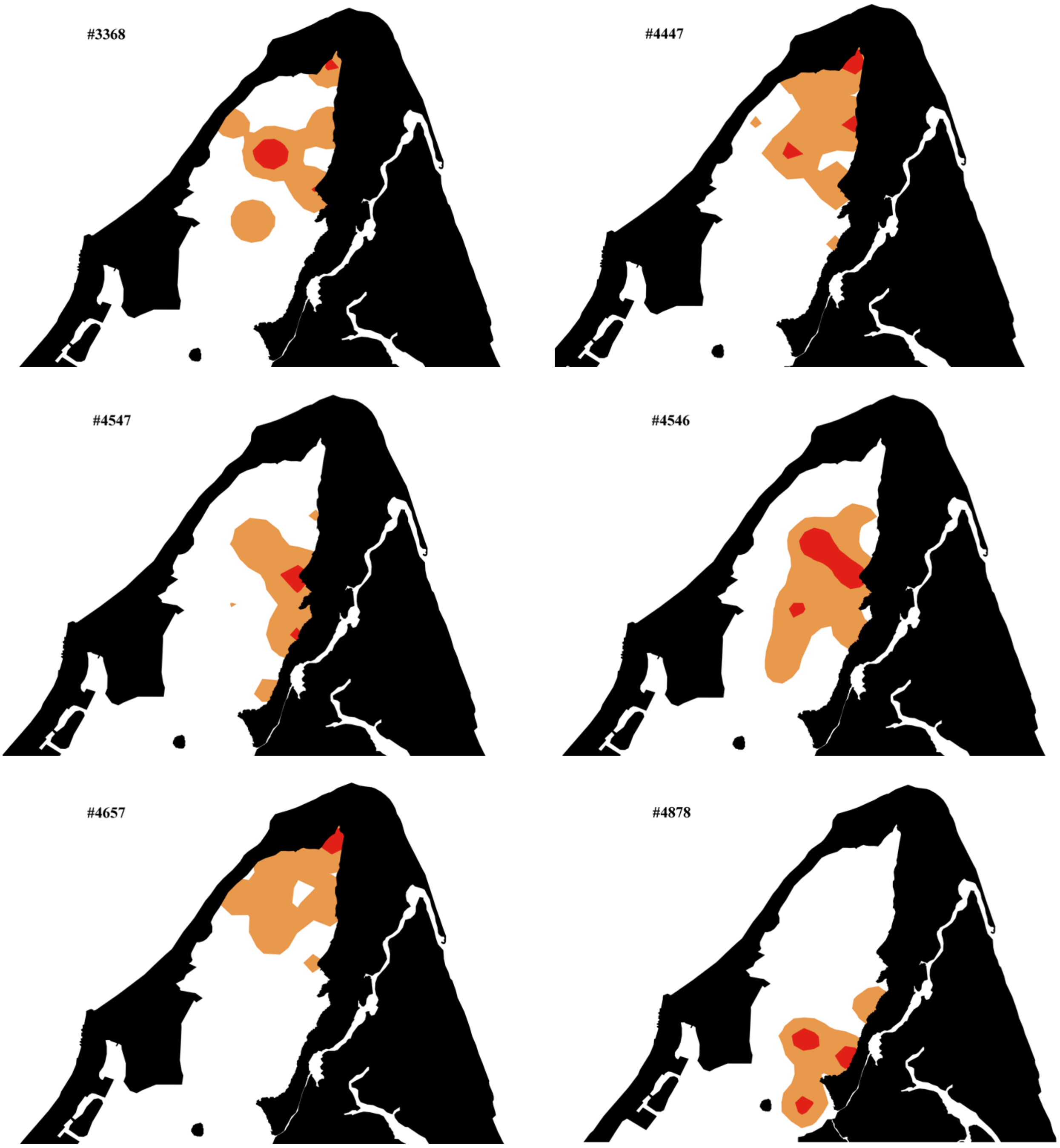
Table 6. Summary table of spatial metrics analyses for tagged juvenile lemon sharks, *Negaprion brevirostris*, in the North Sound, Bimini Islands, Bahamas. MCP is the Minimum Convex Polygon in m^2, 50% MCP corresponding to an estimation of the core area and 95% MCP (minimum convex polygon) enabling a quantification of the extent of the sharks' range in the study area; KUD (kernel utilisation distributions) – 50% KUD – 50% kernel utilisation distribution in m^2 corresponding to the core utilisation area; KUD 95% – 95% kernel utilisation distribution corresponding to home range area in m^2; Core areas is the total number of core areas displayed and COAs is the number of relocations calculated using the methodology described in Simpfendorfer *et al.* (2002).

ID #	50% MCP	95% MCP	50% KUD	95% KUD	Core areas	COAs
5866	-	-	-	-	-	0
4447	453.55	735.31	113.25	1041.91	3	3 972
365	282.95	1074.58	135.90	1087.21	4	3 646
3545	397.20	1296.01	323.67	1474.51	3	1 524
4546	287.12	893.59	198.60	1103.34	2	815
3368	36.34	1017.71	116.57	896.73	3	482
5666	184.07	872.89	85.88	930.43	1	6 028
5667	317.36	788.37	181.20	1064.56	5	5 292
4878	211.50	568.52	140.51	745.83	3	6 508
4888	-	-	-	-	-	0
4547	41.50	728.84	90.60	770.10	2	4 050
4657	188.23	591.97	90.60	996.61	1	4 198

An examination of the localization of the core areas of each sharks revealed a diversity in term of substratum preference (**Appendix III**). Some individuals tended to present a core area centered on relatively dense seagrass patches (#5666, #4657, #4878), others restricted their central area around mangrove fringes (#4547), other individuals spread their core area between sandy bottom, deep areas and mangrove edges (e.g. #365, #3368, #4878). All characteristic habitats of the nursery area were represented, underlying a variability existing between individuals in term of spatial use within their nursery area.

This disparity among individuals was also identifiable regarding the localization of home ranges within the NS (**Fig. 22.**). Each shark presented a different spatial use. For instance, two individuals, #4447 & #4657, established their home range in the northernmost part of the nursery, a very sheltered area. Intriguingly, individual #4657 exhibited a single restrained core area (~ 90 m^2), centered up north of the NS while it displayed a large home range (996.91 m^2), ten times the size of the core area.

Sharks #5667 & #3545 both tended to use mostly the western side of the NS, undergoing radical changes over the study period. However, at a finer resolution, a distinction in spatial occupation was also noticeable. Individual #5667 established its core area close to the shore, whereas juvenile #3454 mostly occupied the central area, deepest part of the NS.



Continued

Fig. 22. Map of core area (50% Kernel Utilization Density; red patch) and home range (95% Kernel Utilization Distribution; orange area) of juvenile lemon sharks, *Negaprion brevirostris*, in their nursery area, North Sound, Bimini Islands, Bahamas.

Spatial analysis estimator accuracy

To provide an analytical insight, comparisons between the 50%MCP & 50%KUD as well as 95%MCP & 95%KUD were performed. The analysis revealed no significant correlation between the 50%MCP and 50%KUD (Rs = 0.5896684, p-value > 0.05) whereas, conversely, a significant relationship was found between the 95%MCP and the 95%KUD estimations (Rs = 0.6848485, p-value < 0.05).

The percentage in change calculated between estimator is reported in **Table 7** and show great variations in term of size estimation between the two models, supported by significant statistical analyses (50%MCP vs. 50%KUD: p-value < 0.05; 95%MCP vs. 95%KUD: p-value < 0.05). This difference is particularly noticeable for the core areas inferences.

ID #	50%MCP vs 50%KUD	95%MCP vs 95%KUD
5866	-	-
4447	-300.48%	29.43%
365	-108.20%	1.16%
3545	-22.72%	12.10%
4546	-44.57%	19.01%
3368	68.82%	-13.49%
5666	-114.33%	6.18%
5667	-75.14%	25.94%
4878	-50.52%	23.77%
4888	-	-
4547	54.19%	5.36%
4657	-107.76%	40.60%

Table 7. Percentage of change between Minimum Convex Polygon and Kernel Utilization Distribution estimates for home range and core area for juvenile lemon sharks, *Negaprion brevirostris*. ID # corresponds to the shark ID. The second column corresponds to the percentage of change between the 50%MCP area and the 50%KUD area. The last column represents the percentage of change between the 95% MCP and the 95% KUD.

III.4.2. Distance from shore

Quite often during active tracking efforts, trackers were able to keep a visual on the detected individual.

Not all sharks were located during every tracking attempt; therefore, the number of locations differed among individuals. The number of days in which a real-time location was assessed for each individual ranged from 3 to 22 (**Table 8**).

A conspicuous result was the wide individual disparity in the distance from the nearest shore currently reported (**Table 8** & **Fig. 23**). The average distance varied from 38.16 m ± 9.12 m (#4547) to 155.38 m ± 40.34 m (#3545). This analysis was the only one performed with shark #4888, demonstrating an averaged distance of 129.73m ± 34.40 m. Individual #4546 was excluded due to lack of locations.

No relationship was found between sex and distance from the shore (p-value > 0.05). Similarly, no correlation was unveiled while evaluating distance from the shore as a function of body size (p-value < 0.05, Rs = 0.4146419).

The examination of the relationship between number of days actively tracked and number of real-time locations revealed no correlation with the DfS (respectively p-value > 0.05, Rs = -0.5321325; p –value > 0.05 , Rs = -0.2622)

Table 8. Summary of the active tracking and distance from the nearest shore of juvenile lemon sharks, *Negaprion brevirostris*, in their nursery area, North Sound, Bimini Islands, Bahamas. Real Time Loc corresponds to the total number of relocation from active tracking effort; Days Track represents the total number of different days the shark was tracked, Last track is the last day the shark was detected during an active tracking effort; DfS corresponds to the distance from the nearest shore; SEM stands for standard error of the mean. Note that individual #4546 is absent. This individual was excluded from further analysis for its number of days of tracking was considered too restrained (2).

ID #	Real Time Loc	Days track	Last track	DfS	SEM
4447	30	14	26-Apr-16	84.45	12.79
365	23	12	15-Apr-16	119.82	22.57
3545	8	3	29-Sep-15	155.38	40.34
3368	4	3	30-Oct-15	82.99	66.86
5666	25	15	15-Apr-16	74.63	10.73
5667	18	10	13-Nov-15	83.76	15.24
4878	39	12	26-Apr-16	104.72	14.63
4888	12	8	18-Mar-16	129.73	28.04
4547	25	14	29-Feb-16	38.16	9.12
4657	12	9	3-Dec-15	89.43	17.80

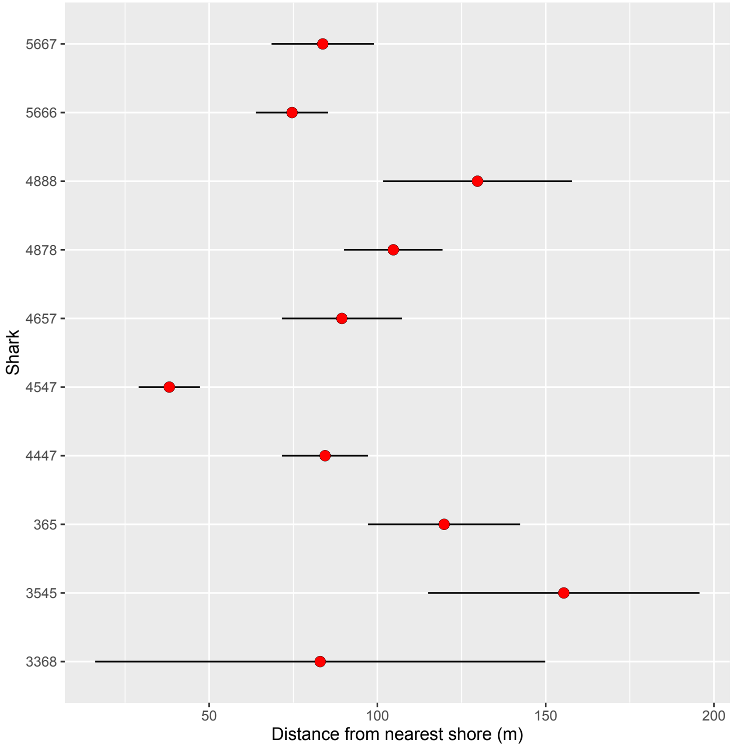


Fig. 23. Distance from nearest shore (m) for each juvenile lemon shark, *Negaprion brevirostris* extracted from active tracking within their nursery area, North Sound, Bimini Islands, Bahamas. Note the absence of individual #5866, never detected, and individual #4546, excluded due to restrained number days with real-time location.

III.5. Spatial ecology & personality traits

Residency index

No significant correlation was found between relative residency index and personality scores (Pearson, p-value > 0.05; Rs = 0.5232764).

The most surprising result was the main outliers (**Fig. 24**), with shark #3368, demonstrating compelling patterns. While this shark exhibited the third smallest exploratory score, its relative residency index appeared to be one of the narrowest (0.38) for a monitored period of over 60% of the study duration.

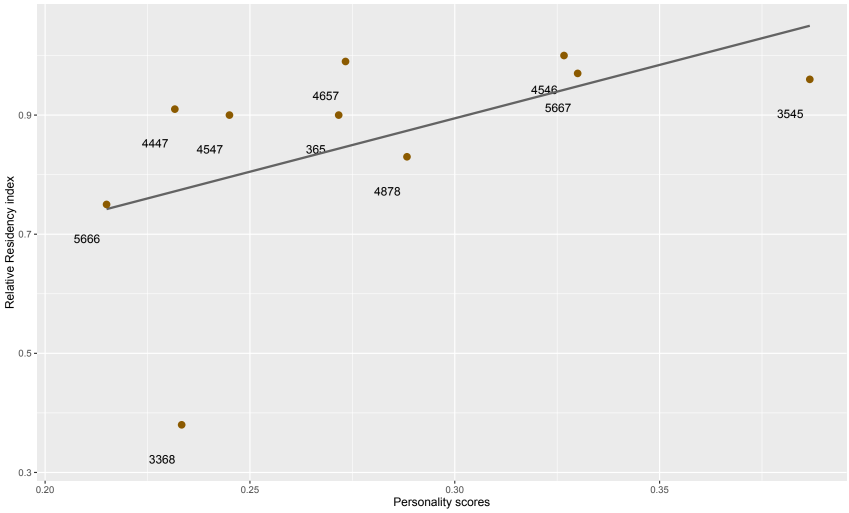


Fig. 24. Personality score of juvenile lemon sharks, *Negaprion brevirostris*, as a function of Relative residency within the nursery area, North Sound, Bimini Islands, Bahamas. Rs = 0.52.

Centers of activity

Concomitantly with the residency index analysis, no signififcant relationship was found between the total number of COA and the personality score from the novel open field test (Pearson, p-value > 0.05; Rs = -0.2765486).

Minimum convex polygons

The analysis of the 50% MCP revealed neither meaningful relationship nor linearity with the personality scores (Pearson, p-value > 0.05; Rs = 0.4877701), certainly due to the presence of three main outliers (**Fig. 25 - A**).

The most unexpected observation is the relationship existing between the personality score and the size of the MCP core area for shark #4447. This individual presented an exploratory score of 0.23, second lowest level reported, while displaying the largest 50% MCP area, reaching 453.55 m^2. It is interesting to note that this feature is not displayed when considering 95% MCP.

Similarly, no significant concordance was established between the 95% MCP size and the personality traits (Pearson, p-value > 0.05; Rs = 0.4065987) (**Fig. 25 - B**).

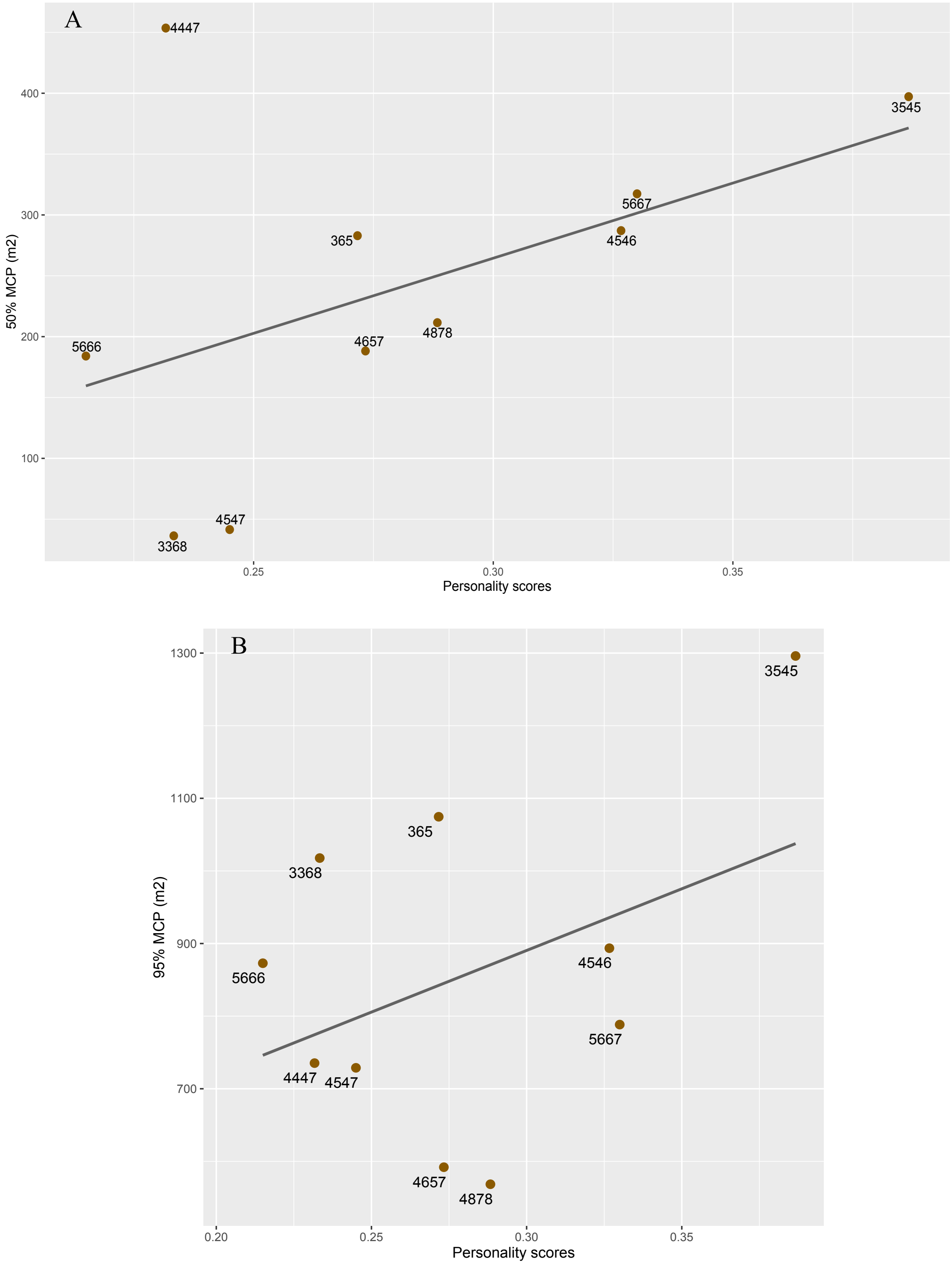


Fig. 25. Relationship between personality score and Minimum Convex Polygon (MCP) area sizes (m^2) in juvenile lemon sharks, *Negaprion brevirostris*. A: 50 % MCP – proxy for core area - vs. Personality score (Rs = 0.48); B: 95% MCP – proxy for home range - vs. Personality score (Rs = 0.40).

Home range and core area

A strong correlation (Spearman, p-value < 0.001; Rs = 0.8449887) was found between personality scores and core areas (50% KUD) (**Fig. 26**). The linear model was significant (F(1,8) = 43.59, p-value < 0.01) and is reported in **Fig. 26**.

Strikingly, the results differed considerably from the 50% MCP analysis, as the graphical position of shark #4447 emphasized. Even though the core area estimated for this juvenile using 50% MCP was the most extensive (453.55 m^2), the results from the kernel modeling produced an opposite outcome, giving this shark a far reduced core area (50% KUD = 113.251 m^2).

On a related observation, individuals #3368 and #4547, two outliers from the 50% MCP exploration, fitted better the linear regression after computing the kernel analysis.

Likewise, the investigation of the relationship between personality scores and home range size (95% KUD) revealed a robust correlation amongst the two components (Pearson, p-value < 0.05; Rs = 0.712368) (**Fig. 27**). In addition, the fitted linear regression shown in **Fig. 27** was significant (F(1,8) = 9, p-value < 0.05).

When comparing these results with the linear model plotted with the 95% MCP, evident disparities are depicted, juveniles #3368 & #4657 expressing the most explicit transpositions, closer to the regression line.

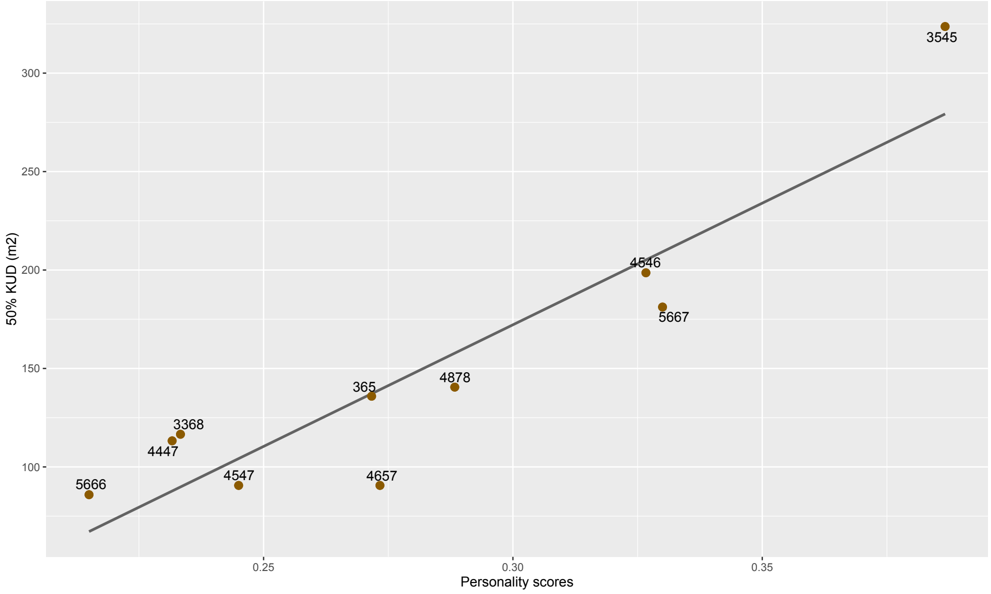


Fig. 26. Core area size (50% Kernel Utilization Distribution) as a function of personality scores in juvenile lemon sharks, *Negaprion brevirostris*. Rs = 0.84.

Noticeably, beside individual #3545, shark #4878 embodies one of the main outliers of the regression, when its exploratory behaviour would lead one to expect a vaster home range size (95% KUD of 745.83 m^2 for a personality score reaching 0.288). The former was constantly represented as an outlier when considering both MCP & KUD home ranges and core areas, exhibiting the highest recorded values (Personality score = 0.38; 50% MCP = 397.20m^2, 95% MCP = 1296.01m^2; 50% KUD = 323.67m^2, 95% KUD = 1474.51m^2).

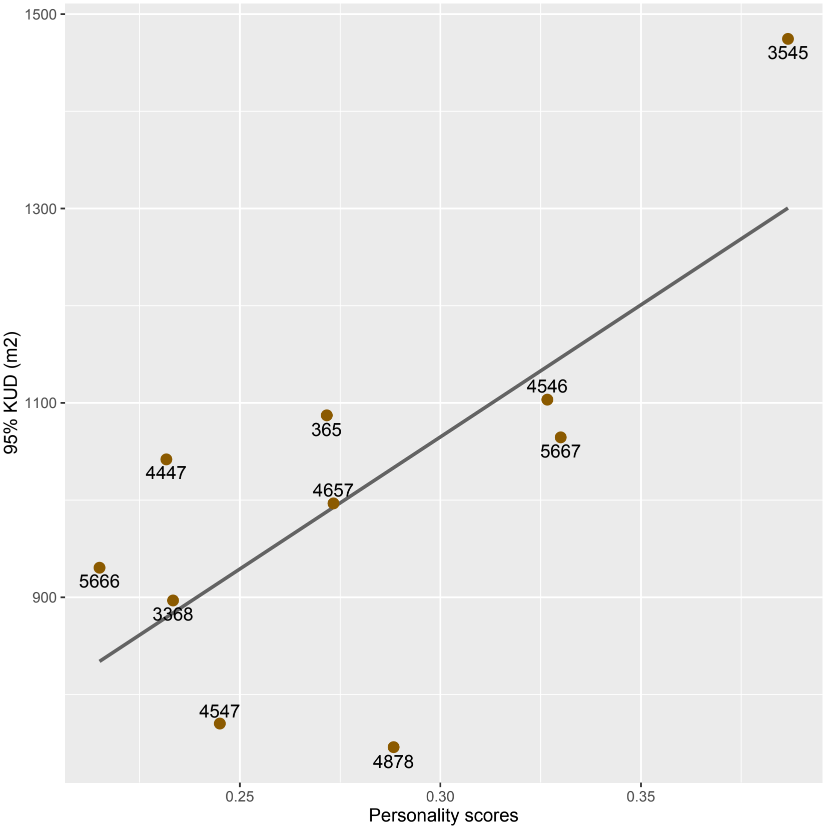


Fig. 27. Home range size (95% Kernel Utilization Distribution) as a function of personality scores in juvenile lemon sharks, *Negaprion brevirostris*. Rs = 0.71.

Distance from nearest shore

The exploration of the relationship between the distance from the nearest shore and the novel open field score unveiled a strong correlation (Pearson, p-value < 0.05; Rs = 0.6989407), concordant with the fitted significant linear model (F(1,8) = 7.641, p-value < 0.05) (**Fig. 28**). A few outliers were noticeable (#4547, #4888, #365, #5667), showing the variability existing between individual.

Shark #3545 was the individual displaying the furthest distance, exhibiting an averaged real-time location of approximately 137 m from the nearest shore, exposing an expected positive relationship with its personality score.

This analysis was the only one incorporating data from juvenile #4888. Individual #4546 was excluded due to limited data.

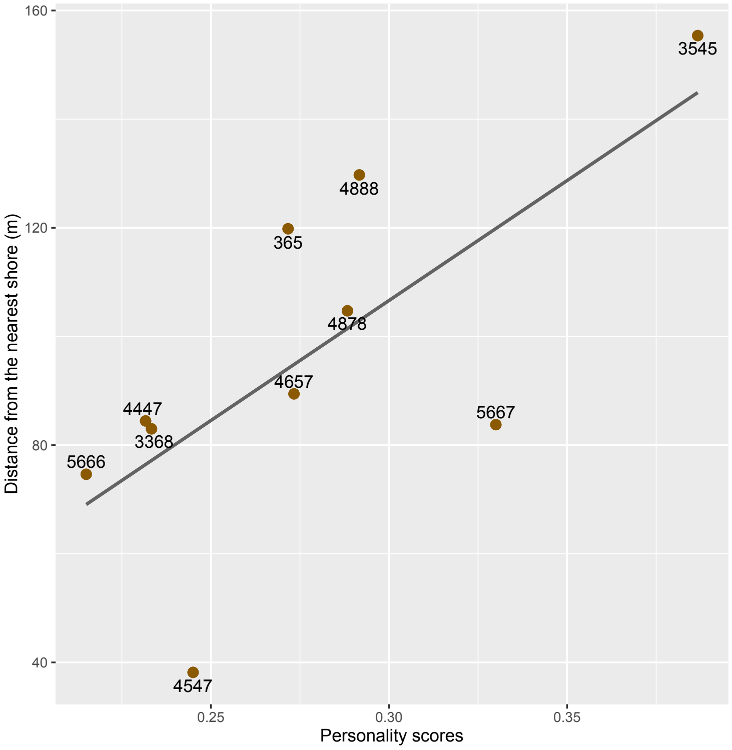


Fig. 28. Distance from the nearest shore (m) as a function of personality score in juvenile lemon sharks, *Negaprion brevirostris*. Rs = 0.69.

IV. DISCUSSION

IV.1. General Observations

This study investigated the relationship between personality and Movement Ecology in natural conditions in juvenile lemon sharks. A personality trait was estimated for each individual from a novel open field test. Home range and core areas were quantified using two methods, MCP and KUD, and movement patterns were assessed by determining an average distance from the nearest shore from real time locations.
The main finding of this research project lies in the observation of a strong correlation between personality traits and movement ecology in juvenile lemon sharks, *N. brevirostris*, in natural conditions. To our knowledge, this is the first research project to combine both behavioral ecology and movement ecology analyses to understand the driving mechanisms of spatial use and movement patterns in the wild in an elasmobranch species.

The preliminary behavioral trial conducted underlines the suitability of novel-open field test as an effective experimental approach to capture personality traits of juvenile lemon sharks in mesocosms. This study also demonstrates the viable use of passive and active acoustic telemetry for the analysis of sharks' movement ecology in a complex and challenging mangrove fringed shallow water environment, providing information that would not be obtained from conventional tagging of a larger number of individuals. The methodological design allowed for accurate and consistent capture of both spatial use and real-time location of the individuals.

Furthermore, this research illustrates both the difficulties of performing optimum home range assessments and the integration of a "case-by-case" individual pattern analysis while using a method investigating population aspects. Besides, the conducted analyses highlight the relative dissimilarities between two methods, MCP and KUD, used to evaluate fine-scale spatial use. The detection range experiments underscored the complexity of the ultrasonic technology involved in this study and underlines the complication in fitting GLMMs for technical analyses, largely applied to living organisms until now.

IV.2. Acoustic monitoring and detection range

Recent improvements in acoustic telemetry technology enabled researchers to monitor the movement patterns of marine species under a multi-dimensional scope (Hussey *et al.*, 2015). The main goal for the current array was to provide 24 hours a day presence/absence data within the listening range of the receivers. The results show that acoustic telemetry is a valuable tool to study the movement patterns of marine species, even in a challenging environment.

Furthermore, to our knowledge, the present work on the detection range capacity of submersible ultrasonic receivers in a shallow water environment provided an interesting insight into detection features scarcely reported until now. The findings of a higher detection rate at 50 m instead of 10 m challenge the commonly accepted idea that the detection probability reaches 100% at the closest of the receivers. Moreover, during this study, this 100% value was never reached, underlining the complexity of acoustic telemetry when exposed to complex environmental conditions. More intriguingly, no reason so far was unveiled to explain either this observation but also to explain the observation of the maximum detection range of 400 m under the most turbid and shallowest conditions. However, the linearity of a relationship between the number of detection/probability of detection and the distance has been described as idealistic. A series of factor have been identified to be responsible for disrupt signal emissions/reception (Leichter *et al.*, 1996; Simpfendorfer *et al.*, 2002; Farmer *et al.*, 2013). The heterogeneity of the sea-bottom, the technical particularities of either the transmitters or the receivers might obstruct or interfere with the sound wave propagation. Farmer *et al.* (2013) suggested that an environment with similar characteristics as the NS could lead, on one hand, to the underestimation of the detection probability for transmitters setup close to the receiver, on the other hand, to the overestimation of the detection probability of a tag far from the receiver. Therefore, although influence of environmental parameters on the detection range was not included within the current analysis, an undergoing testing of Sonotronics Submersible Ultrasonic Receivers in the waters surrounding Bimini Islands intends to further investigate this topic by providing a wider and more diverse sampling. Including habitat type characterization enabling the inclusion into a linear model of seagrass meadow cover, sponge abundance, rock and substrate type might allow a consistent insight into the detection features in the NS.

Overall, all results tended to indicate the reliability of both acoustic telemetry and Sonotronics acoustic equipment during this study. Furthermore, the results demonstrated an impact of the anthropogenic disturbances on the detection range of the receivers on the western side of the NS. However, although the effect appeared evident, such impediment still enabled the detection of resident sharks of this zone. This idea is supported by the total number of detections reported for each shark, independent from the main core area location (**Table 4** & **Fig. 22**). The probability of detection, either on the western flank or in the central area of the NS indicated a very low probability of overlap between the detection ranges of neighboring receivers. This observation was supported by the very restrained number of double detections reported while filtering the data (~350).

The analytical methodology employed to investigate the detection features appeared complex. A GLMM was used to describe the relationship between a response variable (the number of detections) and independent variables (i.e. tidal phase, depth, temperature, turbidity). However, as underlined by Bolker *et al.* (2009) and van Zinnicq Bergmann (2013), the outputs of such statistical analyses are intricate and challenging to interpret when applied to non-biological data *stricto sensu*. More computational efforts are thereby required.

IV.3. Spatial ecology of juvenile lemon sharks

IV.3.1. Sharks monitoring

The residency indexes revealed that most tracked sharks were detected within the monitoring area for varying time, usually through consecutive days, indicating that juveniles are therefore likely to remain within their nursery area for an extended period of time. This almost continuous use of the nursery area through the monitored period was consistent with the findings reported by Morrissey and Gruber (1993a) and Franks (2007) and supported –to a certain extent- by the extremely low number of detections reported at the control receiver (**Fig. 15**).

The observation that seven out of ten individuals were monitored for more than 100 days was coherent with the site-attachment of juveniles described by Gruber *et al.* (1988), Morrissey and Gruber (1993a) and Franks (2007) and implies an efficient monitoring of the early life stages of the lemon sharks.

Equipment failure (i.e. tag battery life deficiency) or fluxes in and out from the NS to another adjacent nursery area (i.e. Sharkland) could be an acceptable reason for the observed limited residency features and restrained detection patterns. However, although the control receiver was only deployed intermittently through the study period, a permanent emigration away from the nursery area of origin is quite unlikely, reported as an isolated event by Gruber *et al.* (2001), recording only a few cases over a 5 years depletion-mark-recapture study. Given that the annual survival rate of juveniles lemon shark in the nursery areas of Bimini Islands varies between 38% to 65% (Gruber *et al.*, 2001), the short-term site fidelity patterns observed were most conceivably due to a premature death of the individual, possibly predated by other animals (i.e. a bull shark, cf. **Material & Methods; section II.5.3.a.**). Natural death was thereby the favored explication for shortened acoustic monitoring periods. For instance, the passive data revealed intriguing features about individual #3545, attributed to the capture of a predation event within the array. The inconsistent swimming speeds over an extended period (~ 3 days) coupled with a space use substantially different from the usually observed patterns supported the idea of the tag being ingested by a large predator.

IV.3.2. Detection features, habitat use and spatial occupation within the nursery area

The design of the acoustic array allowed a maximum coverage of the entire nursery area. The aim of such deployment was to allow the capture of the spatial ecology of the juveniles using a passive array of listening stations, providing presence/absence data in a multi-dimensional perspective. Therefore, an overlap of the detection range of the receivers was not necessary. For most studies investigating home ranges, the underlying objective is to prevent unmonitored movements of the animal beyond the study area (Farmer & Ault, 2014).

The spatial use analysis demonstrated an overall occupation of the entire study area by the juveniles, corroborating the delineation of the nursery ground provided by

Franks (2007). Despite the use of several characteristic habitats of the NS, as revealed by their home range areas (95% KUD and MCP), most sharks exhibited at least one core activity area (50% KUD) along the mangroves, suggesting that it is their preferred habitat. The proportion of detections at the receivers (**Fig. 21**) as well as the localization of the home range of the sharks tended to indicate similar prospects. Interestingly, some sharks presented multiple centers of core activity area, distributed between sandy bottoms and seagrass meadows. Juvenile lemon sharks might use different core centers for diverse reasons (Morrissey & Gruber, 1993a). For instance, the mangrove use might be related to a feeding ground (Newman, 2003) as well as a shelter during high tide (Guttridge *et al.*, 2011b). A habitat preference centered along the mangrove fringe of the NS (**Fig. 15, 21 & 22**) is concomitant with the space use depicted in Morrissey and Gruber (1993a) and Franks (2007). Yet, a several aspects ought to be considered.

First of all, the listening effort was not evenly spread across the monitored area. However, the mangrove edge of the NS represents approximately 3.3 km of coastline against circa 2.9 km on the western flank, which therefore justified the larger number of receivers deployed along the eastern boundaries (6) (**Fig. 7 & 21**). Then, the central area was covered by a listening array of three receivers, accounting for a latitudinal line of ~ 2.3 km, supporting the deployment of a more restrained number of receivers. Secondly, the detection range analysis provided an important insight, weighting the habitat preference inferences. The western receivers exhibited a considerably lower probability of detection than the central area. When compared to the results obtained by van Zinnicq Bergmann (2013), the mangrove fringe, corresponding to the experiments the author lead at the “Finger”, exhibited a 50% probability of detection at 250 m. That is to say, the listening ability was greater on the mangrove edges than anywhere else in the nursery area. Nevertheless, as previously explained, the transducers of the receivers have to be submerged in order to detect a signal from a close-by individual. The eastern side of the NS is the shallowest part (**Appendix III.**), mostly drained during the low tide, therefore, the listening period was reduced to at least 4 tidal phases per day, whereas the deep part as well as the western area were rarely undergoing such drastic changes in depth, enabling an almost constant listening of the SURs (i.e. 6 tidal phases per 24h period). This observation is also nuanced by the fact that juvenile lemon sharks are more likely to frequent safe habitat such as mangrove to shelter during high tide due to higher predation risk (Guttridge *et al.*, 2011b). Indeed deeper waters may induce a greater exposure to large predator, able to swim within the shallow waters of the NS.

In regards to these remarks, mangroves edges can be cautiously considered as the preferred habitat type for juvenile lemon sharks in the NS nursery area.

These last observations also underlined the ecological importance of mangroves as a nursery area for juvenile lemon sharks. The deterioration of the conditions on the western side of the NS might impede the future wellbeing of this nursery. Already Jennings *et al.* (2008) and DiBattista *et al.* (2011) documented the effect of anthropogenic disturbances on populations of juveniles in the NS and outlined the vulnerability of the area. This concern was strengthened by the case of individual #5667. The home range and core area of this juvenile was established around the area most exposed to the current disturbances. The selection of this location raised two main hypotheses with respect to the early loss of track for this shark. The interruption of emissions in January 2015 from the individual corresponded to an intensification of the anthropogenic disturbances, which started in late November 2015. Constructions and resort development might have resulted either in a pressure leading to the migration of the shark out of its original nursery or to the death of the individual. This shark was last detected on SUR7 (**Fig. 21**), localized within its main core area, indicating the former prospect was rather unlikely. Moreover, the conclusions reported by Jennings *et al.* (2008) sustain the likelihood of a premature death of the individual caused by the rapid and intense development around its home range. The authors pointed out the effect of construction developments on the banks of the NS, revealing a decrease in survivorship in juvenile lemon sharks, reporting a 23.5% reduction in first-year survival. This consideration raised concern about the survivorship of future populations of juveniles within this nursery ground. The coming PIT-campaigns might bring interesting results, documenting the current concerns.

An investigation whether anthropogenic disturbances exerted a pressure on the spatial ecology of juveniles, potentially leading to a shift in space use and/or a migration to the adjacent nursery area would produce important knowledge, providing information for conservation and protection purposes. A substantial documentation of the impact of resort development on the spatial utilization and movement ecology of the lemon shark might bring increased awareness on the need of rational protection for the area hosting the future generations of lemon sharks. Mangrove preservation should be an issue of primary concern.

IV.3.3. Inter-individual variability in Movement Ecology of juvenile lemon sharks

First of all, a comparison with different studies on the spatial ecology of juvenile lemon sharks underlined the reliability of the two methods used to delineate and characterize home range sizes. The use of MCP method allowed an assessment of the present estimates (Morrissey & Gruber, 1993a; Franks, 2007) and indicated the inferences were reliable for further comparison with personality scores.
The home range evaluated by Franks (2007) for juveniles from the NS, using MCP estimator, was of circa 1 km^2 for 2 years-old individuals (~ 63 cm total length), a value concordant with the MCP reported in **Table 6**. Likewise, Morrissey and Gruber (1993a) established a MCP area as proxy for home range for juveniles (PCL varying from 48 cm to 100 cm) comprised between 0.23 km^2 and 1.26 km^2. Therefore, both the output extracted from MCP and KUD analyses appear reasonable.

The most striking result of the current study was the high individual variability in Movement Ecology of juvenile lemon sharks. Spatial use differed greatly among individuals **(Fig. 21 & 22** & **Tables 6 & 8**). It is interesting to notice that although home range and core area estimates were highly dependent on the method used, both MCP and KUD analyses underscored this intra-individual variation.
Various factors have been recognized to be responsible for differences between individuals. Environmental factors have been acknowledged to influence spatial ecology of elasmobranchs. Simpfendorfer *et al*. (2011) pointed out a disparity in the response to changes in salinity between individuals. While these differences were identified among a large size-class of juvenile Smalltooth sawfish, *Pristis pectinata*, no specific underlying cause was determined to elucidate this sensitivity, although physiological flexibility to salinity tolerance was a favored hypothesis. Likewise, Franks (2007) underlined the probable influence of seasonal effect on the individual heterogeneity in home range sizes of juveniles, attributing the variations in movement patterns to the wet and dry period that Bimini experiences (Newman, 2003).

However, the current study duration only encompassed the dry season (from November to April; (Newman, 2003)). Therefore this period appeared too restricted to capture both seasonal effects, suggesting it is relatively unlikely that the observed patterns are related to the plasticity of each individual to withstand the seasonal effect differently.

The inter-individual variations could be attributed to the body size of the individuals (Morrissey & Gruber, 1993a, b). During the investigation of home range of juvenile lemon sharks in the NS, Morrissey and Gruber (1993b) identified a positive relationship between MCP size and body size. Likewise, ontogenetic shifts and size-related intra-individual variability in home range sizes have been documented fifteen years later in juvenile lemon sharks from the NS (Franks, 2007). Therefore, for sake of clarity in the investigation of the relationship between Movement Ecology and personality, size variation was evinced by selecting sharks from a restricted size range. Consequently, choosing the juveniles within a similar cohort avoided size related bias. Furthermore, as expected, the absence of significant correlation between the body size of the sharks and the spatial ecology analyses failed to explain the inter-individual variations in movement metrics.

Another factor potentially resulting in the observation of distinctive patterns between individuals could have been the gender of the shark. Sexual disparities in Movement Ecology have been identified in different marine taxa. For instance, Sprogis *et al.* (2016) recently unveiled a sex-specific home range size in Indo-Pacific bottlenose dolphins, *Tursiops aduncus*. Similarly, sexual segregation in term of space use has been extensively described in elasmobranchs (Sims *et al.*, 2001; Sims, 2005; Wearmouth & Sims, 2010). However, the present results demonstrated an absence of correlation between sex and home range or core area size of the juvenile lemon sharks. Differences between individuals were thereby not a result of a sexual variation in juveniles. Nevertheless, it appears reasonable to consider such sexual variations can occur after maturation of the individuals (Gruber *et al.*, 1988; Morrissey & Gruber, 1993a).

The individual differences captured in this study could as well find an explanation in the experimental design. The dissimilarities in monitoring features and detection characteristics existing among individual could have impacted the output of each spatial metric analysis. It could for example be argued that the larger the number of relocations or the more extended the monitoring period, the larger the home range and/or core area. Similarly, the number of days of active tracking or the number of real time locations could have a possible effect on the output of the distance from the shore. Nevertheless, although no asymptote was assessed in this study (March *et al.*, 2009), no substantial association was revealed between the detection features on one hand, and the home range and core area size assessment or DfS on the other hand. The monitoring design was therefore not held responsible for the variability in space use and distance from the shore between individuals.

Competition could be a dynamic for spatial segregation and could explain differences in the spatial ecology of the juveniles (Morris, 2003). Although the current study did not provide information concerning the influence of intraspecifique interactions on the Movement Ecology of juvenile lemon sharks, however, the young of this species have been described as social individuals (Guttridge, 2009; Guttridge *et al.*, 2009; Guttridge *et al.*, 2010; Guttridge *et al.*, 2011a). During his doctoral thesis (Guttridge, 2009), Dr. Tristan Guttridge reported the establishment of size-related hierarchies, with smaller individuals acting as subordinates. Although Brown (2004) reported that the hierarchy among juveniles tended to alternate after six days of starvation, without a strict break of this social organization, Newman (2003) suggested that prey availability was not responsible for competition within the shark nurseries of Bimini. Therefore, resource partitioning was cautiously eliminated as an explanatory variable. This idea was also supported by the fact that Franks (2007) did not uncover the existence of a spatial segregation in juveniles from the same size class.

So far, all typically common characteristics failed to explain the individual variability captured during this study. Unevenness within population is challenging to explain. For most studies, it appeared relatively hazardous to interpret the observed dissimilarities in behavior mainly because of the lack of information about the mechanisms and stimuli responsible for such expression. Most investigations tend to consider environmental parameters such as prey availability, predation risk, competition pressure or abiotic components to explain the captured features in movement and space use but tend to neglect the intrinsic aspect of the nature of the captured spatial metrics, such as personality.

IV.4. Personality-related Movement Ecology of juvenile lemon sharks

IV.4.1. Personality

The personality trait considered for each individual was related to the exploratory behaviour of juvenile lemon sharks while exposed to a novel open field test. As a proxy for personality, the rate of movement of the individuals during very first exposure, determined from the number of section visited per second, was assessed. This process has recently been acknowledged as a reliable technique to assess personality in juvenile lemon sharks (Finger *et al.*, 2016). Furthermore, the repeatability value obtained was similar to the values reported by different studies (Bell *et al.*, 2009; Harrison *et al.*, 2015).
The results allowed determining that this parameter was correlated with movement metrics of the sharks under natural conditions.

IV.4.2. Personality: an intrinsic mechanism for movement ecology?

The results showed the relevance of a key personality trait in shedding light on spatial ecology and movement patterns dynamics in a population of elasmobranchs. Field data combined with behavioral experiments relating personality traits to ecologically important processes such as Movement Ecology remain scarce. This study reports a significant correlation between exploratory behavior and individuals' home range, core area size and distance from the nearest shore. Individuals displaying the highest scores during the very first exposure to the novel open field test were more likely to exhibit the largest home ranges and core areas as well as the furthest distance from the shore.

Individual differences in movement and spatial ecology are particularly described in fish (Conrad *et al.*, 2011; Taylor & Cooke, 2012; Taylor & Cooke, 2014). Until recently, research about individual heterogeneity mainly focused on internal factors, such as the one previously excluded (i.e. sex, body size, external environmental cues) (Lucas *et al.*, 2001). However, in the present study, inter-individual differences persisted even after effects of size, sex or monitoring features were removed. These results provide evidences that individual behavioral traits, not discernible from body size or sex, may have contributed to the determination of movement ecology in natural conditions. The trait correlation analysis suggests the existence of a link between personality and movement ecology in juvenile lemon sharks, affording reasonable explanation of the inter-individual variability in the observed movement patterns. Such findings integrate Movement Ecology into a personality framework.

While few investigations combined experimental behavioral trials in captivity to field movement patterns, divers observational field studies revealed consistent variations in movement by individuals, mostly for short time periods, with the existence of an inter-individual behavioral heterogeneity (Fraser *et al.*, 2001; Conrad *et al.*, 2011; Harrison *et al.*, 2015).
Differences in movement patterns are observed at different life stages of fish. For instance, McLaughlin *et al.* (1992) showed that neonate brook charr *Salvelinus fontinalis* present inter-individual variations in feeding movements inside their home range, supported by various findings such as Grant and Noakes (1987) and Armstrong *et al.* (1997). However, the authors did not clearly interpret the factor responsible for such observations. The present results produced an alternative to explain differences in movement ecology by providing an insight into the potential mechanisms driving spatial use and movement patterns in juveniles of an elasmobranch species. The findings of this project suggest movements can be affected by intrinsic factors, influencing the subsequent spatial patterns.

The correlation between personality traits and movement metrics furnishes evidence for personality being a conceivable driver inherent to the individual. Although the movement ecology of an individual is partly driven as part of a whole (i.e. either the population or the species) and population phenomena are recognized (Schlosser, 1991; Lucas *et al.*, 2001), it appears that at a finer-scale, intrinsic factors influence the individual expression of behaviour. The present results emphasized the importance of animal personality investigations and underlined that this variable might be a key mechanism in shaping the space use of individuals as illustrated by the case of juvenile lemon sharks. Recent work has shown that consistent individual differences in personality traits in animals can be ecologically important (Sih *et al.*, 2004a; Sih *et al.*, 2004b; Réale *et al.*, 2007; Réale *et al.*, 2010), but field studies integrating personality traits with Movement Ecology are scare. Diversity in spatial ecology is complex to capture but the reason behind individual differences appear even more difficult to elucidate. The present finding of a correlation between home range as well as core area and novel open field scores strengthens the conclusions drawn by Minderman *et al.* (2010) reporting a relationship between novel environment exploration and home range size in starlings, *Sturnus vulgaris*. Such interpretations advocate for further investigations in this field of research.

The current results suggested evidence for the relevance of personality in ecological processes such as animal movement. Individual behavioral choices can imply higher energetic costs, leading to a higher predation risk (Heithaus, 2004). The underlying assumption of these results indicate that a higher exploratory score corresponded to a more extended home range and core area as well as a relatively wider distance from the shore than less exploratory individuals. Such inference tends to provide an insight on how personality traits may impact movement strategies in the wild. Indeed, although costs and benefits of different personality types may not be stable with time, if interpreted as a possible surrogate for willingness to take risk, exploratory behaviour may imply a higher predation risk in juveniles exhibiting greater exploratory scores. Therefore, the later variable might suggest a greater increase in predation exposure. The present data set provides an interesting example with the case of shark #3545, supporting such a prospect. Evidence has been found that indicates a predation event on this juvenile. The shark exhibited the greatest personality scores, the most extended home range and core area as well as the furthest distance from the shore. Its core activity was centered in the deepest part of the nursery, the most accessible area for large predators. The predation event might have been related to the willingness of this shark to take risks. Reaction to the presence of a predator has been be clarified by personality traits. Indeed, Jones and Godin (2010) investigated the relationship between exploration behaviour and response latency time to a simulated predator ambush in juvenile convict cichlids (*Amatitlania nigrofasciata*). Response latency time was positively correlated with exploration scores, fast explorers being slower to react to a robotic predator. The probability of such an occurrence cannot be ruled out as far as the death of this individual is concerned and requires more investigation on the consistency in the reaction of juveniles to a predator. A comparison with other personality traits also appears necessary.

According to the findings and the literature about juvenile lemon sharks, it happens to be safer for an individual to remain close to the mangrove fringe shore, were predation risk is lower and where a predator can be more successfully avoided. Thereby, another underlying implication is that personality can influence not only the movement ecology but also the fitness of a population. This reflection underscores the debate around the relationship between personality and natural selection. The question is to comprehend whether a personality traits is favored in comparison to others. For instance, it can be argued that personality can influence a decision based on starvation–predation risk trade-offs. Thus, as to how to explain the existence of individual variability in term of personality traits and Movement Ecology, the most reasonable hypothesis would suggest that such heterogeneity is the result of life-history trade off (Roff, 2002; Roff & Fairbairn, 2007). One main trade-off possibly underlined by the monitoring data concerned the trade-off between growth and mortality (i.e. survivorship). Personality is understood as a consistent behaviour through situations and contexts, differing from that of any other individual within the population. For example, it has been reported that rainbow trouts, *Oncorhynchus mykiss*, adapt their behaviour while undergoing predation pressure by diminishing the use of hazardous habitats (Biro *et al.*, 2004, 2006). Interestingly, such a conclusion supports the hypothesis of individual #3545 being more likely to suffer predation. Indeed, the authors documented a consistency in the anti-predatory response in bold individuals, suggesting a weaker response than shy individuals. Furthermore, as Biro and Stamps (2008) specified, the captured behaviour of juvenile #3545 could fairly be attributed to a “productivity” trade-off, owing to which this juvenile increased its predation risk and was preyed on. It can be hypothesized that an extended home range and a further distance from the shore are a response to higher metabolic requirements due to a more active behaviour (extrapolated from the explanatory trait of the individual). Minderman *et al.* (2010) determined that the strength of the association between the individual scores of the starlings and the size of their maximum range was dependent on the quality of the frequented foraging ground. This hypothesis deserves a deeper interpretation while investigated under an individual-based scope. A similar pattern could occur in the case of juvenile lemon sharks. For instance, more hazardous habitats might be frequented due to a higher presence of items a juvenile could prey on. Such extension of spatial use could thereby correspond to a higher predation exposure. Therefore, from this point of view, personality could influence movement ecology under a trade-off mechanism, driving the expression of space use in relation to the metabolism requirement of the shark.

In order to further investigate the debate around life history influence on the consistency in inter-individual behavioural differences, activity, exploratory behaviour, food intake as well as morphometric measurements (i.e. pectoral girth, TL, PCL, weight but probably also RNA/DNA ratio; Bulow (1970)) should be taken into account in a long-term acoustic monitoring of juvenile lemon sharks. Such studies would not only uncover the relationship between Movement Ecology, activity, exploratory scores, and food intakes and growth rates, but would also determine whether such links would influence the home range of an individual. Also, an investigation of the relationship between anti-predator behaviour and exploratory scores would reveal whether sharks with an extended home range are more likely to undergo predation pressure than others. Similar projects are currently being conducted at the Bimini Biological Field Station, principally investigating the mangrove use in response to a frightening stimulus.

Intriguingly, no correlation was unveiled between both MCP or residency indexes, and individual exploratory scores. This observation contrasts with the finding of Harrison *et al.* (2015), who reported a link between personality and home range and residency. According to this study, a similar relationship would have been expected. However, although the quantity of tracking data appeared adequate to provide suitable output, the number of monitored individuals in the current investigation tended to be low. Therefore, it could be suggested that the absence of correlation is an artifact of a small sample size, being more sensitive to outliers. A similar study involving more specimens might mitigate the effect of such outliers. Nevertheless, this assertion also underscores various interpretations, some of which are being discussed in the following sections.

Firstly, individual variability within a single population is an intriguing aspect, potentially related to the individual phenotype, advocating for a framework encompassing personality and plasticity. Under the scope of evolution, the adaptive nature of personality traits is quite mis-understood. Although some literature tends to attribute the individual variability to plasticity (Wilson, 1998; Nussey *et al.*, 2007), recently, phenotypic variations have been recognized to play an important role (Dall *et al.*, 2004; Sih *et al.*, 2004a; Sih *et al.*, 2004b). The fact that some outliers are present and weaken the relationship between Movement Ecology and personality (i.e. the absence of correlation with Residency or MCP) may be due to a restricted sample size. This emphasizes two aspects: i) it points out that the study might have captured different phenotypes and ii) it stresses that each individual of the study could not express the entire panel of behavioural traits of phenotypes of the population of Bimini, implying the necessity for larger samples. Genetic variations in term of plasticity has been described but field studies should test whether these phenotypes are spatial expressed, that is to say whether the phenotypes correspond to a particular habitat use or home range location/size. For instance, it is noticeable that individual #3368 is a main outlier while computing the relationship between personality and spatial metrics. This individual displayed an average personality score but a relatively low residency index. Thereby, on one hand, it reasonably support the idea of different phenotypes being captured within the 10 sharks tracked, while phenotypic influences are recognized as responsible for heterogeneity in movement behavior (Ketterson & Nolan Jr, 1985; Armstrong *et al.*, 1997). Moreover, in 2009, DiBattista identified two phenotypes in term of habitat use in juvenile lemon sharks in Bimini. During his doctoral thesis, the author underlined the occurrence of small individuals with a slow growth rate, experiencing less predation pressure due to a relatively short distance from the shelter of mangrove roots. As well, he pointed out the existence of an opposite phenotype, that is to say larger and fast growth, experiencing higher predation pressure due to a further distance away from the mangroves. The underlying assumption was that a more demanding metabolic rate in a fast growth specimen implies more frequent foraging episodes but also in more risky situations (DiBattista, 2009). Further research is required on this matter.

On the other hand, the present study only examined one personality trait, related to the individual exploratory behaviour. Personality appears more complex and other features such as sociability should be taken into account and compared with spatial ecology (Brown & Laland, 2001; Hobbs & Munday, 2004). Lemon shark is a social species (Guttridge *et al.*, 2009; Guttridge *et al.*, 2010; Guttridge *et al.*, 2011a); decision about movements may be influenced by social interactions and sociability may contribute to shape movement patterns.

Remarkably, a recent field study on migratory behaviour in a cyprinid fish species unveiled the significant ecological consequences of consistent individual differences on migration dynamics (Chapman *et al.*, 2011). The authors reported bolder individual to be more likely to migrate compared to shy individuals. Therefore the interest of future investigations would lay in the study of the likelihood of mature females to come back – phylopatry (Feldheim *et al.*, 2004) – to their own nursery area to give birth to pups in relation to their personality scores as either juveniles or sub-adults.

IV.4.3. Personality and Movement Ecology

Few studies combined field research and mesocosm experiments. This project produced an interesting meeting ground between behavioral ecology and Movement Ecology. It stresses the importance of future research to focus on such a scientific consortium. These findings also highlight the necessity for ecological rationalization of standardized measures of personality traits in animal in natural conditions. The main assumption emerging from these results tend to indicate a potential influence of personality on the movement ecology of juvenile lemon sharks. If comprehended as a main driver, animal personality may have greater consequences regarding ecological and evolutionary processes than previously acknowledged.

Personality traits determination provided a successful understanding for the individual variability in movement ecology within a population. The results may have captured the mechanisms and drivers of spatial ecology of juvenile lemon sharks within their nursery area. This work provides evidence of an existing relationship between an individual-based decision making mechanism and the expression of a movement-related behaviour. The results indicate the importance and relevance of leading further efforts on the understanding of the mechanisms behind movements. The paradigm expressed by (Nathan, 2008) & Nathan *et al.* (2008) might find relatively strong interpretations and resolution by following this path.

Although this study potentially uncovered an intrinsic motivation for movements, studying Movement Ecology under this framework appears complex and the underlying consequences and mechanisms are difficult to understand. Efforts should be directed to actively investigate the decision-making mechanisms. It is challenging to explicitly link observed movement patterns to the internal behavioral traits of the individual due to the statistical properties of movement and spatial metrics. However, long-term monitoring studies at a fine scale, coupled with behavioral investigation might allow a step forward. Recent advances in telemetry enabling high-resolution spatiotemporal movement analysis might support the association of multi-dimensional aspect of movements into behavioural studies. A study of the consistency in movement patterns, across time and context, over a long-term period might corroborate the present results. For instance Harrison *et al.* (2015) uncovered an influence of personality on home range, site fidelity and movement patterns by investigating the repeatability of spatial metrics in the wild burbot, *Lota lota*. Similar study would allow the comprehension of the influence of personality on the Movement Ecology of juvenile lemon sharks. However, Harrison *et al.* (2015) did not perform personality traits analysis beforehand and attributed the spatial metrics observed directly to a personality traits, identifying “behavioral types” in natural conditions.

Under a certain perspective, an integrative framework associating personality and movement features enables a step forward in Movement Ecology field of research. The aspects personality studies tackle and the approach it provides symbolize this advances. As explained in the introduction, Movement Ecology can be approached under 4 main questions: i) *When*, ii) *Where*, iii) *How* and iv) *Why* (Nathan, 2008; Nathan *et al.* 2008). Common tracking studies mostly provide an insight into *where* and *when* a movement pattern occurs and hypotheses as to *why* such expression happened at an individual scale (Dagorn *et al.*, 2000; Vaudo *et al.*, 2014).

In contrast, personality-related investigations seem to enable furthest apprehension of this later issue. Although understanding *why* a movement happened at a specific location and precise time is challenging, the results suggest that the investigation of personality traits of an individual would enhance the comprehension of movements in natural conditions. Despite the fact that the current project explores the relationships between spatial metrics and personality traits through correlation analyses, the results suggest strong evidences of a significant association between personality and movement ecology. It is undeniable that further studies are required under the scope of an individual-based integrative framework, comprising personality traits, movement ecology, feeding ecology, physiology and growth dynamics. Such association would permit a more elaborated understanding of *why* individual dissimilarities in movements occur at a population level.

IV.4.4. Personality-related Movement Ecology: a component for conservation purposes?

The implication of movement patterns regarding the design of protected areas had already been discussed by Kramer and Chapman (1999). The investigation of the Movement Ecology of juvenile lemon sharks, paired with personality analysis provided not only knowledge about inter-individual variations in home ranges and habitats uses but also an interpretation to explain such heterogeneity. The identification of behavioural differences in terms of extent of spatial use, independent of either body size or sex, may have important consequences for population dynamics and species' management programs. The data show that more exploratory individuals utilized much larger home ranges and core areas. Such information is of a great advantage to define both location and size of a MPA. An effective MPA implantation design requires detailed knowledge on the habitat use, activity patterns and likelihood of the inhabitants to remain within the area. It also appears crucial to provide knowledge on such individual-based movement patterns to consider the extent of use. If the drivers are apprehended and incorporated into a conservation and protection framework, potential habitats of interest, not covered by the array of receivers, could be identified. For instance, as previously hypothesized, a shark exhibiting a higher degree of exploration could frequent more hazardous foraging habitats away from the nursery. Including such habitats and movement patterns under a protection status would permit a rational conservation management, not only for the monitored population but also for the environment, under the condition that most phenotypes were captured during the study.

Additionally, the present study unveiled that some sharks remaining highly site-attached would benefit from high levels of protection of their nursery area. However, others might appear more vulnerable and experience a lesser effect of protection due to the use of the nursery area for varying periods of time. Either related to phenotypic variations or intrinsic factor as personality, such heterogeneity has to be crucially accounted for. Incorporating the variability resulting from *why* such pattern is expressed and understanding what is responsible for such variability would enable a more accurate protection of a population.

The results of this project emphasize the need to integrate personality as a factor for movement ecology and to be incorporated in the decision of protection and conservation status of an area. For example, capturing all phenotypes might indicate whether all are nursery area resident until a certain degree (Egli & Babcock, 2004). Mostly, this study contributes to advocate for large sample size for marine protected areas implantation, encompassing this individual variability at a population level so that a sufficient number of different phenotypes is encompassed. This process would participate to the rationalization of protection. This investigation distinguished a mechanism behind the ability of individuals to exploit the environment. The study of the use and habitat selection by individuals therefore has a fundamental interest in understanding the equilibrium between population and environment.

IV.5. Analytic methodology and home range estimators

Minimum Convex Polygon

The MCP analysis enabled the quantification of the sharks' range but its evaluation tended to overestimate the area sizes – mostly the core area - due to the effect of peripheral locations. The assessment of a 100% MCP was described to be inaccurate due to the large weight of the most marginal COA estimates (March *et al.* 2010). Therefore, in the current study the 100% MCP was evinced and instead, a 95% MCP was applied to the COA. The idea was to enclose only 95% of the detections by connecting the outer locations in such a way it provides a relative space use of the sharks. This method produced a relative estimation of the extent for the home range of an individual.

The most interesting result was the difference between the estimation of the core area (50% MCP) and the home range (95% MCP). The insight produced by the percentage of difference underlined the relative reliability of the 95% MCP as an approximate surrogate for home range, supported by the significant relationship between the 50% MCP estimator and the 95% KUD, whereas a 50% MCP failed to produce appropriate estimation for core area size.

The analytical overview indicated this method was relatively reliable and can still be of considerable use, for instance while dealing with a limited sample size (Seaman & Powell, 1996) or to produce an overall idea of the spatial utilization of an animal when fine scale estimations are not required (Abecasis & Erzini, 2008; Abecasis *et al.*, 2009).

Centers of activity

The failure to corroborate the number of COAs with personality traits underlines the need for further computation. The position estimates obtained by a network of acoustic receivers can be improved using an array design enabling an overlap of the detection ranges of more than one receiver (Hedger *et al.*, 2008; Simpfendorfer *et al.*, 2008).

Indeed the acoustic experimental design did not enable an overlap of the detection range of the receivers. By definition, COAs are relocations based on a triangulation of detections obtained over a Δt within the array of receivers (Simpfendorfer *et al.*, 2002). However, under the current monitoring design, detections occurred at one receiver at a time. This implied that over a Δt, the computation of the COA happened within a one-way axis, that is to say between receiver A, decoding the signal first, and receiver B, decoding the subsequent signal. Therefore, weighed by the number of detection at both receivers over Δt, the COA was relocated within the straight axis between receiver A and receiver B. In that sense, they provided a relatively limited insight into the centers of activity of the shark. Nevertheless, a restricted receiver spacing allowing the overlap of at least 3 receivers at a time might enable the estimation of more accurate COA (Simpfendorfer *et al.*, 2011) and therefore may provide a perception of the degree of activity of an individual at a finer scale.

The following section attempts to propose a theoretical method to assess the potential use of COA as a proxy for personality in natural conditions under such an acoustic design. The first step would be the calculation of original COA following the method employed in this study (Simpfendorfer *et al.*, 2002). Let the considered Δt be of an interval of 15 minutes. In addition to obtaining one COA every 15 minutes, the distance between COA would be evaluated on an hour basis. Ideally, the output would provide 4 different distances. Then a threshold of a certain distance, ideally based on the knowledge of the species and movement patterns of the population, would allow the determination of significant difference in distance between successive COA. For instance, for lemon sharks, a distance comprised between 50 m and 100 m could be relevant – regarding the size of the core area -. Using a limit would contribute to the eviction of relatively close COA, implying the shark did not exhibit strict movement away from the area of origin but rather displayed turnover within the same area. Accordingly, each distance between COA that fell above this threshold would produce a substantial number of COA' (i.e. "COA prime", that is to say, centers of activity substantially different from each other, obtained from the original COA), obtained over a period of one hour, called Δp.

Then, the positive correlation trait unveiled between personality and the DfS allowed to consider the distance from the nearest shore as a surrogate measure of the willingness of the sharks to take risk but also suggested an underlying extended exploratory behaviour in the wild. Therefore, following such reasoning, using these COA', two alternative methods could be assessed. One employing the number of COA' over Δp, the other, using the distance between successive original COA. The distance between COA would be investigated as a potential proxy for activity in the wild, whereas the number of COA' would be examined to be a surrogate for exploration in natural conditions. These results would be compared within behavioral experiments such as novel open field test scores. For instance, the number of COA' obtained per Δp (it could as well be a 24h period) could be compared between individuals. Such result would indicate if an individual exhibit a more exploratory behaviour than another. Similarly, the distance between COA over a determined Δ of time would allow a comparison of activity between individuals. A comparison of the number of COA' per Δp with a personality score (for instance R.O.M.) would enable to determine whether COA' could possibly be employed as a surrogate for exploratory behaviour and if therefore it can substantially document personality in the wild, evincing the requirement for preliminary captivity experiments. This would allow a greater appreciation of the personality in natural conditions, reducing the constraint of mesocosms experiments, allowing the application of this method to a wider number of taxa. Similarly, the distance between COA could be compared with personality scores in order to determine whether this method can be used as a proxy for personality traits assessment in the wild.

Moreover, some studies tend to suggest the existence of a negative relationship between the proportion of detection and movement rate, pointing out a possible decrease in probability of detection for more mobile individuals (Topping *et al.*, 2005). This would imply that individual exhibiting a less vagile activity pattern present greater chances to be detected by the receivers compared to more active ones. According to such reasoning, the relatively high proportion of detection at receivers deployed at the mangrove edges would suggest a less active phase of the juveniles while remaining around mangrove roots. This observation would be consistent with the knowledge about mangrove use by juvenile lemon sharks. During high tide, the juveniles tend to shelter between mangrove roots as predation risk increases due to deeper water column (Gruber *et al.*, 1988; Morrissey & Gruber, 1993a).

Conversely, other investigations supposed that activity pattern are positively correlated with the number of detections, involving an increased probability of detection while the individual is more active (Zeller, 1997; March *et al.*, 2009).

An appreciation of the localization of COA' in regards to tidal phases would allow an insight into this current debate. Comparing both the number of detections with the number of COA' and the distance between successive COA would assert whether the number of detections is related to movement patterns. Then, a Fast Fournier Transform would allow the identification of cyclical patterns in the detection features, allowing the apprehension of the mangrove use related to the time of the day and/or to the tidal phase.

Kernel Utilization Distribution

The results illustrated that Kernel Utilization Distribution tend to provide more adequate perceptions than those of MCP. Bivariate kernel utilization distributions seem to be more robust against outlier COAs (March *et al*. 2010). This method provided accurate insight into the home range and core areas of the individuals. However, the presented methodology underlined the critical need for rational computation of space utilization models. Although increasing literature document the debate around methodologies for home range estimation (Seaman & Powell, 1996; Horne & Garton, 2006; Row *et al.*, 2006; Kie, 2013), *h* smoothing parameter should be thoroughly examined and Kernel models should be adapted to a more adequate design, including efficient tools accounting for the presence of barriers as boundaries the animal cannot cross. The future directions for home range analysis should also consider the habitat use within the study area, relating the probability of space use by the animal to the most frequented habitats according to the knowledge about the species/population.

Considering the proposed theoretical estimation of COA', calculating the distance between each COA' and then computing the Least-Cross Validation for the bandwidth selection using these distances could be an alternative allowing a relatively accurate estimation of *h* parameter for KUD analyses. This hypothesis requires further investigation.

Active tracking and distance from shore

The use of acoustic telemetry for home range analyses of juvenile lemon sharks produced longer monitoring periods than active tracking. However, active tracking allowed more detailed movement data. The challenging aspect of active tracking in this study was to obtain a minimum number of real-time locations for a precise estimate of the distance from the shore. Ensuring large sample size requires both larger investments and more intensive fieldwork efforts. Using another exclusion threshold for the minimum number of real time position, greater than the one currently employed, for decision of incorporating the individual into further analysis would have weakened the output of the relationship with personality.

Moreover, the main asset of the active tracking design developed in this study lies in the use of a standardized transect. Indeed, most studies involving active tracking tend to use random search patterns, which does not enable the coverage of the entire study but also may include human bias (i.e. a shark trying to escape the tracking boat) (Gruber *et al.*, 1988; Morrissey & Gruber, 1993a; Dagorn *et al.*, 2000).

IV.6. Limitations of the study

Study limitations were primarily associated with the choice of methodology. Acoustic telemetry is a valuable tool but very costly. Due to an understandable limitation in the expenses, "only" a restricted number of sharks could be fitted with acoustic transmitters. A small sample size might have weakened the correlation analyses and therefore future research should extend the sample size.

Indeed, noticeably, outliers weaken linear relationships and correlations, and the absence of correlation between either MCP or residency and personality scores might quite likely be an artifact of the small sample size. Furthermore, the correlation coefficient did not appear irrelevant, the absence of significance was underlined by the p-value more than by the strength of the association (i.e. Rs values). This documents the current debate about the use of p-value as a factor for significance of the analysis (Baker, 2016; Greenland *et al.*, 2016; Wasserstein & Lazar, 2016).

Further related limitation is thereby linked to the property of the data, which enabled only correlative analyses. Dingemanse and Dochtermann (2013) underscored the difficulties to detect between-individual differences while correlations coefficient were weaker. Accordingly, this converges to support the idea that the absence of correlation between personality and these two variables does not reflect the biological reality of the relationship but is either an artifact of the reduced number of monitored individuals. Therefore, wider sample sizes should be investigated in future researches on this matter in order to evince such noises.

Another inherent constraint of the present study is related to the type of data involved. To identify causation, experimental data are more likely to be needed as opposed to observational data. Yet, Movement Ecology mostly consists in the observation of the spatial expression of behaviour, resulting in the intrinsic limitation of the correlation trait analyses. From such data, a high degree of correlation can be demonstrated, while causation cannot be established. Studies tend to infer causation by performing randomization tests or by fitting causality models based on Bayesian statistics (Pearl, 2003). However it appears reasonable to consider personality as a driving mechanism influencing the expression of movement patterns. Indeed, flipping the conclusions and describing Movement Ecology as a mechanism for personality makes less sense in regards to the processes previously approached.

CONCLUSIONS

This study investigated the relationship between personality traits and Movement Ecology in natural conditions in juvenile lemon sharks, *N. brevirostris*. A personality trait was estimated for each individual from a novel open field test performed in a mesocosm. Spatial metrics were quantified using active and passive acoustic telemetry. The monitoring design allowed for accurate and consistent capture of both spatial use and real-time location of the individuals. Ultrasonic technics afforded a reliable tool to monitor sharks' movements in a complex mangrove fringed shallow water environment. The detection range experiments performed in the study area underscored the complexity of the ultrasonic technology involved in this study and underlined the complication in fitting GLMMs for technical analyses, largely applied to living organisms until now. Further tests are currently undergoing in the waters surrounding Bimini Islands to allow a better understanding of the underwater sound propagation in challenging environments.

Movement patterns were assessed by determining an average distance from the nearest shore from real time locations. Two main methods, MCP and KUD, were applied to evaluate home range and core area sizes. Theses analyses illustrated the complexity to perform optimum home range assessments and to integrate a "case-by-case" individual pattern analysis while using a method investigating population aspects. A comparison between MCP and KUD highlighted the relative dissimilitude between two methods, yet, possibly due to a restricted sample size. More computational efforts are required to enable accurate fine-scale assessment of movement patterns.

The outcomes related to the spatial ecology of juvenile lemon sharks within their nursery ground corroborated the findings of over 20 years of research on lemon shark at the Bimini Biological Field Station. The results indicated that juveniles are likely to remain within their nursery area for an extended period of time and support the ecological importance of the mangrove for this species of elasmobranchs. Substantial documentation on the impact of resort development on the spatial utilization and movement ecology of the lemon shark might bring increased awareness on the need of rational protection for the area hosting the future generations of lemon sharks. Mangrove preservation should be an issue of primer concern.

Both MCP and KUD approaches reported high individual variability in the movement patterns of the juveniles. Spatial use differed greatly among individuals, yet, common characteristics such as body size, sex but also monitoring design, failed to explain these individual differences captured during the study. Although unevenness within population is challenging to explain, the main finding of this research project laid in the observation of a strong correlation between personality traits and movement ecology in juvenile lemon sharks, *N. brevirostris*, in natural conditions. To our knowledge, this is the first study to combine both behavioral ecology and movement ecology analyses to understand the driving mechanisms of spatial use and movement patterns in the wild in an elasmobranch species. Personality was herein suggested as a mechanism behind home range and core area size in the juveniles. The results allowed determining that this parameter was corroborated with movement metrics. The strong correlations with the personality score underlined the possible influence of intrinsic decision-making mechanisms leading to the expression of movement patterns.

Field data combined with behavioral experiments relating key personality traits to ecologically important processes such as Movement Ecology remain scarce. This study reported a significant corroboration between exploratory behavior and spatial dynamics. Individuals displaying the highest scores during the very first exposure to the novel open field test were more likely to exhibit the largest home ranges and core areas as well as the furthest distance from the shore. This implies evidences on the relevance of personality for ecological processes such as animal movement in the wild. Moreover, individual behavioral choices can imply higher energetic costs, leading to a higher predation risk.

This project produced an interesting meeting ground between behavioral ecology and Movement Ecology. It stressed the importance of future researches to focus on such a scientific consortium. These findings also highlight the necessity for ecological rationalization of standardized measures of personality traits in animal in natural conditions.

Finally, integrating personality as a factor for movement ecology and incorporating such knowledge in the decision of protection and conservation status of an area appears of great relevance while implanting a MPA.

Future researches should involve wider sample sizes, combining acoustic telemetry with elaborated behavioural experiments to uncover the complexity of the influence of personality on Movement Ecology and other evolutionary processes such as individual/population fitness.

"The more clearly we can focus our attention on the wonders and realities of the universe about us, the less taste we shall have for destruction"

Rachel Cason, April 1952

Caribbean reef shark, *Carcharhinus perezii*, South Bimini Island, Bahamas. Early 2016. Credits ©: Charlotte Sams.

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"If the relationship of father to son could really be reduced to biology, the whole earth would blaze with the glory of fathers and sons."

James Arthur Baldwin, **Notes to a Native Son** - 1955

Fair Winds and Following Seas.

Joffrey H. P. Baeyaert,

Alice Town, Bimini Islands, Bahamas
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REFERENCES

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M. & Matthiopoulos, J. (2008) Estimating space - use and habitat preference from wildlife telemetry data. *Ecography*, **31**, 140-160.

Abecasis, D. & Erzini, K. (2008) Site fidelity and movements of gilthead sea bream (Sparus aurata) in a coastal lagoon (Ria Formosa, Portugal). *Estuarine, Coastal and Shelf Science*, **79**, 758-763.

Abecasis, D., Bentes, L. & Erzini, K. (2009) Home range, residency and movements of Diplodus sargus and Diplodus vulgaris in a coastal lagoon: connectivity between nursery and adult habitats. *Estuarine, Coastal and Shelf Science*, **85**, 525-529.

Abecasis, D., Afonso, P. & Erzini, K. (2014a) Combining multispecies home range and distribution models aids assessment of MPA effectiveness. *Mar Ecol Prog Ser*, **513**, 155-169.

Abecasis, D., Afonso, P. & Erzini, K. (2014b) Can small MPAs protect local populations of a coastal flatfish, Solea senegalensis? *Fisheries Management and Ecology*, **21**, 175-185.

Abecasis, D., Bentes, L., Lino, P., Santos, M. & Erzini, K. (2013) Residency, movements and habitat use of adult white seabream (Diplodus sargus) between natural and artificial reefs. *Estuarine, Coastal and Shelf Science*, **118**, 80-85.

Adriaenssens, B. & Johnsson, J.I. (2010) Shy trout grow faster: exploring links between personality and fitness-related traits in the wild. *Behavioral Ecology*, arq185.

Afonso, P., Fontes, J., Holland, K.N. & Santos, R.S. (2009) Multi-scale patterns of habitat use in a highly mobile reef fish, the white trevally Pseudocaranx dentex, and their implications for marine reserve design,. *Marine Ecology Progress Series*, **381**, 273-286.

Andrews, K.S., Tolimieri, N., Williams, G.D., Samhouri, J.F., Harvey, C.J. & Levin, P.S. (2011) Comparison of fine-scale acoustic monitoring systems using home range size of a demersal fish. *Marine biology*, **158**, 2377-2387.

Armstrong, J.D., Braithwaite, V.A. & Huntingford, F.A. (1997) Spatial strategies of wild Atlantic salmon parr: exploration and settlement in unfamiliar areas. *Journal of Animal Ecology*, 203-211.

Arnold, G. & Dewar, H. (2001) Electronic tags in marine fisheries research: a 30-year perspective. *Electronic tagging and tracking in marine fisheries*, pp. 7-64. Springer.

Baggeroer, A.B. (1984) Acoustic telemetry-an overview. *Oceanic Engineering, IEEE Journal of*, **9**, 229-235.

Baker, M. (2016) Statisticians issue warning over misuse of P values. *Nature*, **531**, 151-151.

Baras, E. & Lagardère, J.-P. (1995) Fish telemetry in aquaculture: review and perspectives. *Aquaculture International*, **3**, 77-102.

Barker, M.J., Gruber, S.H., Newman, S.P. & Schluessel, V. (2005) Spatial and ontogenetic variation in growth of nursery-bound juvenile lemon sharks, Negaprion brevirostris: a comparison of two age-assigning techniques. *Environmental Biology of Fishes*, **72**, 343-355.

Bastille-Rousseau, G., Potts, J.R., Yackulic, C.B., Frair, J.L., Ellington, E.H. & Blake, S. (2016) Flexible characterization of animal movement pattern using net squared displacement and a latent state model. *Movement Ecology*, **4**, 1-12.

Bell, A.M. (2007) Future directions in behavioural syndromes research. *Proceedings of the Royal Society of London B: Biological Sciences*, **274**, 755-761.

Bell, A.M., Hankison, S.J. & Laskowski, K.L. (2009) The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, **77**, 771-783.

Bergmüller, R. & Taborsky, M. (2010) Animal personality due to social niche specialisation. *Trends in Ecology & Evolution*, **25**, 504-511.

Biro, P.A. & Stamps, J.A. (2008) Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, **23**, 361-368.

Biro, P.A., Beckmann, C. & Stamps, J.A. (2010) Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society of London B: Biological Sciences*, **277**, 71-77.

Biro, P.A., Abrahams, M.V., Post, J.R. & Parkinson, E.A. (2004) Predators select against high growth rates and risk–taking behaviour in domestic trout populations. *Proceedings of the Royal Society of London B: Biological Sciences*, **271**, 2233-2237.

Biro, P.A., Abrahams, M.V., Post, J.R. & Parkinson, E.A. (2006) Behavioural trade‐offs between growth and mortality explain evolution of submaximal growth rates. *Journal of Animal Ecology*, **75**, 1165-1171.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in ecology & evolution*, **24**, 127-135.

Brown, C. & Laland, K. (2001) Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology*, **59**, 471-493.

Brown, C.A. & Gruber, S.H. (1988) Age assessment of the lemon shark, Negaprion brevirostris, using tetracycline validated vertebral centra. *Copeia*, 747-753.

Buchan, K.C. (2000) The Bahamas. *Marine Pollution Bulletin*, **41**, 94-111.

Bulow, F.J. (1970) RNA-DNA ratios as indicators of recent growth rates of a fish. *Journal of the Fisheries Board of Canada*, **27**, 2343-2349.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. (1988) Design and analysis methods for fish survival experiments based on release-recapture. *Journal of Applied Ecology*,

Bushnell, P., Lutz, P. & Gruber, S. (1989) The metabolic rate of an active, tropical elasmobranch, the lemon shark (Negaprion brevirostris). *Exp. Biol*, **48**

Calenge, C. (2006) The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecological modelling*, **197**, 516-519.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D. & Wardle, D.A. (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59-67.

Chapman, B.B., Hulthén, K., Blomqvist, D.R., Hansson, L.A., Nilsson, J.Å., Brodersen, J., Anders Nilsson, P., Skov, C. & Brönmark, C. (2011) To boldly go: individual differences in boldness influence migratory tendency. *Ecology Letters*, **14**, 871-876.

Chapman, D.D., Babcock, E.A., Gruber, S.H., Dibattista, J.D., Franks, B.R., Kessel, S.A., Guttridge, T., Pikitch, E.K. & Feldheim, K.A. (2009) Long-term natal site-fidelity by immature lemon sharks (Negaprion brevirostris) at a subtropical island. *Molecular Ecology*, **18**, 3500-3507.

Chateau, O. & Wantiez, L. (2008) Human impacts on residency behaviour of spangled emperor, Lethrinus nebulosus, in a marine protected area, as determined by acoustic telemetry. *Journal of the Marine Biological Association of the UK*, **88**, 825-829.

Chatzisavvas, K. (2005) The Benefits of Etymology in the Vocabulary Development of Greek ESL Students. *ESL, Kean University, NJ, USA*,

Compagno, L.J. (2001) *Sharks of the world: an annotated and illustrated catalogue of shark species known to date*. Food & Agriculture Org.

Conrad, J.L., Weinersmith, K.L., Brodin, T., Saltz, J. & Sih, A. (2011) Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *Journal of Fish Biology*, **78**, 395-435.

Cooke, S., Chandroo, K., Beddow, T., Moccia, R. & McKinley, R. (2000) Swimming activity and energetic expenditure of captive rainbow trout Oncorhynchus mykiss (Walbaum) estimated by electromyogram telemetry. *Aquaculture Research*, **31**, 495-505.

Cortés, E. & Gruber, S.H. (1990) Diet, feeding habits and estimates of daily ration of young lemon sharks, Negaprion brevirostris (Poey). *Copeia*, 204-218.

Dagorn, L., Josse, E. & Bach, P. (2000) Individual differences in horizontal movements of yellowfin tuna (Thunnus albacares) in nearshore areas in French Polynesia, determined using ultrasonic telemetry. *Aquatic Living Resources*, **13**, 193-202.

Dall, S.R., Houston, A.I. & McNamara, J.M. (2004) The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology letters*, **7**, 734-739.

Díaz, S., Fargione, J., Chapin III, F.S. & Tilman, D. (2006) Biodiversity loss threatens human well-being. *PLoS Biol*, **4**, e277.

Dibattista, J., Feldheim, K., Gruber, S. & Hendry, A. (2007) When bigger is not better: selection against large size, high condition and fast growth in juvenile lemon sharks. *Journal of Evolutionary Biology*, **20**, 201-212.

DiBattista, J.D. (2009) *Evolutionary Potential of a Large Marine Vertebrate: The Lemon Shark (Negaprion Brevirostris)*. McGill University,

DiBattista, J.D., Anisman, H., Whitehead, M. & Gilmour, K.M. (2005) The effects of cortisol administration on social status and brain monoaminergic activity in rainbow trout Oncorhynchus mykiss. *Journal of Experimental Biology*, **208**, 2707-2718.

DiBattista, J.D., Feldheim, K.A., Garant, D., Gruber, S.H. & Hendry, A.P. (2009) Evolutionary potential of a large marine vertebrate: quantitative genetic parameters in a wild population. *Evolution*, **63**, 1051-1067.

DiBattista, J.D., Feldheim, K.A., Garant, D., Gruber, S.H. & Hendry, A.P. (2011) Anthropogenic disturbance and evolutionary parameters: a lemon shark population experiencing habitat loss. *Evolutionary applications*, **4**, 1-17.

Dingemanse, N.J. & Réale, D. (2005) Natural selection and animal personality. *Behaviour*, **142**, 1159-1184.

Dingemanse, N.J. & Dochtermann, N.A. (2013) Quantifying individual variation in behaviour: mixed ‐ effect modelling approaches. *Journal of Animal Ecology*, **82**, 39-54.

Dingemanse, N.J., Kazem, A.J., Réale, D. & Wright, J. (2010) Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution*, **25**, 81-89.

Dingemanse, N.J., Both, C., Drent, P.J., Van Oers, K. & Van Noordwijk, A.J. (2002) Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, **64**, 929-938.

Dollard, J. & Miller, N.E. (1950) *Personality and psychotherapy*.

Dulvy, N.K. & Forrest, R.E. (2010) Life histories, population dynamics and extinction risks in chondrichthyans. *Sharks and Their Relatives*, **2**, 639-679.

Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J., Cortes, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P. & Gibson, C. (2008) You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **18**, 459-482.

Ebstein, R.P., Novick, O., Umansky, R., Priel, B., Osher, Y., Blaine, D., Bennett, E.R., Nemanov, L., Katz, M. & Belmaker, R.H. (1996) Dopamine D4 receptor (D4DR) exon III polymorphism associated with the human personality trait of novelty seeking. *Nature genetics*, **12**, 78-80.

Edrén, S.M.C. & Gruber, S.H. (2005) Homing ability of young lemon sharks, Negaprion brevirostris. *Environmental Biology of Fishes*, **72**, 267-281.

Egli, D. & Babcock, R. (2004) Ultrasonic tracking reveals multiple behavioural modes of snapper (Pagrus auratus) in a temperate no-take marine reserve. *ICES Journal of Marine Science: Journal du Conseil*, **61**, 1137-1143.

Ehlinger, T.J. & Wilson, D.S. (1988) Complex foraging polymorphism in bluegill sunfish. *Proceedings of the National Academy of Sciences*, **85**, 1878-1882.

Espinoza, M., Farrugia, T.J., Webber, D.M., Smith, F. & Lowe, C.G. (2011) Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. *Fisheries Research*, **108**, 364-371.

Farmer, N.A. & Ault, J.S. (2014) Modeling Coral Reef Fish Home Range Movements in Dry Tortugas, Florida. *The Scientific World Journal*, **2014**

Farmer, N.A., Ault, J.S., Smith, S.G. & Franklin, E.C. (2013) Methods for assessment of short-term coral reef fish movements within an acoustic array. *Movement ecology*, **1**, 1-13.

Feldheim, K., Gruber, S. & Ashley, M. (2001) Population genetic structure of the lemon shark (Negaprion brevirostris) in the western Atlantic: DNA microsatellite variation. *Molecular Ecology*, **10**, 295-303.

Feldheim, K.A., Gruber, S.H. & Ashley, M.V. (2002) The breeding biology of lemon sharks at a tropical nursery lagoon. *Proceedings of the Royal Society of London B: Biological Sciences*, **269**, 1655-1661.

Feldheim, K.A., Gruber, S.H., Ashley, M.V. & Orti, G. (2004) Reconstruction of parental microsatellite genotypes reveals female polyandry and philopatry in the lemon shark, Negaprion brevirostris. *Evolution*, **58**, 2332-2342.

Feldheim, K.A., Gruber, S.H., DiBattista, J.D., Babcock, E.A., Kessel, S.T., Hendry, A.P., Pikitch, E.K., Ashley, M.V. & Chapman, D.D. (2014) Two decades of genetic profiling yields first evidence of natal philopatry and long‐term fidelity to parturition sites in sharks. *Molecular ecology*, **23**, 110-117.

Finger, J., Dhellemmes, F., Guttridge, T., Kurvers, R., Gruber, S. & Krause, J. (2016) Rate of movement of juvenile lemon sharks in a novel open field, are we measuring activity or reaction to novelty? *Animal Behaviour*, **116**, 75-82.

Finger, J.S.G., T.L.; Wilson, A.; Dochtermann, N.; Gruber S.H.; Krause, J. (2013) Investigating personality in juvenile lemon sharks (*Negaprion brevirostris*). *Joint Meeting of Ichthyologists and Herpetologist & American Elasmobranch Society*, **Albuquerque, New Mexico**

Franks, B.R. (2007) *The spatial ecology and resource selection of juvenile lemon sharks(Negaprion brevirostris) in their primary nursery areas*.

Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N. & Skalski, G.T. (2001) Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *The American Naturalist*, **158**, 124-135.

Gosling, S.D. (2001) From mice to men: what can we learn about personality from animal research? *Psychological bulletin*, **127**, 45.

Graham, J.B., DeWar, H., Lai, N., Lowell, W.R. & Arce, S.M. (1990) Aspects of shark swimming performance determined using a large water tunnel. *Journal of Experimental Biology*, **151**, 175-192.

Grant, J.W. & Noakes, D.L. (1987) Movers and stayers: foraging tactics of young-of-the-year brook charr, Salvelinus fontinalis. *The Journal of Animal Ecology*, 1001-1013.

Greenland, S., Senn, S.J., Rothman, K.J., Carlin, J.B., Poole, C., Goodman, S.N. & Altman, D.G. (2016) Statistical tests, P values, confidence intervals, and power: a guide to misinterpretations. *European journal of epidemiology*, 1-14.

Groothuis, T.G. & Trillmich, F. (2011) Unfolding personalities: the importance of studying ontogeny. *Developmental psychobiology*, **53**, 641-655.

Gruber, S.H., Nelson, D.R. & Morrissey, J.F. (1988) Patterns of activity and space utilization of lemon sharks, Negaprion brevirostris, in a shallow Bahamian lagoon. *Bulletin of Marine Science*, **43**, 61-76.

Gruber, S.H., De Marignac, J.R. & Hoenig, J.M. (2001) Survival of juvenile lemon sharks at Bimini, Bahamas, estimated by mark–depletion experiments. *Transactions of the American Fisheries Society*, **130**, 376-384.

Guttridge, T. (2009) *The social organisation and behaviour of the juvenile lemon shark, Negaprion brevirostris*. University of Leeds,

Guttridge, T., Gruber, S., Gledhill, K., Croft, D., Sims, D. & Krause, J. (2009) Social preferences of juvenile lemon sharks, Negaprion brevirostris. *Animal Behaviour*, **78**, 543-548.

Guttridge, T., Gulak, S., Franks, B., Carlson, J., Gruber, S., Gledhill, K., Bond, M., Johnson, G. & Grubbs, R. (2015) Occurrence and habitat use of the critically endangered smalltooth sawfish Pristis pectinata in the Bahamas. *Journal of fish biology*, **87**, 1322-1341.

Guttridge, T.L., Gruber, S.H., Krause, J. & Sims, D.W. (2010) Novel acoustic technology for studying free-ranging shark social behaviour by recording individuals' interactions. *PLoS One*, **5**, e9324.

Guttridge, T.L., Gruber, S.H., DiBattista, J.D., Feldheim, K.A., Croft, D.P., Krause, S. & Krause, J. (2011a) Assortative interactions and leadership in a free-ranging population of juvenile lemon shark Negaprion brevirostris. *Marine Ecology Progress Series*, **423**, 235-245.

Guttridge, T.L., Gruber, S.H., Franks, B.R., Kessel, S.T., Gledhill, K.S., Uphill, J., Krause, J. & Sims, D.W. (2011b) Deep danger: intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks Negaprion brevirostris. *Marine Ecology Progress Series*, **445**, 279-291.

Harrison, P.M., Gutowsky, L.F.G., Martins, E.G., Patterson, D.A., Cooke, S.J. & Power, M. (2015) Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (Lota lota). *Behavioral Ecology*, **26**, 483-492.

Hatase, H., Takai, N., Matsuzawa, Y., Sakamoto, W., Omuta, K., Goto, K., Arai, N. & Fujiwara, T. (2002) Size-related differences in feeding habitat use of adult female loggerhead turtles Caretta caretta around Japan determined by stable isotope analyses and satellite telemetry. *Marine Ecology Progress Series*, **233**, 273-281.

Hedger, R.D., Martin, F., Dodson, J.J., Hatin, D., Caron, F. & Whoriskey, F.G. (2008) The optimized interpolation of fish positions and speeds in an array of fixed acoustic receivers. *ICES Journal of Marine Science: Journal du Conseil*, **65**, 1248-1259.

Heisey, D.M. & Fuller, T.K. (1985) Evaluation of survival and cause-specific mortality rates using telemetry data. *The Journal of wildlife management*, 668-674.

Heithaus, M. (2004) Predator-prey interactions. *Biology of sharks and their relatives. CRC, Boca Raton*, 487-521.

Heithaus, M.R., Frid, A., Wirsing, A.J. & Worm, B. (2008) Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, **23**, 202-210.

Heupel, M., Semmens, J. & Hobday, A. (2006) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Marine and Freshwater Research*, **57**, 1-13.

Hobbs, J.-P. & Munday, P. (2004) Intraspecific competition controls spatial distribution and social organisation of the coral-dwelling goby Gobiodon histrio. *Marine Ecology Progress Series*, **278**, 253-259.

Hockersmith, E.E. & Beeman, J.W. (2012) A history of telemetry in fishery research. *Telemetry techniques: a user guide for fisheries research. Edited by NS Adams, JW Beeman, and JH Eiler. American Fisheries Society, Bethesda, Md*, 7-19.

Horne, J.S. & Garton, E.O. (2006) Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. *Journal of Wildlife Management*, **70**, 641-648.

Huntingford, F. & Adams, C. (2005) Behavioural syndromes in farmed fish: implications for production and welfare. *Behaviour*, **142**, 1207-1221.

Huntingford, F.A. (1976) The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, Gasterosteus aculeatus. *Animal Behaviour*, **24**, 245-260.

Huntingford, F.A. (1982) Do inter-and intraspecific aggression vary in relation to predation pressure in sticklebacks? *Animal Behaviour*, **30**, 909-916.

Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., Holland, K.N., Iverson, S.J. & Kocik, J.F. (2015) Aquatic animal telemetry: a panoramic window into the underwater world. *Science*, **348**, 1255642.

Jacoby, D.M., Fear, L.N., Sims, D.W. & Croft, D.P. (2014) Shark personalities? Repeatability of social network traits in a widely distributed predatory fish. *Behavioral Ecology and Sociobiology*, **68**, 1995-2003.

Jennings, D.E., Gruber, S.H., Franks, B.R., Kessel, S.T. & Robertson, A.L. (2008) Effects of large-scale anthropogenic development on juvenile lemon shark

(Negaprion brevirostris) populations of Bimini, Bahamas. *Environmental Biology of Fishes*, **83**, 369-377.

Johansen, I.B., Sørensen, C., Sandvik, G.K., Nilsson, G.E., Höglund, E., Bakken, M. & Øverli, Ø. (2012) Neural plasticity is affected by stress and heritable variation in stress coping style. *Comparative Biochemistry and Physiology Part D: Genomics and Proteomics*, **7**, 161-171.

Jones, K.A. & Godin, J.-G.J. (2010) Are fast explorers slow reactors? Linking personality type and anti-predator behaviour. *Proceedings of the Royal Society of London B: Biological Sciences*, **277**, 625-632.

Kareiva, P. (1983) Local movement in herbivorous insects: applying a passive diffusion model to mark-recapture field experiments. *Oecologia*, **57**, 322-327.

Kessel, S., Cooke, S., Heupel, M., Hussey, N., Simpfendorfer, C., Vagle, S. & Fisk, A. (2014) A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries*, **24**, 199-218.

Ketterson, E.D. & Nolan Jr, V. (1985) Intraspecific variation in avian migration: evolutionary and regulatory aspects. *Migration: mechanisms and adaptive significance*, **27**, 553-579.

Kie, J.G. (2013) A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. *Animal Biotelemetry*, **1**, 1.

Kilfoyle, D.B. & Baggeroer, A.B. (2000) The state of the art in underwater acoustic telemetry. *Oceanic Engineering, IEEE Journal of*, **25**, 4-27.

King, J.E. & Figueredo, A.J. (1997) The five-factor model plus dominance in chimpanzee personality. *Journal of research in personality*, **31**, 257-271.

Koolhaas, J., Korte, S., De Boer, S., Van Der Vegt, B., Van Reenen, C., Hopster, H., De Jong, I., Ruis, M. & Blokhuis, H. (1999) Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews*, **23**, 925-935.

Kramer, D.L. & Chapman, M.R. (1999) Implications of fish home range size and relocation for marine reserve function. *Environmental biology of Fishes*, **55**, 65-79.

Krebs, C. (1989) Estimating abundance: mark-and-recapture techniques. *Ecological methodology*, 654.

Krejcar, O. (2011) *Modern Telemetry*. InTech.

Laskowski, K.L. & Pruitt, J.N. (2014) Evidence of social niche construction: persistent and repeated social interactions generate stronger personalities in a social spider. *Proceedings of the Royal Society of London B: Biological Sciences*, **281**, 20133166.

Leichter, J.J., Wing, S.R., Miller, S.L. & Denny, M.W. (1996) Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. *Limnology and Oceanography*, **41**, 1490-1501.

Lino, P.G., Bentes, L., Oliveira, M.T., Erzini, K. & Santos, M.N. (2011) The African hind's (Cephalopholis taeniops, serranidae) use of artificial reefs off sal island (Cape Verde): a preliminary study based on acoustic telemetry. *Brazilian Journal of Oceanography*, **59**, 69-76.

Lucas, M.C., Baras, E., Thom, T.J., Duncan, A. & Slavík, O. (2001) *Migration of freshwater fishes*. Wiley Online Library.

MacDonald, P. & Smith, H.D. (1980) Mark-recapture estimation of salmon smolt runs. *Biometrics*, 401-417.

March, D., Palmer, M., Alós, J., Grau, A. & Cardona, F. (2009) Short-term residence, home range size and diel patterns of the painted comber Serranus scriba in a temperate marine reserve. *Marine Ecology Progress Series*, **400**, 195.

Matich, P. & Heithaus, M.R. (2015) Individual variation in ontogenetic niche shifts in habitat use and movement patterns of a large estuarine predator (Carcharhinus leucas). *Oecologia*, 1-13.

McClellan, D.B. & Cummings, N.J. (1997) Preliminary analysis of tag and recapture data of the greater amberjack, Seriola dumerili, in the southeastern United States. *Proceedings of the 49th Annual Gulf and Caribbean Fisheries Institute, Christ Church, Barbados (1996)*, **49**, 25-45.

McLaughlin, R.L., Grant, J.W. & Kramer, D.L. (1992) Individual variation and alternative patterns of foraging movements in recently-emerged brook charr (Salvelinus fontinalis). *Behaviour*, **120**, 286-301.

Minderman, J., Reid, J.M., Hughes, M., Denny, M.J., Hogg, S., Evans, P.G. & Whittingham, M.J. (2010) Novel environment exploration and home range size in starlings Sturnus vulgaris. *Behavioral Ecology*,

Mittelbach, G.G., Ballew, N.G., Kjelvik, M.K. & Fraser, D. (2014) Fish behavioral types and their ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences*, **71**, 927-944.

Morris, D.W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, **136**, 1-13.

Morrissey, J.F. & Gruber, S.H. (1993a) Habitat selection by juvenile lemon sharks, Negaprion brevirostris. *Environmental Biology of Fishes*, **38**, 311-319.

Morrissey, J.F. & Gruber, S.H. (1993b) Home range of juvenile lemon sharks, Negaprion brevirostris. *Copeia*, 425-434.

Nathan, R. (2008) An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences*, **105**, 19050-19051.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, **105**, 19052-19059.

Newman, S.P. (2003) Spatial and temporal variation in diet and prey preference of nursery-bound juvenile lemon sharks (Negaprion brevirostris) at Bimini, Bahamas.

Newman, S.P., Handy, R.D. & Gruber, S.H. (2010) Diet and prey preference of juvenile lemon sharks Negaprion brevirostris. *Marine Ecology Progress Series*, **398**, 221-234.

Nixon, A.J. & Gruber, S.H. (1988) Diel metabolic and activity patterns of the lemon shark (Negaprion brevirostris). *Journal of experimental Zoology*, **248**, 1-6.

Nussey, D., Wilson, A. & Brommer, J. (2007) The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of evolutionary biology*, **20**, 831-844.

Øverli, Ø., Sørensen, C., Pulman, K.G., Pottinger, T.G., Korzan, W., Summers, C.H. & Nilsson, G.E. (2007) Evolutionary background for stress-coping styles: relationships between physiological, behavioral, and cognitive traits in non-mammalian vertebrates. *Neuroscience & Biobehavioral Reviews*, **31**, 396-412.

Pearl, J. (2003) Causality: models, reasoning and inference. *Econometric Theory*, **19**, 675-685.

Pervin, L.A. & John, O.P. (1999) *Handbook of personality: Theory and research*. Elsevier.

Pradel, R. (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics*, 703-709.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T. & Dingemanse, N.J. (2007) Integrating animal temperament within ecology and evolution. *Biological reviews*, **82**, 291-318.

Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V. & Montiglio, P.-O. (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 4051-4063.

Robson, D. & Regier, H. (1964) Sample size in Petersen mark–recapture experiments. *Transactions of the American Fisheries Society*, **93**, 215-226.

Roff, D. & Fairbairn, D. (2007) The evolution of trade ‐ offs: where are we? *Journal of evolutionary biology*, **20**, 433-447.

Roff, D.A.D.A. (2002) *Life history evolution*.

Rogers, K.B., White, G.C., Guy, C. & Brown, M. (2007) Analysis of movement and habitat use from telemetry data. *Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland*, 625-676.

Rogerson, P. (2001) *Statistical methods for geography*. Sage.

Row, J.R., Blouin-Demers, G. & Fox, S. (2006) Kernels are not accurate estimators of home-range size for herpetofauna. *Copeia*, **2006**, 797-802.

Schjolden, J., Backström, T., Pulman, K.G., Pottinger, T.G. & Winberg, S. (2005) Divergence in behavioural responses to stress in two strains of rainbow trout (Oncorhynchus mykiss) with contrasting stress responsiveness. *Hormones and Behavior*, **48**, 537-544.

Schjolden, J., Pulman, K., Pottinger, T., Metcalfe, N. & Winberg, S. (2006) Divergence in locomotor activity between two strains of rainbow trout Oncorhynchus mykiss with contrasting stress responsiveness. *Journal of Fish Biology*, **68**, 920-924.

Schlosser, I.J. (1991) Stream fish ecology: a landscape perspective. *BioScience*, **41**, 704-712.

Seaman, D.E. & Powell, R.A. (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, **77**, 2075-2085.

Sih, A., Bell, A. & Johnson, J.C. (2004a) Behavioral syndromes: an ecological and evolutionary overview. *Trends in ecology & evolution*, **19**, 372-378.

Sih, A., Bell, A.M., Johnson, J.C. & Ziemba, R.E. (2004b) Behavioral syndromes: an integrative overview. *The quarterly review of biology*, **79**, 241-277.

Simpfendorfer, C.A., Heupel, M.R. & Hueter, R.E. (2002) Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 23-32.

Simpfendorfer, C.A., Heupel, M.R. & Collins, A.B. (2008) Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 482-492.

Simpfendorfer, C.A., Yeiser, B.G., Wiley, T.R., Poulakis, G.R., Stevens, P.W. & Heupel, M.R. (2011) Environmental influences on the spatial ecology of juvenile smalltooth sawfish (Pristis pectinata): results from acoustic monitoring. *PLoS One*, **6**, e16918.

Sims, D., Nash, J. & Morritt, D. (2001) Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. *Marine Biology*, **139**, 1165-1175.

Sims, D.W. (2005) Differences in habitat selection and reproductive strategies of male and female sharks. *Sexual segregation in vertebrates: Ecology of the two sexes*, 127-147.

Singh, L., Downey, N., Roberts, M., Webber, D.M., Smale, M., Van den Berg, M., Harding, R., Engelbrecht, D. & Blows, B. (2009) Design and calibration of an acoustic telemetry system subject to upwelling events. *African Journal of Marine Science*, **31**, 355-364.

Spoolder, H.A., Burbidge, J.A., Lawrence, A.B., Simmins, P.H. & Edwards, S.A. (1996) Individual behavioural differences in pigs: intra-and inter-test consistency. *Applied animal behaviour science*, **49**, 185-198.

Sprogis, K.R., Raudino, H.C., Rankin, R., MacLeod, C.D. & Bejder, L. (2016) Home range size of adult Indo‐Pacific bottlenose dolphins (Tursiops aduncus) in a coastal and estuarine system is habitat and sex‐specific. *Marine Mammal Science*, **32**, 287-308.

Stevens, J., Bonfil, R., Dulvy, N. & Walker, P. (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science: Journal du Conseil*, **57**, 476-494.

Sundström, L.F. (2015) Sundström, L.F. 2015. Negaprion brevirostris. The IUCN Red List of Threatened Species 2015: e.T39380A81769233. http://dx.doi.org/10.2305/IUCN.UK.2015.RLTS.T39380A81769233.en . Downloaded on 16 September 2015. *The IUCN Red List of Threatened Species 2015*,

Sundström, L.F., Gruber, S.H., Clermont, S.M., Correia, J.P., de Marignac, J.R., Morrissey, J.F., Lowrance, C.R., Thomassen, L. & Oliveira, M.T. (2001) Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, Negaprion brevirostris, around Bimini Islands, Bahamas. *Environmental Biology of Fishes*, **60**, 225-250.

Taylor, E.B. (1990) Phenotypic correlates of life-history variation in juvenile chinook salmon, Oncorhynchus tshawytscha. *The Journal of Animal Ecology*, 455-468.

Taylor, M. & Cooke, S. (2014) Repeatability of movement behaviour in a wild salmonid revealed by telemetry. *Journal of fish biology*, **84**, 1240-1246.

Taylor, M.K. & Cooke, S.J. (2012) Meta-analyses of the effects of river flow on fish movement and activity. *Environmental Reviews*, **20**, 211-219.

Techera, E.J. (2012) Fishing, finning and tourism: trends in Pacific shark conservation and management. *The International Journal of Marine and Coastal Law*, **27**, 597-621.

Thompson, B., Beasley, M. & Wilson, C. (1999) Age distribution and growth of greater amberjack, Seriola dumerili, from the north-central Gulf of Mexico. *Fishery Bulletin*, **97**, 362-371.

Toms, C.N., Echevarria, D.J. & Jouandot, D.J. (2010) A methodological review of personality-related studies in fish: focus on the shy-bold axis of behavior. *International Journal of Comparative Psychology*, **23**

Topping, D., Lowe, C. & Caselle, J. (2005) Home range and habitat utilization of adult California sheephead, Semicossyphus pulcher (Labridae), in a temperate no-take marine reserve. *Marine Biology*, **147**, 301-311.

Topping, D.T. & Szedlmayer, S.T. (2011) Site fidelity, residence time and movements of red snapper Lutjanus campechanus estimated with long-term acoustic monitoring. *Marine Ecology Progress Series*, **437**, 183-200.

Udyawer, V., Chin, A., Knip, D.M., Simpfendorfer, C.A. & Heupel, M.R. (2013) Variable response of coastal sharks to severe tropical storms: environmental cues and changes in space use. *Mar Ecol Prog Ser*, **480**, 171-183.

van Zinnicq Bergmann, M. (2013) Testing the acoustic detection range of submersible ultrasonic receivers in relation to environmental factors at two shallowwater environments in Bimini, Bahamas.

Vaudo, J.J., Wetherbee, B.M., Harvey, G., Nemeth, R.S., Aming, C., Burnie, N., Howey‐Jordan, L.A. & Shivji, M.S. (2014) Intraspecific variation in vertical habitat use by tiger sharks (Galeocerdo cuvier) in the western North Atlantic. *Ecology and evolution*, **4**, 1768-1786.

Ward-Paige, C.A., Mora, C., Lotze, H.K., Pattengill-Semmens, C., McClenachan, L., Arias-Castro, E. & Myers, R.A. (2010) Large-scale absence of sharks on reefs in the greater-Caribbean: a footprint of human pressures. *PloS one*, **5**, e11968.

Wasserstein, R.L. & Lazar, N.A. (2016) The ASA's statement on p-values: context, process, and purpose. *The American Statistician*,

Watsky, M.A. & Gruber, S.H. (1990) Induction and duration of tonic immobility in the lemon shark, Negaprion brevirostris. *Fish Physiology and Biochemistry*, **8**, 207-210.

Wearmouth, V. & Sims, D. (2010) Sexual segregation in elasmobranchs. *Biol Mar Mediterr*, **17**, 236-239.

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S. & Holmes, R.T. (2002) Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution*, **17**, 76-83.

Weimerskirch, H., Brothers, N. & Jouventin, P. (1997) Population dynamics of wandering albatross Diomedea exulans and Amsterdam albatross D. amsterdamensis in the Indian Ocean and their relationships with long-line fisheries: conservation implications. *Biological conservation*, **79**, 257-270.

Weiss, A., King, J.E. & Figueredo, A.J. (2000) The heritability of personality factors in chimpanzees (Pan troglodytes). *Behavior genetics*, **30**, 213-221.

Wetherbee, B.M., Gruber, S.H. & Cortés, E. (1990) Diet, feeding habits, digestion, and consumption in sharks, with special reference to the lemon shark, Negaprion brevirostris. *NOAA Technical Report NMFS*, **90**, 29-47.

Wilson, D.S. (1998) Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **353**, 199-205.

Wilson, D.S., Coleman, K., Clark, A.B. & Biederman, L. (1993) Shy-bold continuum in pumpkinseed sunfish (Lepomis gibbosus): an ecological study of a psychological trait. *Journal of Comparative Psychology*, **107**, 250.

Wilson, D.S., Clark, A.B., Coleman, K. & Dearstyne, T. (1994) Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, **9**, 442-446.

Wolf, M. & Weissing, F.J. (2012) Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, **27**, 452-461.

Wolf, M. & McNamara, J.M. (2012) On the evolution of personalities via frequency-dependent selection. *The American Naturalist*, **179**, 679-692.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B., Lotze, H.K., Micheli, F. & Palumbi, S.R. (2006) Impacts of biodiversity loss on ocean ecosystem services. *science*, **314**, 787-790.

Worton, B.J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**, 164-168.

Zeller, D.C. (1997) Home range and activity patterns of the coral trout Plectropomus leopardus (Serranidae). *Marine Ecology Progress Series*, **154**, 65-77.

Appendix I. Methodology of Submersible Ultrasonic Receivers (Sonotronics Inc., ® Tucson, Arizona, U.S.A.) retrieval, data downloading & maintenance

I. Background and anatomy of the SURs

Sonotronics Submersible Ultrasonic Receivers "SUR-3" (Sonotronics Inc. ®, Tucson, Arizona, U.S.A.) are delicate equipment that need to be handled with a lot of caution. Any shock or damage could induce the loss of the stored data and malfunction of the device.

The receiver consists of different components put together in a plastic housing (**Fig. 1 & 2**). The receiving unit (the yellow transducer), is located on the top of the gear, and is the most fragile part of the device (**Fig. 1. & 2. A, B & E**). Therefore, it is imperative to never shock this part. The screw next to the transducer serves as a cap for the serial port connector (**Fig.1 & 2.A - E**). It is highly recommended to avoid the use of wrenches to unscrew it. Typically, it is manually tightened. The SUR serial number is printed on a white label, on the upper part of the circuits assembling (**Fig. 1**

& 2.H). The two D. 3.6 Volts lithium batteries are kept in the bottom part of the device (**Fig. 1 & 2.B**). The operating DEL, a red light flashing at frequent intervals, indicating that the receiver is “On”, is situated just above the batteries compartment. It is discernable owing to its reference designator “D5”. The “On – Off” switch is positioned on the bottom of the receiver, on the circuit assembling. The receiver was only switched off while batteries were being replaced. An unfortunate switch to the “Off” position would lead to an erroneous time setting of the internal clock of the SUR. The mounting eyebolt is located on the bottom of the receiver (**Fig. 1 & 2.G**).

II. Field method

The precise location of all the receivers has been previously determined using a Garmin handheld GPS, over the first deployment. Following these coordinates, each SUR was efficiently localized.

The receivers were contained inside Polyvinyl chloride (“PVC”) housings, closed on the top by a screwing lid, set up on a concrete base, easily identifiable from the bow of the skiff (**Fig. 3 & 4. A - E**). Upon each retrieval, the housing was scrubbed to clear away the epibiota and the lid was loosened using wrenches. This manipulation had to be performed with caution since the lid possesses a slot through which the transducer and connector outstrip. Once the device was being collected, the time, depth, SUR serial number, location name as well as a new set of GPS coordinates were taken.

Aboard the skiff, the receivers were carefully wrapped up in bubble packing paper, interposed between towels and kept inside an insulated dry box until arrival at the Shark Lab. During unfavorable sea conditions, considered as possibly involving damages to the gear over transportation, no planning (i.e. high speed) was authorized with the boat.

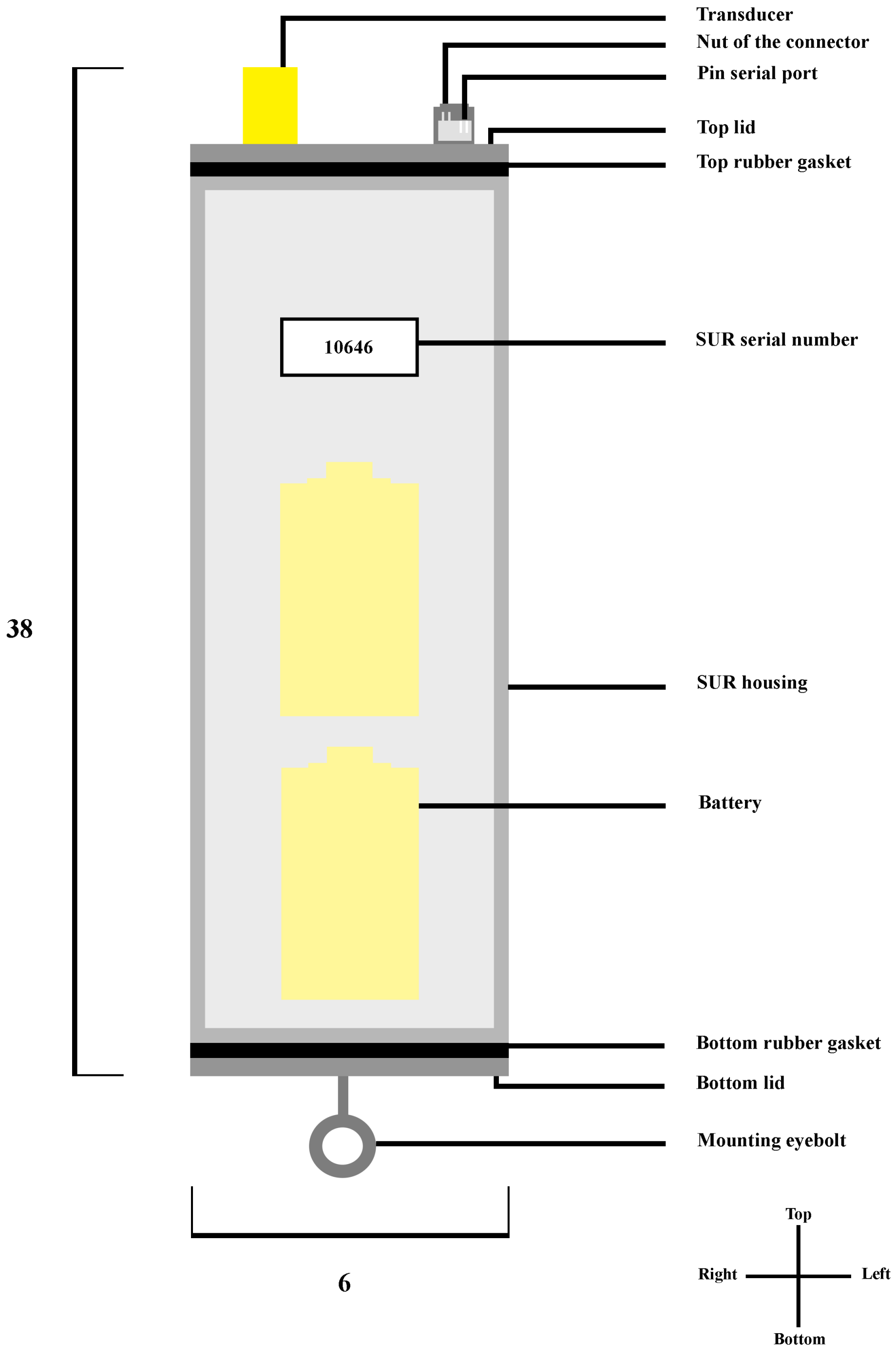

Fig. 1. Diagram of the anatomy of a Submersible Ultrasonic Receiver "SUR" (Sonotronics Inc., ® Tucson, Arizona, U.S.A.).

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Fig. 2. Components and structure of a Submersible Ultrasonic Receiver "SUR" (Sonotronics Inc., ® Tucson, Arizona, U.S.A.). A: side view of the top lid of the SUR, revealing the transducer (yellow) and the serial connecter bolt – the nut has been previously unscrewed -; B: mid-upper part of the SUR, exhibiting the two batteries; C & D: nut of the serial port connector; E: top view of the upper lid, showing the pin serial "COM" port connector; F: the two sorts of rubber gasket used to seal the SUR; G: Bottom of the SUR, showing the mounting eyebolt fixed to the lid; H: SUR serial number; I: empty SUR housing.

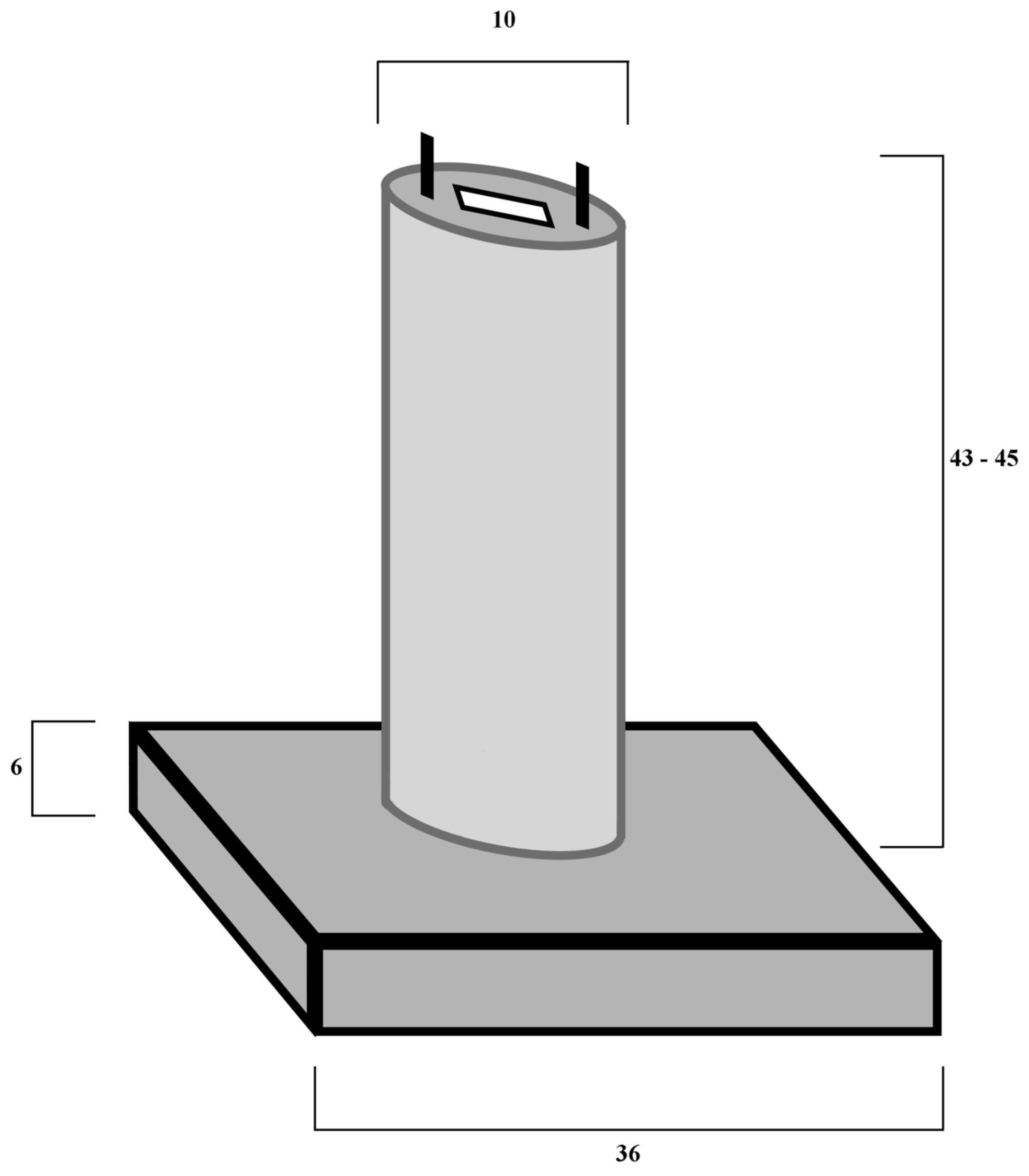

Fig. 3. Diagram of a typical PVC housing used to contain Submersible Ultrasonic Receivers (Sonotronics Inc., ® Tucson, Arizona, U.S.A.) in shallow areas.

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Fig. 4. Underwater photography of a Submersible Ultrasonic Receiver “SUR” (Sonotronics Inc., ® Tucson, Arizona, U.S.A.) and PVC housings deployed in the North Sound nursery area, North Bimini, Bahamas. A, C & E: Underwater view of SURs deployed inside their PVC housing (April 2016); B: PVC housing used to contain the SURs in a shallow area; D: top view of a SUR inside a housing, showing the transducer and connector outstripping from the slot of the lid.

III. Laboratory procedures

III.1. Common maintenance

After disembarking, each SUR was cautiously unwrapped and immersed in a freshwater bath for a few minutes. Then, the housings were washed and dried. Afterwards, the top of the receivers was thoroughly cleaned (transducer and connector) using a rag and a toothbrush in order to remove the epibiosis. Then, the nut of the connector was manually unscrewed and brushed, as were the pitches and bolt of the plug.

In order to maintain a water-tight seal at the serial port, any foreign particles found on the rubber gasket were removed and extra caution was taken to ensure the gasket was not damaged.

III.2. Data processing

The data processing included two main steps, the downloading of the data and the operative setting-up of the receiver. Both processes involved the use of SONOTRONICS free software "*SURsoft*", available for Windows operating systems. The application benefits from a simple interface and each stage of the process is straightforward.

III.2.1. Data downloading

After running the program, the SUR was plugged into the USB port of the PC via its pin serial "COM" port connector (**Fig.1 & 2.E**), using the adapter cable. The SUR was kept "On" during the entire procedure. The next step consisted of connecting and synchronizing the receiver for the software to access the stored information. In order to do so, a communication port "COM" – corresponding to the USB terminal of the

PC configured to host the cable - had to be selected. Information related to the synchronization status and number of detections saved in the internal memory of the receiver are displayed on the bottom left corner of the screen (e.g. "error", "connected") (**Fig. 5. A - D**).

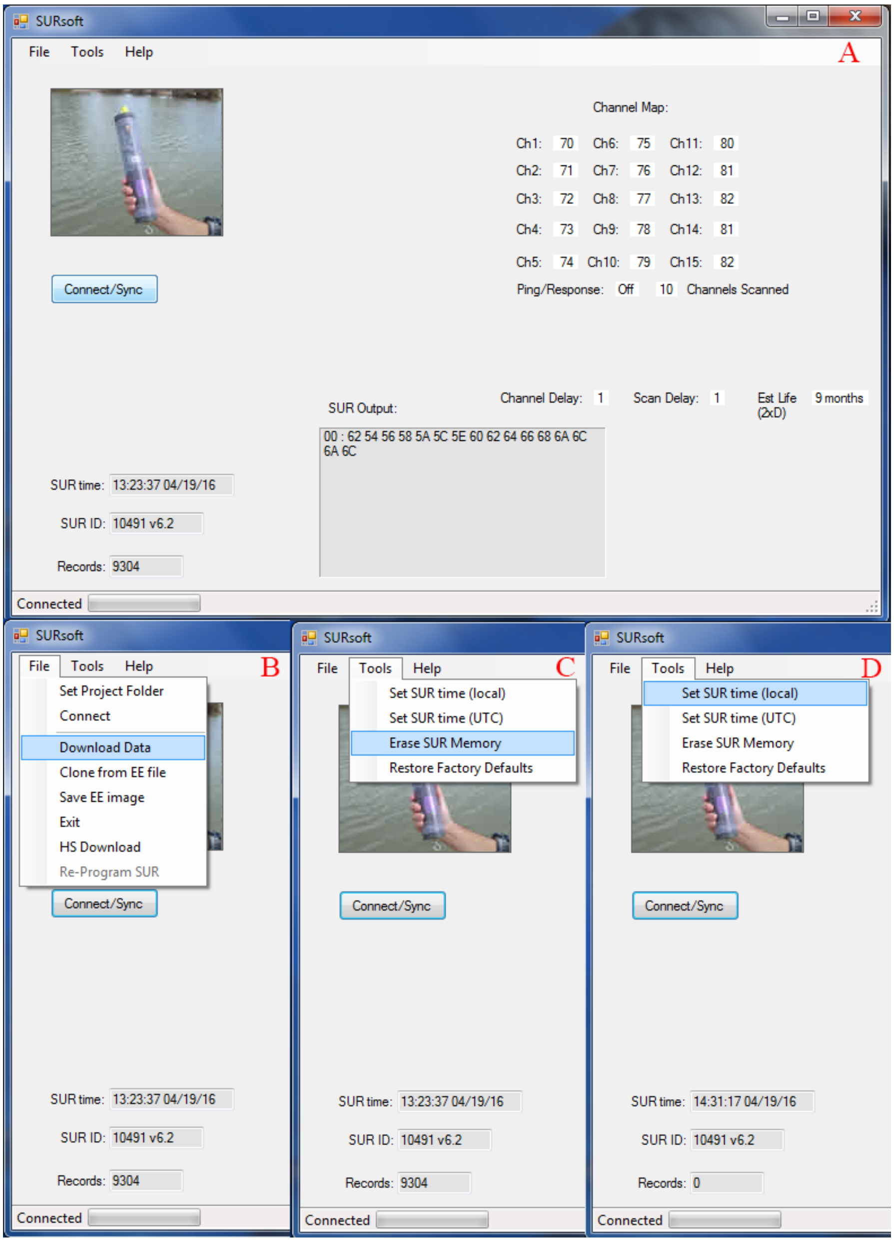
The final stage of the data saving was completed by selecting the option "Data download" under the "File" tab (**Fig. 5.B**). As a matter of precaution, SURs outputs were stored in two distinct folders, one of which was contained in an online data storage service, as well as on an external hard-drive.

III.2.2. SUR setup

Once the information contained in the SUR was saved, upon verification of the files for putative corruption (e.g. missing or anomalous data due to incomplete download or connection failure between the SUR and the PC), its internal memory was erased (**Fig. 5.C**). Subsequently, the internal clock of the receiver was setup at local time (**Fig. 5.D**) and the frequencies were inspected to ensure the 10 inputted scanned channels matched those of the tags (70 kHz to 79 kHz).

III.3. Battery replacing

Common data downloads did not necessitate the opening of the housing. However, the batteries were regularly tested (every 4 to 6 months) with a voltmeter and replaced if needed. For precautionary measures, the procedure always occurred after the download of the data. During this manipulation, the SURs were first unscrewed from the top by gripping the gray rim of the lid, whilst the handler had to take care not to hold the device by the transducer or the nut of the connector.



Channel Map:

Ch1: 70 Ch6: 75 Ch11: 80
Ch2: 71 Ch7: 76 Ch12: 81
Ch3: 72 Ch8: 77 Ch13: 82
Ch4: 73 Ch9: 78 Ch14: 81
Ch5: 74 Ch10: 79 Ch15: 82
Ping/Response: Off 10 Channels Scanned

Channel Delay: 1 Scan Delay: 1 Est Life (2xD) 9 months

SUR Output:

```
00 : 62 54 56 58 5A 5C 5E 60 62 64 66 68 6A 6C
6A 6C
```

SUR time: 13:23:37 04/19/16
SUR ID: 10491 v6.2
Records: 9304

SUR time: 13:23:37 04/19/16
SUR ID: 10491 v6.2
Records: 9304

SUR time: 13:23:37 04/19/16
SUR ID: 10491 v6.2
Records: 9304

SUR time: 14:31:17 04/19/16
SUR ID: 10491 v6.2
Records: 0

Fig. 5. Sonotronics SURsoft interface (Sonotronics Inc., ® Tucson, Arizona, U.S.A.). A: Screen of the software interface while a SUR is synchronized; B: Data download; C: Memory erasing; D: Local time setup of the SUR.

Then, the bottom lid was removed following the same method. Before replacement of the batteries, the receiver was switched "Off". The batteries inserted in the receivers were specific Lithium Thionyl Chloride - 1/2AA, ER14250/W 3.6V – batteries acquired through Energy One Electronics Inc. with an estimated life of 9 months under the current use (more technical information accessible online at http://energyoneinc.com/specs/er14250w_e1.pdf).

Once the two new batteries installed, the receivers were turned “On” and their functioning status was confirmed by checking the operating LED “D5”.

III.4. Detailed maintenance of the housing and sealing system

Concurrently with the batteries replacement, a thorough cleansing of the housing and sealing system was carried out.

All rubber gasket rings were removed and the remaining silicone layer was cleaned with a wood fiber lab wiper. If considered damaged or distorted, the gaskets were replaced. The circuit assembling was dusted and checked for any unplugged wire or anomalies. The screwing pitches of the housing and lids were scrubbed with a damp rag (and Q-tips if necessary) and wiped using a lab wiper. Before reassembling the receiver, a very thin layer of silicone grease was applied on all sealing components (gasket rings, screwing pitches) to ensure better insulation of the electronic system.

After properly repositioning the gaskets, the first element to be re-embedded was the top lid with the fixed circuits, then, the bottom lid.

Only a slight pressure between the lid, the gasket ring and the housing was sufficient for an optimal sealing. If too tight, the gasket would splay, leading to a loss of the waterproof property of the closing and generating leaks.

Finally, after verifying the state of the gaskets and seals (top & bottom), a slight amount of contact cleaner was sprayed over the serial port connector, left to dry a few minutes, and then manually closed with its nut.

Information on the technological characteristics and performances of the receivers are also available online on the website of the manufacturer at http://sonotronics.com/wp-content/uploads/2010/07/SURmanual.pdf

Appendix II. Mapping of the spatial ecology of juvenile lemon sharks within their nursery area: outputs from the centers of activity & Minimum Convex Polygon analyses.

- **I. Centers of activity**
- **II. Minimum convex Polygon**
- **III. Overall abacus**
- **IV. *h* smoothing parameter**

I. Centers of activity

#365

#3368

#3545

#4447

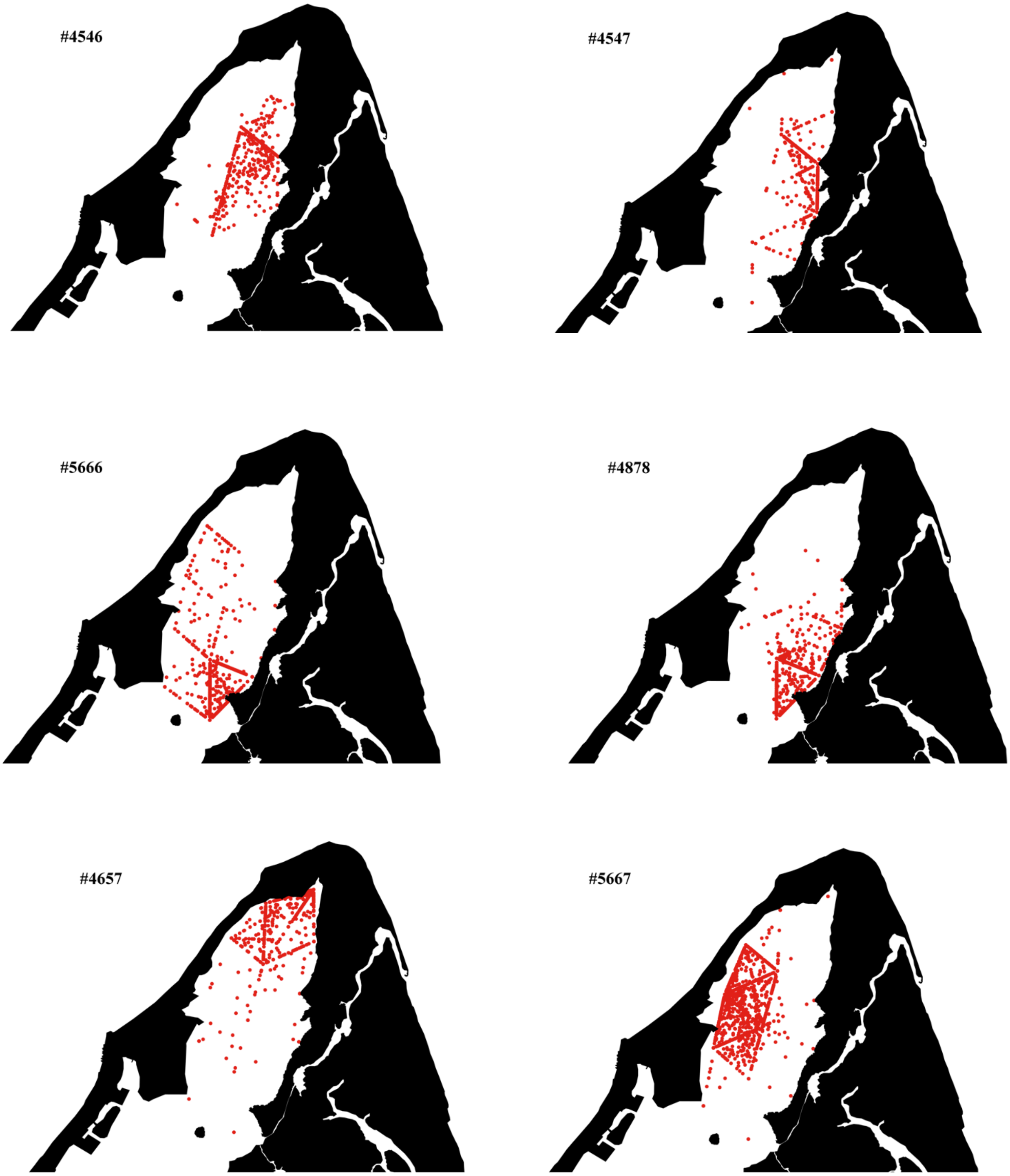
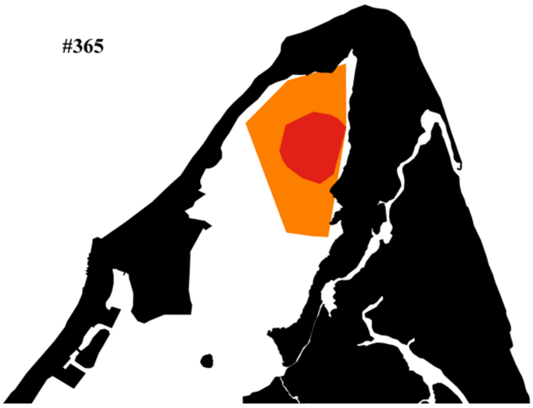


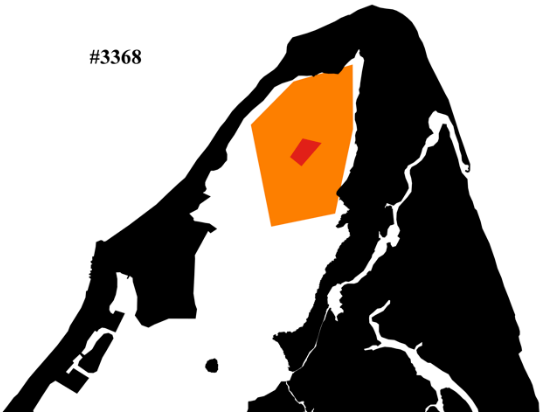
Fig. 1. Centers of activity, as calculated from the arithmetic method developed by Simpfendorfer *et al.* (2002), of juvenile lemon sharks, *Negaprion brevirostris*, within their nursery area, North Sound, Bimini Islands, Bahamas.

II. Minimum Convex Polygon

#365



#3368



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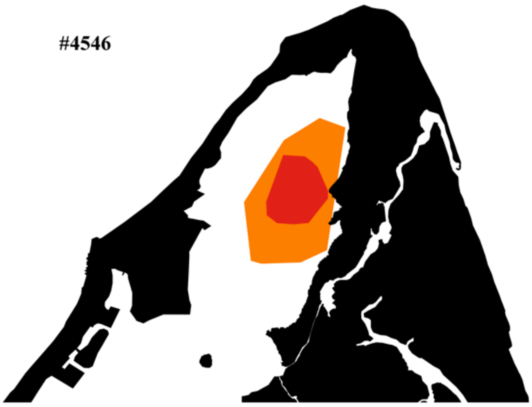

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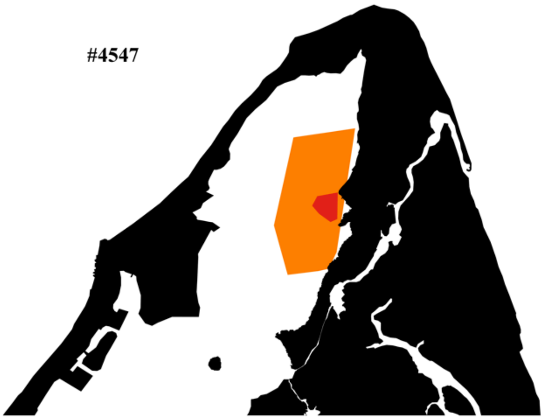

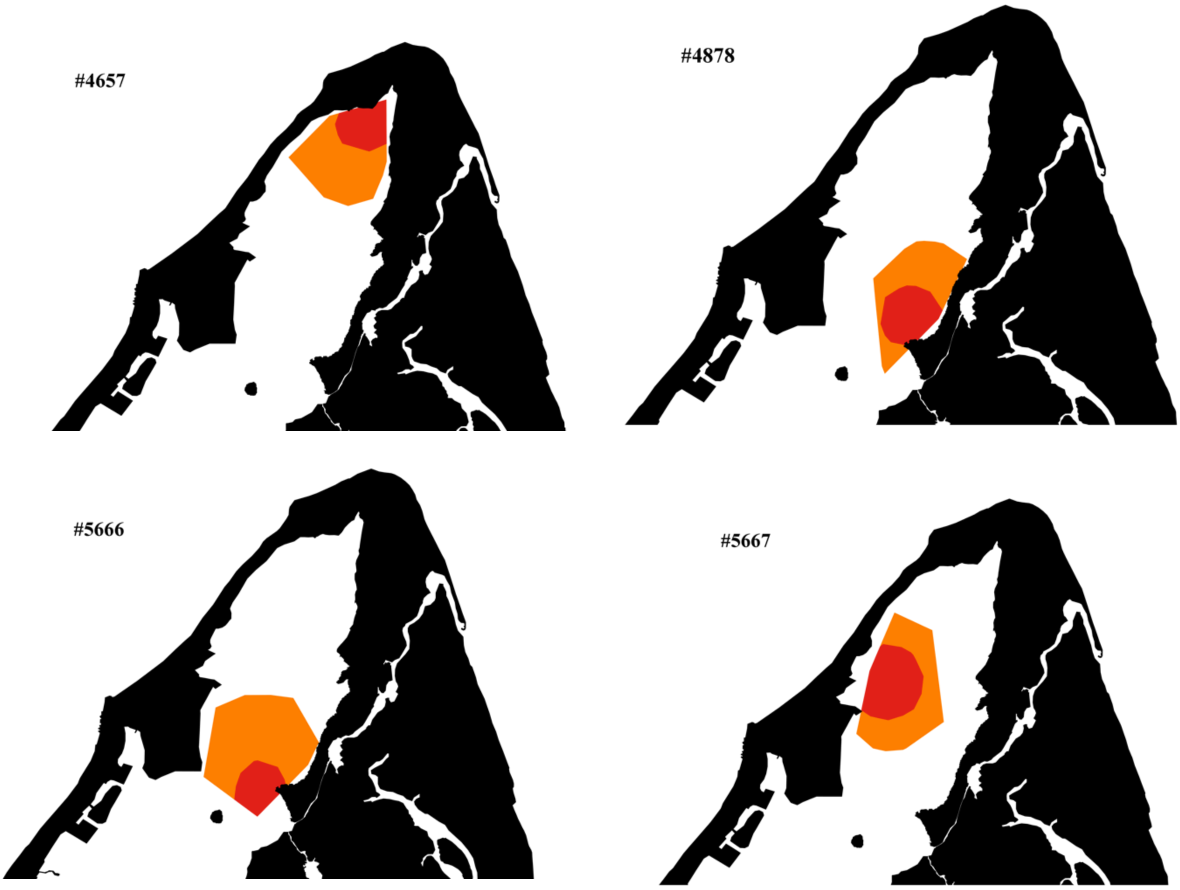

Fig. 2. Minimum Convex Polygon of juvenile lemon sharks, Negaprion brevirostris, within their nursery area. Orange represents the 95% MCP while the red patches correspond to the 50% MCP

III. Overall abacus

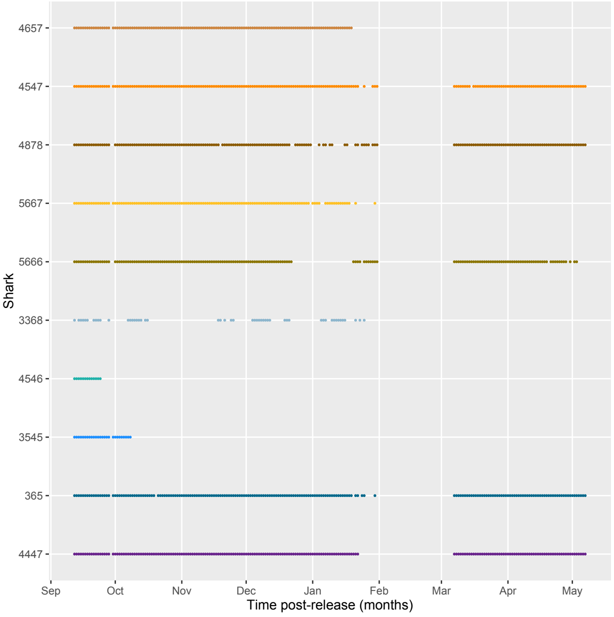

Fig. 3. Overall abacus plot of daily presence of the ten juvenile lemon sharks, *Negaprion brevirostris*, monitored within their nursery area, between September 2015 and May 2016, North Sound, Bimini Islands,

IV. *h* smoothing parameter

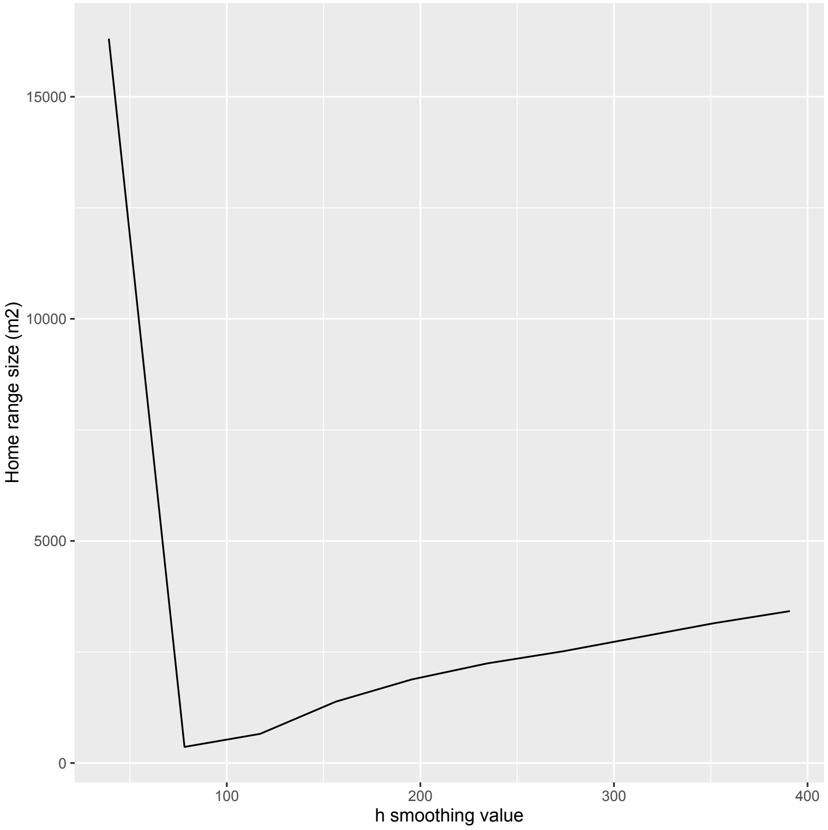

Fig. 4. Original figure for *h* smoothing parameter selection, including 0.1 *href*. Note the out-of-bound home range value it produces.

Reference

Simpfendorfer, C.A., Heupel, M.R. & Hueter, R.E. (2002) Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 23-32.

Appendix III. Supplementary material: Cartography and geography of Bimini Islands, Bahamas & characterization of the study area, North Sound, Bimini Islands, Bahamas.

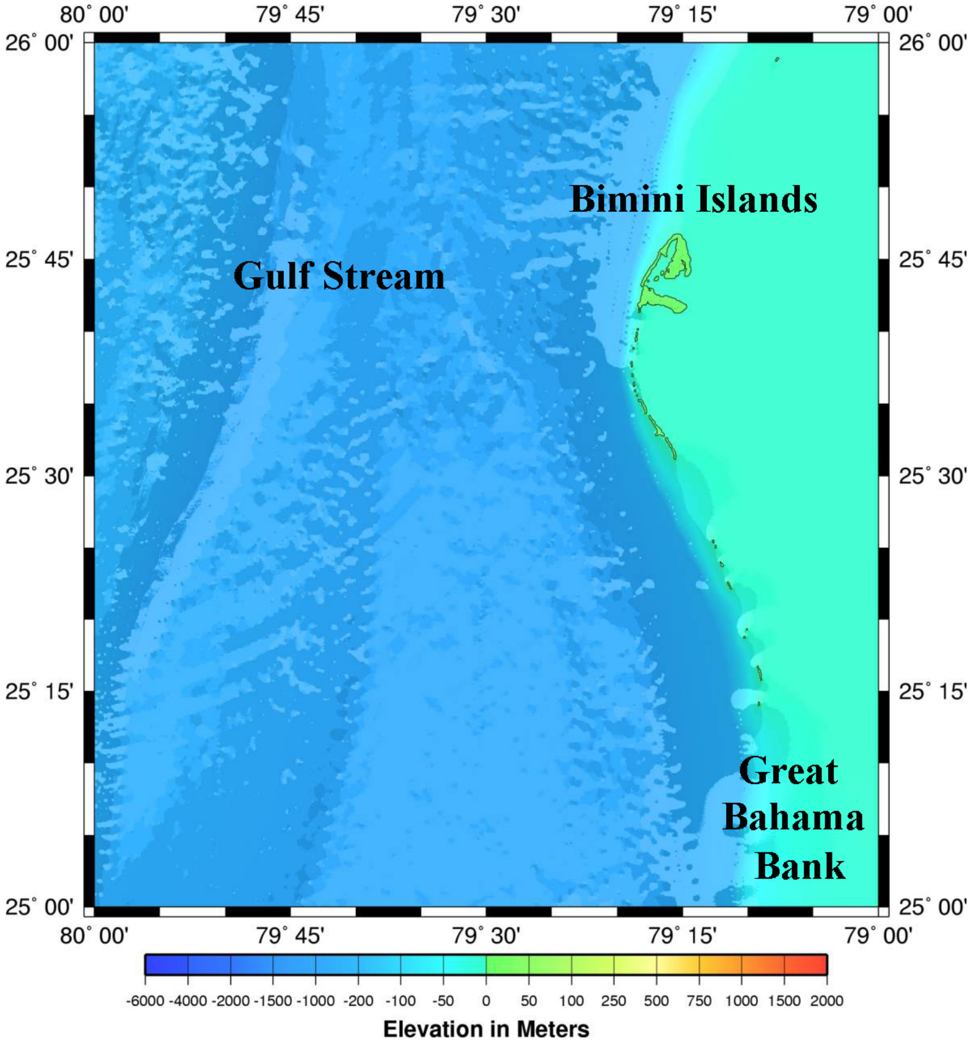

Fig. 1. Bimini Islands, Bahamas.

The islands of South Bimini and North Bimini, situated northwest of the Great Bahama Bank, are recognized as part of the shallowest tropical waters in the Western Atlantic Ocean.

Source: *NOAA National Centers for Environmental Information, U.S. Coastal Relief Model, Retrieved date goes here,* http://www.ngdc.noaa.gov/mgg/coastal/crm.html

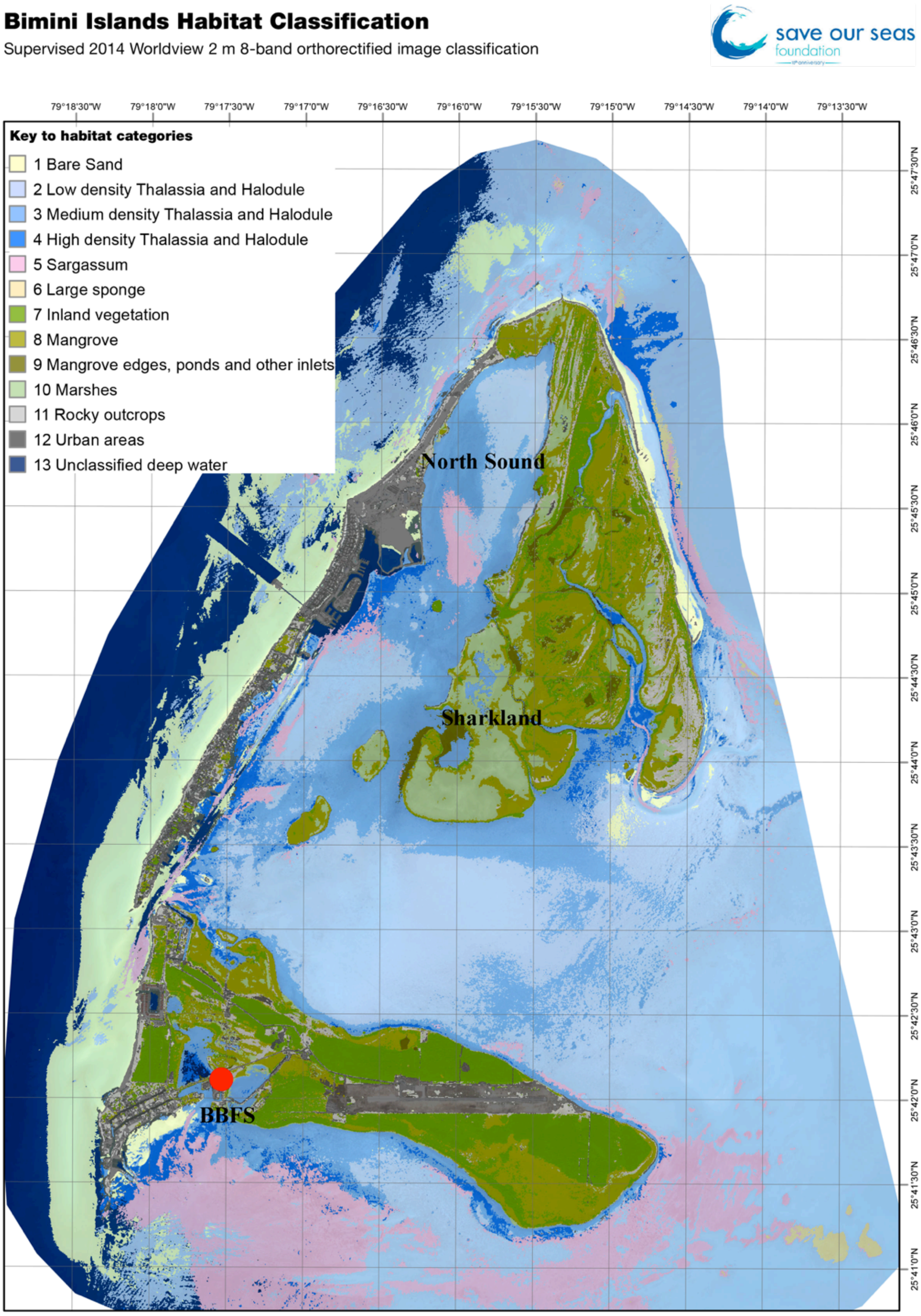

Fig. 2. Bimini islands habitats classification.

The eastern part of the study area, the North Sound, is mainly characterized by a dense mangrove canopy, a suitable environment to give birth for mature female lemon sharks exhibiting phylopatry.

BBFS: Bimini Biological Field Station.

Adapted from: *Save our Seas Foundation*

Supervised 2014 Worldview 2 m 8-band orthorectified image classification.

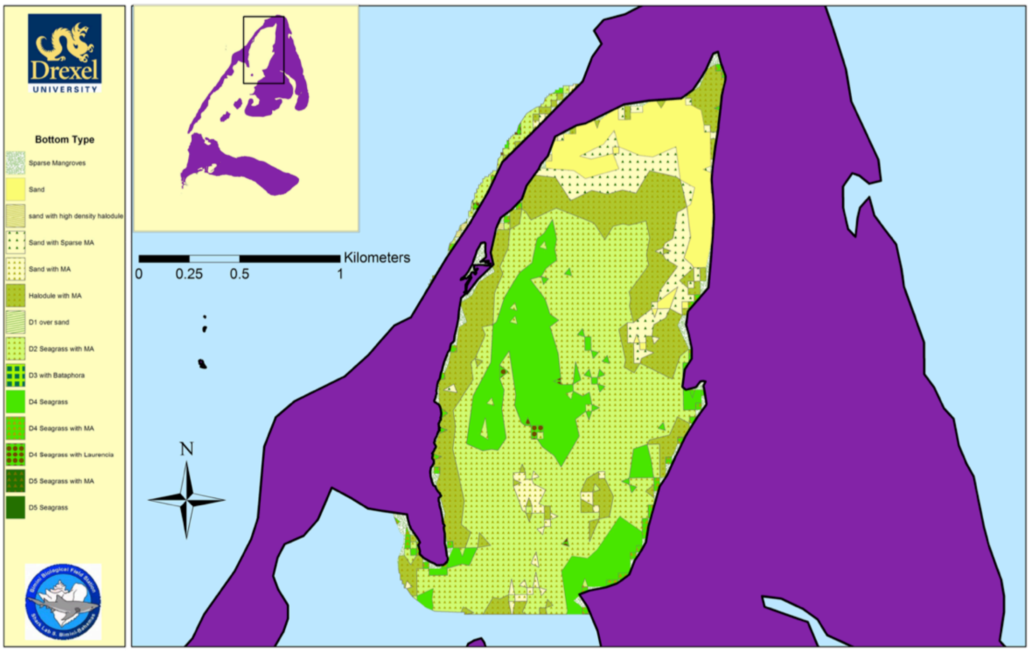

Fig. 3. Dominant bottom type of areas within the North Sound primary nursery area assessed between 2003-2006, extracted from Franks (2007). Bottom types were estimated from a LandSat 7 satellite image and groundtruthed using GPS and systematic surveys. Seagrass density ranges from D1 (sparse seagrass) to D5 (high density seagrass beds). MA is various macroalgae species. Note the mapping process occurred prior to the main disturbances.

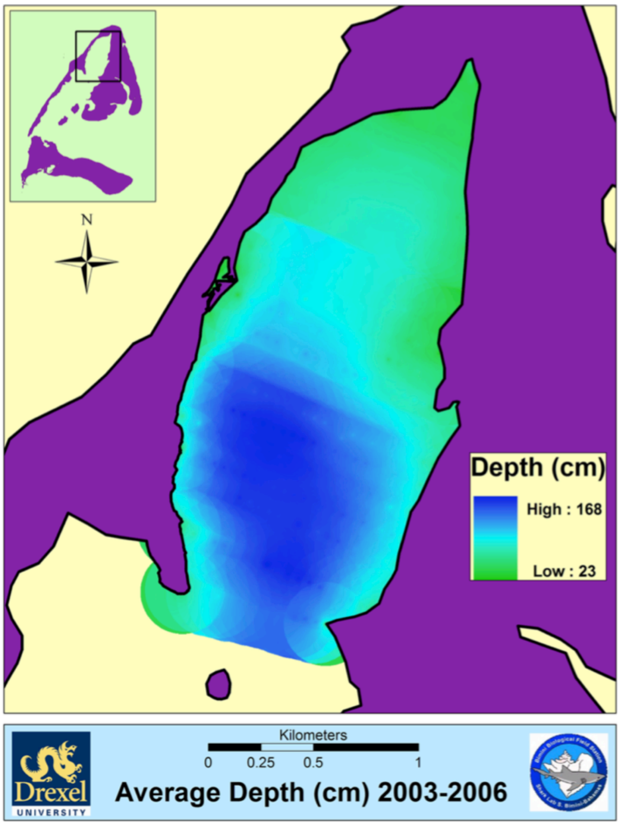

Fig. 4. Depth contour map of the North Sound nursery area showing average depth as monitored between 2003-2006. Extracted from Franks (2007).

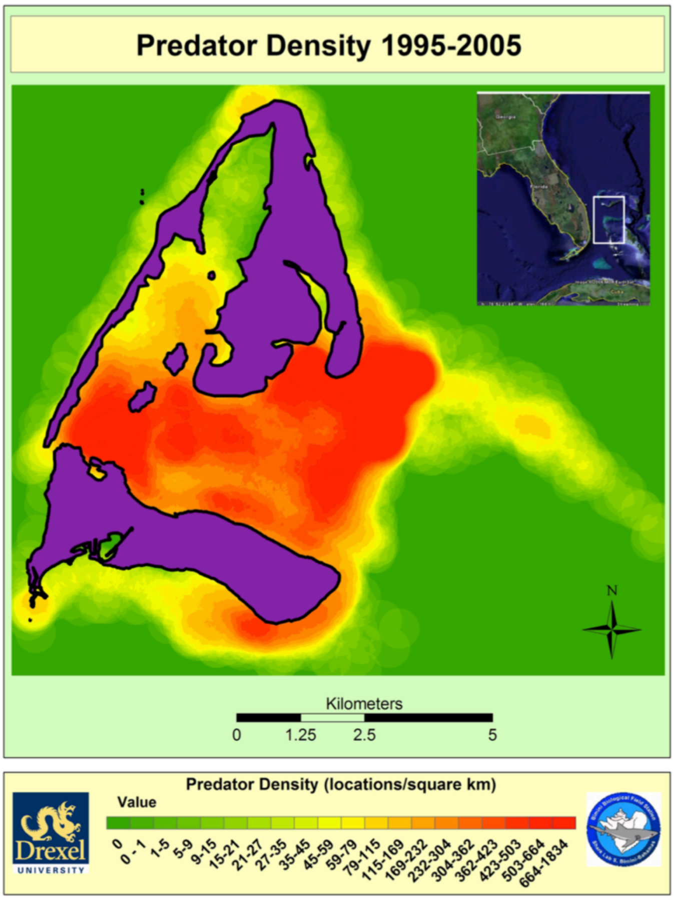

Figure 5. Predator density in the areas around Bimini, Bahamas. Density was estimated using telemetry locations of subadult lemon sharks greater than 120 cm. Green represents areas on the map that had lower numbers of subadult sharks recorded in those areas. Red represents areas on the map that have had greater numbers of subadult telemetry locations recorded in those areas. Extracted from Franks (2007).

Reference

Franks, B.R. (2007) *The spatial ecology and resource selection of juvenile lemon sharks(Negaprion brevirostris) in their primary nursery areas*.