Portfolio effect and bet-hedging adaptations in sea turtles

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Portfolio effect and bet-hedging adaptations in sea turtles

By

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Abstract

A great proportion of marine species are at risk of going extinct as a result of profound changes in the world's oceans, primarily driven by human activities. Sea turtles are not exempt from this fate. Despite sea turtles being exposed to a range of environmental conditions and threats that vary in frequency and intensity, these ancient marine reptiles have persisted for millennia. In the past, sea turtles have been able to adapt to natural perturbations while other animal groups have not. The ability of sea turtles to adapt to contemporary changes in conditions, produced by human activities, has become limited.

The persistence of sea turtles may be explained by the application of a concept termed "portfolio effect". An aggregate system is more stable and less prone to fluctuations over time (i.e. portfolio effect) if a diversity of finer components comprises the entire system and displays asynchronous fluctuations over time. Biological entities (e.g. species measured by the abundance trend) may achieve long-term stability even though the individual components (e.g. populations measured in abundance trend) display weak or negative correlations with each other in space and time. Different sea turtle populations may display independent trends in abundances over time, resulting in a portfolio effect at species levels.

Trends in sea turtle abundances may be affected by individual behaviour. The adoption of bet-hedging adaptations may enable populations to thrive despite environmental changes or stochasticity, by lowering short-term fitness in exchange for maximising long-term fitness. Individual sea turtles may exhibit bet-hedging adaptations through changes in their temporal nesting behaviour, including the remigration interval. Since remigration interval length regulates the number of nesting females per nesting season, changes in remigration interval will affect abundance trends. The ability of individuals to change their remigration interval allows them to "skip" the breeding migration when environmental conditions seem unfavourable.

The overall aim of this thesis was to investigate potential reasons for observed sea turtle abundance trends at species, population, and rookery levels. I tested whether the portfolio effect applies to sea turtles by analysing and interpreting spatiotemporal trends in loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) abundances at the population and species levels using global datasets. The application of bet-hedging strategies was tested at a local level using data from the long-term monitoring program for South African nesting sea turtles.

The majority of loggerhead rookeries displayed an increase in abundance over time, while most leatherback rookeries declined (Chapter 2). Population growth rates also differed among rookeries within Regional Management Units (RMUs) (Chapter 2). This diversity in abundance trends among rookeries suggested spatiotemporal variation in environmental conditions, threats and/or level of protection accompanying sea turtles. The species-level growth rate for both species displayed an overall increase in abundance over time. However, larger (more turtles) leatherback rookeries/RMUs experienced more rapid declines in abundance compared to smaller rookeries/RMUs, resulting in a recent species-level decline. Uncorrelated trends in abundances at the RMU-level could have stabilised species-level trends.

Differences in the remigration intervals as a possible bet-hedging adaptation could potentially explain differences in population recovery rates between South Africa's loggerhead and leatherback sea turtles (Chapter 3), but found no evidence that individuals from either species exhibit bet-hedging adaptations. Loggerheads, however, have increased their remigration intervals over time, while leatherbacks have not. These increases were accompanied by declines in adult body size (previously established) which could be an effect of diminishing foraging area quality. The increased remigration interval shown by loggerheads may be a response rather than an adaptation to the prevailing environmental conditions that impact their food supply in their foraging areas. The population growth rate of leatherback sea turtles may surpass that of the loggerheads in the near future, although there is a global decline in abundance (Chapter 2).

This dissertation provides information on possible reasons for observed trends in sea turtle abundances at various levels of biological organisation. While a variety of factors have the potential to influence trends in sea turtle abundance, the possible occurrence of portfolio effects and investigating nesting behaviour may resolve any uncertainties regarding the reasons for observed trends in abundance.

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Chapter 1 | **Introduction**

Biodiversity loss and the ongoing "Sixth Mass Extinction"

Since the emergence of life on Earth approximately 4.3 to 2.7 billion years ago (Jheeta 2013; Woolfson 2015; Jheeta 2017; Schopf et al. 2018), five mass extinction events have resulted in the massive depletion of biodiversity within short intervals of geological time (Barnosky et al. 2011; Palombo 2021; Cowie et al. 2022). Natural phenomena, such as drastic changes in Earth's temperature (Finnegan et al. 2012; Bond and Grasby 2020), eustatic sea level changes (Hallam and Wignall 1999; Sandberg et al. 2002; Kaljo et al. 2008), severe volcanic activity (Percival et al. 2017), alterations to the atmospheric concentration of oxygen (Wignall and Hallam 1992; Brennecka et al. 2011; Qiu et al. 2022), asteroid impacts and/or meteor strikes (Chiarenza et al. 2020) and the acidification of oceanic waters (Henehan et al. 2019) were primarily responsible for the rapid loss of terrestrial and aquatic diversity during these major extinction events. Even though the last mass extinction event occurring approximately 66 million years ago (Kaiho et al. 2016; Chiarenza et al. 2020), life on Earth has been exposed to multiple environmental events that have influenced the persistence of various species (Shivanna 2020). These continue into the present and are exasperated by human activities (Sandy 2017; Ceballos et al. 2020). Yet, a range of ancient species continue to survive regardless of the detrimental impacts on the biotic and abiotic components of the modern world.

In recent centuries, many component populations or entire species have vanished because of unsustainable conditions imposed by anthropogenic activities (Ceballos et al. 2017; Cowie et al. 2022). Habitat deterioration and loss (Henderson and Loreau 2018), the unsustainable use of bioresources (McDaniel and Borton 2002; Balatsky et al. 2015) and the amplification by climate change are mainly responsible for ecosystem degradation and accelerated biodiversity losses (Shivanna 2020). Consequently, direct and indirect human-related impacts on the environment have forced earth's "Sixth Mass" or "Holocene" extinction event (Barnosky et al. 2011; Cowie et al. 2022), whereby species are disappearing at unprecedented rates compared to natural background losses (De Vos et al. 2015). In contrast to historical mass extinction events, the ongoing "Sixth Mass Extinction" is thought to be driven solely by unsustainable human actions (Sandy 2017; Dasgupta and Ehrlich 2019; Ceballos et al. 2020). These losses are not only taking place on land but also in marine systems despite our perceived reduced impact on marine systems.

Marine species in peril

The marine environment has been altered greatly through the direct and indirect impacts of human activities. The overharvesting of marine resources (Myers and Worm 2003; Meissa and Gascuel 2014) and the use of the ocean as a dumping site for an excessive amount of pollutants (McKinley and Johnston 2010) has resulted in shifting oceanic temperatures (Wabnitz et al. 2018), decreased ocean productivity (Hoegh-Guldberg and Bruno 2010), the loss of critically important spawning, rearing and living habitats (Jones et al. 2004; Sánchez et al. 2019), changes in oceanic pH levels (i.e. ocean acidification, Jiang et al. 2019) and altered food web dynamics (Ullah et al. 2018; Tekwa et al. 2022). The contemporary deterioration in ocean health (Gyles 2011; Halpern et al. 2017) yields detrimental consequences for marine communities, species, and individual populations. As a consequence, a great proportion of marine species are at risk of extinction due to the profound human-induced changes in the world's oceans (Webb and Mindel 2015; Boyce et al. 2022).

Migratory marine species are not exempt from the current pressures prevailing in the earth's natural ecosystems; they are dependent on a range of environmental conditions as they migrate between various ocean regions to reproduce and/or to find food and shelter (Dingle and Drake 2007). Because they move beyond national boundaries it is complicated to protect or manage these species (Dunn et al. 2019). As a result, many migratory marine species experience population extirpations and/or extinction (Lascelles et al. 2014). For example, whale shark (*Rhincodon typus*) sightings at Ningaloo Reef, Western Australia, have shown major declines even though whale sharks were protected within Australian waters (Bradshaw et al. 2008). The broad range of these whale sharks exposed them to lower levels of protection when migrating outside national boundaries.

Sea turtles have multiple ecological roles and perform a variety of ecosystem services, ranging from serving as food sources to having sociocultural value. They also regulate ecosystem functioning by reducing the transmission rate of infectious diseases, influencing nutrient cycles (e.g. Williams et al. 2018) and maintaining overall natural ecosystem functioning by structuring communities (e.g. green turtle *Chelonia mydas*) grazing on seagrass meadows;

Scott et al. 2020). As such, it is a concern that many marine species, including sea turtles, are experiencing population declines. The continued persistence of sea turtles is critical to ensuring that all the benefits provided by them are maintained.

Sea turtle populations continue to persist

Sea turtles are under pressure from both natural and non-natural sources. Natural threats such as terrestrial and marine predators also influence the survival of sea turtles (Marco et al. 2015; Wilson et al. 2019). Despite these threats, many populations have recently increased in abundance (Mazaris et al. 2017). Common anthropogenic (non-natural) threats faced by sea turtles include fisheries bycatch (Wallace et al. 2010b; Swimmer et al. 2017), the introduction and/or spread of pathogens and ingestion of pollutants e.g. plastic pollution (Sarmiento-Ramírez et al. 2014; Eastman et al. 2020), entanglement in “ghost gear” (Wilcox et al. 2016; Duncan et al. 2017), targeted harvesting of eggs or adults (Fendjalang et al. 2017; Pheasey et al. 2020), habitat loss through infrastructure development on or near sea turtle rookeries (Lopez et al. 2015; Fuentes et al. 2020) and/or climate change (Fuentes et al. 2011; Katselidis et al. 2014).

Explaining trends in sea turtle abundances: “Portfolio effect” and bet-hedging adaptations

Sea turtles are an ancient group of animals that has roamed the ocean for over 100 million years and some species outlived the dinosaurs even when the earth experienced drastic environmental changes and catastrophes (Nie et al. 2015; Lovich et al. 2018; Martín-Del-Campo and Garcia-Gasca 2019). In the past, sea turtles have been able to adapt to changing conditions and some species have subsequently persisted. However, modern anthropogenic activities have added additional pressures on populations. As a result, various conservation efforts have been established to counteract human interference. However, trends in sea turtle abundances continue to fluctuate independently, even though the conservation efforts put in place and the frequency and intensity of threats might be similar.

The conditions to which sea turtle populations are exposed to vary over space and time, producing different trends in abundance. As a result, some sea turtle populations are experiencing increases in population size, while other populations are declining during similar time periods (Mazaris et al. 2017). For example, the annual number of loggerhead (*Caretta*

caretta) sea turtle nests located along the shoreline of Grand Cayman, Cayman Islands, increased from the 2000s to the late 2010s (Blumenthal et al. 2021), while a rapid decline in the number of loggerhead nests was evident during the same time interval at Masirah Island, Oman (Willson et al. 2020). Individuals from some populations have been able to adapt to their local changes in conditions, while other populations have not. Because some populations may be increasing in abundance and act as a buffer to other populations in decline, it is possible that a "portfolio effect" is evident at the species-level, facilitating persistence.

The "Portfolio effect"

A financial portfolio proposes that an investor can minimise the risk of financial ruin and (probabilistically) guarantee (more) stable returns by splitting capital investments into a range of schemes resulting in a diversified portfolio (Markowitz 1952; Ball and Brown 1969; Omisore et al. 2012). This portfolio concept has been used to explain stability in ecological systems across different components such as populations, species, and communities (Schindler et al. 2015). The portfolio effect predicts that biological entities may achieve long-term stability if individual components are weak or negatively correlated with each other in space and time (Schindler et al. 2015) by responding to the immediate environment.

Various studies have illustrated how an increase in species richness and diversity can stabilise entire ecosystems and communities, if the species comprising the community show varied responses to environmental changes, whereby a decline in the abundance of one species is buffered by the increase of another species (Hooper et al. 2005; Cleland 2011). For example, an experiment illustrated how the species composition of plankton communities changed drastically following the acidification of lakes, but total plankton biomass displayed limited changes (Schindler 1990). Total plankton biomass remained stable because some species were able to adapt to the change in lake conditions, while other populations declined.

Portfolio effects were expressed at the community level (i.e. total plankton biomass) as a result of the diversity of species and varied responses to changing conditions within the system. Individuals, populations, or species are more susceptible to change than collective systems (e.g. populations, species, or communities). A change in a particular property (e.g. abundance of a single population) may not affect the success of the collective system (e.g. species decline/growth), because the populations operate independently by being distributed unevenly through space. Thus, the particular demographic, behavioural or phenological parameter may remain stable at the species or population level across space and time because the individual components (i.e. populations or individuals, respectively) respond independently to their own prevailing environmental conditions and/or threats. It is therefore likely that different sea turtle populations display independent trends in abundances over time, if the rookeries are independent (i.e. geographically isolated). A diversity of demographic responses may reflect portfolio effects at species or global levels, which could serve as a possible explanation as to why sea turtles may have persisted for millions of years, when other reptiles could not.

Bet-hedging adaptations

The abundance of sea turtle species at the local scale may include bet-hedging strategies to deal with environmental stochasticity. Highly variable environments may favour particular organismal traits during modal conditions, while disfavouring them during disrupted periods (Childs et al. 2004; Simons 2009; Greene et al. 2010). As a result, individuals comprising a population, or the population itself, may have a reduced risk of losing an entire generation of offspring by utilizing a bet-hedging strategy that lowers the short-term fitness (e.g. between years, between generations etc.) in exchange for maximising the long-term fitness of the individual or population (Olofsson et al. 2009; Simons 2011). These bet-hedging strategies differ among species and locations.

Three types of bet-hedging strategies have been identified; “conservative”, “diversified” and “adaptive coin flipping” behaviours (Olofsson et al. 2009), which are differentiated based on the number of tactics used and when they are applied. These range from single strategies to consistent multiple strategies or varied strategies. The simplest of these being conservative strategies. “Conservative” bet-hedging involves organisms expressing only a single trait/strategy to avoid individual-level risk of either dying and/or losing a great number of offspring (Olofsson et al. 2009; Childs et al. 2010; Haaland et al. 2019). For example, by commencing flowering earlier in the growth season, Indian tobacco/puke weed (*Lobelia inflata*) avoid potentially unpredictable environmental conditions near the end of the growing season (Simons and Johnston 2003). Gremer and Venable (2014) illustrated how winter annual plants in the Sonoran Desert delayed seed germination to reduce overall variability in survival over time. A proportion of the seeds remained dormant and acted as a buffer should the germinating seeds experience a complete germination failure. Because the main purpose of flowering in plants is to reproduce, the adoption of a conservative bet-hedging strategy might enable various populations of angiosperms to avoid complete extirpation.

Another bet-hedging strategy minimises the overall variability in survival by occupying a range of different strategies (Olofsson et al. 2009). This kind of behaviour is known as a "diversified" bet-hedging strategy, which is centred around not "putting all your eggs into one basket" and instead spreading the risk of losing an entire generation of offspring (Childs et al. 2010; White et al. 2013) by minimising the correlation in the probability of survival between individuals comprising the same population (Starrfelt and Kokko 2012), which may ultimately result in lowering variation in the long term fitness of an individual and/or of offspring.

Diversified bet-hedging strategies are evident in San Diego (*Branchinecta sandiegonensis*) and Riverside (*Streptocephalus woottoni*) fairy shrimp that occupy vernal/ephemeral pools situated in Southern California, United States (Simovich and Hathaway 1997). The unpredictability in the frequency and intensity of rainfall events has resulted in both species being exposed to unpredictable environmental conditions, increasing the variability in survival of shrimp that need a substantial volume of water to mature and successfully reproduce. As a result, both species use a diversified bet-hedging strategy whereby only a proportion of cysts produced hatch upon first contact with water, while the remaining cysts remain dormant until another point in time (Simovich and Hathaway 1997). Spreading hatching dates reduced the risk of losing an entire generation of shrimp during periods when water volume was low.

Another example of diversified strategy is Agassiz's desert tortoises (*Gopherus agassizii*) in Palm Springs, California, United States (Lovich et al. 2015). The terrestrial environment for these tortoises is highly variable with unpredictable resource availability. The tortoises spread their reproductive risk of losing a large seasonal clutch by laying multiple small clutches annually regardless of rainfall and/or food resource availability (Lovich et al. 2015). This example illustrates how not "putting all your eggs into one basket" could potentially reduce the risk of losing an entire generation of offspring. In a world characterised by environmental unpredictability and uncertainty, the use of conservative and/or diversified bet-hedging strategies may enable multiple species to persist in highly variable natural ecosystems.

A third type of bet-hedging strategy, called "adaptive coin flipping" involves individuals selecting which strategy to use at any given point in time, whereas a different strategy may be adopted in the future (Olofsson et al. 2009) depending on the predicted and perceived environmental conditions. For example, wild boar (*Sus scrofa*) residing in stochastic environments minimised the among-year variation in reproductive success by large females with a heavier body mass producing mixed-weight offspring with a mixture of both heavy and light piglets over time (15-year period), whereas lighter-weight adults produced offspring of similar sizes (Gamelon et al. 2013). Larger-bodied females exhibit an "adaptive coin flipping" bet-hedging strategy within their unpredictable environment by taking a chance to produce lighter (more vulnerable) offspring during some years and heavier offspring (less vulnerable) during other time periods.

The main difference between conservative bet-hedging, diversified bet-hedging, and adaptive coin flipping is that the latter does not exhibit a strategy based on an informed decision but rather a stochastic/random choice made by an individual. Conservative and diversified bet-hedging attempt to minimise the variation in fitness among years. It is possible that some sea turtle species (and/or populations) exhibit bet-hedging adaptations, which could potentially help explain why some sea turtle populations have been able to persist for as long as they have.

The ability of organisms to change their behaviour (i.e. exhibit bet-hedging adaptations) over time reflects whether they can be regarded as being specialists or generalists. Specialist species include organisms with narrow niche breadths and limited capabilities to change their habitat, dietary needs and/or behaviour as environmental conditions change (Kassen 2002; Terraube et al. 2011). In contrast, generalists utilise a wide range of resources and/or exhibit the ability to change behaviour and can survive in a diversity of environments (Ducatez et al. 2015; Böhm et al. 2017; Mills et al. 2020). Generalist species may have a lower risk of extirpation resulting from their plasticity in distribution, diet and/or behaviour and, consequently, survive environmental changes, including human-induced changes (Ramiadantsoa et al. 2018). Some sea turtle populations are suggested to be generalists with diversified and/or adaptive coin flipping bet-hedging strategies (e.g. displaying variable remigration periods), which would improve the overall fitness of individuals and populations.

Individual sea turtles may exhibit bet-hedging adaptations through temporal changes in their nesting behaviour, specifically altering the remigration interval. The remigration interval, defined as the time period between two successive nesting seasons, is critical in determining lifetime reproductive success or fitness (Cheng et al. 2018). Shorter remigration intervals may be associated with healthier foraging ground conditions (Saba et al. 2007; Hatase et al. 2013), shorter distances between nesting grounds and foraging sites (Troëng and Chaloupka 2007) or may be linked to the health of individual sea turtles (Hatase and Tsukamoto 2008). Sea turtles respond to changing environmental conditions in their foraging area by either shortening or lengthening their remigration intervals during favourable and unfavourable environmental conditions, respectively (Hays 2000; Reina et al. 2009; Girard et al. 2021). If conditions improve, shortened remigration intervals will result in more frequent nesting seasons.

As a result, trends in sea turtle abundance in the nesting area may (partly) be explained by the changes (and synchronicity) of the remigration interval of individuals. If sea turtles are able to "bet-hedge" their remigration intervals it may allow populations to prosper. Bet-hedging seasonal nesting migrations may buffer reproductive success against environmental disruptions, which would ultimately increase survival. Variability in sea turtle abundances at the rookery scale could be explained by the flexible temporal nesting intervals of individuals.

The subdivision of sea turtles into individual populations: Regional Management Units (RMUs)

Sea turtles have seven extant species with the family Cheloniidae consisting of the six hard-shelled turtle species, including the Loggerhead, and family Dermochelyidae having a single representative (Steele et al. 2008), the Leatherback (*Dermochelys coriacea*). Wallace et al. (2010a) divided the world's extant marine turtle species into a total of 58 Regional Management Units (RMUs), based on satellite telemetry distribution, nest location, and genetic data. These RMUs are separate population segments, comprising one or several rookeries (Wallace et al. 2010a; Wallace et al. 2023). Loggerhead and leatherback sea turtles are composed of 10 and seven RMUs, respectively, and will act as study species for this investigation. By investigating the temporal trends in loggerhead and leatherback sea turtle abundances across their RMUs, it could indicate that the portfolio effect is evident at the species-level. Only loggerhead and leatherback sea turtle trends will be investigated here but it is assumed that the result is relevant to the other species and serves as a possible explanation as to why extant sea turtle species may have persisted.

It is possible that variability in an abundance trend is related to the size of the RMU. Habitat diversity increases with area (Kallimanis et al. 2008; Macdonald et al. 2018), and population segments that exploit a larger ocean space should sample a greater diversity of environmental conditions (which has a positive effect) and threats (which could have a negative effect), which may result in differing responses by populations and/or individual sea turtles. Sea turtle populations using larger ocean space (i.e. larger RMU areas) may have a more stable abundance trend over time, while sea turtle populations using smaller ocean spaces may have greater variability in abundance over time as a result of lower habitat heterogeneity.

Regional Management Units as part of a metapopulation

Every sea turtle species may potentially be regarded as being a metapopulation, because every species consists of several population segments (i.e. RMUs) that are spatially segregated (Wallace et al. 2010a; Wallace et al. 2023). Metapopulations are thought to be more resilient than a species consisting of only a single large population occupying a single geographic location (Molofsky and Ferdy 2005). A metapopulation, however, is defined as a large population consisting of various smaller populations that are spatially separated but with some level of interaction among population segments i.e. dispersal of individuals between populations (Kritzer and Sale 2004; Shtilerman and Stone 2015; Lin 2022) and structured genetically by gene flow (Harrison and Hastings 1996; Kunz et al. 2021).

Despite some similarities shared between portfolio effect and metapopulation theory (Anderson et al. 2013) in the form of spreading risk among population segments, differences exist. Gene flow associated with the exchange of individuals among populations is a key characteristic of metapopulations, while portfolio effects may solely be evident as a result of different populations responding independently to changing local conditions (Schindler 1990). Portfolio effects may thus be evident at higher levels of biological organisation (e.g. species-level) as a result of populations showing contrasting responses in their productivity (Hilborn et al. 2003) or abundance, irrespective of whether gene flow occurs or not.

Because of fairly strict natal philopatry (Lohmann et al. 2013), sea turtles cannot convincingly be considered as metapopulations. However, the overlap in portfolio effect concept and metapopulation theory is that sea turtle species are composed of several populations that are spatially (and mostly genetically) segregated and sea turtle species may be more likely to persist, because the loss of one component population will not result in the extinction of the entire species.

South African sea turtles as a case study for bet-hedging

Two species of sea turtles nest along the sandy beaches of iSimangaliso Wetland Park in Maputaland, South Africa, namely the loggerhead and leatherback sea turtles. Historically, nesting South African sea turtles were harvested as a source of nutrition (McAllister et al. 1965) and potential monetary value (Hughes 1980). Given the growing concern at the time regarding the survivorship of South African sea turtles, a field-based protection and monitoring program was established in 1963. Since then, loggerhead and leatherback sea turtles have received increasing protection efforts through the implementation of a series of coastal and marine protected areas (Hughes 1973; Nel et al. 2013) in an attempt to increase population growth rates.

Given the equal treatment of both species, nesting South African sea turtles serve as appropriate candidates to investigate the nesting behaviour and strategies of sea turtles. Because South African sea turtles have been monitored since 1963, one of the most extensive global datasets on nesting patterns are available. Further, even though these sea turtles have received identical levels of conservation protection in iSimangaliso Wetland Park, the population recovery rates between the two species differ with the loggerheads increasing in abundance over time, while leatherbacks are stable. The reasons for these differences are uncertain (Nel et al. 2013). Various possible reasons have been proposed including differing reproductive outputs, male to female ratio disparities, incorrect quantification of abundances as a result of unobserved nests/tracks or possible differences in their offshore mortality rates (Nel et al. 2013). However, it is also possible that potential differences in the temporal nesting behaviour of loggerhead and leatherback sea turtles could serve as an explanation for the observed differences in seasonal abundances.

Temporal nesting behaviours that could affect trends include remigration period. Loggerhead sea turtles may, for example, have shorter remigration intervals compared to the leatherback sea turtles, which would encourage more rapid population growth rates in the former. Shorter remigration intervals may be associated with a larger number of nesting females (Bjorndal et al. 1999; Troëng and Chaloupka 2007) and, thus, a greater total number of clutches per nesting season, while longer remigration intervals may be related to fewer total clutches being deposited per season (Price et al. 2004; Shaver et al. 2016). It is possible that the behaviour differs between the species; individuals from one species may show consistency in their remigration period, whereas individuals from the other species may have changed their remigration intervals as conditions changed (Nel et al. 2013) or as an individual becomes an experienced nester (e.g. learn to change remigration interval with age to improve hatching success/hatchling survival).

The ability of organisms to change their remigration intervals may, however, benefit the entire population if individuals are able to undertake the breeding migration less frequently and thus limiting their exposure to adverse environmental conditions. Thus, sea turtles may deploy a "diversified" bet-hedging strategy by changing their remigration interval to nest during optimal conditions, or deploy an "adaptive coin flipping" strategy, whereby they return to the nesting sites with no particular pattern in their remigration interval regardless of favourable conditions or not. Sea turtles that use "diversified" and/or "adaptive coin flipping" bet-hedging remigration strategies may be regarded as temporal generalists, while individuals with consistent remigration interval values may be referred to as temporal specialists.

There is, however, a trade-off between short term and long term reproductive fitness using bet-hedging strategies. The adoption of a bet-hedging strategy by individuals of one population may lower fitness during shorter time periods in exchange for the average long-term fitness becoming maximised (Olofsson et al. 2009; Simons 2011). Such a population may appear to be in decline during certain time periods compared to a population whereby bet-hedging adaptations are absent with consistent numbers arriving irrespective of environmental conditions. Thus, it may appear that South Africa's nesting leatherback sea turtles are doing poorly compared to the loggerheads (Nel et al. 2013), but it is possible that the leatherback sea turtles are better equipped to deal with anticipated environmental challenges by exhibiting variation in the remigration intervals of individual sea turtles.

Dissertation outline

Given the potential explanations provided by portfolio effect to stabilise species and population trends or bet-hedging strategies to explain variations in interannual nesting abundance, the overall aim of this thesis is to test some of these potential reasons for observed sea turtle abundance trends at species, population and rookery levels. Firstly, I will investigate if the portfolio effect applies to sea turtles by i) analysing spatiotemporal trends in loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) abundances at the RMU (population) and species levels, ii) determining if there is a relationship between RMU extent (exploiting larger oceanic space) and population stability, i.e. show if the fluctuation in abundance is inversely related to RMU size. Secondly, I will analyse remigration periods for the South African rookery and test if the abundance trends could be explained by their temporal nesting behaviour (and possible associated bet-hedging adaptations). If there are differences among the species it could potentially explain the different population recovery rates between South African loggerhead and leatherback sea turtles.

The breakdown for this dissertation is as follows:

Chapter 1 – Introduction: The aim of this chapter was to review literature related to the current state of sea turtles, introduce the portfolio effect and bet-hedging strategy concepts. It is also to discuss the potential relationship between theory and practice by applying it to abundance trends and remigration intervals of sea turtles.

Chapter 2 – The portfolio effect and persistence of sea turtle species and populations: The aim of this chapter is to compare RMU abundance trends over time (due to differences in sea turtle life histories and/or threats across RMUs) and whether the diversity of abundance trends across RMUs resulted in stable species trends i.e. a portfolio effect at the species-level. Also, this chapter aims to determine whether the extent of variability in sea turtle abundances is a function of the relative size of each RMU (i.e. area).

Chapter 3 – Nesting behaviour and bet-hedging adaptations in loggerhead (Caretta caretta) and leatherback (Dermochelys coriacea) sea turtles: This chapter aims to determine whether differences in the remigration intervals and the possible occurrence of bet-hedging adaptations could serve as explanations for the differences in population recovery rates between South Africa’s nesting loggerhead and leatherback sea turtles.

Chapter 4 – Conclusion: The final chapter of this thesis includes a brief summary and interpretation of the findings from the various content chapters of this dissertation, as well as a discussion on what the findings suggests in relation to sea turtle conservation and management.

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Chapter 2 | **The portfolio effect and persistence of sea turtle species and populations**

Abstract

Understanding the persistence of threatened species requires information regarding both past and recent trends in abundance. Environmental conditions and threats differ spatiotemporally, which may produce asynchronous trends in abundance among populations of a single species. If the overall species-level trend in abundance is stabilised, it is referred to as a "portfolio effect". Population trends for loggerhead, *Caretta caretta*, and leatherback, *Dermochelys coriacea*, sea turtles were obtained from time series data sets of annual nesting abundance for 173 rookeries (n=98 for *C. caretta* and n=75 for *D. coriacea*). Most loggerhead rookeries displayed an increase in number of nests, whereas most leatherback rookeries declined. When abundance trends were averaged within Regional Management Units (RMUs) using both "unweighted by rookery size" and "weighted by rookery size" methods, five loggerhead RMUs displayed increasing abundances, and four RMUs declined. For leatherbacks, four of seven RMUs displayed declines in abundance using an "unweighted" method, while only two RMUs experienced declines using the "weighted method. At the species-level, loggerheads have been reasonably stable, with a slight (contemporary) increase in the number of nests. Leatherbacks have also experienced an (initial) increase in abundance at the time of monitoring despite some RMUs displaying clear declines. However, when weighted, leatherbacks experienced a rapid decline since the 1980s while when unweighted, declines were observed since the 2000s. Larger leatherback rookeries declined faster than smaller rookeries. Nevertheless, both species appear to have "portfolio effects" at both RMU and species-levels. Maintaining diversity, even of small rookeries/populations, should be the central focus of conserving biodiversity.

Keywords

Portfolio effect; time series; annual nesting abundance; Regional Management Unit; *Caretta caretta*; *Dermochelys coriacea*

Introduction

Sea turtles are considered to be one of the most threatened groups of animals globally (Lascelles et al. 2014) and face a multitude of threats in the terrestrial and marine environments (e.g. Wallace et al. 2010b; Sarmiento-Ramírez et al. 2014). In addition, they are highly migratory (Briscoe et al. 2016; Godley et al. 2020), long-lived (Gibbons and Semlitsch 1982), slow maturing (Scott et al. 2012), exhibiting iteroparous reproduction with high fecundity (Davenport 1997) but low survivorship from hatchling to adulthood (Campbell and Lagueux 2005; Robinson et al. 2021). Most of these life-history characteristics of sea turtle populations render them vulnerable to (rapid) change in conditions.

Sea turtles have, however, persisted for over 100 million years (Martín-Del-Campo and Garcia-Gasca 2019; Godley et al. 2020) and have been able to adapt to changing conditions. However, human activities have contributed towards ongoing global changes (e.g. climate change). Sea turtles are forced to adapt to local changes in conditions to persist. Populations at a regional scale have shown both increasing (Mazaris et al. 2017) and decreasing (e.g. Willson et al. 2020) trends in abundance, possibly resulting in the species trend remaining more-or-less stable over long periods of time. Therefore, it is hypothesised that the portfolio effect may have facilitated the persistence of sea turtles in the past.

The portfolio theory borrowed from finance supposes that an investor can minimise the risk of financial devastation and (probabilistically) guarantee stable returns by investing capital into a range of financial schemes resulting in a diversified financial portfolio (Markowitz 1952; Ball and Brown 1969; Omisore et al. 2012). Similarly, the portfolio effect as a concept has been applied to biological systems including communities, species or populations (Schindler et al. 2015). The portfolio concept in ecology (also applied as bet-hedging; Simons 2011) predicts that larger systems are more stable in the long term if the individual components comprising the larger system do not behave in the same manner in space and time (Schindler et al. 2015). Individual components comprising a larger system will show different trends and/or patterns in some biological parameter due to the non-uniformity of the prevailing environmental conditions. The portfolio concept therefore suggests that individual biological components (species, populations, subpopulations, or individuals) are more susceptible to change than the combined system (communities, species or populations) resulting from weak/negative correlations among the finer-scale components over time (Schindler et al. 2015).

A classic example of the portfolio effect operating on a natural population is the sockeye salmon stock complex (*Oncorhynchus nerka*) situated in Bristol Bay, Alaska. This sockeye salmon stock complex demonstrates how diverse population-level adaptations in a range of life history characteristics result in overall stability (Hilborn et al. 2003). The entire stock comprises of multiple sockeye salmon populations with the individual populations residing in different habitats that experience distinct environmental conditions. The numerous sockeye salmon populations have become adapted to their own unique spawning and incubation environments, resulting in dissimilar life history traits (e.g. spawning times, extent of rearing periods, time spent at sea, time of adult arrivals to freshwater etc.; Hilborn et al. 2003).

The diversity of life history traits evident among the different sockeye salmon populations has allowed the Bristol Bay stock complex to retain long-term stability even though unfavourable local environmental conditions result in instability within separate populations (Hilborn et al. 2003). Naknek-Kvichak, Egegik and Nushagak represent three of the primary locations where fishermen commonly target sockeye salmon within Bristol Bay (Dann et al. 2013; Schoen et al. 2017). From the early 1900s to the early 2000s, all three stocks fluctuated, experiencing periods of both high and low productivity. However, the independent responses through local adaptations enabled the Bristol Bay sockeye salmon stock to remain relatively stable for a century and so to survive through various environmental disruptions (Hilborn et al. 2003). It is possible that the portfolio effect (spread of risk among diverse locations and with a suite of local adaptations) has enabled other marine animals, such as sea turtles, to avoid complete extirpation.

Trends in sea turtle abundance is influenced by multiple factors, such as clutch frequency (Mazaris et al. 2008) and/or clutch size which can also be related to the size of adults (Le Gouvello et al. 2020), nesting season period and the extent of foraging times i.e. remigration interval (Hays 2000). Also, the foraging behaviour of individuals (Hawkes et al. 2006) and the quality of foraging grounds may have an influence on abundance (Arendt et al. 2013; Cardona et al. 2014). However, a change in local conditions may result in some populations adapting to such a change by displaying behavioural or phenological modifications. Populations may, for example, respond to changing environmental conditions by altering their remigration intervals (Reina et al. 2009). As a result, changing local environmental conditions, in combination with type and intensity of anthropogenic threats, may drive differences in abundance trends among spatially segregated populations.

Similar to the sockeye salmon stock complex of Bristol Bay, all seven sea turtle species are divided into different population segments referred to as Regional Management Units (RMUs), each comprising single or multiple rookeries (Wallace et al. 2010a; Wallace et al. 2023). These 58 RMU designations were based on satellite telemetry distribution, nest location and genetic data (Wallace et al. 2010a; Wallace et al. 2023) and are maintained by various life history traits, such as natal philopatry. The distribution during the nesting season as opposed to non-nesting seasons drive the genetic differentiation among different RMUs.

The prevailing environmental conditions and threats within RMUs vary spatially and temporally, and as a result, trends in sea turtle abundance vary among RMUs. For example, the number of loggerhead nests of Grand Cayman, Cayman Islands in the Caribbean Sea, showed a significant increase in density from the 2000s to the late 2010s (Blumenthal et al. 2021), while the annual number of loggerhead nests showed a rapid decrease during the same time period at Masirah Island, Oman in the Indian Ocean (Willson et al. 2020). Populations unable to adapt to their local conditions may experience declines in abundance, while other populations may experience increased abundances by employing effective adaptive mechanism(s) to their conditions. Portfolio effects may be evident in RMU and species trends. Rookeries experiencing an increase in abundance may have a buffering effect on declining rookeries, and RMU trends may buffer species trends. Global loggerhead and leatherback abundance trends (respectively) could remain stable over time, because declines in abundance across a particular time period within one RMU may be counteracted by rapid increases in abundances in other sea turtle RMUs.

The extent of variability in sea turtle abundances may be related to the size of the area that a RMU covers. Habitat diversity increases with area (Kallimanis et al. 2008; Macdonald et al. 2018). RMUs which occupy a larger ocean space may sample a greater diversity of environmental conditions and threats, which may result in differing responses by populations and/or individual sea turtles. Thus, it might be possible that broader distributed populations (i.e. larger RMU areas) may have a more stable overall trend in abundance over time, whereas sea turtle populations using smaller ocean spaces may have greater overall variability in abundance over time resulting from lower habitat heterogeneity.

The Theory of Island Biogeography (IBT) states that island size and distance from mainland influences immigration and extinction rates (MacArthur and Wilson 1967; Whittaker et al. 2017), whereby larger islands can support more species and/or larger populations as a result of greater habitat diversity and resources. Because habitat diversity increases with area (Kallimanis et al. 2008; Macdonald et al. 2018), larger oceanic spaces may provide populations with more opportunities to adapt should local conditions change compared to populations utilising smaller ocean spaces. If variability in population abundance is a function of RMU size (i.e. area), and thus the diversity of environmental conditions or habitats, then it becomes important to detect a diverse range of habitats that requires protection and management, which would limit variability in sea turtle abundance.

The ability of individuals to adapt to changes in local conditions may be more likely compared to populations utilising smaller areas with limited ranges. In addition, since conditions experienced among rookeries occupying larger RMU areas may differ, some populations may be able to adapt to local conditions while others will not. Increasing populations may thus have a buffering effect on declining populations (Schindler et al. 2015), resulting in a more stable RMU trend. Turtles utilising nesting habitats in smaller RMUs may be exposed to the same conditions and will be more likely to respond (i.e. adapt) in the same manner. This will result in a greater degree of RMU-level fluctuations in abundance, if conditions change within smaller RMU areas. Investigating whether the portfolio effect applies to sea turtles, as well as whether variability in sea turtle abundances is a function of RMU size (i.e. area), may provide insights as to whether local adaptations to conditions has allowed sea turtles to persist at species levels.

Investigating whether the portfolio effect is evident within global-scale sea turtle abundance trends by comparing species-level and RMU-level trends in abundance over time should provide insights into the robustness of populations to survive future perturbations (Schindler et al. 2015). Further, determining if populations occupying small versus large habitat spaces/areas are more prone to fluctuations in abundances over time will reveal the importance of maintaining a diversity of oceanic habitats to sea turtles.

It is thus possible that the occurrence of a set of sub-populations, all of which experience independent trends in abundances over time as a consequence of differences in the life histories and threats faced by sea turtles, may have resulted in the global sea turtle trend in abundance remaining "stable" over long periods of time, facilitating their persistence.

The aim of this investigation is to determine if different sea turtle RMUs display synchronous variation in abundance trends over time or not. It is assumed that if variation in abundance is not synchronous, the diversity of abundance trends across RMUs (i.e. time effect) resulted from biological complexity in each population and habitat (i.e. space effect) which is evidence of the portfolio effect at the species-level. The objectives are to (1) investigate global trends over time in both loggerhead and leatherback abundances within their respective RMUs and to (2) determine whether the extent of variability in abundance is a function of RMU size. It is hypothesised that loggerhead and leatherback sea turtles within rookeries and their RMUs will display independent trends in abundance over time (because of experiencing different environmental conditions and local adaptations to resist change) with an overall stabilising effect on their respective RMU and species-level abundance trends. Further, it is hypothesised that populations of sea turtles that exploit a greater (surface) area of oceanic environments (i.e. larger RMUs) show less overall variability in abundance (because populations are exposed to a greater diversity of environmental conditions and have a larger habitat available) compared to populations exploiting smaller areas.

Materials and methods

Ethics

Secondary data were sourced from published and unpublished literature. No primary data were collected.

Data collection

Time series of loggerhead and leatherback sea turtle nesting numbers were collated from various literature sources, including data for individual rookeries from peer-reviewed and grey literature (e.g. annual monitoring reports, newsletters, symposium conference proceedings and internet sources). Nesting locations for each sea turtle species were identified using the Marine Turtle Specialist Group Reports (MTSGP reports, available at https://www.iucn-mtsg.org/regional-reports) and The State of the World's Sea Turtle Database (SWOT, Kot et al. 2023). In addition, data sources were retrieved by making use of Internet searches using keywords relating to abundance estimates in a given location or variations thereof (e.g. “number of nests", “population abundance of”, “abundance estimates”, “time series of”). Targeted data searches were performed in cases where data gaps were evident in a collected time series.

In all accessed reports/journal publications, the original references contained within these sources were also retrieved and used for data collection/verification. Supplementary data/information (when available) were gleaned from published and unpublished literature. In some cases, annual estimates were reported in graphs without stating numbers. In such cases numbers were estimated from the reported figures using plotting software (http://www.graphreader.com/). Google Translate (https://translate.google.com/) was used if the original publication was published in a foreign language to ensure the correct index of abundance (e.g. number of nests vs number of females) was used.

Sea turtle abundance metrics are reported in a variety of indices e.g., the number of nests per season, the number of nesting females etc. When necessary, abundance values were converted to the same units for the analyses, i.e. number of nests per season. If the nesting trend was reported as the number of nesting females over time, it was multiplied by the average clutch frequency per female calculated in the same study and/or in a study conducted during a similar time period in the same location.

A “rookery” was defined as a discrete nesting beach for which data were consistently recorded and systematically reported; therefore, rookeries include individual nesting sites, beach sections, the entire coastline of a country/island based on the spatial extent for which data were reported. A “population” was referred to as a collection of beaches within the same area experiencing the same threats as per the Regional Management Unit (RMU) assigned in Wallace et al. (2010a).

Time series data for a particular rookery were, in some cases, collected from more than a single literature source. In such cases, data reported by the various publications were either combined to increase the range of annual estimates available (only if the same methods and/or monitoring efforts were used to record such estimates) or the publication(s) with the lowest data availability was removed. In total, abundance time series for 103 loggerhead and 104 leatherback sea turtle nesting sites from across the globe were collected.

Individual rookeries for which less than three years of abundance data were collected were removed from further analyses (n=5 for loggerheads; n=29 for leatherbacks). This specific data manipulation was implemented to avoid generating growth rates for individual rookeries (and ultimately RMUs and at the species-level) with very limited data because modelling population data using two data points may prove to be problematic and unreliable (Hathout 2013). It is critically important that a time series has a sufficient number of points to capture the phenomena of interest (see Supplementary Tables 2.1-2.4 in Supplementary Material I). For this study, "complex RMUs" will be referred to sea turtle RMUs that are composed of a compilation of individual rookeries, while "simple RMUs" are those with only one or two rookeries.

Relevant shapefiles (containing attribute and/or spatial data) were also collected from secondary data sources. A geodatabase containing global distributions and coverages for loggerhead and leatherback sea turtle RMUs were retrieved (Wallace et al. 2023). Maps were generated using QGIS [version 3.32.3] (QGIS Development Team 2009).

Statistical analyses

Abundance trends in rookeries, populations and species

Data processing and analyses were conducted in R [version R-4.0.5] (R Core Team 2021). Data points for which the annual number of nests were 0, were converted to 0.1, to calculate the log-value. For this analysis, rookeries with a minimum of three data entries were included (n=98 for loggerheads; n=75 for leatherbacks).

Three different growth models were fitted to individual rookeries to investigate the change in annual numbers across nesting sites (see Supplementary Figures 2.1 and 2.2 in Supplementary Material I). These models were exponential, log-logistic and breakpoint growth models. All three models have different formulae. These formulae were saved as functions within the R software (see below for formulas). The best fit for each individual model was obtained using the built in optimization function *nlminb* (Gay 1990).

The *nlminb* function iteratively estimates parameters (associated with the particular model) to find the best set of values that ultimately best describes the trend in the data provided. In other words, the *nlminb* function rotates the values of each one of the parameters until the best series of values (for each of the individual parameters), associated with the particular model, are generated. To determine which collection of values for the individual parameters best describes the time series data, *the negative log-likelihood* for each fitted model was also computed. Lower negative log-likelihood values are associated with models that best describe time series data and the values of each parameter associated with the lowest generated negative log-likelihood values were stored for further analyses. Both *exponential growth* models and *log-logistic growth* models were applied to individual nesting sites for which at least three years of annual nest numbers were available.

Exponential Growth Model

The exponential growth pattern shows a greater increase/decrease in population size as the number of individuals in the population increase/decrease over time; the rate of population increase/decrease is proportional to the number of individuals at any given point in time (Snider and Brimlow 2013). Prior to using the *nlminb* function, to determine the best set of parameters that describes the exponential growth (based on the lowest negative log likelihood value), the exponential growth rate formula and an initial starting estimate for each one of the parameters were required. The exponential growth rate formula is:

$$\boldsymbol{\widehat{N_{t+1}} = \widehat{N_t}(1 + r)}$$

Where: $\boldsymbol{\widehat{N_t}}$ = the estimated number of nests in year *t*

$\mathbf{r}$ = the intrinsic growth rate

The likelihood of observing N_t nests when the predicted number was $\widehat{N_t}$was assumed to be distributed with a negative binomial likelihood. In addition to the exponential growth rate formula, three parameters were included in the *nlminb* function to determine the series of values that best describes an exponential rate of growth: (1) the intercept (the number of nests for the earliest year for which data were available), (2) the slope/growth rate (the selected starting estimate was retrieved from the linear growth rate generated using the *lm* function from the *lme4* package (Bates et al. 2015)) and (3) the variance (a starting estimate of 1 was used). The *nlminb* function was used to determine which set of values for each of the three parameters associated with the exponential growth model best describe the pattern in the data over time based on the lowest negative log likelihood value obtained.

The Log-Logistic Growth Model

The log-logistic growth model is similar to the exponential growth model, but where the population's growth rate remains proportional to population size in the exponential growth model, a log-logistic model may be more representative of density-dependent states. In nature, populations may initially experience an exponential increase until resource availability and/or competition slows or halts the rate at which the population increases (Tsoularis and Wallace 2002; Edwards and Edwards 2011). The log-logistic model takes some of these limiting factors into account by including a limited carrying capacity value into the formula (Wisniewski 1980; Deangelis et al. 2020). In logistic growth, a population's growth rate decelerates as the population size nears the carrying capacity (Tsoularis and Wallace 2002). The following formula was used to model logistic growth:

$$\widehat{N_{t+1}} = \widehat{N_t} + r\widehat{N_t}\left(1 - \frac{\widehat{N_t}}{k}\right)$$

Where: $\widehat{N_t}$ = the estimated number of nests in year *t*

$\mathbf{r}$ = the intrinsic growth rate

$\mathbf{k}$ = the carrying capacity

Again, the likelihood of observing a specific number of nests in any year was assumed to be negatively binomially distributed around the predicted number. Four parameters were incorporated into the *nlminb* function to determine which values best describes a log-logistic growth rate with 1 – 3 the same as in the exponential model: (1) the intercept, (2) the slope/growth rate, (3) the variance and (4) the carrying capacity (a starting estimate of 2 x maximum nest count value for any particular year for which we have data was used). The *nlminb* function was then used to determine which set of values for each of the four parameters associated with the logistic growth model best described the pattern in the data over time based on the lowest negative log likelihood value obtained.

Breakpoint Model

The final model fitted to the individual nesting sites was the breakpoint model. A breakpoint model detects if there is a substantial change in the rate at which the population increases/declines at one particular moment in time (e.g. Ji and Haralick 1998). Breakpoints are particularly useful to detect changes in responses to environmental or management interventions. It is possible that populations experience an increase/decline in size prior to the break year may experience a faster rate of increase/decline after the break year.

For these models, only rookeries with a minimum of six datapoints were fitted with breakpoint models. The model was:

$$\widehat{\boldsymbol{N_{t+1}}} = \widehat{\boldsymbol{N_t}}(\mathbf{1} + \boldsymbol{r_1}) \quad \boldsymbol{if\ t \leq\ t^*}$$

$$\widehat{\boldsymbol{N_{t+1}}} = \widehat{\boldsymbol{N_t}}(\mathbf{1} + \boldsymbol{r_2}) \quad \boldsymbol{if\ t >\ t^*}$$

Where: $\widehat{\boldsymbol{N_t}}$ = the estimated number of nests in year *t*

$\mathbf{r}$ = the intrinsic growth rate

t* = the predicted breakpoint year

Because t* is an integer, the best fit was found by iterating over t*, for each value of t* finding the values for the parameters that best fit the data. Four parameters were used to model the growth rates for each individual rookery/nesting site: (1) the predicted break point year (t*) (the year at which an abrupt change in the exponential growth rate took place), (2) growth rate prior to the predicted break point year (r_1), (3) the growth rate after the predicted break point year (r_2) and (4) the variance of the negative binomial distribution (a starting estimate of 1 was used). The *nlminb* function was used to determine which set of values for each of the four parameters, associated with the breakpoint model's (i.e. exponential model's) formula, best describe the pattern in the data over time based on the lowest negative log likelihood value obtained. To calculate the mean overall growth rate value for breakpoint models, the growth rate was quantified by calculating the annual growth rate from one year to the next and taking the mean of these values. Using this method ensures that the growth rate after/before the breakpoint year was given more weight if the growth rate was observed for a longer time period compared to the growth rate before/after the breakpoint year.

After extracting the best-fit exponential, logistic, and breakpoint model for each one of the loggerhead and leatherback nesting sites based on the minimum negative log-likelihood values, the best-fit model was determined. The Akaike information criterion (AIC) was used to estimate and compare among the models with the lowest calculated AIC value having the best fit to the data trend over time (Bozdogan 2000; Stoica and Selen 2004; Wagenmakers and Farrell 2004). The AIC values for each of the fitted models were calculated by using the following formula:

$$AIC_m = 2k_m - 2In\ (L_m)$$

Where: k = the number of parameters (4)

L = the negative log-likelihood value

The model type and associated parameter values that best fit each loggerhead and leatherback sea turtle rookery trend in abundance over time was stored, along with the predicted abundance for that rookery.

RMU and species-level trends

To compare trends over time, an abundance trend per RMU and per species (i.e. combining all RMUs) were generated using similar methods to the Living Planet Index (LPI 2023). Using the best fit model's abundance values for each individual rookery, the rate of increase/decrease for each year was calculated. Next, the annual growth rates across rookeries were averaged to obtain a mean RMU-level growth rate for each year. These values were used to generate average RMU-level trends which were used as the predicted overall trends in abundance within each individual RMU over time. The same method was used to generate species-level trends in abundance over time except for taking the average of all rookeries (across all RMUs) to calculate the average growth rate for each year.

Two different methods were used to generate the RMU and species-level plots. The first (unweighted) method simply calculated the average annual growth rate by weighting each growth rate per rookery equally regardless of the number of nests per annum in the rookery, whereas the weighted method calculated the average annual growth rate by weighting the contribution proportionate to the rookery's average annual number of nests. Thereby giving larger rookeries (i.e. those with a larger average annual number of nests) a greater influence on the RMU and species-level trends compared to smaller rookeries.

Relationship between variability in abundance and RMU area

The area (km²) of each loggerhead and leatherback RMU was extracted using QGIS and the values were stored (see Supplementary Tables 2.5 and 2.6 in Supplementary Material I). For this analysis, time series with a minimum of three years of data were included. A total of 98 loggerhead and 75 leatherback rookeries were included in this analysis.

Inter-annual variability index values (VIV) in nest numbers

To determine variability in sea turtle abundances, methods as used by Hays et al. (2022) were applied, termed "inter-annual variability index". These values are calculated for each pair of values from successive years in a time series using annual nest numbers; the larger abundance value was divided by the smaller abundance value (irrespective of which came first so ignoring the direction of the variability) to obtain a series of inter-annual variability index values (VIV) for each rookery. This process was repeated for every pair of successive years in each time series, and then finally calculating the mean inter-annual VIV for each rookery. The following formula was used to calculate inter-annual VIVs:

$$\boldsymbol{VIV = \frac{N_t}{N_{t+1}} \quad if\ N_t > N_{t+1}}$$

$$\boldsymbol{VIV = \frac{N_{t+1}}{N_t} \quad if\ N_t < N_{t+1}}$$

Where: $\boldsymbol{VIV}$ = the inter-annual variability index value

$\boldsymbol{N_t}$= the population size in year *t*

For example, consider five years of data with population abundance values of 200 in 2015, 300 in 2016, 150 in 2017, 450 in 2018 and 900 in 2019. For each pair of successive years, the inter-annual VIV would be 1.5, 2, 3 and 2 with a mean value of 2.125 (i.e. the mean difference in abundance between successive years is 2.125-fold). This rookery would thus be assigned an overall inter-annual VIV of 2.125. The inter-annual variability index value for each RMU was determined by calculating the mean overall inter-annual VIV.

Relationship between variability in abundance and RMU size

For this analysis, linear regression models were used to determine if there was a relationship between the RMU inter-annual VIV and RMU area. The first model combined both loggerhead and leatherback data, while the second and third models tested species independently (i.e. model 2 included only loggerheads and model 3 included only leatherbacks). Ultimately, three linear regression models were fitted for this analysis. The *lme4* (Bates et al. 2015), *lmerTest*

(Kuznetsova et al. 2017) and *DHARMa* (Hartig 2022) packages were used to fit the linear model, obtain the relevant p value, and provide diagnostic plots to investigate whether the model assumptions were met or not, respectively.

To test whether the relationship between the dependent and independent variable was linear, scatterplots were initially generated. It appeared as if some form of linear relationship existed between the two variables for all three models. To test whether each predictor X_i and the outcome Y was linear, the residuals were plotted against the fitted values. The linearity assumption appeared to have been satisfied. For the assumption concerning the constant variance of errors, the points for all three models appeared to be scattered and not show any discernible shape, resulting in the assumption being met. Based on the use of boxplots and histograms (visual assessments), the conduction of Anderson-Darling tests for normality, and assessing the diagnostic plots, the distribution of errors appeared to be relatively normal for the combined dataset, as well as for both species' individual inter-annual variability index values. To improve and satisfy the assumption regarding normality, both log and square root transformations were performed. Neither transformation improved normality regardless of the dataset used. As a result, data were kept in the original format (i.e. untransformed).

For this analysis, it was tested whether the **inter-annual variability index value** is a function of **RMU size** (fixed effect) using the following formula:

$$\boldsymbol{Model\,1 = lm\,(IAVIV \sim Size)}$$

Where: ***lm*** = the function used to fit a linear regression model (using *lme4* package)

IAVIV = the RMU's Inter-annual variability index value

Size = the size of the RMU (km²)

Results

Abundance trends in rookeries, populations and species

Loggerhead RMU trends

Models were fitted to 98 rookeries across 9 RMUs (except for the data-deficient Northeast Indian Ocean loggerhead subpopulation; Table 2.1). A summary of the trends is in Table 2.1

(The references from where the data were obtained and the years for which data were available are in Supplementary Table 2.2 in Supplementary Material I).

In the Atlantic Ocean, the **Northwest Atlantic RMU** constitute 16 rookeries of which 12 sites experienced increasing trends while the remaining four rookeries showed declining patterns. The average number of clutches per year ranged from 8.3 to 67 914.7 with growth rates from -0.085 (Querepare, Cipara, Parguito Beach, and between Moron and Yaracuy) to 0.24 (Aruba). The **Southwest Atlantic** RMU had three rookeries with increasing trends in abundance over time, and one rookery that experienced a decline in abundance over time. Growth rates ranged from -0.019 (Farol, Comboios, Povoação, Interlagos, Guarajuba, and Praia do Forte) to 0.174 (Rio de Janeiro). The average number of clutches per year varied from 583.5 to 4 914 in the Southwest Atlantic RMU. Three nesting sites in the **Northeast Atlantic** RMU displayed an increase in the annual number of clutches deposited over time, while the largest nesting site within this RMU (Boa Vista Island) showed a decrease in abundance. The average number of clutches ranged from 889.7 to 8 264.4.

The Mediterranean Sea has a single loggerhead RMU and in the **Mediterranean** RMU, 31 out of 51 nesting sites showed an increase in sea turtle abundance over time, while declining abundance trends were observed for the remaining 20 sites. The average number of clutches per year ranged from 5.2 to 1 229.1 within individual rookeries. Growth rates ranged from -0.431 (Marzuga) to 0.437 (Cirali beach).

The Indian Ocean has four RMUs where the **Northwest Indian** RMU, which included a single rookery (Masirah Island) for which data were available, depicting an exponential decline in loggerhead abundance over time from 30 380 nests to 11 020 nests, with a growth rate of -0.138. Both rookeries within the **Southwest Indian** RMU increased in abundance over time with growth rates of 0.028 (Kosi Bay Mouth to Mabibi) and 0.04 (Between Ponta do Ouro and Bazaruto Archipelago), while the mean number of nests deposited annually ranged from 818.6 to 1 695.1. All rookeries in the **Southeast Indian** RMU showed declines in the annual number of nests over time. In the Southeast Indian RMU, growth rates from -0.009 (Ningaloo Region) to -0.036 (Gnaraloo Bay) were observed, and the average number of clutches per year ranged from 375.4 to 515.8 within individual rookeries.

Only two loggerhead RMUs are recognised in the Pacific Ocean; in the **North Pacific**, 10 out of a possible 14 nesting sites experienced declines in loggerhead sea turtle abundance over time, while only four nesting sites showed increases in abundance. The average number of clutches per year ranged from 13.5 to 4 012.3 with growth rates from -0.272 (Minabe Iwashiro beach) to 0.095 (Omaezaki beach). Three nesting sites from the **South Pacific** showed declines in the annual number of nests, while the remaining rookery displayed an increase in abundance over time. The average number of clutches per year ranged from 30.4 to 173 in rookeries situated within the South Pacific RMU, with growth rates from -0.114 (Wreck Island) to 0.065 (Sunshine coast).

Table 2.1: Growth rates in nest numbers and average annual number of nests deposited for individual rookeries situated within loggerhead sea turtle RMUs

Regional Management Unit (RMU)	Country	Rookery/nesting location	Average annual number of nests (Rank)	Growth model[1]	Growth rate[2]
Northwest Atlantic	United States	North Carolina beaches	**1 416** (3)	Exponential	0.025
	United States	Northern Recovery Unit (North Carolina, South Carolina and Georgia)	**5 433.1** (2)	Exponential	0.006
	United States	Peninsular Florida	**67 914.7** (1)	Breakpoint (2008)	-0.007; 0.056 (0.015)
	United States	Dry Tortugas National Park	602.3 (6)	Exponential	-0.007
	United States	Northwest Management Unit of Florida	173.2 (8)	Breakpoint (2004)	-0.092; 0.05 (0.004)
	United States	Northern Gulf of Mexico	906.3 (5)	Exponential	-0.047
	Mexico	Half Moon Bay, Akumal Bay, Jade Bay, and South Akumal Bay	140.8 (9)	Breakpoint (2005)	-0.039; 0.096 (0.04)
	Mexico	Quintana Roo, Paarmul, Kanzul, San Juan, Xel Ha	**1 221.6** (4)	Breakpoint (2006)	-0.012; 0.081 (0.021)
	Cuba	Guanahacabibes Peninsula	19 (14)	Exponential	0.007
	Cuba	Guanahacabibes NP, San Felipe NP, Sur de la Isla PAMR, Jardines de la Reina NP	256.5 (7)	Breakpoint (2009)	0.182; -0.15 (0.054)
	Cayman Islands	Little Cayman	72.3 (10)	Exponential	0.063

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[1] Akaike Information Criterion (AIC) was utilised for reported model selection; For breakpoint models, the year at which the breakpoint occurs is reported in brackets

[2] Rookeries/nesting sites for which two growth rate values were provided includes locations for which the breakpoint model was selected, where the first growth rate value includes the rate of increase/decrease prior to the break year, while the second reported growth rate value is the growth rate following the break year. The value in brackets depicts the average growth rate value for locations where the breakpoint model was selected as the best fit model. Values in red indicate negative population growth.

	Cayman Islands	Cayman Brac	42.4 (12)	Exponential	-0.005
	Cayman Islands	Grand Cayman	65.5 (11)	Exponential	0.120
	Aruba	Aruba	14.8 (15)	Exponential	0.24
	Bonaire	Klein Bonaire	21.1 (13)	Exponential	0.016
	Venezuela	Querepare, Cipara, Parguito Beach, and between Moron and Yaracuy	8.3 (16)	Exponential	-0.085
Southwest Atlantic	Brazil	Farol, Comboios, Povoação, Interlagos, Guarajuba, and Praia do Forte	**4 914** (1)	Exponential	-0.019
	Brazil	Bahia	**1 137.5** (2)	Exponential	0.061
	Brazil	Espirito Santo	688.3 (3)	Exponential	0.015
	Brazil	Rio de Janeiro	583.8 (4)	Exponential	0.174
Northeast Atlantic	Cape Verde	Santa Luzia	889.7 (4)	Exponential	0.333
	Cape Verde	Sal	**2 193.8** (3)	Exponential	0.269
	Cape Verde	Boa Vista Island	**8 264.4** (1)	Exponential	-0.108
	Cape Verde	Maio Island	**7 948.3** (2)	Exponential	0.298
Mediterranean	Greece	Kyparissia Bay	555 (3)	Breakpoint (1997)	0.006; 0.102 (0.07)
	Greece	Zakynthos	**1 229.1** (1)	Breakpoint (2017)	-0.013; 0.158 (0.007)
	Greece	Keroni	53 (24)	Exponential	0.001
	Turkey	Dalaman beach	86.9 (13)	Exponential	0.001
	Turkey	Dalyan beach	209.6 (7)	Breakpoint (1995)	-0.056; 0.067 (-0.003)
	Turkey	Fethiye Bay	101.3 (11)	Breakpoint (2006)	-0.055; 0.03 (-0.012)
	Turkey	Patara beach	129.7 (10)	Breakpoint (1996)	-0.083; 0.081 (0.047)
	Turkey	Kale beach	66.7 (19)	Exponential	0.007
	Turkey	Demre coast	70.2 (17)	Exponential	0.028
	Turkey	Finike-Kumluca	183.8 (8)	Exponential	-0.031
	Turkey	Cirali beach	70.5 (16)	**Logistic**	0.437
	Turkey	Belek beach	833.4 (2)	Breakpoint (1995)	0.004; 0.106 (0.07)
	Turkey	Kizilot beach	139.2 (9)	Exponential	0.057

Turkey	Anamur beach	300.5 (5)	Exponential	0.098
Turkey	Goksu Delta	90.6 (12)	Exponential	0.026
Turkey	Alata beach	25.3 (31)	Exponential	-0.125
Turkey	Kazanli beach	11.8 (44)	Exponential	0.108
Turkey	Akyatan beach	19 (34)	Exponential	0.117
Turkey	Samandag beach	12.1 (41)	Exponential	0.123
Cyprus	Northern Cyprus	234.4 (6)	Exponential	0.024
Cyprus	Alagadi beach	60.4 (22)	Exponential	0.003
Cyprus	Chrysochou Bay	372.4 (4)	Exponential	0.113
Cyprus	West coast	67.8 (18)	Breakpoint (2003)	0.049; 0.216 (0.1)
Lebanon	El Mansouri beach	45.5 (25)	Exponential	0.076
Israel	Israeli coast	42.1 (27)	Exponential	0.113
Libya	Bananes	12 (43)	Exponential	-0.114
Libya	Al-Hasi	9.9 (48)	Exponential	0.065
Libya	Ain Ghazala	37.5 (28)	Exponential	-0.09
Libya	Jarjaruma	11 (45)	Exponential	0.019
Libya	Zaafaran	14 (37)	Exponential	0.399
Libya	Shash	76.8 (15)	Exponential	-0.052
Libya	Mtefla	42.5 (26)	Exponential	-0.043
Libya	Al-Thalateen	59 (23)	Exponential	-0.01
Libya	Al-Gbeba	66.5 (20)	Exponential	-0.08
Libya	West Camp	36 (29)	Exponential	0.024
Libya	Al-Arbaeen (Tamet)	80.4 (14)	Exponential	-0.064
Libya	Al-Khamseen	61.3 (21)	Exponential	0.31
Libya	Al-Nakhla	13 (38)	Exponential	0.106
Libya	Elkhowada	12.3 (40)	Exponential	-0.049
Libya	Al-bwerat	19.3 (33)	Exponential	0.219
Libya	Almjaren	16 (36)	Exponential	-0.189
Libya	Almerekeb	5.6 (50)	Exponential	-0.175
Libya	Al-Ghwezat	16 (35)	Exponential	-0.234
Libya	Al-Malfa	11 (46)	Exponential	-0.194
Libya	Marzuga	9 (49)	Exponential	-0.431
Libya	Smeda	29.8 (30)	Exponential	-0.164

	Libya	AlMahbula	12 (42)	Exponential	-0.228
	Libya	Arar	20.5 (32)	Exponential	0.094
	Libya	Ugla	12.7 (39)	Exponential	-0.082
	Libya	Ugla Misratah	5.2 (51)	Exponential	0.121
	Tunisia	Great Kuriat Island	10.8 (47)	Exponential	0.056
Northwest Indian	Oman	Masirah Island	**23 562.7** (1)	Exponential	-0.138
Southwest Indian	Mozambique	Ponta do Ouro to Bazaruto Archipelago	818.6 (2)	Breakpoint (2013)	0.177; -0.091 (0.04)
	South Africa	Kosi Bay Mouth to Mabibi	**1 695.1** (1)	Breakpoint (1989)	0.011; 0.041 (0.028)
Southeast Indian	Australia	Ningaloo Region	515.8 (1)	Exponential	-0.009
	Australia	Gnaraloo Bay	375.4 (2)	Exponential	-0.036
North Pacific	Japan	Japan	**4 012.3** (1)	Breakpoint (1997)	-0.158; 0.065 (-0.021)
	Japan	Omaezaki beach	381.9 (6)	Breakpoint (1991)	0.183; -0.065 (0.095)
	Japan	Minabe Senri beach	153.1 (7)	Breakpoint (1991)	0.088; -0.148 (-0.023)
	Japan	Minabe Iwashiro beach	27.3 (12)	Exponential	-0.272
	Japan	Hiwasa	73.4 (8)	Breakpoint (1993)	0.011; -0.23 (-0.116)
	Japan	Nobeoka beach	32 (10)	Breakpoint (1994)	-0.357; 0.038 (-0.097)
	Japan	Miyakazi beach	488.1 (4)	Breakpoint (1990)	0.097; -0.026 (0.038)
	Japan	Nichinan beach	31.6 (11)	Exponential	-0.053
	Japan	Shibushi beach	37.7 (9)	Exponential	0.086
	Japan	Nagasakibana beach	13.5 (14)	Exponential	-0.218
	Japan	Inakahama beach	523.2 (3)	Breakpoint (1991)	0.086; -0.067 (-0.003)
	Japan	Yakushima	**1 062.7** (2)	Exponential	0.037
	Japan	Maehama beach	448.8 (5)	Exponential	-0.102
	Japan	Ishigakijima Island	22 (13)	Breakpoint (2009)	0.162; -0.209 (-0.052)
South Pacific	Australia	Wreck Island	173 (1)	Exponential	-0.114
	Australia	Heron Island	30.4 (4)	Breakpoint (1999)	-0.077; 0.065 (-0.028)
	Australia	Sunshine coast	55.3 (3)	Exponential	0.065
	Australia	Batemans Bay	75.5 (2)	Exponential	-0.04

Leatherback RMU trends

Models were fitted to 75 individual nesting sites across all seven leatherback turtle RMUs (Table 2.2). Most leatherback nesting sites were also best fit by exponential increases/declines, followed by breakpoint trends, while the log-logistic model fitted best to only three rookeries. In contrast to loggerheads, more leatherback sites showed declines in abundance (n=39), whereas 36 sites increased in the number of nests over time. (The references from where the data were obtained are in Supplementary Table 2.4 in Supplementary Material I).

A comparison of patterns among RMUs differ substantially. In the Atlantic Ocean, a total of 26 out of 43 nesting sites within the **Northwest Atlantic** RMU showed an increase in leatherback nest numbers over time. The average annual number of nests among rookeries in the Northwest Atlantic RMU varied with orders of magnitude from 3 (North Carolina) to 16 825.5 (Amana). A diversity of growth rates was consequently observed ranging from -1.366 (St Kitts and Nevis) to 0.754 (Soana Island and Del Este National Park). The only nesting site (Espirito Santo, Brazil) with available quantitative data in the **Southwest Atlantic** RMU showed an increase in abundance over time. A growth rate of 0.056 was observed within this RMU. This is one of the smallest rookeries in the world with abundances ranging from 8 to 213 nests per annum with an annual average of 55.9. For the **Southeast Atlantic** population, one of the largest leatherback populations in the world, growth rates varied from -0.955 (Palmeirinhas) to 0.052 (Gabon). The average annual number of clutches deposited within these individual rookeries ranged from 3 to 84 400.

In the Indian Ocean, the **Southwest Indian** RMU showed contrasting patterns. One rookery (in Mozambique) showed a decline in leatherback nest numbers over time, while the other (in South Africa) showed an increase in abundance. The growth rates were -0.068 (between Ponta do Ouro and Bazaruto Archipelago, Mozambique) and 0.038 (Kosi Bay Mouth to Mabibi, South Africa). The average annual number of clutches deposited within these individual rookeries ranged from 58.5 (Mozambique) to 283.5 (South Africa). In the **Northeast Indian** RMU both rookeries (on the Little Andaman Island) experienced an increase in leatherback sea turtle nests over time. Growth rates within the Northeast Indian RMU included 0.011 (South Bay, Little Andaman) and 0.156 (West Bay, Little Andaman), with the average number of clutches per year ranging from 37 to 83.3 per annum.

In the Pacific Ocean, data from five rookeries in the **West Pacific** RMU were analysed. One rookery increased in nest numbers, whereas four nesting sites declined in nest numbers over time. The growth rates ranged from -0.717 (Suka Made) to 0.156 (Huon coast), with an average number of nests per year ranging from 7.7 to 3 022.7. The **East Pacific** RMU showed an overall decrease in nest numbers, with only four out of 17 rookeries displaying an increase in the number of nests over time. Growth rates in this RMU ranged from -0.295 (Caletas) to 0.612 (Cabuyal), with the average number of clutches per year ranging from 2.5 to 3 733.3.

Table 2.2: Growth rates in nest numbers and average annual number of nests deposited for individual rookeries situated within leatherback sea turtle RMUs.

Regional Management Unit (RMU)	Country	Rookery/nesting location	Average annual number of nests (Rank)	Growth model[3]	Growth rate[4]
Northwest Atlantic	United States	North Carolina	3 (43)	Exponential	-0.032
	United States	Florida	287.8 (24)	Breakpoint (2010)	0.118; -0.045 (0.067)
	Dominican Republic	Jaragua National Park	127.8 (31)	Exponential	0.411
	Aruba	Aruba	50.8 (36)	Breakpoint (2009)	0.176; -0.143 (0.029)
	Dominican Republic	Saona Island and Del Este National Park	5.3 (42)	Exponential	0.754
	Puerto Rico	Maunabo	167.8 (28)	Exponential	0.078
	Puerto Rico	Luquillo-Fajardo	205.2 (26)	Breakpoint (2002)	0.261; -0.012 (0.148)
	Puerto Rico	Culebra	157.9 (29)	Breakpoint (2003)	0.049; -0.14 (-0.027)
	United States	Sandy Point National Wildlife Refuge	398.4 (21)	Breakpoint (2007)	0.083; -0.159 (0.02)
	British Virgin Islands	British Virgin Islands	22.7 (39)	Breakpoint (2003)	0.159; -0.212 (0.118)
	British Virgin Islands	BVI Archipelago	24.7 (38)	Breakpoint (2003)	0.161; -0.08 (0.061)
	Anguilla	Anguilla	11 (40)	Exponential	-0.089
	St. Eustatius	Zeelandia beach	7.3 (41)	Exponential	-0.082
	St Kitts	St Kitts and Nevis	149.3 (30)	**Logistic**	-1.366
	Guadeloupe	Guadeloupe	108.7 (32)	Breakpoint (2005)	0.486; 0.034 (0.208)
	Grenada	Levera	769.5 (15)	Exponential	0.136
	Tobago	Tobago	460.2 (19)	Exponential	0.005
	Trinidad and Tobago	Grande Riviere	**13 657.1** (3)	Exponential	-0.016
	Trinidad and Tobago	Matura	**5 640.7** (5)	Breakpoint (2006)	0.198; -0.025 (0.109)
	Trinidad and Tobago	Fishing Pond	**3 968.8** (9)	Exponential	-0.17
	Venezuela	Cipara	101.5 (34)	Exponential	-0.035

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[3] Akaike Information Criterion (AIC) was utilised for reported model selection; For breakpoint models, the year at which the breakpoint occurs is reported in brackets

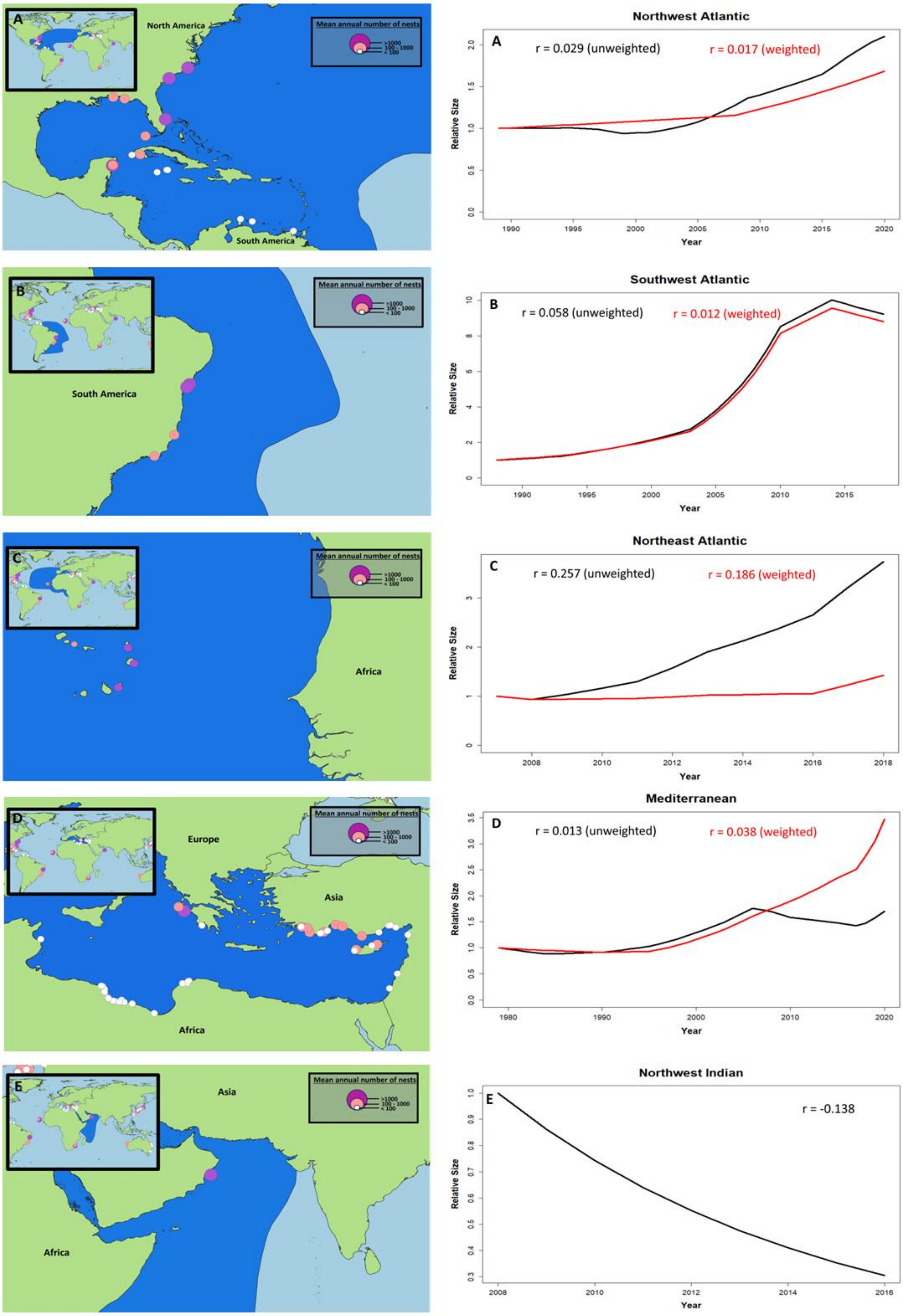
[4] Rookeries/nesting sites for which two growth rate values were provided includes locations for which the breakpoint model was selected, where the first growth rate value includes the rate of increase/decrease prior to the break year, while the second reported growth rate value is the growth rate following the break year. The value in brackets depicts the average growth rate value for locations where the breakpoint model was selected as the best fit model. Values in red indicate negative population growth.

	Venezuela	Querepare	107.3 (33)	Breakpoint (2007)	0.318; -0.043 (0.077)
	Guyana	Guyana	442.6 (20)	Breakpoint (2006)	0.126; -0.178 (0.013)
	Suriname	Matapica beach	**1 517** (14)	Breakpoint (1985)	0.18; -0.235 (0.017)
	Guianas/Trinidad	Suriname	**5 129** (7)	Breakpoint (2001)	0.051; -0.106 (-0.038)
	Suriname	Galibi nature reserve	**5 526.1** (6)	Breakpoint (1985)	0.253; 0.066 (0.15)
	Suriname	Samsambo sandpit	**1 606.3** (13)	Exponential	0.682
	French Guiana	Awala-Yalimapo	**13 127.8** (4)	Breakpoint (1990)	0.128; -0.131 (-0.03)
	French Guiana	Yalimapo beach	**15 643.9** (2)	Breakpoint (1977)	0.668; 0.037 (0.28)
	French Guiana	Amana	**16 825.5** (1)	Breakpoint (1985)	0.264; -0.058 (0.117)
	French Guiana	Western beaches	**2 643.9** (12)	Breakpoint (2009)	0.081; -0.361 (-0.148)
	French Guiana	Cayenne	**3 657.8** (10)	Breakpoint (2010)	0.187; -0.164 (0.067)
	French Guiana	Eastern beaches	**3 276.3** (11)	Breakpoint (2013)	0.143; -0.433 (-0.048)
	Nicaragua	Nicaragua	59.8 (35)	Exponential	-0.245
	Mexico	Playa Norte	45.2 (37)	Exponential	-0.1
	Costa Rica	Tortuguero	567.7 (17)	Exponential	-0.114
	Costa Rica	Playa Pacuare	331.6 (23)	Exponential	-0.046
	Costa Rica	Estacion La Tortuga	379.3 (22)	Exponential	0.008
	Costa Rica	Pacuare Nature Reserve	733.1 (16)	Breakpoint (1995)	0.366; -0.013 (0.042)
	Costa Rica	Playa Moin	229 (25)	Exponential	0.089
	Costa Rica	Cahuita	199.9 (27)	Exponential	-0.011
	Costa Rica	Gandoca	535.2 (18)	Breakpoint (1997)	0.21; -0.077 (0.024)
	Panama	Chiriqui	4601.4 (8)	Exponential	0.014
Southwest Atlantic	Brazil	Espirito Santo	55.9 (1)	Exponential	0.056
Southeast Atlantic	Equatorial Guinea	Bioko Island	**2 386.3** (2)	Exponential	-0.02
	Gabon	Gabon	**84 400** (1)	Exponential	0.052
	Congo	Republic of Congo	265.3 (3)	Exponential	-0.193
	Congo	Banana, Tonde, Nsiemfumu and Tshiende beaches	3 (5)	Exponential	-0.234
	Angola	Palmeirinhas	13.3 (4)	Exponential	-0.955
	Mozambique	Ponta do Ouro to Bazaruto Archipelago	58.5 (2)	Exponential	-0.068

Southwest Indian	South Africa	Kosi Bay Mouth to Mabibi	283.5 (1)	Breakpoint (1970)	0.351; -0.001 (0.038)
Northeast Indian	India	West Bay Little Andaman	83.3 (1)	Exponential	0.156
	India	South Bay Little Andaman	37 (2)	Exponential	0.011
West Pacific	Malaysia	Terengganu	**2 308.4** (2)	Breakpoint (1995)	-0.113; -0.55 (-0.195)
	Indonesia	Suka Made	7.7 (5)	**Logistic**	-0.717
	Indonesia	Jamursba-Medi	**3 022.7** (1)	Exponential	-0.07
	Indonesia	Wermon	**1 361.1** (3)	Breakpoint (2014)	-0.184; 0.43 (-0.027)
	Papua New Guinea	Huon coast	196.2 (4)	**Logistic**	0.156
East Pacific	Mexico	Mexiquillo beach	**1 838** (3)	Exponential	-0.223
	Mexico	Index beaches in Mexico	**3 733.3** (1)	Breakpoint (2012)	-0.1; 0.138 (-0.09)
	Mexico	Tierra Colorada beach	284.3 (6)	Exponential	-0.092
	Mexico	Cahuitan beach	260.6 (7)	Exponential	-0.188
	Mexico	Chacahua beach	**1 846.7** (2)	Exponential	-0.169
	Mexico	Barra de la Cruz beach	367.9 (5)	Exponential	-0.192
	Guatemala	Guatemala	2.5 (17)	Exponential	-0.059
	El Salvador	El Salvador	9 (14)	Exponential	0.109
	Nicaragua	Juan Venado	16.3 (12)	Exponential	-0.289
	Nicaragua	Salamina	22.25 (11)	Exponential	0.209
	Nicaragua	Veracruz	31.2 (8)	Exponential	-0.168
	Costa Rica	Naranjo	30.7 (9)	Exponential	-0.073
	Costa Rica	Cabuyal	13.8 (13)	Exponential	0.612
	Costa Rica	Nombre de Jesus	8.5 (15)	Exponential	0.394
	Costa Rica	Parque Nacional Marino Las Baulas	**1 803.6** (4)	Exponential	-0.136
	Costa Rica	Ostional	26.7 (10)	Exponential	-0.058
	Costa Rica	Caletas	6.9 (16)	Exponential	-0.295

Loggerhead Portfolio

The majority (56) of loggerhead rookeries had positive abundance trends (Table 2.1). Therefore, it is not surprising that five of the nine loggerhead RMUs displayed positive trends, using both unweighted and weighted models (Figure 2.1). The Northwest Atlantic (unweighted r = 0.029; weighted r = 0.017), Southwest Atlantic (unweighted r = 0.058; weighted r = 0.012), Northeast Atlantic (unweighted r = 0.257; weighted r = 0.186), Mediterranean (unweighted r = 0.013; weighted r = 0.038) and the Southwest Indian (unweighted r = 0.034; weighted r = 0.032) showed an increase in abundance over time. In contrast, the Northwest Indian (unweighted and weighted r = -0.138), Southeast Indian (unweighted r = -0.031; weighted r = -0.027), North Pacific (unweighted r = -0.065; weighted r = -0.009) and South Pacific (unweighted r = -0.022; weighted r = -0.06) RMUs experienced declines in abundance over time. Combining all the RMUs (Figure 2.1J) for a species assessment, loggerheads seem to have expanded with an increase in the global abundance over time (unweighted r = 0.013; weighted r = 0.015).

A
North America
Mean annual number of nests
>1000
100 - 1000
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South America
Northwest Atlantic
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r = 0.029 (unweighted)
r = 0.017 (weighted)
Relative Size
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Mean annual number of nests
>1000
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< 100
South America
Southwest Atlantic
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r = 0.058 (unweighted)
r = 0.012 (weighted)
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Mean annual number of nests
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Northeast Atlantic
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r = 0.257 (unweighted)
r = 0.186 (weighted)
Relative Size
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Year
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Mean annual number of nests
>1000
100 - 1000
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Africa
Mediterranean
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r = 0.013 (unweighted)
r = 0.038 (weighted)
Relative Size
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Mean annual number of nests
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r = -0.138
Relative Size
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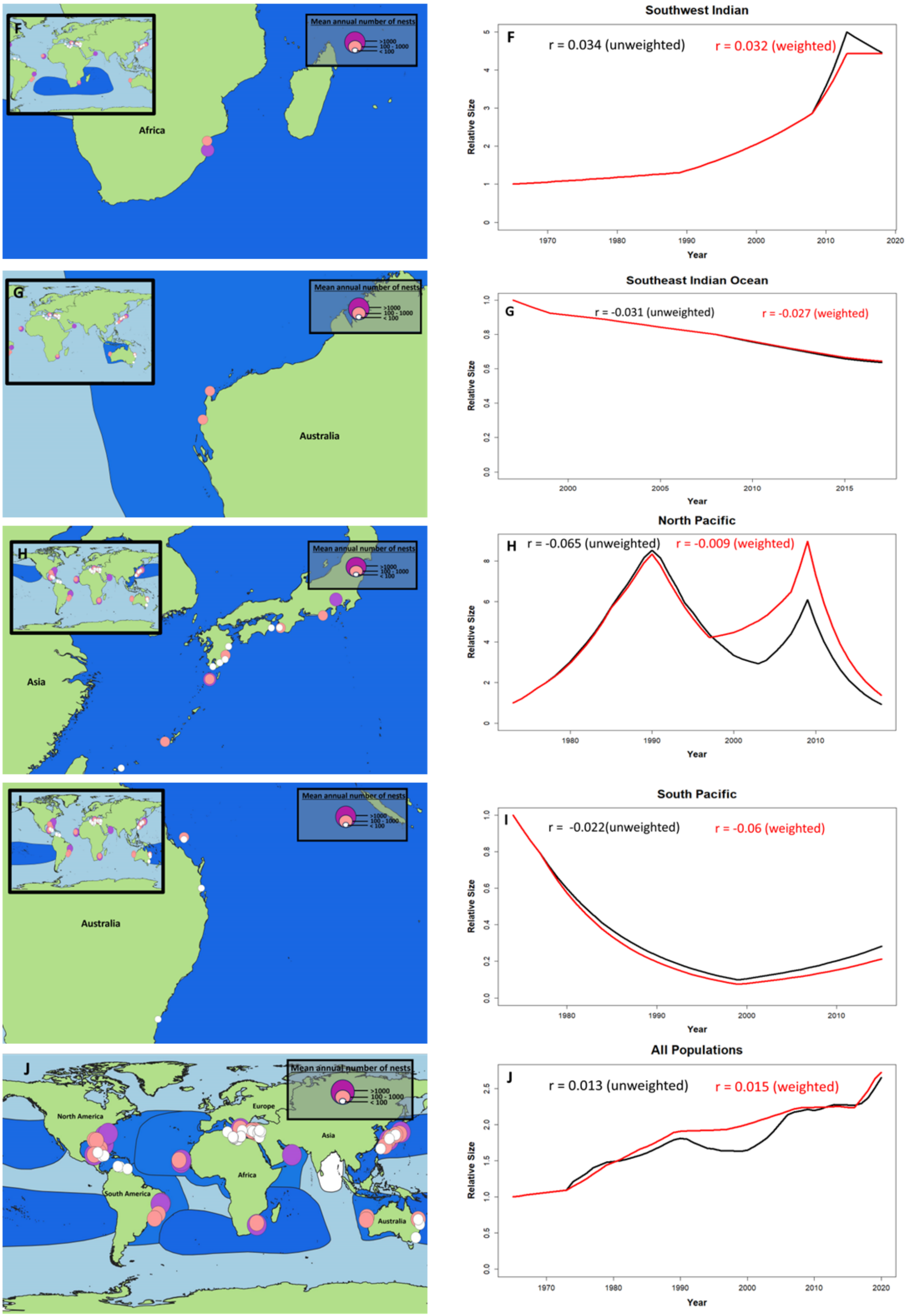


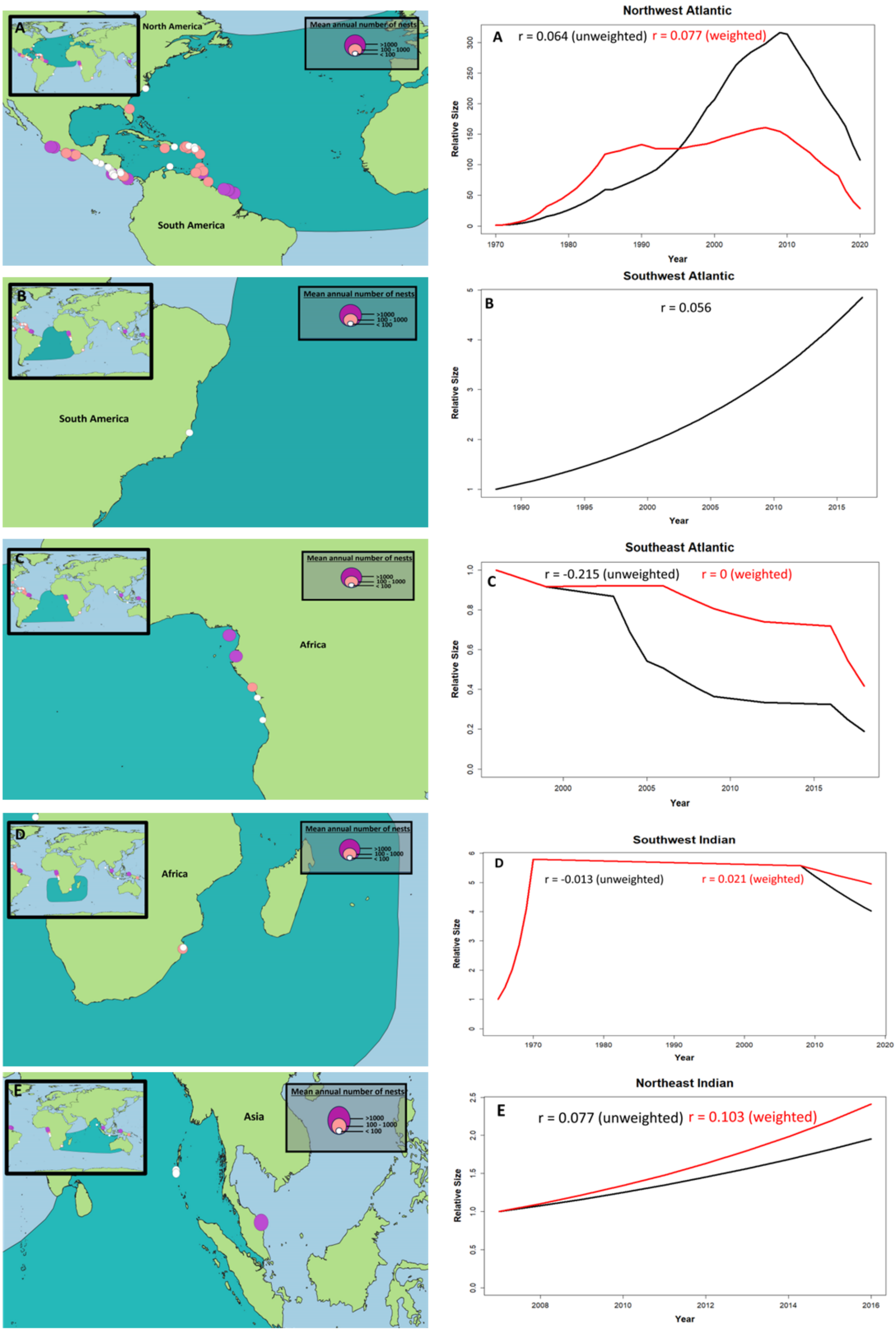
Figure 2.1: Loggerhead sea turtle RMU and species-level trends in abundance over time: (A) Northwest Atlantic, (B) Southwest Atlantic, (C) Northeast Atlantic, (D) Mediterranean, (E) Northwest Indian, (F) Southwest Indian, (G) Southeast Indian, (H) North Pacific, (I) South Pacific and the (J) species-level trend. The location and mean annual number of nests for each rookery within each RMU are depicted by circle size and colour.

Leatherback Portfolio

Of the 75 rookeries monitored about half (36) had positive trends (Table 2.2), but the trend at an RMU level is complicated and dependent on whether it is weighted or unweighted. Three of the seven leatherback RMUs displayed positive trends using an unweighted model and four were positive when the model was weighed by rookery size (Figure 2.2). One RMU, the Southeast Atlantic, was considered stable using a weighted model.

The Northwest Atlantic (unweighted r = 0.064), Southwest Atlantic (unweighted r = 0.056) and Northeast Indian (unweighted r = 0.077) RMUs showed an increase in abundance over time when growth rates were unweighted by mean rookery size, while the Southeast Atlantic (unweighted r = -0.215), Southwest Indian (unweighted r = -0.013), East Pacific (unweighted r = -0.02) and West Pacific (unweighted r = -0.055) RMUs declined in abundance over time. Combining all unweighted trends from the RMUs, leatherback sea turtles, at the species-level, seems stable/weakly positive (unweighted r = 0.017) with recent declines.

When the RMU-level (Figure 2.2A-G) and species abundance trends (Figure 2.2H) were calculated using weighted mean rookery size, the outcomes are different at the RMU-level. Only two of the seven RMUs had negative trends: the East (weighted r = -0.126) and West (weighted r = -0.096) Pacific RMUs. The other five were stable or increasing. These were the Northwest Atlantic (weighted r = 0.077), Southwest Atlantic (weighted r = 0.056), Southeast Atlantic (weighted r = 0), Southwest Indian (weighted r = 0.021) and Northeast Indian (weighted r = 0.103) RMUs. When RMU trends were weighted by mean population size, the leatherback sea turtle species-level trend was overall positive but mildly so (weighted r = 0.029) and was considered stable with a decline during the most recent decades.


A
North America
South America
Mean annual number of nests
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Northwest Atlantic
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r = 0.064 (unweighted)
r = 0.077 (weighted)
Relative Size
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Year
B
South America
Mean annual number of nests
>1000
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< 100
Southwest Atlantic
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r = 0.056
Relative Size
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Africa
Mean annual number of nests
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Southeast Atlantic
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r = -0.215 (unweighted)
r = 0 (weighted)
Relative Size
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0.4
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Year
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Africa
Mean annual number of nests
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Southwest Indian
D
r = -0.013 (unweighted)
r = 0.021 (weighted)
Relative Size
0
1
2
3
4
5
6
1970
1980
1990
2000
2010
2020
Year
E
Asia
Mean annual number of nests
>1000
100 - 1000
< 100
Northeast Indian
E
r = 0.077 (unweighted)
r = 0.103 (weighted)
Relative Size
0.0
0.5
1.0
1.5
2.0
2.5
2008
2010
2012
2014
2016
Year

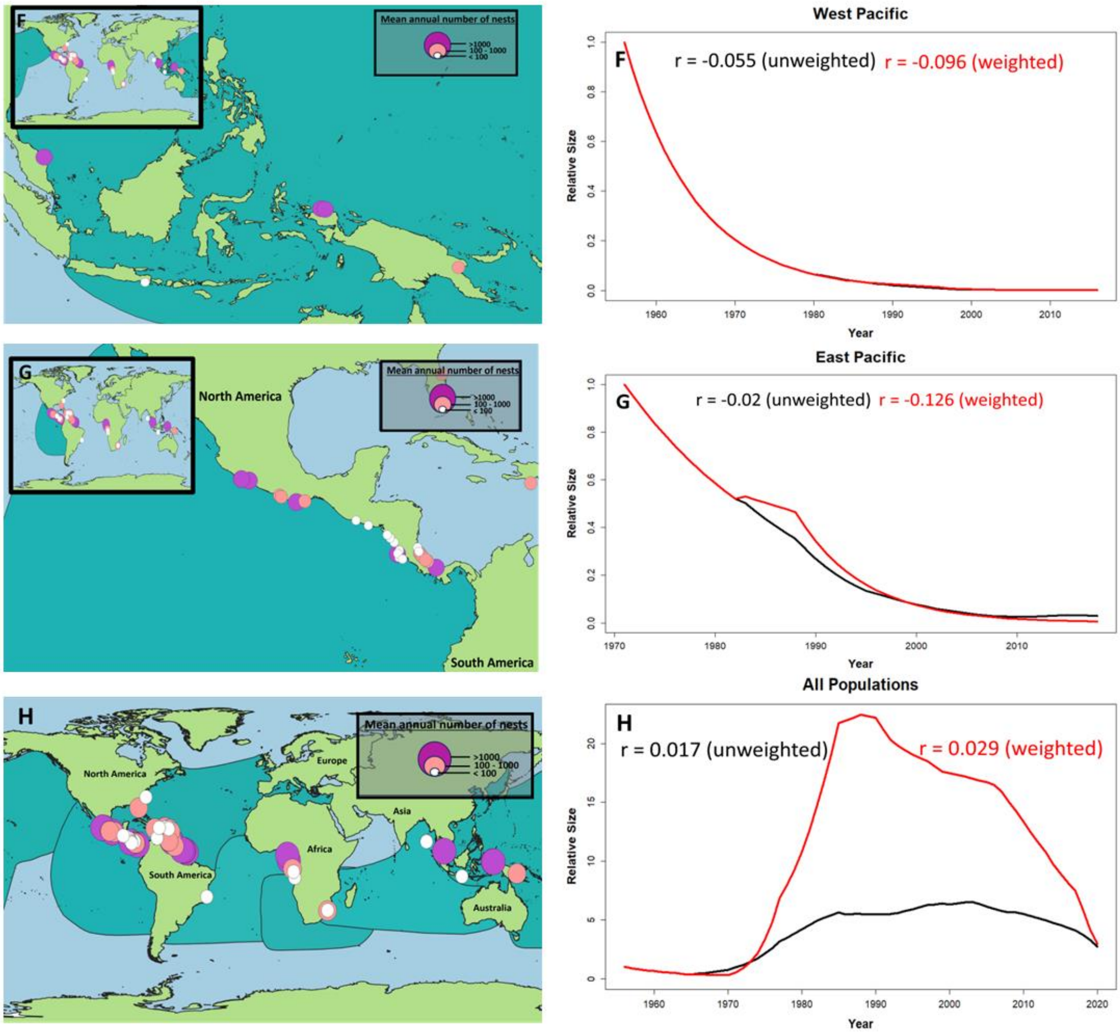

Figure 2.2: Leatherback sea turtle RMU and species-level trends in abundance over time: (A) Northwest Atlantic, (B) Southwest Atlantic, (C) Southeast Atlantic, (D) Southwest Indian, (E) Northeast Indian, (F) West Pacific, (G) East Pacific and the (H) species-level trend. The location and mean annual number of nests for each rookery within each RMU are depicted by circle size and colour.

Relationship between variability in abundance and RMU area

One potential factor that could influence the variability in abundance over time is the RMU area (i.e. size), assuming that larger areas should provide a greater diversity of environmental conditions and threats. Linear regression models were fitted to test whether a relationship exists between the inter-annual variability index values and RMU size (Model 1). The results indicated that no statistically significant relationship exists between the inter-annual variability index value and RMU size when both species' values were included (Figure 2.3; r^2 = <0.001; F statistic = 0.001; p value >0.05).

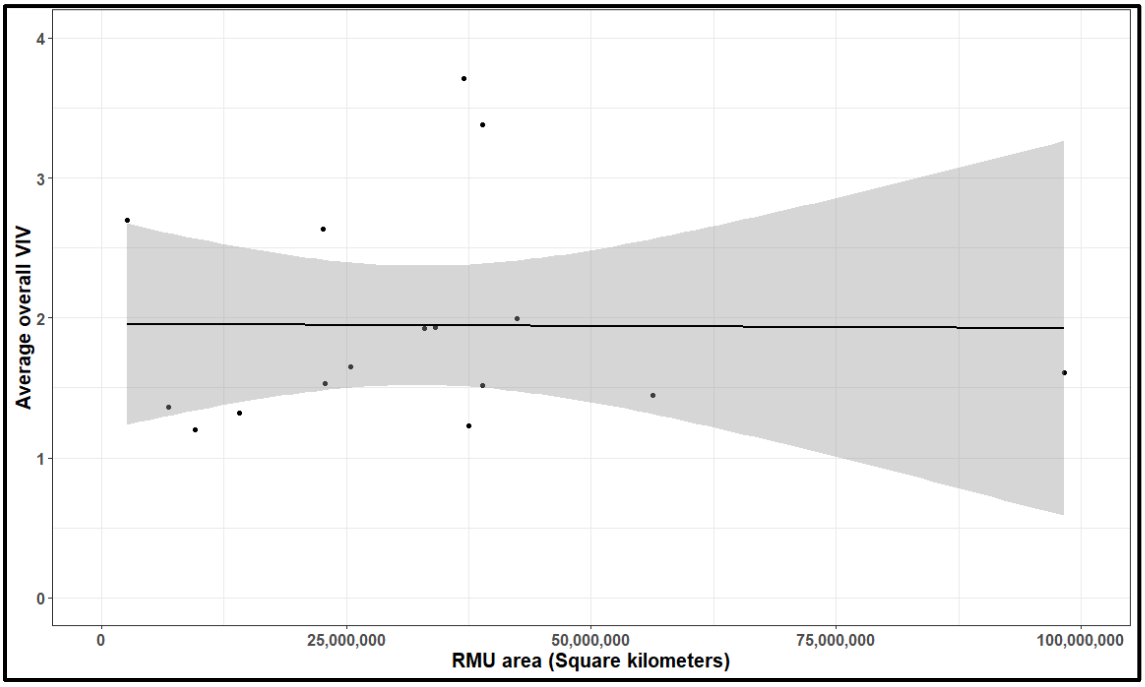

Figure 2.3: Relationship between variability in abundance (expressed as average overall Variability Index Value (y-axis) and Regional Management Unit area (in square kilometres; x-axis) for loggerhead and leatherback sea turtles combined. Each dot represents a unique loggerhead or leatherback Regional Management Unit (total n=16). The black line represents the change in the extent of variability in abundance as RMU size increases. A 95% confidence envelope was added to the model.

No statistically significant relationship exists between the inter-annual variability index value (VIV) and RMU size when only loggerheads were included in the model (Figure 2.4; $r^2 = 0.081$; F statistic = 0.618; p value >0.05).

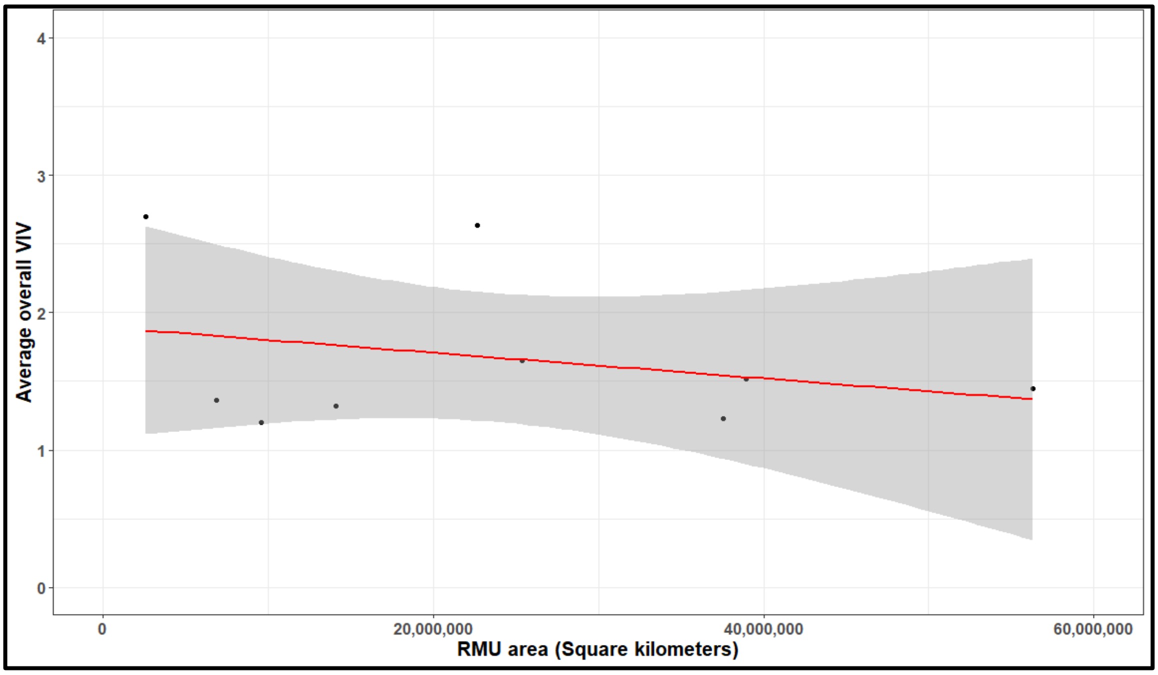

Figure 2.4: Relationship between variability in abundance (expressed as average overall Variability Index Value (y-axis) and Regional Management Unit area (in square kilometres; x-axis) for loggerhead sea turtles. Each dot represents a unique

loggerhead Regional Management Unit (total n=9). The red line represents the change in the extent of variability in abundance as RMU size increases. A 95% confidence envelope was added to the model.

As in loggerheads, the relationship between the inter-annual variability index value and RMU size was nonsignificant in leatherbacks (Figure 2.5; $r^2 = 0.047$; F statistic = 0.248; p value >0.05).

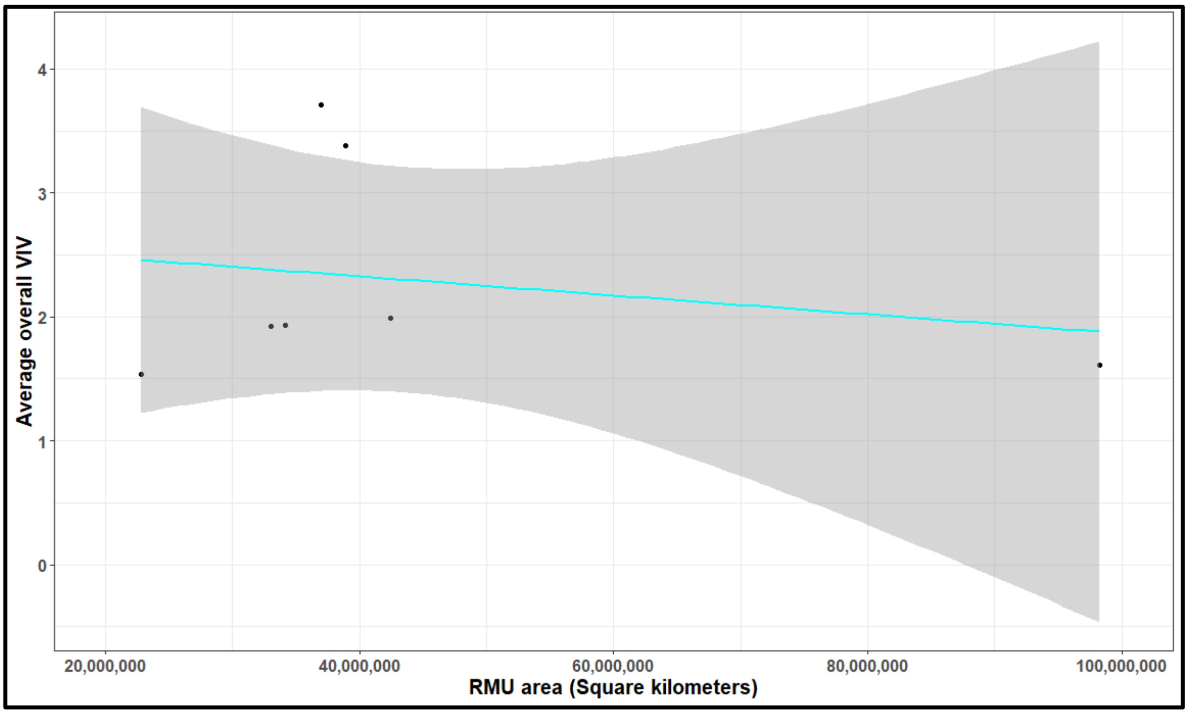

Figure 2.5: Relationship between variability in abundance (expressed as average overall Variability Index Value (y-axis) and Regional Management Unit area (in square kilometres; x-axis) for leatherback sea turtles. Each dot represents a unique leatherback Regional Management Unit (total n=7). The blue line represents the change in the extent of variability in abundance as RMU size increases. A 95% confidence envelope was added to the model.

Discussion

The aim of this investigation was to determine whether the portfolio effect could apply to sea turtles (without testing any specific mechanism) using the trend in the number of clutches oviposited (abundance trends) over time for two species of sea turtles (i.e. loggerhead and leatherback) as indicators. Specifically considered were the ideas that abundance trends per RMU were stabilised by rookeries reacting independently, and at a species-level, if RMUs reacted independently. It was hypothesised that different loggerhead and leatherback RMUs would display independent trends in abundance over time because they are subjected to different pressures in different ocean basins, which would result in long-term stabilised species-level abundance trends. Similarly, it was expected that the portfolio effect may buffer population abundances (RMU-level), with individuals nesting in specific rookeries utilising different developmental and foraging grounds and, therefore, facing different challenges (see Supplementary Material I & II) but being adapted to different environments.

The various loggerhead and leatherback rookeries per RMU displayed independent trends in abundances over time (Table 2.1 and Table 2.2, respectively) with the patterns differing between the two species. Most loggerhead nesting sites displayed an increase in the number of nests (Table 2.1), whereas most leatherback nesting sites showed a decrease in the number of nests over time (Table 2.2). In addition, the growth rates in the number of nests at individual rookeries differed. Wallace et al. (2011) considered these contrasting patterns as the result of the spatiotemporal variability in risk and threat status of sea turtles across RMUs, whereas Mazaris et al. (2017) ascribed these contrasting growth rates to variation in local conditions. It seems advantageous to spread risk by having broad distributions and experiencing a range of local conditions, which results in a range of growth rates experienced among rookeries, and thus have stabilising effects on abundance trends at the RMU-level (i.e. portfolio effect).

At the species-level, loggerhead sea turtles appear to have experienced a reasonably stable, gentle increase in the number of nests over time (Figure 2.1J). This stability in the relative abundance of nests at the species-level is attributed to a diversity of growth rates across RMUs, which is a characteristic associated with the portfolio effect theory. Despite four loggerhead sea turtle RMUs displaying declining abundance trends, five RMUs increased in population size (Figure 2.1). The diversity in environmental conditions, threats and level of protection across RMUs (Wallace et al. 2010b; Wallace et al. 2011; Wallace et al. 2023) have resulted in uncorrelated trends among loggerhead populations, and as a result, loggerheads benefit from the diversified portfolio (Schindler et al. 2015).

The pattern is, however, more complicated for leatherbacks. Only three out of the seven leatherback RMUs show an increase in abundance over time (i.e. when rookeries are unweighted by mean size) but the species-level trend increased nevertheless (Figure 2.2H). The same pattern is observed when larger rookeries are given more weight (Figure 2.2), but the trend is not consistent over time. Leatherback nest abundance increased during the 1970s to the 1980s, but a steep decline followed to the 2020s. In contrast, when rookeries are equally weighted, the species-level trend appears stable, with a slight decline after 2000. These patterns suggest that the number of clutches laid at larger leatherback sea turtle rookeries are currently declining more rapidly compared to smaller sea turtle rookeries.

A number of studies reported that leatherbacks are declining in abundance across various oceanic basins (e.g. Troëng et al. 2004; Witt et al. 2011; Ábrego et al. 2020; Benson et al. 2020), with some smaller rookeries (e.g. Sandy Point; Table 2.2; Dutton et al. 2005) showing trends of population increase. These smaller increasing sea turtle rookeries seem to buffer the declines evident in larger rookeries. The portfolio effect is evident when sea turtle rookeries are unweighted by size, while the same remark cannot be made for the weighted abundance trend, suggesting a current global decline in the total number of leatherbacks nesting per annum.

The analysis between the relationship of variability in RMU-level abundance and RMU current spatial distribution (i.e. RMU size/area) showed that no significant relationship existed (Figure 2.3-2.5). The environmental conditions and threats in the natural environment may be too variable in space and time to observe a trend at the RMU-level, or that the use across space is not uniform enough to be useful. Loggerheads may spend a disproportionate amount of time in neritic areas, but it was still expected to hold for leatherbacks with a pelagic distribution (Harris et al. 2015; Robinson et al. 2018). It is also possible that the inclusion of currently unavailable and/or unacquired data may have yielded opposite results. Nevertheless, from this analysis, it does not appear that the relative size of a particular RMU influences the extent of variability in sea turtle numbers.

The findings of this research reveal the importance of conserving sea turtles at an RMU-level (rather than at a species-level), as well as the significance of managing and maintaining a diversity of sea turtle RMUs to facilitate survival of species as a whole. Wallace et al. (2011) developed a “conservation priorities portfolio” system wherein each individual sea turtle RMU was assigned two scores. The first score, termed “risk matrix”, involved giving each RMU a score based on the status of the population (i.e. using population size, recent trend, long-term trend, rookery vulnerability, and genetic diversity). The second score was termed “threats matrix”, wherein each RMU was given a score based on the severity of threats faced by sea turtles within the RMU (i.e. fisheries bycatch, take, coastal development, pollution/pathogens, and climate change). It was shown that each individual sea turtle RMU is unique with regards to their risk and threat levels (Wallace et al. 2011). This suggests that sea turtles cannot be effectively conserved at the species-level, because their population statuses as well as the type and/or severity of threats vary across RMUs, with some populations having a poor risk/threat score, while other populations are thriving and display a good risk/threat score.

A single sea turtle RMU may display an increasing trend in population size over time, while another RMU may experience declines within the same time period (Figure 2.1-2.2). These patterns may, however, change in the future. As a result, a RMU with a large number of sea turtles cannot be considered as having a greater importance compared to a smaller RMU with fewer turtles. In the future, the larger RMU may experience a drastic decline in sea turtle abundance, while smaller RMUs may experience an increase and thereby provide a "buffering effect" for the declining population.

Despite being incorporated as a relatively new concept in ecology, the portfolio effect has been shown to serve relevance at multiple levels of biological organisation (Schindler et al. 2015). At the community level in ecology, the portfolio effect indicates that natural ecosystems should be better buffered against environmental fluctuations when species diversity is high as opposed to species-poor communities (Loreau et al. 2021). At the species-level, the temporal variability of a particular characteristic (e.g. abundance, behaviour) is reduced when the parameter shows great variation among individual populations comprising the species. Entire communities or species may also be stabilised through diversity at alternative levels of organisation (Thibaut and Connolly 2013), such as through diverse functional groups (Bai et al. 2004) or genotypic and phenotypic diversity in/among populations (Norberg et al. 2001).

Examples of the portfolio effect operating on natural populations are scarce, but some case studies do exist. In aquatic ecology, much of the existing literature on the portfolio effect theory has centred on explanatory mechanisms for observed stability in fish populations (Hilborn et al. 2003; Siple and Francis 2016; Moore et al. 2021; Price et al. 2021; Vargas et al. 2022). Some studies have concluded that diversification at one level of biological organisation could be stabilised as a result of diversification at lower levels; for example, greater phytoplankton species and population diversity increases the stability of entire phytoplankton communities (Corcoran and Boeing 2012). Further, more diverse phytoplankton communities may encourage ecosystem stability (Vallina et al. 2017). It is likely that a wide diversity of other marine species display similar adaptations.

These results have clear implications for sea turtle conservation and management. It suggests that breeding strategies (i.e. philopatry and risk spread among rookeries and RMUs) have a naturally stabilising effect on populations to withstand natural variation. However, the anthropogenic pressures, such as bycatch, pollution, and disturbance at nesting grounds, need to be managed. It is the diverse range of anthropogenic threats that have made these extant marine reptiles prone to population declines. Sea turtles have remained resilient for centuries and some populations, with adequate protection and threat-management, continue to thrive (e.g. green turtles from Samandağ beach, Turkey; Sönmez et al. 2023). It is concluded that the portfolio effect operates in sea turtles since the portfolio effect allows entire species to achieve temporal stability in abundance as a result of population-level diversity (Anderson et al. 2013; Loreau et al. 2021).

Conclusion

The portfolio effect is new in the field of biology and deserves greater attention. It serves as a possible explanation why various marine species have persisted for millennia, including sea turtles. In this study, the portfolio effect appears to operate within populations/RMUs (i.e. diversity of rookeries) where a diversity of growth rates were evident in each region. Maintaining diversity, even of small rookeries and populations, should be a priority. In this particular analysis and the persistence of sea turtles in general, diversity has a stabilising effect and highlights the importance to monitor, manage and conserve sea turtles on a rookery and/or population (i.e. RMU) basis; environmental conditions and threats experienced by these marine reptiles varies spatiotemporally and the spread creates resilience.

Protective measures at one rookery or RMU may aid the recovery of just that one population, and not necessarily other populations that are geographically isolated. But conserving a diversity of rookeries and/or RMUs allows populations that are experiencing a period of success to “buffer” populations that are under pressure. The persistence of sea turtles is unpredictable and uncertain in this anthropogenically-dominated world. Conservation and management measures should be designed to lessen human impacts and to allow these well-adapted species to flourish in the environment in which they have thrived in for so long.

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Chapter 3 | **Nesting behaviour and bet-hedging adaptations in loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtles**

Abstract

The iSimangaliso Wetland Park hosts nesting loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) populations that have been protected and monitored since 1963 as a result of past exploitation. Loggerhead numbers have increased rapidly while leatherbacks have been "recovering" much slower, with no clear explanation. Here, it is hypothesised that loggerheads may exhibit bet-hedging strategies (i.e. altering remigration periods to capitalise on favourable seasons), a characteristic associated with generalist species, that facilitated population growth compared to the leatherbacks. The results indicated that most loggerheads had 2-4 year remigration intervals but with substantial variation, whereas leatherbacks typically remigrate every 2-3 years. Both species were, however, considered temporal specialists with neither species exhibiting bet-hedging adaptations. No interspecific difference was found when comparing how remigration interval changes with experience. However, the variability in remigration period of loggerheads seem to be due to an increase in remigration period over time. A significant difference between species existed when comparing whether remigration interval has changed through time, whereby loggerheads increased their remigration period while leatherbacks retained consistent patterns as conditions changed. It suggests that loggerheads experienced declines in fitness, because an increase in remigration intervals results from deteriorating conditions in foraging area(s) and/or a decline in individual health. If current conditions continue or become unfavourable, loggerhead sea turtles may experience a slowing, or even a decline, in their population growth rate in the near future while leatherbacks may retain or experience an increase in their population growth rate.

Keywords

Bet-hedging; generalist species; remigration interval; foraging grounds; individual health; fitness; population growth rate; *Caretta caretta*; *Dermochelys coriacea*

Introduction

Sea turtles are well adapted to their (pristine) environment and have persisted through various past mass extinctions. Currently they face a range of anthropogenic threats (such as direct harvesting (Lopes et al. 2022), incidental bycatch (Carpio et al. 2022), pollution (Roslan Harun 2023), coastal development (Costa et al. 2023), boat strikes (Foley et al. 2019) etc., which necessitated conservation initiatives at rookeries to protect nesting populations where they occur predictably in high abundances. These conservation actions may involve the implementation of nest monitoring and protection programs, as well as the establishment of terrestrial and marine protected areas within sea turtle nesting and foraging habitats (Mazaris et al. 2017; Patrício et al. 2022).

A number of sea turtle populations have shown signs of recovery since protection, such as green sea turtles (*Chelonia mydas*) in Aldabra which have been protected since 1968 (Mortimer et al. 2011; Pritchard et al. 2022). Other green turtle populations that have shown recent increases include an increase in the annual number of nests along the Floridian coastline in the North Atlantic (Valdivia et al. 2019) and along the Hawaiian coastline (Mazaris et al. 2017). In addition, other nesting populations of sea turtles have shown at least some increase in nesting numbers (e.g. hawksbill sea turtles (*Eretmochelys imbricata*) in the Dominican Republic (Revuelta et al. 2015) and leatherback sea turtles (*Dermochelys coriacea*) in Florida (Stewart et al. 2011) and Sandy Point on St. Croix (Dutton et al. 2005)). These conservation successes illustrate that protection can boost recovery.

The establishment of conservation areas, however, has not always been successful. It is possible that the conservation measures are not appropriate or enforced adequately or are not matched with the behaviour of the species they are trying to protect. Harris et al. (2015) suggested that the distribution of internesting and nesting habitat used by leatherbacks is much broader than the monitored areas in Southwestern Indian Ocean (SWIO) Regional Management Unit (RMU) and, thus, may not provide a good representation of the nesting trends. Therefore, it is useful to investigate the SWIO RMU to establish if the animal behaviour and conservation measures are mismatched.

Five species occur along the sandy beaches of iSimangaliso Wetland Park in Maputaland, South Africa, i.e. hawksbill, green, loggerhead (*Caretta caretta*), olive ridley (*Lepidochelys* *olivacea*) and leatherback sea turtles (Hughes 1970; Hughes 1973) but only two nest here. Historically, these nesting turtles were harvested as a source of nutrition (McAllister et al. 1965) and income (Hughes 1980), but the growing concern about the number of harvested turtles sparked a field-based protection and monitoring program.

Since 1963 loggerhead and leatherback sea turtles have received increasing protection through the implementation of a series of coastal and marine protected areas and measures (Hughes 1973; Nel et al. 2013) to increase population growth rates. It was expected that both species would benefit from protection and show similar population recovery rates. Initially this was the case and both species did respond, with some recovery for the first decade (Nel et al. 2013). However, after that the trends diverged. Despite South African loggerhead and leatherback sea turtles receiving similar conservation efforts in the iSimangaliso Wetland Park, loggerheads appeared to have experienced a rate of population recovery that is rapid compared to the leatherback population (Nel et al. 2013). Loggerhead sea turtles have experienced an increase in abundance over time, while leatherback sea turtles have stabilised with no or minimal change over time (based on annual nest counts; Nel et al. 2013).

Explanations for the observed differences in population recovery rates were investigated through a number of student projects; these include testing differing reproductive outputs per species (Tucek 2014), male to female ratios (Maxwell et al 1988, Tucek 2014), differing predation rates and survivorship (De Wet 2012), correcting quantification of abundances caused by unobserved nests/tracks or different offshore mortality rates (Thorson et al 2012; Nel et al. 2013), and different nest habitat preferences (King 2023). Although these may contribute to the decline (or recovery) of the population, additional information needs to be considered. The between-season behaviour of individual sea turtles (e.g. remigration period) may serve as a possible explanation for observed differences in population growth rates. The frequency at which sea turtles return to nest may influence the number of clutches deposited per season and the overall reproductive output of individuals. If true, this would affect population growth.

The remigration interval is defined as the time period between two successive nesting seasons (Cheng et al. 2018). Individual sea turtles respond to changing environmental conditions in their foraging areas by either lengthening (i.e. increasing) or shortening (i.e. decreasing) their remigration intervals during unfavourable and favourable environmental conditions, respectively (Hays 2000; Reina et al. 2009; Girard et al. 2021). Because remigration interval regulates the number of female nesters per season (Bjorndal et al. 1999; Troëng and Chaloupka 2007), recovery rates may be affected. Shorter remigration intervals from healthy foraging areas (Saba et al. 2007; Hatase et al. 2013), shorter distances between nesting beaches and foraging areas (Troëng and Chaloupka 2007), and/or health of individual sea turtles (e.g. larger body sizes; Hatase and Tsukamoto 2008), should increase the rate of population growth and/or recovery. A short remigration interval facilitates more frequent nesting and potentially greater lifetime reproductive output. Sea turtles with short remigration intervals may enhance population growth rates, providing that the total generation length (reproductive duration) and clutch frequency stays constant.

During the sea turtle nesting season in South Africa (between mid-October and mid-March), loggerhead and leatherback sea turtles typically return from their distant foraging grounds to lay approximately 3-5 and 6-8 nests per adult female, respectively (Nel et al. 2013). Nesting South African sea turtles do not, however, return to the sandy beaches of Maputaland to nest every year. South African loggerhead and leatherback sea turtles have remigration intervals of similar mean duration (Nel et al. 2013) of approximately three years. However, the remigration interval of individuals in a species may be different or change over time (resulting in differences in the total annual number of nests deposited per nesting season between species) or individuals from either species may have changed their remigration intervals over time with experience or as environmental conditions change.

Stochastic environments make it challenging for individual organisms to predict and effectively respond to the prevailing and future stressors. Highly variable environments may result in species' traits being optimal during one particular period (i.e. modal conditions), whereas the same traits may be a disadvantage under more extreme or abnormal conditions (Childs et al. 2004; Simons 2009; Greene et al. 2010). As a result, individuals in a population, or a population itself, may adapt their default behaviour to a strategy that lowers the fitness in the short term (e.g. between breading cycles, years, or successive generations etc.) in exchange for maximum long-term fitness of the individual or population (Olofsson et al. 2009; Simons 2011). This behaviour is known as "bet-hedging", wherein individuals living in unpredictable and/or highly variable environments reduces their temporal fitness between cohorts by diversifying their phenotype (Philippi and Seger 1989; Starrfelt and Kokko 2012).

For example, asynchrony in the hatching times of fairy shrimp (*Branchinella longirostris*) eggs acts as a buffer against the probability of experiencing a complete reproductive failure during one period (Pinceel et al. 2017). Increased long-term population growth of fairy shrimp (*Branchipodopsis wolfi*) results from the asynchronous hatching times of dormant eggs (Pinceel et al. 2021); a diversified bet-hedging strategy. With the current rapid climate change and unpredictable natural environments, animals using bet-hedging strategies might be particularly well-equipped to avoid extirpation.

Bet-hedging strategies range from "conservative" (expressing only a single trait/strategy to avoid risk), to a diversified strategy (using a range of adaptations), or "adaptive coin flipping" use different strategies at different times (Olofsson et al. 2009). Diversified and/or adaptive coin flipping behaviours are considered typical for generalist species which have broader environmental tolerances. Specialist species, however, are organisms with narrow niche breadths, utilising specific habitats, with specialised diets (Terraube et al. 2011) and/or other environmental requirements (Dennis et al. 2011; Botts et al. 2013). Specialist species thrive in (near) constant environments whereas generalist species tolerate highly variable environments or periods of environmental instability (Colles et al. 2009; Peers et al. 2012). Generalists can alter breeding behaviours in response to environmental change by changing the timing (onset or intervals) of recurring key biological events such as the migration (Reina et al. 2009), breeding or spawning events (Walther et al. 2002). Generalist and specialist species are thus not equally vulnerable to global or local change (Wilson et al. 2008; Clavel et al. 2010; De Gabriel Hernando et al. 2022).

Even though specialist species may outcompete generalist during stable environmental conditions, generalists may benefit in the longer term since they have a greater capacity to tolerate and withstand changing environmental conditions (Colles et al. 2009; Peers et al. 2012). Therefore, it is possible that sea turtle population recovery rates could be explained by the use of bet-hedging adaptations, with the ability to change a behaviour as environmental conditions change, such as the case of South Africa's loggerhead and leatherbacks. Sea turtles may be regarded as "temporal generalists" by showing variability in their remigration intervals, or as "temporal specialists" if individuals are consistent in their nesting interval. If one of the two species is a "temporal generalist" it may alter their remigration intervals using a diversified and/or adaptive coin flipping bet-hedging behaviour. As a result, it may skip nesting seasons when conditions become unfavourable. Sea turtles may, however, change their remigration if an individual's body condition declines as a result of injury, disease, or if food availability diminishes.

The aim of this investigation was to determine the consistency of individual loggerheads and leatherbacks nesting in iSimangaliso and to assess the use of the bet-hedging concept in the evaluation of the behaviours. Two key questions were investigated. First, do loggerhead or leatherback individuals change their remigration intervals? It is hypothesised that loggerheads have a generalist temporal nesting behaviour exhibiting bet-hedging adaptations and the ability to change their remigration intervals whenever conditions become unfavourable. Such flexibility in behaviour may have allowed loggerheads to increase in abundance much faster than leatherbacks (Nel et al. 2013). Second, has the remigration interval of leatherbacks lengthened? It is hypothesised that the remigration interval of leatherback sea turtles has increased over time resulting in less frequent nesting since the abundance of the leatherback population has not increased as rapidly as the loggerhead sea turtles (Nel et al. 2013).

Materials and Methods

Ethics statement

Nesting data used for this particular investigation were collected by Ezemvelo KZN Wildlife in compliance with their legislated conservation mandate. Permission to use the long-term dataset was granted under a research agreement.

Study site & Data collection

The study site for this investigation was iSimangaliso Wetland Park, which includes a sandy coastline spanning ~220 km situated along the northeastern coastline of Kwazulu-Natal, South Africa (Claudino-Sales 2019), where sea turtles have been monitored and studied annually along a ~52km stretch of beach within the park (from Kosi Bay Mouth to Mabibi; Figure 3.1). The study site map (Figure 3.1) was created using QGIS [version 3.32.3] (QGIS Development Team 2009).

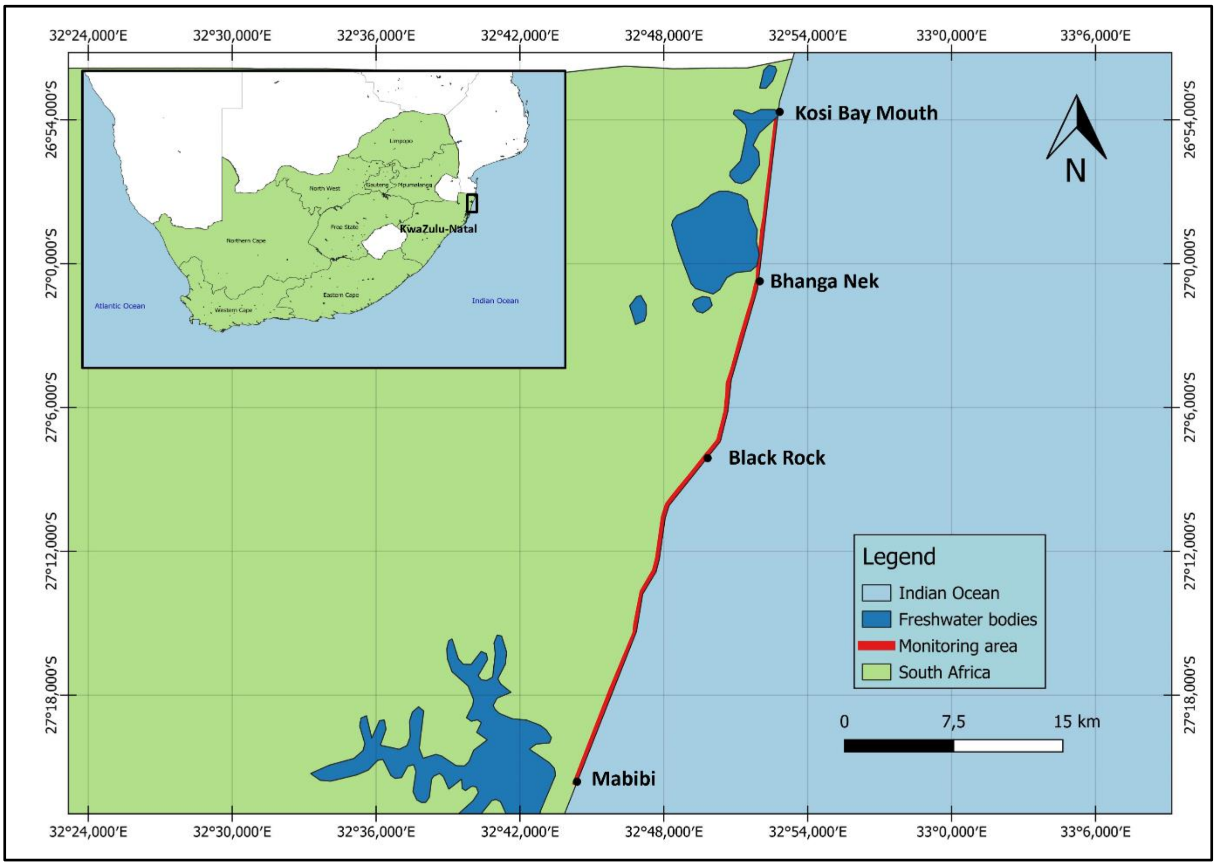

Figure 3.1: The South African sea turtle monitoring area (i.e. from Kosi Bay Mouth, situated ~4km south of the Mozambique border, to Mabibi, situated ~56km south from the Mozambique border)

iSimangaliso Wetland Park experiences a subtropical climate and is influenced by both tropical and temperate weather systems (iSimangaliso Wetland Park Authority 2017). The average summer temperature across the region is approximately 26 °C, with annual rainfall averaging between 1 000 and 1 100 mm, and with a relatively high annual humidity (Tucek 2014). The warm Agulhas Current borders the study area and flows towards the southwest, transporting warm oceanic waters from northern South Africa that coincides with the sea turtle nesting season (Tucek 2014).

In 1963, the Maputaland program was established to conserve and monitor the status of South African sea turtles. Between mid-October and mid-March, adult female loggerhead and leatherback sea turtles migrate from their respective foraging grounds to the park to lay several clutches (Nel et al. 2013). Loggerhead and leatherback sea turtles are commonly regarded as South Africa's only two nesting sea turtle species. Today, the Maputaland sea turtle program has collated over 60 years' worth of monitoring data for South African sea turtles, making this program one of the longest sea turtle monitoring programs globally (Hughes et al. 1967; Nel et al. 2013; De Geer et al. 2022).

The initial sea turtle monitoring area included a 12.8 km stretch of beach from 3.2 to 16 km south of the Mozambique border (i.e. from the Kosi Estuary mouth southwards to the research station), which was defined as the “Index area” (Nel et al. 2013). However, since the 1973/74 nesting season, South African adult sea turtle and nesting data have been collected between from the Kosi Estuary mouth (3.2 km south of the Mozambique border) to 56 km south of the border (Mabibi). This enlarged monitoring area was denoted as the “monitoring area” (Nel et al. 2013) and includes a 52.8 km stretch of beach. As a result of the increasing monitoring efforts, a greater quantity of data pertaining individual adult sea turtle health, size and behaviour, as well as clutch size, hatching success and overall condition, have been collected.

During the pioneering work of the Maputaland Program tagging methods and type of tags used have changed. Initially (1965/66 to 1972/73), plastic numbered Rototags were used (McAllister et al. 1965; Hughes et al. 1967) which included small sheep tags or larger cattle (large) tags which were normally used for shark tagging (Hughes 1970). Newly sighted sea turtles were given a single Rototag (McAllister et al. 1965; Hughes et al. 1967). Later (post 1973/74), turtles were fitted with strong, durable metal tags made of monel/titanium with an associated locking mechanism (Hughes 1970; Hughes 1975). In addition to alterations in the type of flipper tags used, the number of tags applied to each individual sea turtle also changed. Leatherbacks were double tagged in the hind flippers because of the high tag loss whereas loggerheads were fitted with a single tag on the front proximal position between the scales. Beginning in the 2007/08 season, both loggerhead and leatherbacks were routinely double flipper tagged. Double flipper tagging greatly increases the probability that previously tagged individuals will retain at least one of the flipper tags upon return for identification which increases the likelihood of identification upon return to the nesting beach (Casale et al. 2017).

The correct identification of individuals relies on flipper tags to remain attached, intact and readable to monitors without human error. Any unrecorded nesters and/or misidentifications will influence the remigration interval values calculated for each sea turtle, and hence the results obtained for this investigation. Because of tag loss or tag confusion which could not be solved with cross-validation or data verification, different analyses relied on different subsets of data.

Data manipulation

The remigration intervals of individual sea turtles were calculated from reconstructions of the nesting season histories per individual from the seasons they were observed. Only individuals sighted for two seasons or more were used.

Statistical analyses

Data processing and analyses were conducted in R [version R-4.0.5] (R Core Team 2021). As a result of changes in the tag types, tagging methods and the size of the monitoring area within the study site over time, different sections of this analysis make use of different subsets of data.

Remigration interval between loggerheads and leatherbacks

A total of 3 924 unique loggerheads were identified, with a total of 6 159 remigration interval values. A total of 463 unique leatherback histories were recorded, with 757 remigration interval values. Based on these data, descriptive statistics were calculated for each species (range, mode, and median remigration interval values). After ensuring the assumptions of the test were met, a Mood's median test was conducted (using the *coin* package; Hothorn et al. 2006) to determine if there was a significant difference in the median remigration period between the two species.

Remigration interval and nesting experience

Individual sea turtles with a minimum of three remigration periods (i.e. a minimum of four observations) were included (495 unique loggerhead individuals with 1894 remigration interval values, and 80 unique leatherbacks with 272 remigration interval values). A mixed-effects model was used to determine if the remigration interval per species changed with nesting experience. The *lme4* (Bates et al. 2015), *lmerTest* (Kuznetsova et al. 2017), and *DHARMa* (Hartig 2022) packages were used to fit the mixed effects model, obtain the relevant p values and provide diagnostic plots to investigate whether the model assumptions were met.

For this analysis, it was tested whether the remigration interval varied with nesting experience (fixed effect) for each **species** (fixed effect). Nesting experience for any observation was initially computed as the number of years since the year in which that individual's first nest was recorded (relative year), but was subsequently standardised by subtracting relative year from the mean of relative years in the dataset. This latter operation allows model intercepts to be expressed relative to the average nesting experience within the dataset, rather than relative to "zero experience", thereby allowing intercepts to represent remigration intervals per species for an individual with "average" experience. In this analysis, the individual sea turtle identities (**ID**s) were treated as a random effect to account for potential pseudo-replication introduced by repeated observations of the same specimens.

The assumptions considered for the model included verification of a linear relationship between variables, independence of errors, constant variance of errors and the normal distribution of residuals. The residuals were not perfectly normally distributed but appeared to exhibit some form of normality, nonetheless. In an attempt to improve normality, both a log and a square root transformation of the response variable was performed. Neither of these transformations improved the model. As a result, data were kept in the original format (i.e. untransformed). The model formula for this analysis can be written as follows:

$$\boldsymbol{Model\ 1 = lmer\ (RI \sim Spp * RelYear + (1|ID)}$$

Where: ***lmer*** = the function used to fit a mixed effects model (using *lme4* package)

RI = the remigration interval

Spp = the particular species (fixed effect)

RelYear = nesting year relative to average year of nesting experience (fixed effect)

(1|ID) = various individual sea turtle replicates (random effect)

Stability in remigration intervals over time

Similar to the previous analysis, all individual sea turtles with a minimum of three remigration interval values (i.e. a minimum of four observations) were used. This totalled 495 individual loggerheads, with 1 894 remigrations, and 80 individual leatherback sea turtles, with 272 remigrations. Again, a mixed-effects model was used, but this time to determine whether remigration intervals per species varied over time. This analysis included a year effect, i.e. the actual year that a sea turtle was observed as a nesting individual, again centred relative to its mean, allowing intercepts to be interpreted more meaningfully.

The *lme4* (Bates et al. 2015), *lmerTest* (Kuznetsova et al. 2017), and *DHARMa* (Hartig 2022) packages were used to fit the mixed-effects model, obtain the relevant p values and provide diagnostic plots to investigate whether the model assumptions were met or not, respectively. For this analysis, it was tested whether the remigration interval is a function of **species** (fixed effect) and **time** (i.e. year; fixed effect). In this analysis, time refers to the specific year that an individual nested relative to the average year that a sea turtle nested. The individual sea turtle **ID**s were treated as a random effect to account for potential pseudo-replication introduced by repeated observations of the same specimens.

The assumptions considered for the model included verification of a linear relationship between variables, independence of errors, constant variance of errors, and the normal distribution of residuals. The residuals were not perfectly normally distributed but appeared to exhibit some form of normality, nonetheless. To improve normality, both a log and a square root transformation of the response variable was performed, but neither improved the model. As a result, data were kept in the original format (i.e. untransformed). For this analysis, we tested whether the remigration interval is a function of **species** (fixed effect) and **year** (fixed effect) using the following formula:

$$\boldsymbol{Model\,2 = lmer\,(RI \sim Spp * Year + (1|ID)}$$

Where: ***lmer*** = the function used to fit a mixed effects model (using *lme4* package)

RI = the remigration interval

Spp = the particular species (fixed effect)

Year = the specific year relative to the average year of nesting (fixed effect)

(1|ID) = various individual sea turtle replicates (random effect)

Results

Remigration interval between loggerheads and leatherbacks

Basic descriptive statistics regarding the temporal nesting behaviour of both species would serve as an appropriate first step for this study. Table 3.1 indicates the results from various tests conducted to compare various statistics between the loggerhead and leatherback sea turtles. The remigration interval range was 1 to 26 years for loggerheads and 1 to 15 years for leatherbacks. The most frequently occurring remigration interval value (i.e. the mode) for both species was 2, suggesting that sea turtles most commonly return to the nesting beaches every two years. When comparing the median remigration interval between the two species, both species had a median remigration interval value of 3. However, the output from Mood's Median Test suggested that the differences between the median weights were statistically significant (p value <0.01).

Table 3.1: Sample size and remigration interval statistics of loggerhead and leatherback sea turtles (1965-2019)

	# individual IDs	**# remigration interval values**	**Remigration interval range**	**Mode remigration interval**	**Median remigration interval**
C. caretta	3 924	6 159	1-26	2	3
D. coriacea	463	757	1-15	2	3
p value	-	-	-	-	0.001 (Mood's Median test)

The frequency of each remigration interval value for loggerhead sea turtles (expressed as a count and in percentage) were calculated. The median remigration interval value was 3 years (depicted in red colouration; Figure 3.2). The most frequently occurring remigration interval values for loggerhead sea turtles included 2 years (40%), 3 years (22%) and 4 years (12%). Most remigration intervals were 2-4 years in length (~74%), while 1-year migrants were common (9%). The remaining remigration interval values occurred much less frequently. Remigration intervals longer than the median remigration interval value of 3 years (i.e. >3 years) constituted ~29% of the total frequency. A steep increase in frequency is evident from 1-year intervals to 2-year intervals (i.e. increase of 31%).

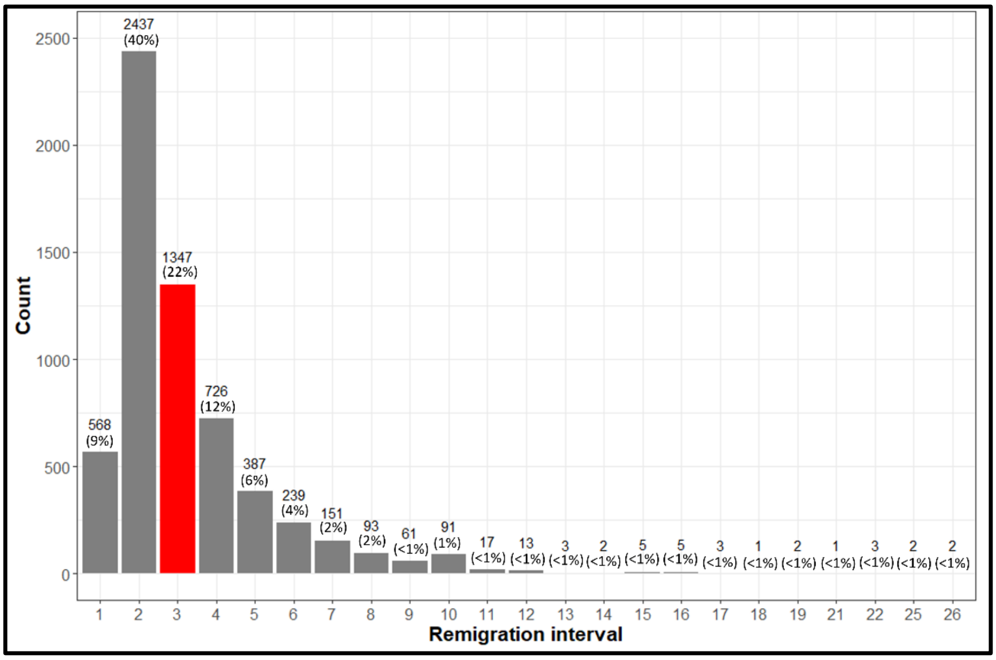

Figure 3.2: Frequency bar graph of the remigration interval values for loggerhead sea turtles (total n = 6 159; 1965-2019). The remigration interval value is illustrated on the x-axis (expressed in years), while the frequency of each remigration interval value is depicted on the y-axis (expressed as a count and percentage in brackets). The red bar illustrates the median remigration interval of loggerheads (3 years).

The frequency of each remigration interval value for leatherback sea turtles (expressed as a count and in percentage) were calculated. The median remigration interval value was 3 years (depicted in cyan coloration; Figure 3.3). The most frequently occurring remigration interval values included 2 years (46%) and 3 years (28%). The majority of remigration interval lengths were 2-3 years (~74%), while 4-year remigration interval values were also common (9%). A very small percentage of remigration intervals included 1-year intervals (i.e. 2%), while the remaining remigration interval values were also negligible. Remigration intervals longer than the median remigration interval value of 3 years (i.e. >3 years) constituted ~24% of the total frequency. A steep increase in frequency is evident from 1-year intervals to 2-year intervals (i.e. increase of 44%), while a reduction in the frequency of remigration intervals exists from 3-year intervals to 4-year intervals (i.e. decline of 19%).

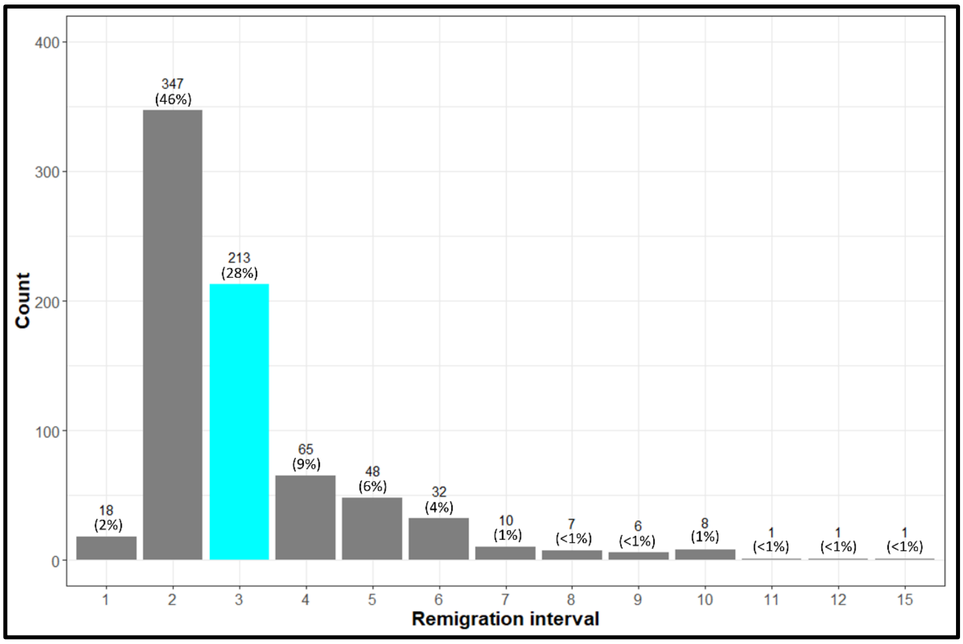

Figure 3.3: Frequency bar graph of the remigration interval values for leatherback sea turtles (total n = 757; 1965-2019). The remigration interval value is illustrated on the x-axis (expressed in years), while the frequency of each remigration interval value is depicted on the y-axis (expressed as a count and percentage in brackets). The blue bar illustrates the median remigration interval of leatherbacks (3 years).

Remigration interval and nesting experience

One potential factor that could be contributing to differences in population growth rates may be related to greater changes in the remigration intervals of individuals (which itself would be related to the overall number of clutches deposited per season if clutch frequency stays constant) from one species compared to the other species. A mixed-effects model was fitted to test whether individuals from one species changed their remigration intervals with experience to a greater or lesser extent compared to the individuals from the other species (Model 1). The results indicated that, for loggerhead sea turtles, the remigration interval of individuals with an average level of experience was significantly greater than zero (Estimate = 2.759; p value <0.001; Table 3.2).

For leatherback sea turtles, even though the adjustment to the loggerhead sea turtle's intercept was positive (adjusted estimate = 0.007), this difference was nonsignificant (p value >0.05). Therefore, there was no significant difference in remigration intervals between species when comparing individual turtles with an "average" level of nesting experience (Table 3.2; Figure 3.4). For loggerheads, the actual slope for the regression line was positive (Estimate = 0.103 years/year) and significant (p value <0.001; Table 3.2), suggesting that the loggerhead sea turtles were increasing the length of their remigration intervals with experience. For the leatherback sea turtles, the adjustment to the loggerhead's sea turtle's slope was slightly less positive (still a positive slope; adjusted estimate = -0.04 years per year). The difference between the slopes of the two sea turtle species were, however, nonsignificant (adjusted p value >0.05).

The sequential removal of nonsignificant terms did not change the final patterns obtained and, therefore, does not change the interpretation of the results. These findings suggested that individuals from both sea turtle species increased their remigration intervals with experience, but that this relationship did not differ measurably between the two species (Table 3.2; Figure 3.4).

Table 3.2: Results from the mixed effects model (Model 1) comparing whether individuals from either sea turtle species changed their remigration intervals to a greater/lesser extent with experience compared to the other species

	Estimate	**Standard Error (SE)**	**Degrees of freedom (df)**	**t value**	**p value**
Intercept (*C. caretta*)	2.759	0.042	551.2	66.242	<0.001
Adjusted intercept (*D. coriacea*)	0.007	0.117	659.9	0.063	0.95
Slope (*C. caretta*)	0.103	0.009	2162	11.717	<0.001
Adjusted slope (*D. coriacea*)	-0.04	0.031	2110	-1.316	0.188

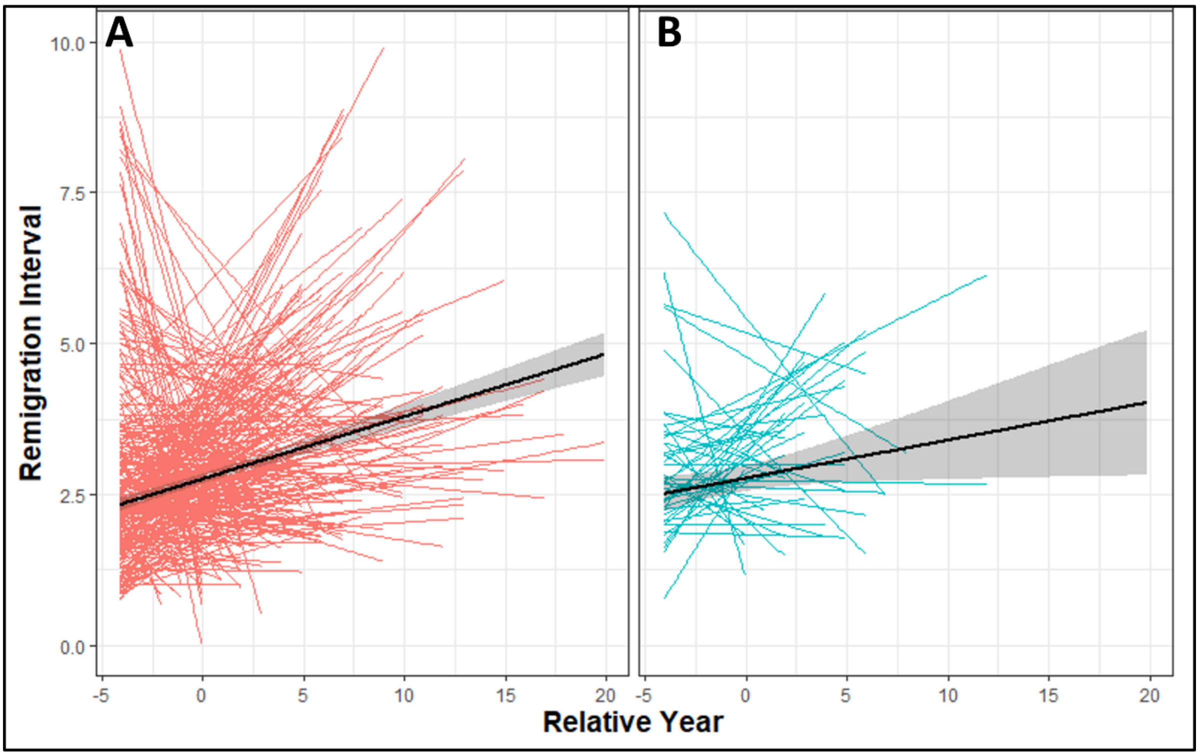

Figure 3.4: Change in remigration intervals with experience for loggerhead (A) and leatherback (B) sea turtles. Each individual red or blue line represents a unique individual loggerhead or leatherback sea turtle, respectively. The remigration interval is indicated on the y-axis (expressed in years), while the relative year is found on the x-axis. The black line represents the mean overall change in remigration interval as a sea turtle becomes more experienced. A 95% confidence envelope was added to the model.

Stability in remigration intervals over time

Testing whether sea turtles from either species change their remigration interval over time is of central importance, as this could allow for the verification of whether sea turtles have changed their remigration intervals due to a change in their environments. A mixed-effects model was used to test whether individuals from one species changed their remigration intervals over time to a greater or lesser extent compared to individuals from the other species (Model 2). In the case of this mixed-effects model, there was no significant difference in the remigration intervals of individuals with average levels of nesting experience between the two species (as in the previous analysis; Table 3.3), but there was a significant difference in the rate of change in remigration intervals over time when compared between species (Table 3.3; Figure 3.5).

For loggerheads, the slope of the regression line was positive (Estimate = 0.036) and significant (p value <0.001; Table 3.3), indicating that the remigration intervals of the loggerhead sea turtles was increasing over time. The adjustment to this slope for leatherback sea turtles, on the other hand, was negative (adjusted estimate = -0.041 years/year; Table 3.3) and the difference in remigration intervals between species over time was significant (adjusted p value <0.001; Table 3.3). When inspecting the fitted plot of the relationship for leatherbacks, the 95% confidence envelope suggests that the rate of change in remigration interval (an actual estimate of -0.005 years per year), is not discernible from zero. These findings indicate that individual loggerhead sea turtles have increased their remigration intervals over time, while leatherback sea turtles displayed no change in their remigration intervals over time (Table 3.3; Figure 3.5).

Table 3.3: Results from the mixed effects model (Model 2) comparing whether individuals from either sea turtle species changed their remigration intervals to a greater/lesser extent over time compared to the other species

	Estimate	**Standard Error (SE)**	**Degrees of freedom (df)**	**t value**	**p value**
Intercept (*C. caretta*)	2.716	0.042	509.757	64.264	<0.001
Adjusted intercept (*D. coriacea*)	-0.026	0.128	630.984	-0.206	0.837
Slope (*C. caretta*)	0.036	0.004	774.237	9.964	<0.001
Adjusted slope (*D. coriacea*)	-0.041	0.008	742.664	-4.873	<0.001

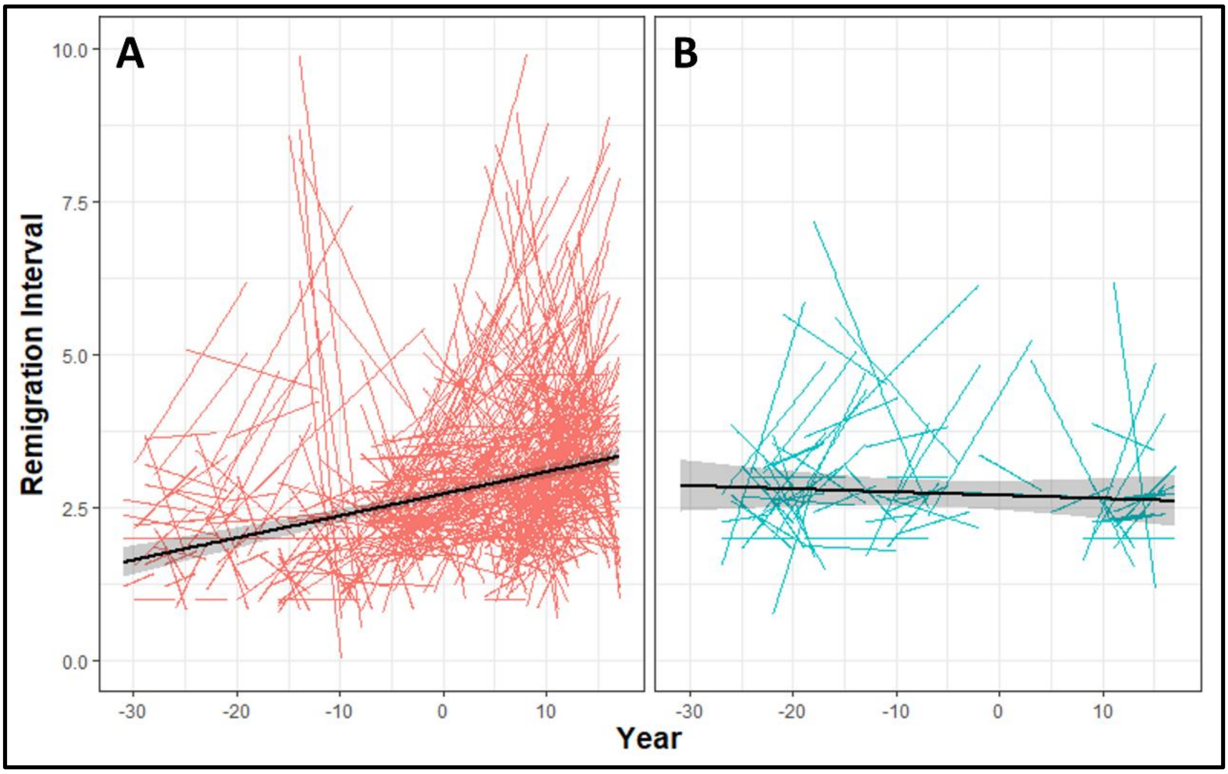

Figure 3.5: Change in remigration intervals over time (years) for loggerhead (A) and leatherback (B) sea turtles. Each individual red or blue line represents a unique individual loggerhead or leatherback sea turtle, respectively. The remigration interval is indicated on the y-axis (expressed in years), while year is found on the x-axis. The black line represents the mean overall change in remigration interval over time. A 95% confidence envelope was added to the model.

Discussion

No previous study has investigated the temporal changes in remigration intervals (i.e. the number of years between two subsequent nesting seasons; Cheng et al. 2018) of South Africa's loggerhead and leatherback sea turtles. The aims of this investigation were to determine whether differences existed in the remigration intervals of loggerhead and leatherback sea turtles and to examine the potential of bet-hedging adaptations as an explanation for the differences in population recovery rates between these two sea turtles that nest at iSimangaliso Wetland Park. In addition, this investigation aimed to determine if individual loggerhead and leatherback sea turtles change their remigration intervals with experience and if the remigration interval of leatherback sea turtles lengthened through time.

The growth potential of a sea turtle population may depend on the remigration intervals of individual sea turtles, with shorter remigration intervals leading to more females nesting per season and, thus, a higher total number of nests per season (Shaver et al. 2016; Heppell et al.

2022) for the rookery despite individuals laying fewer clutches per season as a result of having shorter foraging times in between more frequent migrations. When comparing South Africa's loggerhead and leatherback sea turtles, the median remigration interval value for both species was 3 years but the distributions (peaks) were significantly different between the species (Table 3.1). Some loggerhead sea turtles had longer remigration intervals (to 26 years) that skewed the distribution of the intervals (Figure 3.2 and Figure 3.3).

Various factors affect remigration interval. Longer remigration intervals may be associated with distant foraging grounds (Troëng and Chaloupka 2007), poor foraging ground conditions (Solow et al. 2002; Saba et al. 2007), and/or low individual health (Hatase and Tsukamoto 2008; Cheng et al. 2018). Loggerhead sea turtles have retained a relatively consistent foraging distribution and typically feed near central Mozambique on the Sofala Bank off the Zambezi delta (Nel unpublished data). Leatherback sea turtles, on the other hand, appear to utilise a diversity of foraging grounds with some individuals feeding on the south coast of the African continent and off the west coast of South Africa (Luschi et al. 2006), while others have more recently exhibited a northerly migration and forage in the Mozambique channel as well (Harris et al. 2015; Harris et al. 2018). Because a greater proportion of loggerhead sea turtles appear to feed near nesting areas compared to the proportion of leatherbacks, distance between foraging sites and nesting grounds does not appear to be responsible for the longer remigration intervals of loggerhead sea turtles (Troëng and Chaloupka 2007). If foraging distance were the only factor to influence the remigration intervals of individual sea turtles, leatherbacks should have had longer remigration intervals compared to the loggerheads.

Loggerhead sea turtles also had a greater proportion of 1-year migrants compared to the leatherback sea turtles (9% and 2%, respectively; Figure 3.2 and Figure 3.3). Individual sea turtles who foraged in closer proximity to breeding sites typically have shorter remigration intervals (Troëng and Chaloupka 2007). The shorter distance between foraging grounds and breeding sites therefore facilitates more frequent breeding migrations for some loggerhead sea turtles.

However, loggerheads had a larger proportion of 4-year remigrants compared to the leatherback sea turtles (12% and 9%, respectively; Figure 3.2 and Figure 3.3). Loggerhead sea turtles thus displayed a greater variation in their remigration intervals with the highest frequency ranging 2-4 years (~74% of remigration interval values), while 1-year migrants were also common (~9% of remigration interval values; Figure 3.2). In contrast, leatherbacks typically nest every 2-3 years (~74% of remigration interval values), with a small proportion of individuals nesting every 4 years (~9% of remigration interval values; Figure 3.3). In addition, the overall remigration interval range for loggerheads was 1 to 26 years, while leatherback remigration interval values ranged from 1 to 15 years. These descriptive statistics suggest that loggerheads displayed greater variation in their remigration intervals depending on environmental conditions, whereas leatherbacks remigrate every 2-3 year.

The mechanism of variation in loggerhead sea turtles is uncertain; it could be an adaptation, where individuals alter their remigration intervals when environmental conditions change (Reina et al. 2009) or a trade-off by spending more time building up an adequate energy reserve on foraging grounds, delaying remigration but subsequently lay more clutches during nesting seasons (Plot et al. 2012). The ability to alter the remigration interval when conditions change may improve the long-term fitness of individual sea turtles, which may potentially explain why loggerhead sea turtles have recovered much faster compared to the leatherback sea turtles.

It is possible, however, that the longer and more varied remigration intervals of loggerhead sea turtles is a response to changing environmental conditions (e.g. Reina et al. 2009) rather than an adaptation, which would suggest that loggerhead sea turtles may be experiencing some difficulty in coping with the current, changing and/or stochasticity of environmental conditions (Le Gouvello et al. 2020a). Interpreting the results obtained from the respective key questions may reveal the reason(s) for the differences in remigration intervals when comparing the loggerhead and leatherback sea turtles.

Analysing the data on the plasticity in remigration intervals between these species revealed that both loggerhead and leatherback sea turtles increased their remigration intervals with experience and there was no difference in the rate of change between species (Table 3.2; Figure 3.4). This finding suggests that older turtles extend the remigration period and more time is spent on the foraging grounds. Both species can be considered as being temporal specialists, with individuals from both species increasing the lengths of their remigration intervals with experience. South Africa's loggerheads are spatial specialists with individual females decreasing the distance between consecutive nests over time, whereas leatherbacks are spatial generalists with no change in the distance between subsequent nests over time

(King 2023). However, being a temporal generalist modifying the remigration interval has the potential to increase the fitness of individual sea turtles by allowing them to only undertake the breeding migration when conditions are favourable.

This study defined individuals using bet-hedging adaptations as being temporal generalists; they can alter their remigration intervals over time and limit their exposure to unfavourable environmental conditions. Various studies have illustrated how the adoption of diversified and/or adaptive coin flipping strategies has the potential to improve the fitness of an individual and/or an entire population (e.g. Simovich and Hathaway 1997; Lovich et al. 2015). However, here both sea turtle species are classified as temporal specialists with individuals from both species displaying lengthened remigration intervals with experience. There is no compelling evidence that individuals from either species exhibit bet-hedging adaptations because there exists no difference in the change in remigration intervals with experience between the species. Therefore, the hypothesis is rejected and it is concluded that no difference in the variability of the remigration intervals with experience existed between species.

The remigration intervals of individuals from either species may change over time as conditions change (Reina et al. 2009). Environmental conditions drove these behavioural responses, such as the measured alteration of the length of remigration intervals and not the level of experience for each species (Table 3.3; Figure 3.5). The lengthening of loggerhead sea turtle remigration intervals with time is small but significant (Table 3.3; Figure 3.5). In comparison, leatherbacks exhibited a very slight decrease/no change over time (Table 3.3; Figure 3.5). The hypothesis of no difference in the change in remigration intervals between the species is rejected because the remigration interval of loggerhead sea turtles has increased over time resulting in less frequent nesting seasons, while the leatherback remigration interval has not.

Leatherback sea turtles have retained relatively consistent remigration intervals over time, suggesting that the quality/quantity/availability of food in their foraging areas has remained stable for decades or they have started to exploit alternative, yet productive foraging areas (see Harris et al. 2015; Harris et al. 2018). Because the remigration intervals of loggerhead sea turtles have increased over time it is possible that individuals are either utilising new foraging grounds that are located further from nesting sites, experiencing declines in individual health, and/or the exploited foraging grounds are becoming less productive of the necessary food resources.

Results from various case studies have illustrated how distance to foraging grounds may influence the remigration intervals of individual sea turtles. For example, green sea turtles from Tortuguero, Costa Rica, exploiting distant foraging grounds were shown to exhibit longer remigration intervals compared to individuals making shorter trips towards other foraging sites that are in closer proximity to nesting areas (Troëng and Chaloupka 2007). South Africa's loggerheads have retained a relatively consistent foraging distribution along the coasts of the Mozambique channel as evidenced from flipper tag returns and satellite tagging (Hughes 1974; Harris et al. 2018; Nel unpublished data). Leatherback sea turtles have a much broader range, with individuals foraging on the south and west coast of South Africa, while some individuals have moved northwards and started to utilise the same foraging areas as the loggerheads (i.e. Sofala Bank, Harris et al. 2015; Robinson et al. 2016; Harris et al. 2018). Distance between nesting beaches and foraging grounds does not appear to be the reason for the observed increase in the remigration intervals of loggerhead sea turtles, because individuals have continued to exploit the same foraging areas for decades.

The next possible explanation for the increase in loggerhead remigration intervals (Table 3.3; Figure 3.5) is that the health of individuals and/or the quality of foraging grounds has deteriorated. South African loggerhead sea turtles have experienced declines in body size (i.e. straight carapace length) over time, while leatherbacks have retained a stable mean female body size (i.e. curved carapace length; Le Gouvello et al. 2020a). Previous studies have also shown that a relationship exists between maternal body size and clutch size, where larger females are able to produce larger clutches compared to smaller females (Le Gouvello et al. 2020b; Jorgewich-Cohen et al. 2022; Mortimer et al. 2022). In addition, within a Japanese loggerhead sea turtle nesting population, smaller females exhibited longer remigration intervals compared to larger females (Hatase and Tsukamoto 2008). South Africa's loggerhead sea turtles appear to exhibit a similar trend with an increase in remigration interval length over time (Table 3.3; Figure 3.5), which may share some relationship with the reported declines in the mean female body size of individuals (Le Gouvello et al. 2020a).

Because the remigration interval of individual loggerhead sea turtles is increasing with an associated decline in mean adult body size, while no change in distance between foraging areas and nesting sites being evident, it appears that possible declines in foraging ground conditions may be influencing the fitness of individuals. An increase in food availability and/or the quality of foraging grounds may be associated with a decrease in remigration interval length (Price et al. 2004; Ceriani et al. 2015; Heppell et al. 2022). It is possible that the quality of foraging areas on the Sofala Bank has diminished, resulting in a decline in individual fitness (and body size) with an associated increase in remigration interval durations.

The diet of loggerhead and leatherback sea turtles differ substantially. Loggerhead sea turtles are carnivorous and feed on bottom dwelling invertebrates, which includes a variety of crustaceans and fish (Dodd 1988; Molter et al. 2022; Mariani et al. 2023), whereas leatherback diets primarily consist of soft-bodied, gelatinous organisms such as free-swimming medusae (i.e. jellyfish) and other invertebrates (Bjorndal 1985; Heaslip et al. 2012; Nordstrom et al. 2020). It is possible that the availability of prey items for loggerheads have decreased, leading to an increase in time spent within foraging grounds to obtain sufficient resources for upcoming breeding seasons. Jellyfish, on the other hand, have shown to proliferate in recent years (Brotz et al. 2012; Condon et al. 2013; Lee et al. 2023). Leatherback sea turtles may be exploiting good quality foraging areas that contain an abundance of resources, allowing individuals to retain a consistent remigration interval while individual loggerheads are exploiting foraging areas that have limited resource availability and/or are of poor quality.

From these results, it appears that South Africa’s leatherback sea turtles have higher fitness compared to the loggerheads that appear to have entered a period of decline. Even though loggerhead sea turtles have experienced rapid recent population growth rates (Nel et al. 2013), it is possible that this pattern may soon be reversed in favour of the leatherbacks. A potential foraging area quality decline may have been responsible for the reduction in the adult female body size of loggerheads, with a concomitant increase in their remigration intervals (Troëng and Chaloupka 2007). This fitness compromise may lower reproductive output (Le Gouvello et al. 2020b).

It is possible that loggerhead sea turtles exhibit a trade-off between remigration interval and clutch frequency. In a previous investigation, it was found that individual green sea turtles nesting in Cyprus with remigration intervals of less than three years had a clutch frequency that was 25% lower compared to individuals with longer remigration intervals (Stokes et al. 2014). Leatherback sea turtles nesting in French Guiana have displayed similar patterns with higher estimated clutch frequencies being associated with individuals with longer remigration intervals (Plot et al. 2012). It is possible that South Africa's loggerhead sea turtles display a similar behaviour and exhibit a trade-off between the remigration interval and number of clutches, where longer remigration intervals would allow individuals to obtain an adequate supply of energy and subsequently lay more clutches during nesting seasons. Such an adaptation might have allowed loggerheads to experience more rapid population growth rates compared to the leatherbacks.

However, despite loggerheads potentially exhibiting such a trade-off, it is more likely that the loggerheads are currently in peril. Increasing remigration intervals could result in a reduction in the number of nests per season (Shaver et al. 2016), while longer remigration intervals may not necessarily be associated with larger reproductive outputs per female (Price et al. 2004). The decline in adult body size (and thus individual fitness; Le Gouvello et al. 2020a) with an associated increase in the remigration intervals over time (Table 3.3; Figure 3.5) makes it more plausible that it is not an adaptive strategy or trade-off exhibited by loggerheads. The lengthening of loggerhead remigration intervals is suggested to be a response to possible declines in foraging habitat conditions.

Conclusion

Similarities as well as differences in the temporal remigration intervals of South Africa's loggerhead and leatherbacks exist. Both species were shown to increase their remigration intervals with experience and can be classified as being temporal specialists. No evidence of bet-hedging adaptations being occupied by individuals from either species was found. Between the two species, only loggerhead sea turtles increased their remigration intervals over time. This increase in their remigration intervals may be the result of the decrease in individual health and adult body size, which may reflect a possible decline in the quality of their foraging habitats. Even though loggerhead sea turtles may potentially exhibit a trade-off between the length of their remigration interval and clutch frequency, which may have encouraged population growth rates, it is more likely that their increasing remigration intervals is a response rather than an adaptation to the prevailing environmental conditions. Leatherbacks appear to be in better condition compared to the loggerheads. Even though the loggerhead population within iSimangaliso Wetland Park has been recovering faster than the leatherback population for decades, it becomes apparent that the differences in population growth rates may potentially be reversed in the near future.

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Chapter 4 | **Conclusion**

The implementation of effective sea turtle management and protection strategies has resulted in the successful recovery of several modern-day populations (Mazaris et al. 2017). Because of the high and ever-expanding number of threats faced by sea turtles, which includes both natural (e.g. climate change, Fuentes et al. 2011; Gammon et al. 2023) and anthropogenic perturbations (e.g. bycatch, Carpio et al. 2022; illegal harvesting, Pheasey et al. 2023; pollution, Arienzo 2023; etc.), many populations have experienced declines in abundance and this ancient group has consequently been identified as one of the most threatened groups of animals in the world (Lascelles et al. 2014). However, despite the establishment of conservation actions potentially halting or reversing such declines, sea turtles have shown to exhibit their own form of resilience to environmental changes as they have existed for millions of years while other major taxa have gone extinct (Martín-Del-Campo and Garcia-Gasca 2019; Godley et al. 2020).

The overall aim of this thesis was to investigate potential reasons for observed trends in sea turtle abundances at species, population, and rookery levels. This dissertation is split into the portfolio effect (Chapter 2) which focused on populations to species and the temporal renesting interval and associated bet-hedging adaptations (Chapter 3) within two species using the South African population data.

Species and RMU level loggerhead and leatherback abundance trends and the portfolio effect

To test whether the portfolio effect (Schindler et al. 2015) applies to sea turtles using nesting abundance trends over time for two species (i.e. loggerhead and leatherback sea turtles), it was determined whether different RMUs display independent trends in abundance over time, which would result in a stabilising effect on the overall species-level abundance trend (Schindler et al. 2015). The majority of rookeries situated within loggerhead RMUs displayed increasing trends in abundance over time, while most leatherback rookeries showed declines. In addition, population growth rates differed among rookeries situated within both loggerhead and leatherback RMUs. This diversity in abundance trends within rookeries were suggested to be a reflection of the spatiotemporal variation in environmental conditions, threats, and/or level of protection accompanying sea turtles.

At the species-level, irrespective of whether growth rates were weighted or unweighted by mean population size, loggerhead sea turtles experienced an increase in abundance over time. Recently loggerheads have been reported to show increasing abundances within various ocean basins, such as in the North Atlantic (Laloë et al. 2020), Mediterranean and Southwest Indian (Mazaris et al. 2017). However, some loggerhead populations in other RMUs have shown rapid declines in the annual number of clutches (e.g. Northwest Indian Ocean, Willson et al. 2020). Uncorrelated trends in abundances at the RMU-level (caused by different sea turtles experiencing different environmental conditions and/or protection levels) resulted in a stabilised species-level trend (*sensu* Schindler et al. 2015). In this context, loggerhead sea turtles exhibit a diversified portfolio, allowing for their persistence at the species-level. It follows that conserving sea turtles across multiple rookeries/RMUs, irrespective of population size, is essential to maintaining a diversified portfolio.

Leatherback species-level abundance increased when rookeries were weighted or unweighted by mean population size. However, the species-level trend for leatherbacks increased during the 1970s up to the 1980s, while a steep decline in abundance was evident for the remaining decades when trends were weighted by mean population size. In contrast, when rookeries were unweighted by mean population size, the species-level trend displayed minimal fluctuations in abundance over time (apart from a decline from the 2000s to the 2020s).

Larger leatherback rookeries/RMUs showed more rapid declines in abundance than smaller rookeries/RMUs. Leatherbacks have declined in various ocean basins in recent decades, such as in the Atlantic (Hays et al. 2024) and in the Pacific (Benson et al. 2020). However, leatherbacks have been reported to show signs of increasing trends in nesting abundance in other areas (Mazaris et al. 2017). The results from this study suggested that smaller leatherback rookeries/RMUs with fewer mean clutch deposits per season, which were either experiencing increasing or less rapidly declining trends in abundance compared to larger populations, may have a buffering effect on declines evident in the larger leatherback rookeries/RMUs. These patterns suggested that smaller rookeries were facilitating survival of leatherbacks at the species-level. However, similar to loggerheads, it is essential that conservation efforts are allocated to various rookeries/RMUs to maintain diversity and to increase species resilience to changing conditions.

It was also determined whether a relationship exists between variability in abundance and RMU size. It was found that the extent of variability in abundance of RMUs shared no relationship with the RMU size (i.e. area). Some RMUs may be large in area and encompass many rookeries receiving increased levels of protection efforts, while other RMUs may cover large oceanic spaces but sample a greater number of environmental conditions/threats. This situation may result from environmental conditions and threats in the natural environment being too variable in space and time to observe a trend at the RMU-level or that the spatial use within the RMU is not even. Indices like kernel density or some space metric that identifies utilization distribution may be a more relevant approach (Peckham et al. 2008). Many of the hard-shelled species have a more coastal distribution and rarely use the high seas evenly (Hughes 1974; Harris et al. 2018).

The portfolio effect serves as a possible explanation of how sea turtles have persisted for millennia. Although this concept is relatively new in the field of biology (Schindler et al. 2015), it provides a useful perspective from which to examine the response of populations to changing conditions. In this study, the portfolio effect appeared to operate within populations/RMUs where a diversity of growth rates were evident within the region. From this, it was suggested that maintaining diversity should be the central focus of conserving biodiversity. Sea turtles should be monitored and protected on a rookery and/or population (i.e. RMU) basis, because the environmental conditions and threats experienced by these marine reptiles varies spatiotemporally (Mazaris et al. 2013). The protective measures put in place in one rookery/RMU may aid the recovery of one population, but not necessarily another population that is geographically isolated. In addition, conserving a diversity of rookeries and/or RMUs allows populations that are experiencing a period of increasing abundances to act as a “buffer” for declining populations.

While portfolio effects were evident within both loggerhead and leatherback sea turtles, while other taxa have also shown to exhibit similar patterns (see Schindler et al. 2015), some improvements to the current study may have produced better/alternative results. One of the major factors that may have resulted in the acquisition of different results is the presence of data gaps. A great proportion of data entries remain unpublished/unreported and are thus inaccessible (Omeyer et al. 2022). In addition, data collection protocols and the extent of human-produced observation/data entry errors will vary across rookeries, resulting in sampling biases. Therefore, it becomes important that monitoring data be collected consistently and is available for future studies.

Also, it is essential that data entries are treated with caution, because the inclusion of human-related errors and differences in methods used may render some data unusable. In this study, the Living Planet Index method (LPI 2023) was used to derive RMU and species-level trends in abundances. There are other methods available to derive large scale trends using finer scale components, such as making use of state-space models (Auger-Méthé et al. 2021), which may produce different trends and may have result in different interpretations of findings. Future studies that include time-series data should carefully consider the appropriateness of different models when analysing the data.

Temporal nesting behaviour of South African loggerhead and leatherback sea turtles

To test if differences and/or changes in remigration intervals, as well as the possible occurrence of bet-hedging adaptations, could serve as explanations for the differences in population recovery rates, loggerhead and leatherback sea turtles nesting along the coastline of iSimangaliso Wetland Park was used as a model system. 2-year remigration intervals were the most frequent intervals for both species. Loggerhead sea turtles had a greater variation in remigration interval compared to the leatherbacks, with loggerheads typically undergoing the breeding migration every 1-4 years, while leatherbacks typically nested every 2-3 years. Other studies have reported how shorter distances between nesting and foraging grounds may result in shorter remigration intervals (Troëng and Chaloupka 2007). It was suggested that 1-year remigration intervals within loggerheads were attributable to their foraging areas being in close proximity to their nesting grounds (Nel unpublished data). Foraging distance does not, however, explain why loggerheads had a higher proportion of 4-year remigration intervals compared to leatherbacks.

The change in remigration intervals within individuals with experience did not differ between loggerheads and leatherback sea turtles. Both species were classified as being temporal specialists, whereby individuals from both species showed consistent increases in remigration intervals with experience. As a result, no evidence that individuals from either species exhibit bet-hedging adaptations (Philippi and Seger 1989; Starrfelt and Kokko 2012) was found. It is possible that individuals bet-hedge in space by varying the distribution of their nests across nesting beaches (King 2023). However, individuals from both species do not exhibit bet-hedging adaptations associated with remigration intervals.

South African loggerheads have been increasing their remigration intervals through time (rather than with experience) while the leatherback sea turtles did not display such an increase. This increase in loggerhead remigration interval is suggested to be driven by a change in conditions (Reina et al. 2009). Previous investigations have found that a lengthening in remigration intervals may result from increasing foraging area distances (Troëng and Chaloupka 2007), diminishing foraging ground qualities (Saba et al. 2007), and/or a decline in the health of individual sea turtles (Hatase et al. 2013; Cheng et al. 2018). Previous studies have reported that smaller individual sea turtles (which may have lower fitness) may have shorter remigration intervals than larger individuals (e.g. Hatase and Tsukamoto 2008). In addition, South African loggerhead sea turtles exhibit signs of decreasing body sizes (straight carapace length), while leatherbacks have not (curved carapace length; Le Gouvello et al. 2020a). Smaller adult females may lay smaller/fewer clutches compared to larger individuals (Le Gouvello et al. 2020b; Mortimer et al. 2022).

Because the remigration intervals of individual loggerhead sea turtles are increasing with an associated decline in mean adult body size and assuming no change in distance between foraging areas and nesting sites a decline in the foraging area conditions may be impacting the health of individuals. The quantity/quality of prey items of carnivorous loggerhead sea turtles may be decreasing, while an abundance of dietary items may be available to leatherbacks because jellyfish populations have been increasing and spreading globally (Brotz et al. 2012; Lee et al. 2023). South Africa's leatherback sea turtles appear to exhibit higher fitness levels compared to the loggerheads. Even though previous investigations have shown loggerhead population growth rates that could be considered as being rapid compared to those of leatherbacks for decades (Nel et al. 2013), it is possible that environmental change in the foraging areas may cause a reverse in this pattern.

While an increase in remigration interval lengths may serve as an indication of declining foraging area and/or individual health, it was suggested that loggerhead sea turtles may possibly exhibit a trade-off between remigration interval and clutch frequency. Previous studies have indicated that longer remigration intervals may result in higher clutch frequencies (e.g. Plot et al. 2012; Stokes et al. 2014). Such an adaptation may have allowed loggerheads to outcompete leatherbacks in terms of their population growth rates, because undertaking the breeding migration less frequently, spending more time within foraging areas and building up a larger energy reserve would have limited the exposure of individual loggerheads to a diversity of conditions.

However, even though it is possible that the loggerheads exhibit such adaptations, it is more likely that the loggerheads are in peril. The decline in adult body size (and thus individual fitness; Le Gouvello et al. 2020a) with an associated increase in the remigration intervals makes it plausible that loggerheads do not exhibit an adaptive strategy through a trade-off between remigration interval length and clutch frequency, but rather that individuals were responding to possible declines in foraging habitat quality. Because remigration interval length regulates the number of adult females that are reproducing during a given nesting season (Bjorndal et al. 1999; Troëng and Chaloupka 2007), the annual number of loggerhead nests may enter a period of decline.

Individual leatherbacks appear to be in better condition compared to the loggerheads with individuals showing no increase in their remigration intervals over time, while they have retained consistent 2-3 year remigration intervals and subsequently experienced a stable population recovery rate. From these results, bet-hedging adaptations were not evident and do not serve as explanations for current rates of population growth. However, changes/differences in the remigration intervals between species may influence population growth rates (Bjorndal et al. 1999; Troëng and Chaloupka 2007), while the remigration interval may predict future trends in abundance.

Other factors may have influenced the results obtained from this investigation. The reliability of results obtained are limited by the accurate identification of all tagged individuals over time. It was assumed that all individuals were identified correctly across nesting seasons. In addition, it is possible that individual sea turtles were missed during a particular nesting season (Thorson et al. 2012), resulting in a missing, as well as a prolonged, remigration interval value. Individuals may lose their flipper tag(s) at sea, resulting in a “new” individual being recorded. In addition, because loggerhead sea turtles are spatial specialists while leatherbacks distribute their nests over a wider area (King 2023), it is possible that a greater proportion of adult loggerheads, as well as nests, were successfully recorded in comparison to leatherbacks.

If this is the case, differences in the accuracy of results obtained in terms of the remigration intervals and annual nest counts between species would exist, influencing the reliability of any comparisons made. However, large sample sizes and the extensive database help to buffer any major inaccuracies in the results being obtained.

Implications for management

A single theme emerges when the results from both analyses are combined for interpretation. In order to understand trends in nesting abundances, it is important to first investigate patterns within finer components before analysing larger systems. For example, to conserve an entire community, it is important to understand the species composition. In addition, if the aim is to conserve an entire community, the community needs to be monitored for diversity and numerical composition. A range of ecological studies have illustrated how species diversity improves community stability (e.g. Goodman 1975; Cleland 2011; Wisnoski et al. 2023). At following levels of biological organisation the same principle applies.

To conserve an entire species, it is important that the individual population(s) comprising the particular species are conserved. For example, metapopulations are classified as being a large population comprising various smaller populations that are spatially separated but also includes some level of interaction between them (i.e. dispersal of individuals between populations) (Shtilerman and Stone 2015; van Nouhuys 2016; Lin 2022). A metapopulation consisting of several smaller interconnected populations is, however, thought to be more likely to persist compared to a species consisting of only a single large population situated within a single pre-defined geographic location (Molofsky and Ferdy 2005). Therefore, to conserve an entire species the individual populations comprising a particular species should be protected and monitored continuously. As mentioned, sea turtles may potentially function as a metapopulation (potentially with very limited migration of individuals between populations) where the respective RMUs constitute the individual subpopulations. Thus, to conserve any sea turtle species, it is important that the different RMUs are effectively managed and protected.

Next, to effectively conserve a (meta)population, the behaviour and overall fitness of individuals comprising the population must be understood. Various studies have illustrated how the behaviour of individuals may influence population growth rates. For example, biased sex ratios have the potential to directly influence individual fitness resulting in a decline in effective population size and increasing the odds of inbreeding (Telschow et al. 2006; Dubreuil et al. 2010; Heppell et al. 2022), both of which may influence the long-term survival of a population. This is because a reduction in the proportion of males within sea turtle populations has demographic consequences (Hays et al. 2023) resulting in fewer nests being laid annually, slowing population growth rates. Therefore, knowledge regarding male to female sex ratios may help to explain observed population growth rates.

The foraging distribution of individual sea turtles may be indicative of prevailing trends in abundance of turtles. The abundance of herbivorous green sea turtle (*Chelonia mydas*) is influenced by their foraging distribution and/or the quality of foraging grounds, whereby a reduction in seagrass density coincided with a decline in sea turtle abundance (Kale et al. 2022). These two case studies illustrate how an improvement in the knowledge regarding the individual sea turtles comprising a particular population may help explain current trends in abundance. Thus, to effectively conserve a population, it becomes paramount that individuals undergo extensive investigation.

In summary, portfolio effects and the remigration interval of individual sea turtles are two of many factors to consider when assessing trends in abundance at the species, RMU/population and/or rookery levels. A diversified portfolio enables sea turtles to avoid complete extirpation, with varied population growth rates among rookeries acting to stabilise RMU-level trends, and RMU patterns stabilising species-level trends in nesting abundance. The remigration interval of individual sea turtles has an impact on abundance trends, but that is unlikely an effect of bet-hedging adaptations. Therefore, it is important that the contribution of portfolio effects and of the remigration interval of individuals are investigated in studies conducted to remedy any uncertainties regarding the reasons for observed trends in abundance at the species, population and/or rookery levels.

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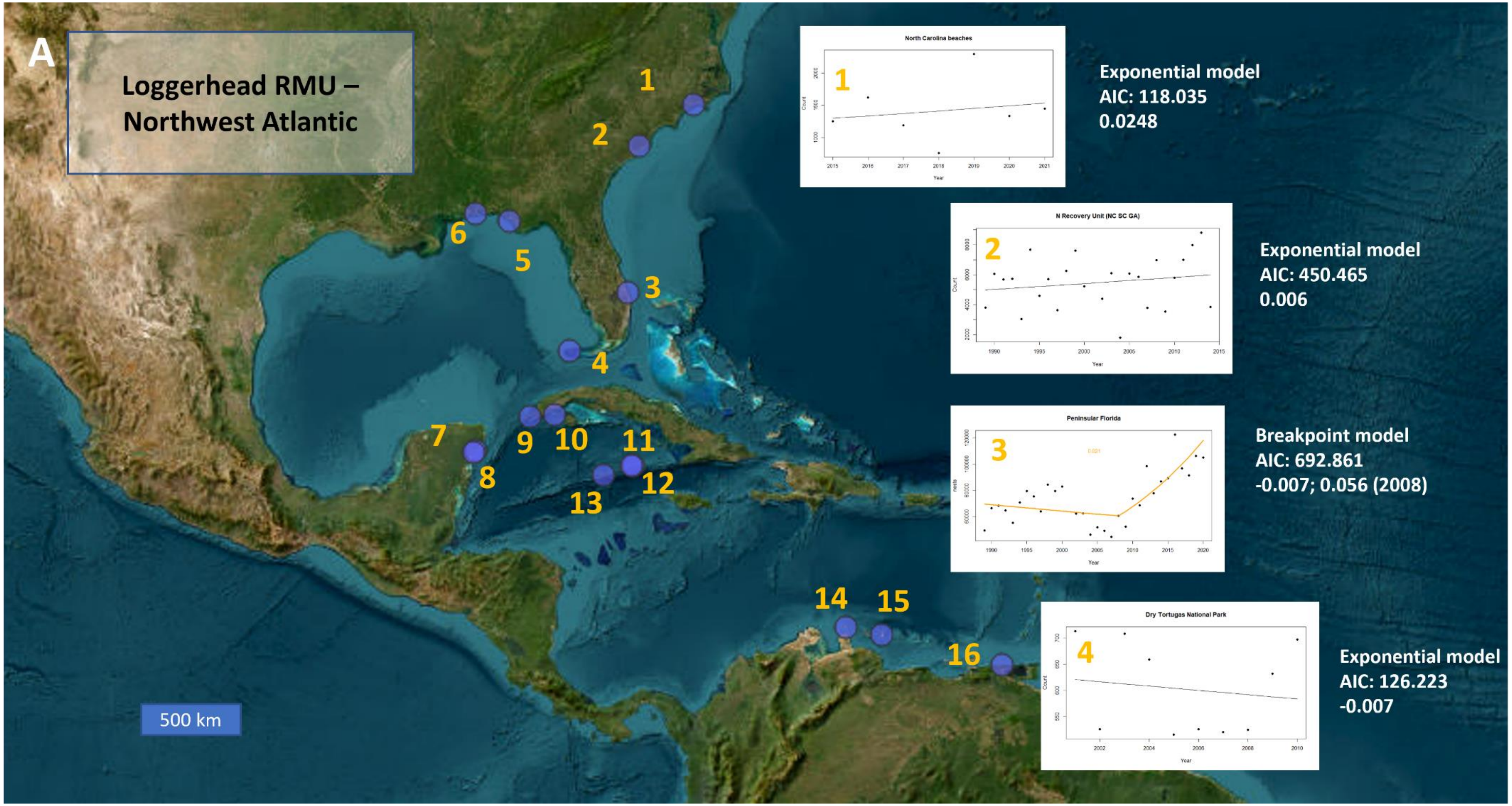
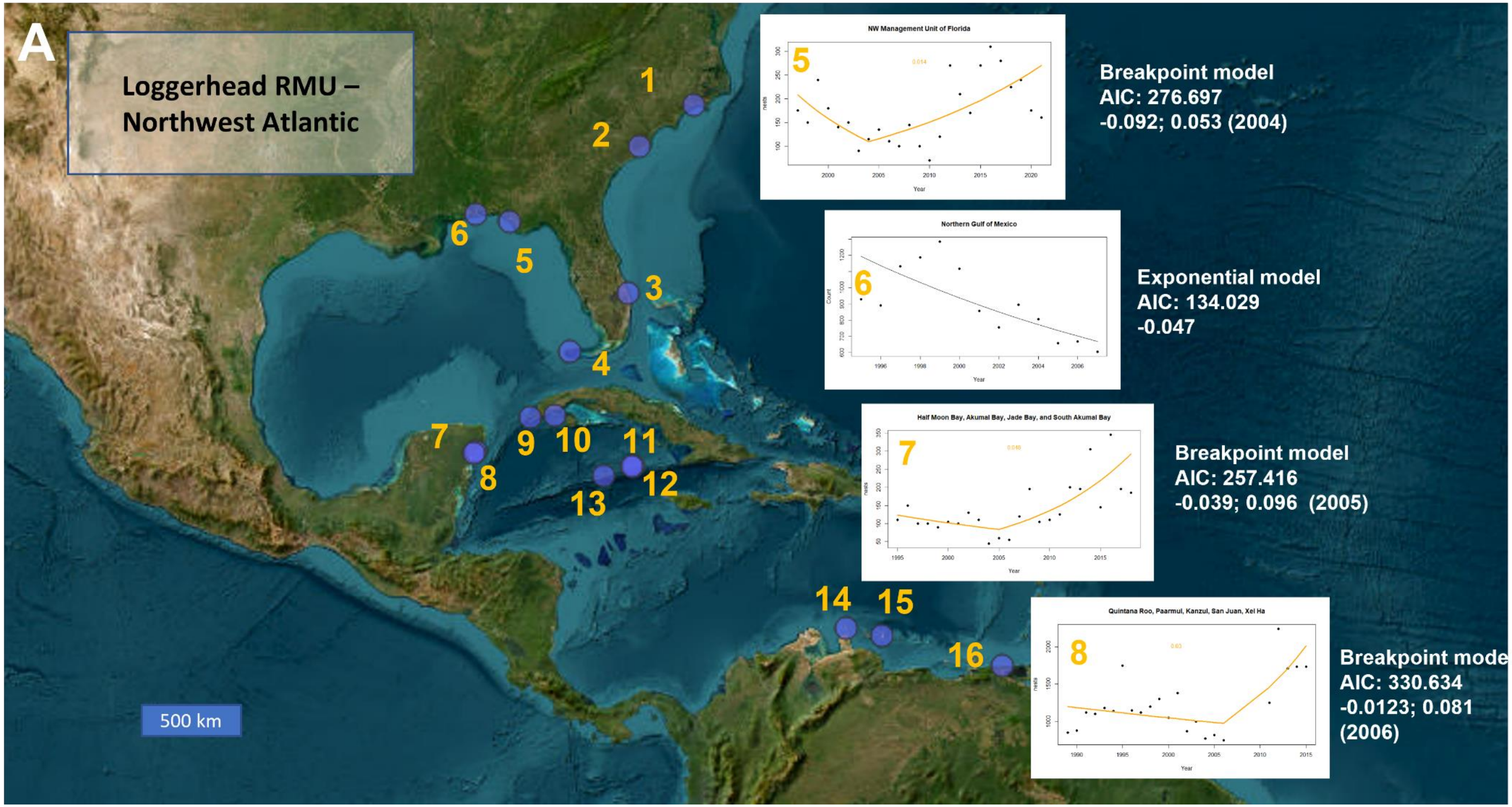
Supplementary Material I:

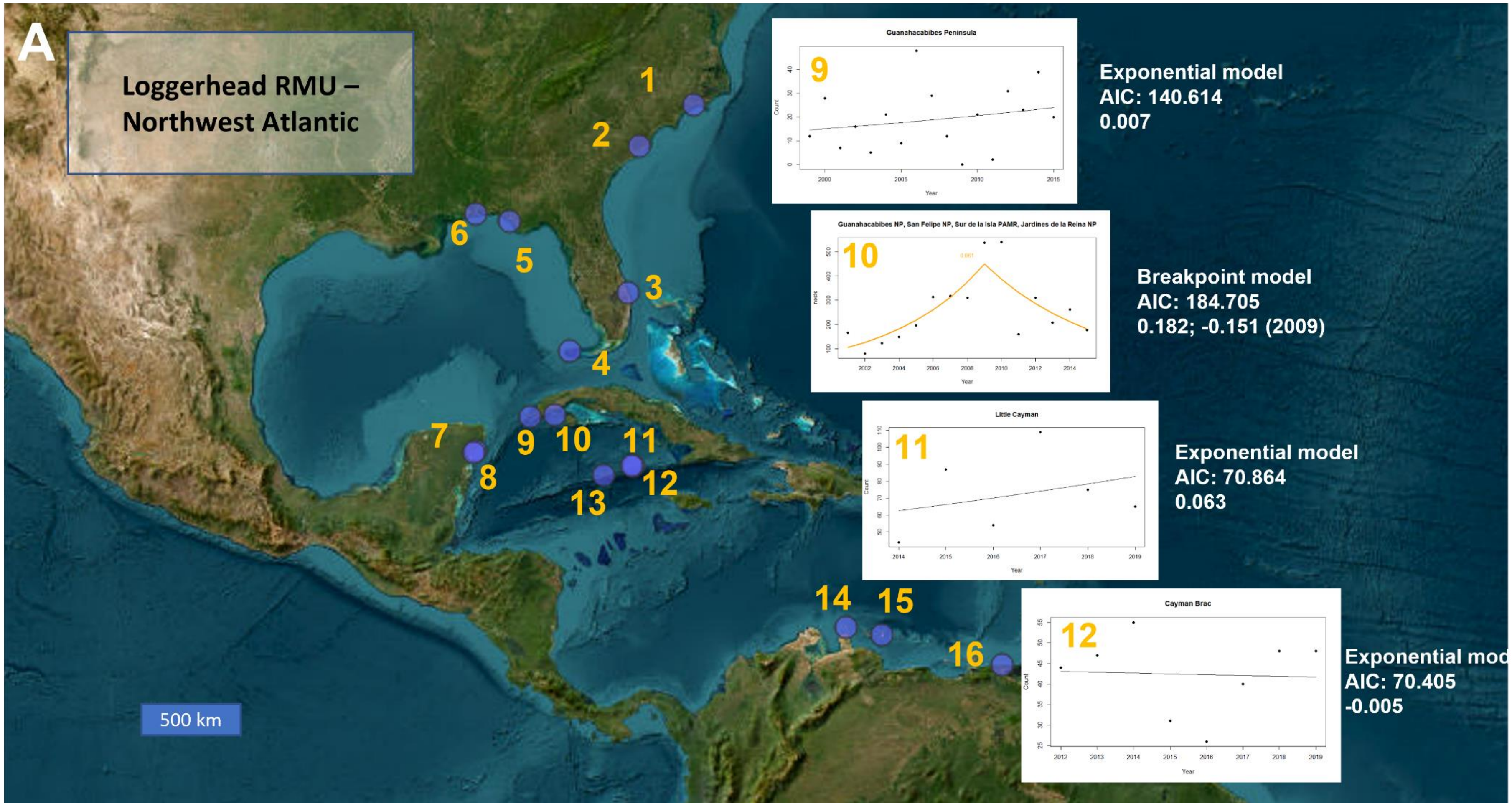
Chapter 2 | The portfolio effect and persistence of sea turtle species and populations

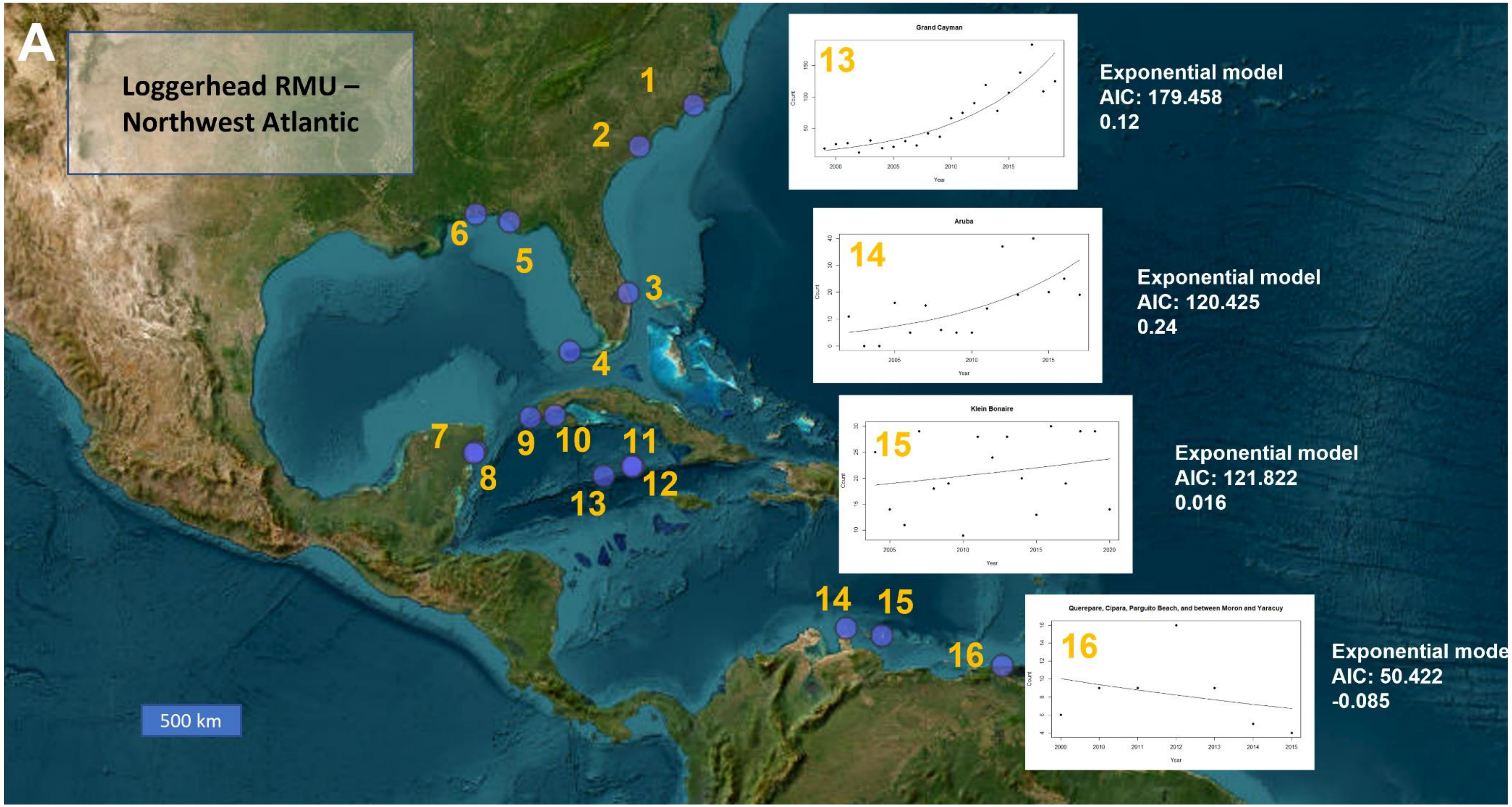
Supplementary Table 2.1: Loggerhead sea turtle Regional Management Units (excluding the Northeast Indian RMU; Wallace et al. 2023)

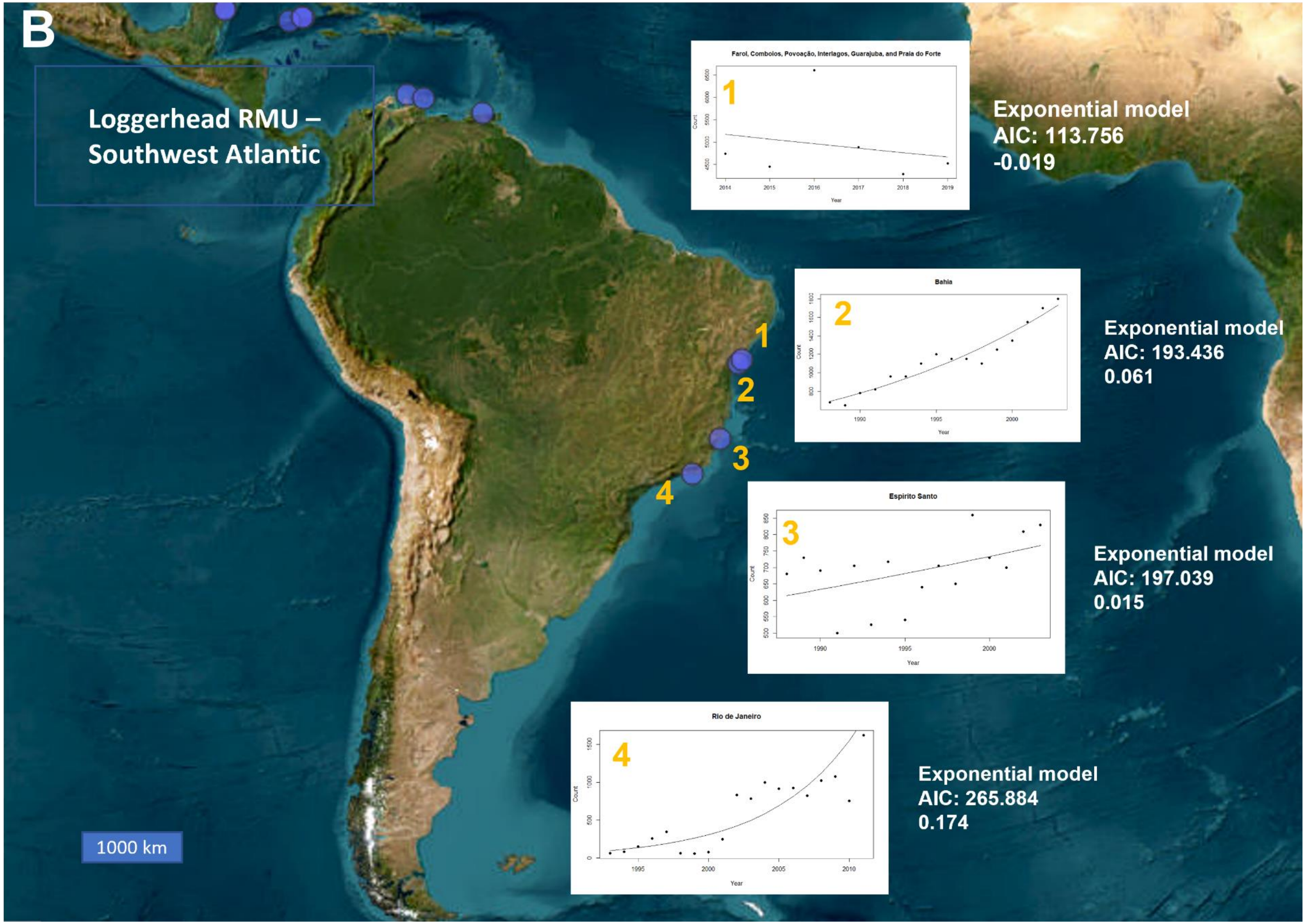
Number	Regional Management Unit
A	Northwest Atlantic
B	Southwest Atlantic
C	Northeast Atlantic
D	Mediterranean
E	Northwest Indian
F	Southwest Indian
G	Southeast Indian
H	North Pacific
I	South Pacific

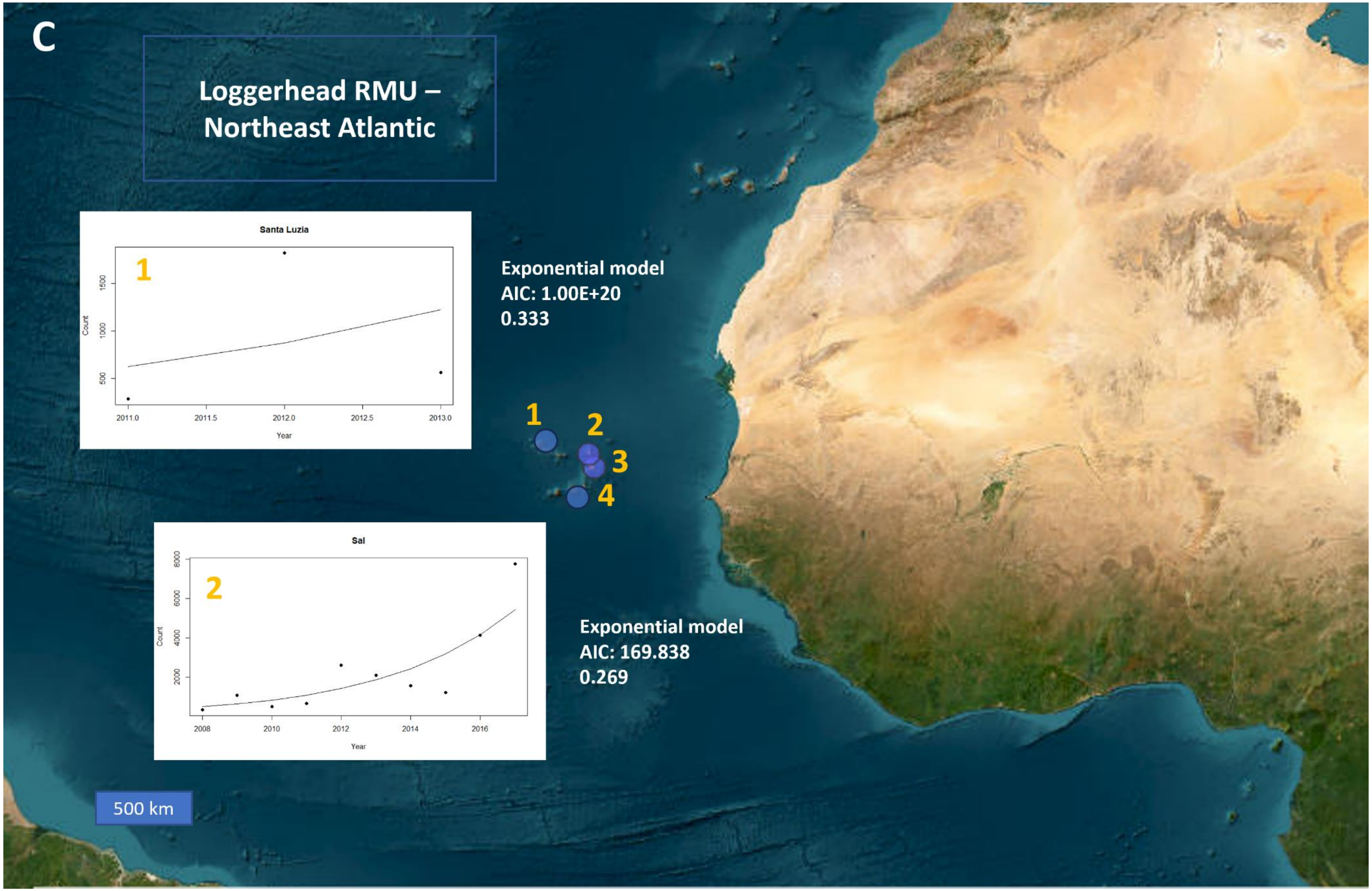

A
Loggerhead RMU – Northwest Atlantic
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
500 km
North Carolina beaches
Count
Year
Exponential model
AIC: 118.035
0.0248
N Recovery Unit (NC SC GA)
Count
Year
Exponential model
AIC: 450.465
0.006
Peninsular Florida
Nests
Year
Breakpoint model
AIC: 692.861
-0.007; 0.056 (2008)
Dry Tortugas National Park
Count
Year
Exponential model
AIC: 126.223
-0.007


A
Loggerhead RMU –
Northwest Atlantic
1
2
6
5
3
4
7
9
10
11
8
12
13
14
15
16
500 km
NW Management Unit of Florida
5
0.014
nests
Year
Breakpoint model
AIC: 276.697
-0.092; 0.053 (2004)
Northern Gulf of Mexico
6
Count
Year
Exponential model
AIC: 134.029
-0.047
Half Moon Bay, Akumal Bay, Jade Bay, and South Akumal Bay
7
0.016
nests
Year
Breakpoint model
AIC: 257.416
-0.039; 0.096 (2005)
Quintana Roo, Paarmul, Kanzul, San Juan, Xel Ha
8
0.03
nests
Year
Breakpoint mode
AIC: 330.634
-0.0123; 0.081
(2006)


A
Loggerhead RMU – Northwest Atlantic
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
500 km
Guanahacabibes Peninsula
9
Count
Year
Exponential model
AIC: 140.614
0.007
Guanahacabibes NP, San Felipe NP, Sur de la Isla PAMR, Jardines de la Reina NP
10
nests
Year
Breakpoint model
AIC: 184.705
0.182; -0.151 (2009)
Little Cayman
11
Count
Year
Exponential model
AIC: 70.864
0.063
Cayman Brac
12
Count
Year
Exponential model
AIC: 70.405
-0.005


A
Loggerhead RMU –
Northwest Atlantic
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
500 km
Grand Cayman
13
Count
Year
2000
2005
2010
2015
Exponential model
AIC: 179.458
0.12
Aruba
14
Count
Year
2005
2010
2015
Exponential model
AIC: 120.425
0.24
Klein Bonaire
15
Count
Year
2005
2010
2015
2020
Exponential model
AIC: 121.822
0.016
Querepare, Cipara, Parguito Beach, and between Moron and Yaracuy
16
Count
Year
2009
2010
2011
2012
2013
2014
2015
Exponential mode
AIC: 50.422
-0.085

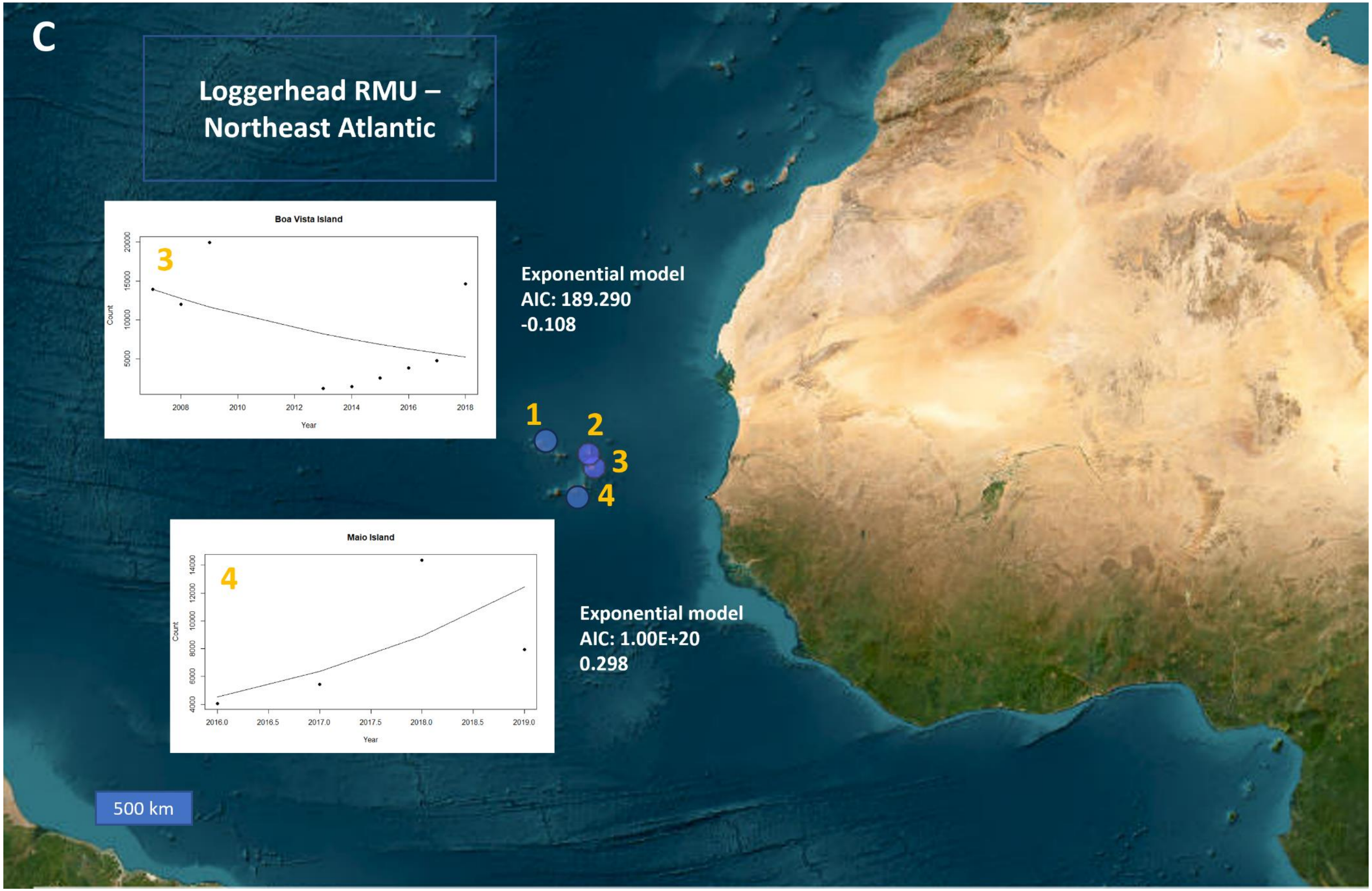

B
Loggerhead RMU – Southwest Atlantic
1
2
3
4
1000 km
Farol, Comboios, Povoação, Interlagos, Guarajuba, and Praia do Forte
Count
Year
2014
2015
2016
2017
2018
2019
Exponential model
AIC: 113.756
-0.019
Bahia
Exponential model
AIC: 193.436
0.061
Espirito Santo
Exponential model
AIC: 197.039
0.015
Rio de Janeiro
Exponential model
AIC: 265.884
0.174



Loggerhead RMU – Northeast Atlantic

Exponential model
AIC: 1.00E+20
0.333

Exponential model
AIC: 169.838
0.269

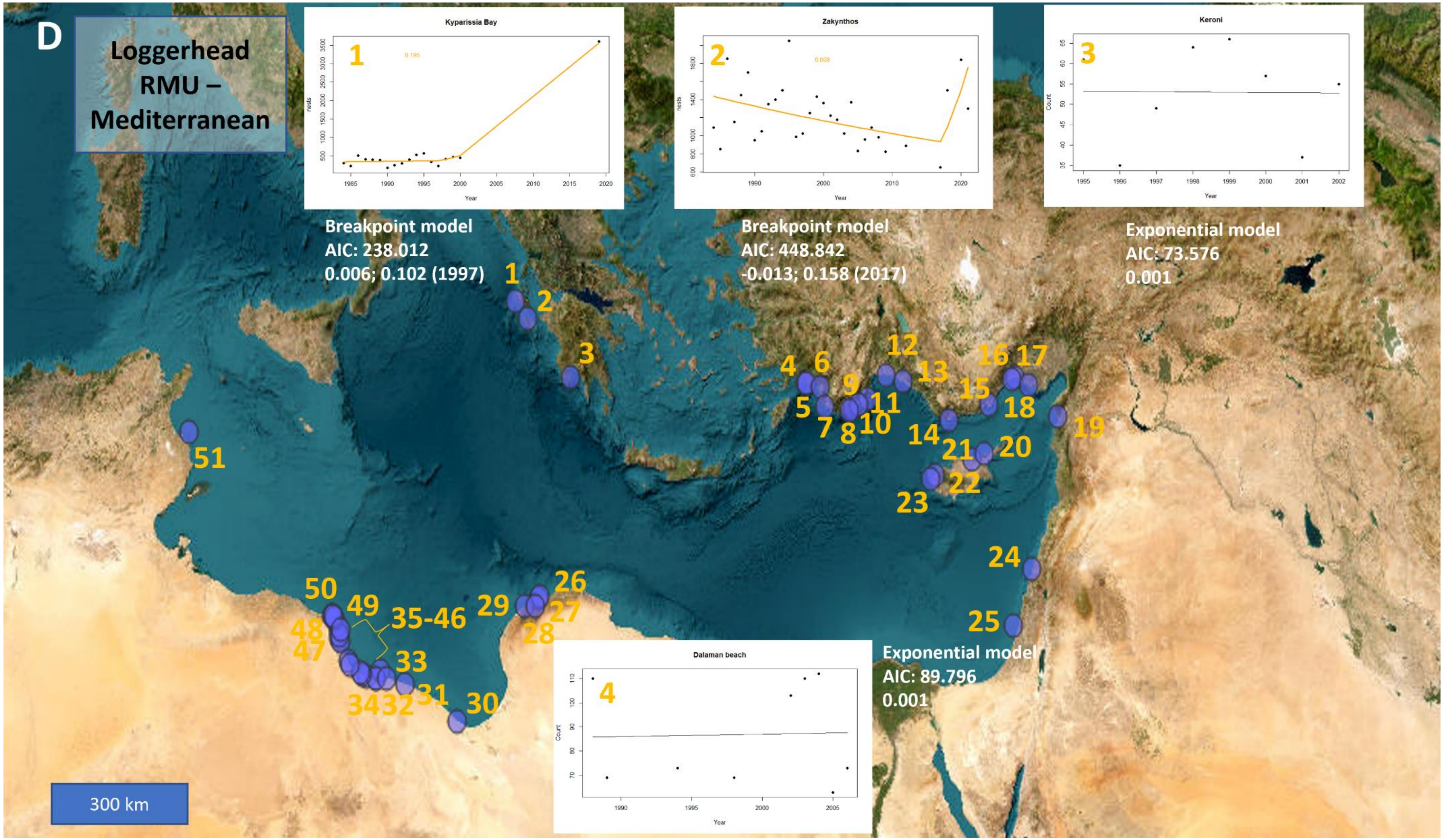


C

Loggerhead RMU – Northeast Atlantic

Exponential model
AIC: 189.290
-0.108

Exponential model
AIC: 1.00E+20
0.298



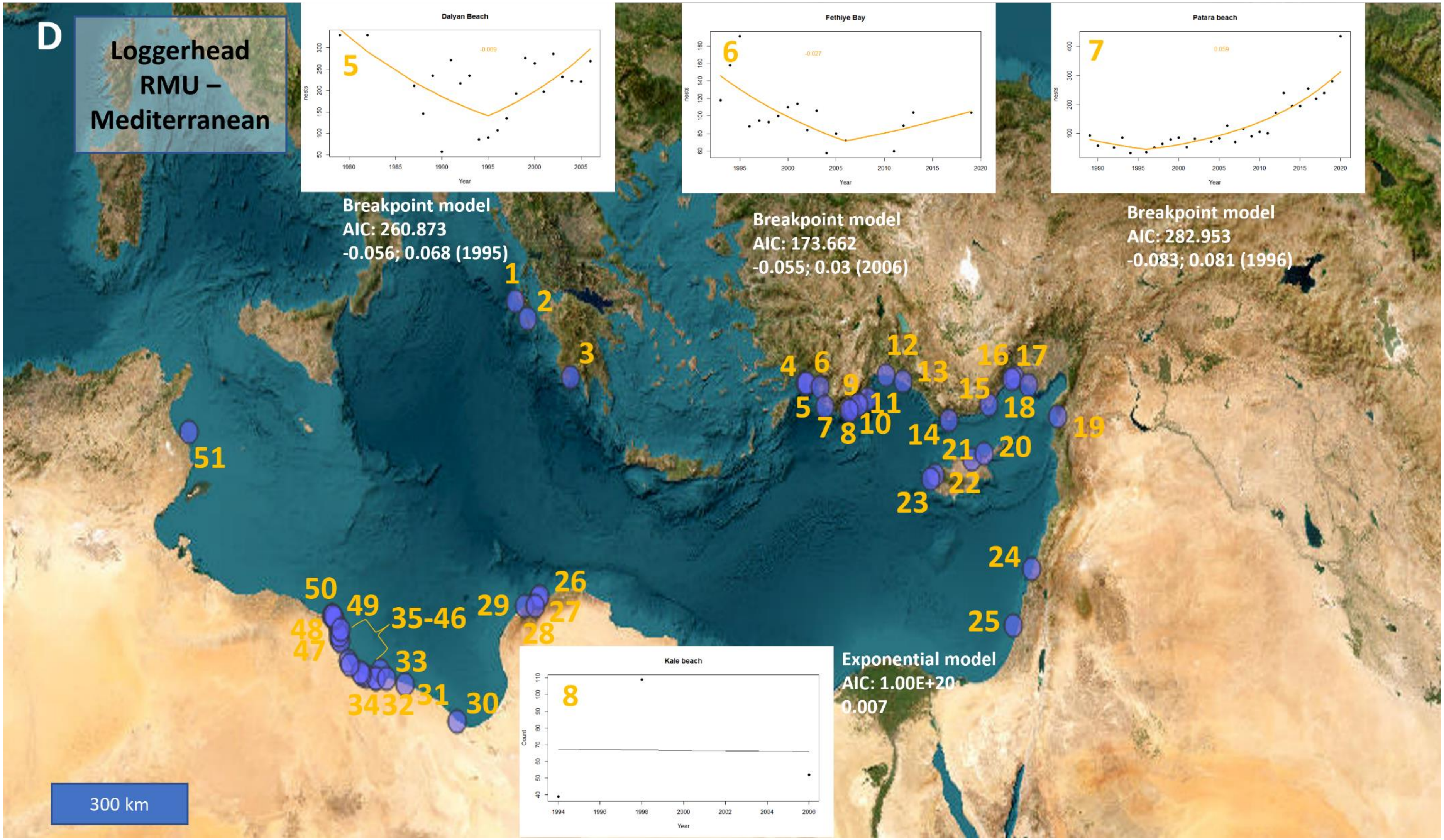
Loggerhead RMU – Mediterranean

Breakpoint model
AIC: 238.012
0.006; 0.102 (1997)

Breakpoint model
AIC: 448.842
-0.013; 0.158 (2017)

Exponential model
AIC: 73.576
0.001

Exponential model
AIC: 89.796
0.001

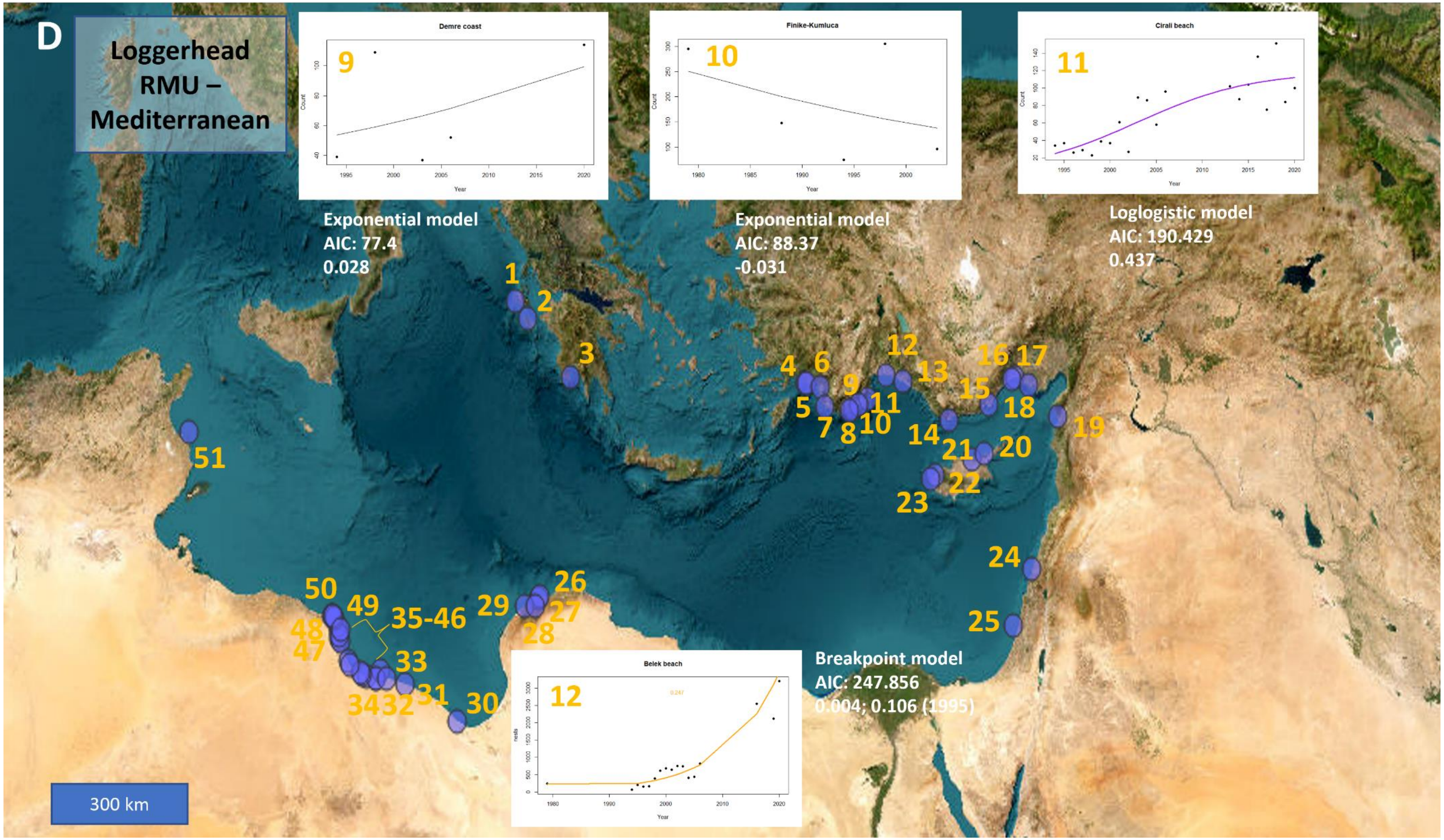


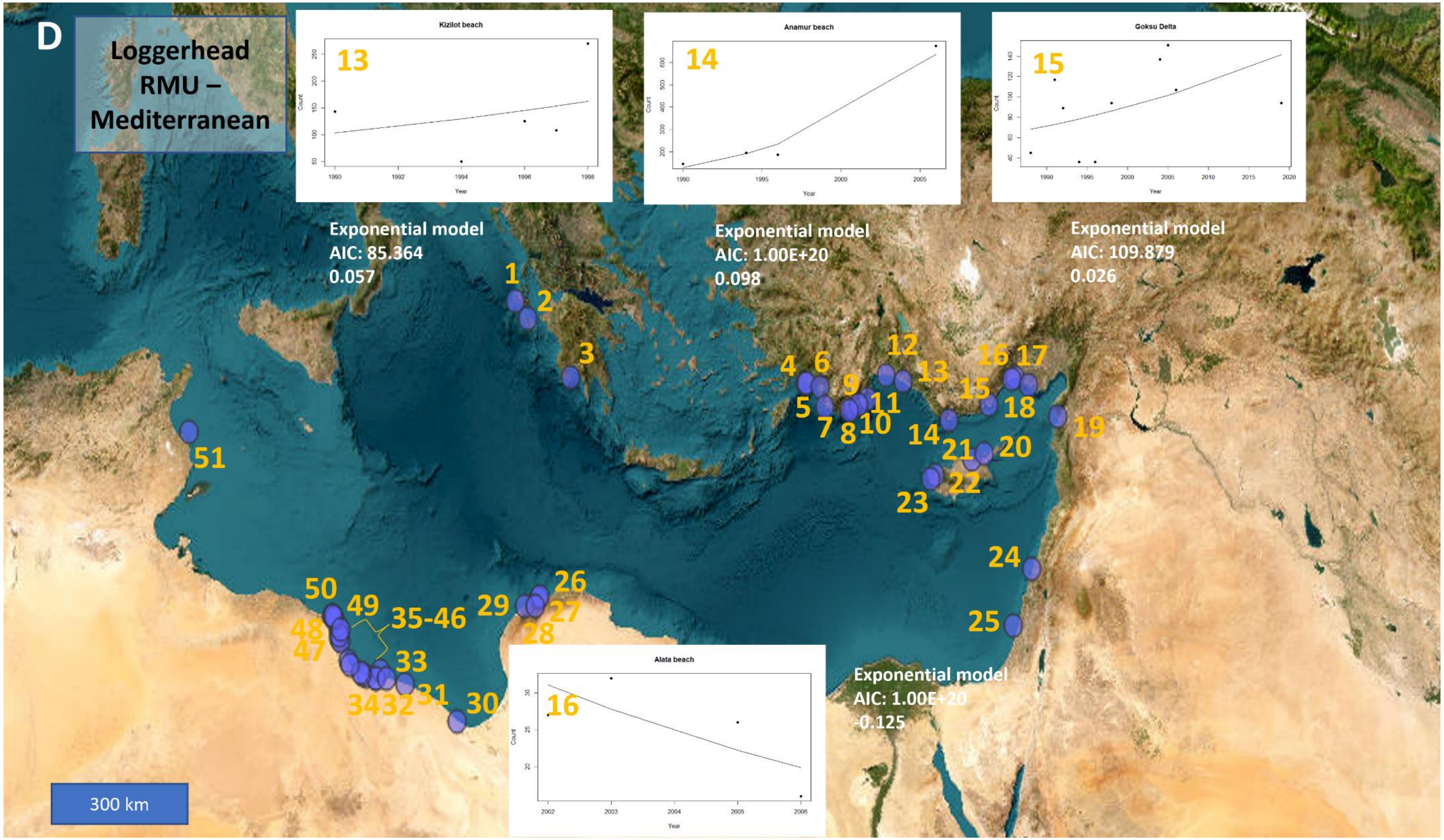
Breakpoint model
AIC: 260.873
-0.056; 0.068 (1995)

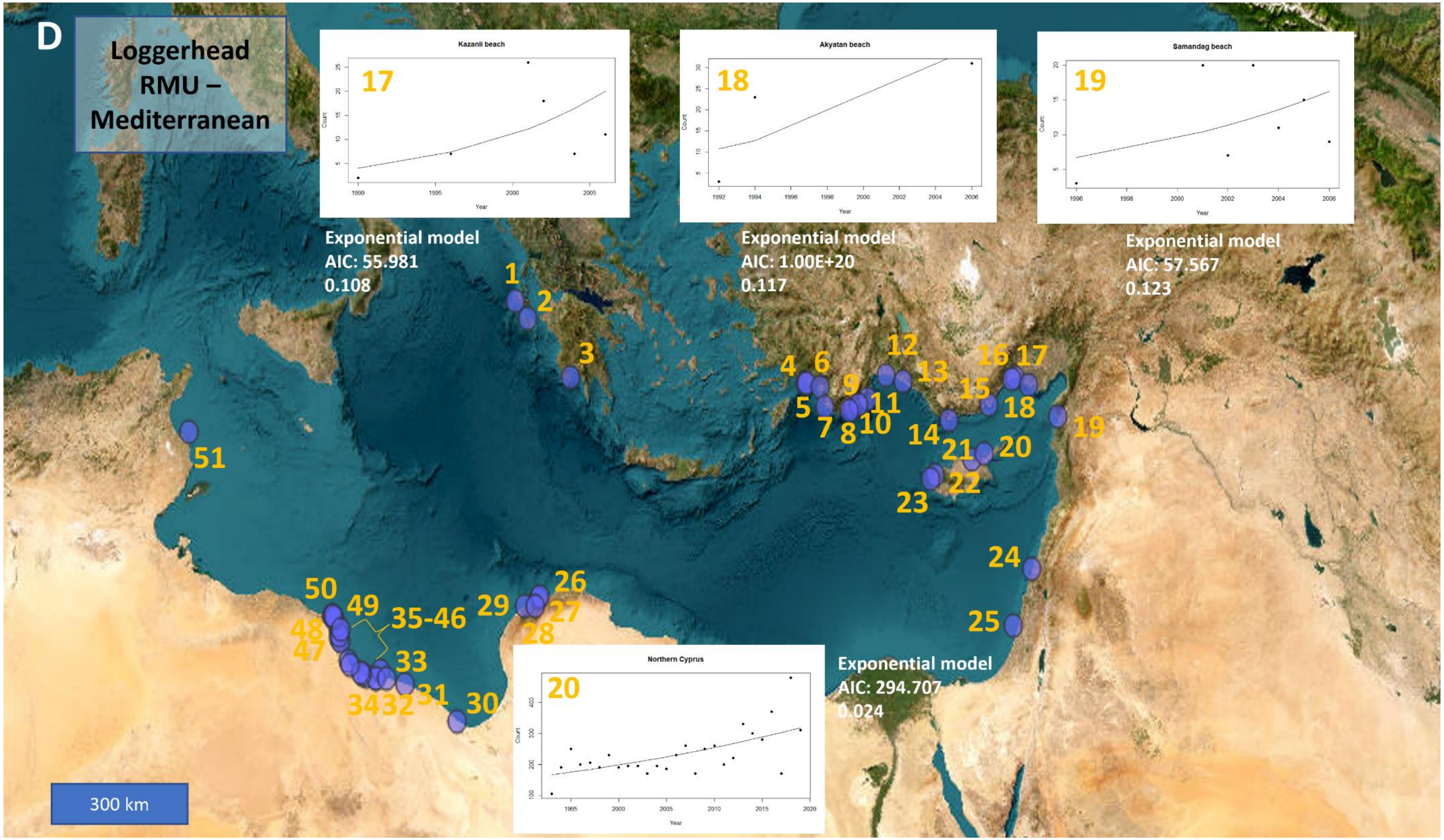
Breakpoint model
AIC: 173.662
-0.055; 0.03 (2006)

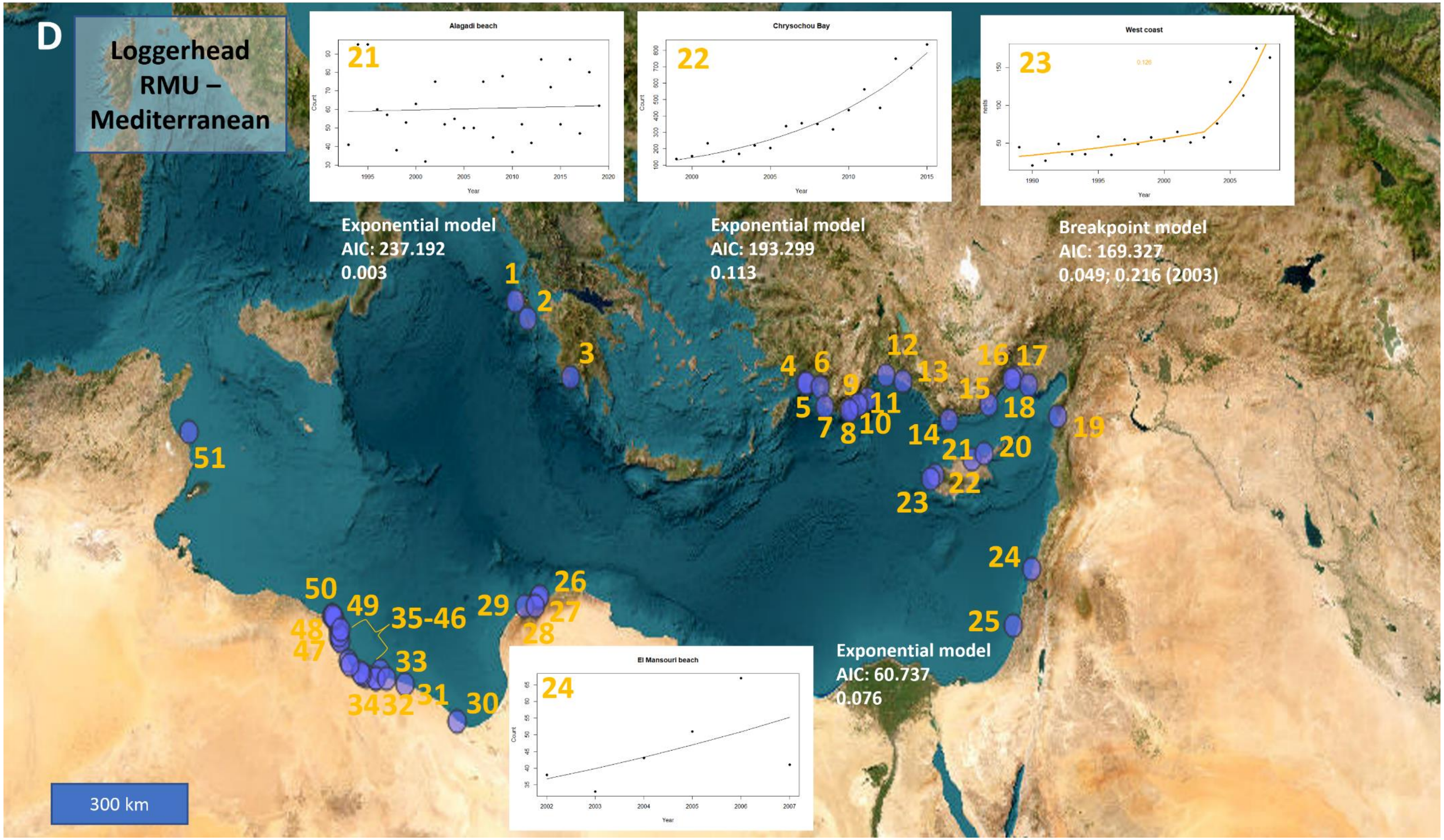
Breakpoint model
AIC: 282.953
-0.083; 0.081 (1996)

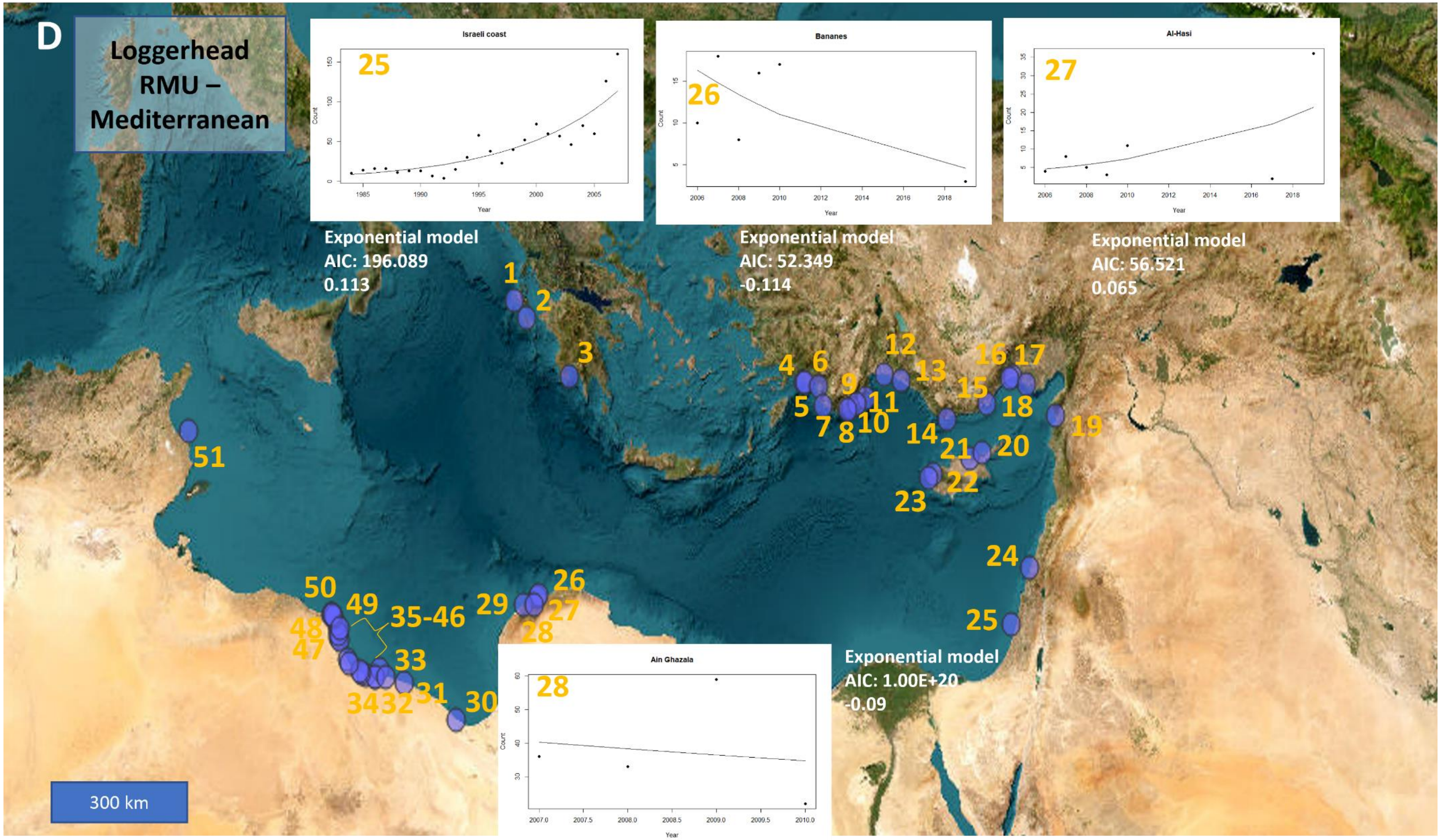
Exponential model
AIC: 1.00E+20
0.007


D
Loggerhead RMU – Mediterranean
Demre coast
9
Count
Year
Exponential model
AIC: 77.4
0.028
Finike-Kumluca
10
Count
Year
Exponential model
AIC: 88.37
-0.031
Cirali beach
11
Count
Year
Loglogistic model
AIC: 190.429
0.437
Belek beach
12
0.247
nests
Year
Breakpoint model
AIC: 247.856
0.004; 0.106 (1995)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35-46
47
48
49
50
51
300 km


D
Loggerhead RMU – Mediterranean
Kizilot beach
13
Count
50
100
150
200
250
1990
1992
1994
1996
1998
Year
Exponential model
AIC: 85.364
0.057
Anamur beach
14
Count
200
300
400
500
600
1990
1995
2000
2005
Year
Exponential model
AIC: 1.00E+20
0.098
Goksu Delta
15
Count
40
60
80
100
120
140
1990
1995
2000
2005
2010
2015
2020
Year
Exponential model
AIC: 109.879
0.026
Alata beach
16
Count
20
25
30
2002
2003
2004
2005
2006
Year
Exponential model
AIC: 1.00E+20
-0.125
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35-46
47
48
49
50
51
300 km


D
Loggerhead RMU – Mediterranean
Kazanli beach
17
Count
Year
1990
1995
2000
2005
5
10
15
20
25
Exponential model
AIC: 55.981
0.108
Akyatan beach
18
Count
Year
1992
1994
1996
1998
2000
2002
2004
2006
5
10
15
20
25
30
Exponential model
AIC: 1.00E+20
0.117
Samandag beach
19
Count
Year
1996
1998
2000
2002
2004
2006
5
10
15
20
Exponential model
AIC: 57.567
0.123
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35-46
47
48
49
50
51
Northern Cyprus
20
Count
Year
1995
2000
2005
2010
2015
2020
100
200
300
400
Exponential model
AIC: 294.707
0.024
300 km


D
Loggerhead RMU – Mediterranean
Alagadi beach
21
Count
Year
Exponential model
AIC: 237.192
0.003
Chrysochou Bay
22
Count
Year
Exponential model
AIC: 193.299
0.113
West coast
23
0.126
nests
Year
Breakpoint model
AIC: 169.327
0.049; 0.216 (2003)
El Mansouri beach
24
Count
Year
Exponential model
AIC: 60.737
0.076
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35-46
47
48
49
50
51
300 km

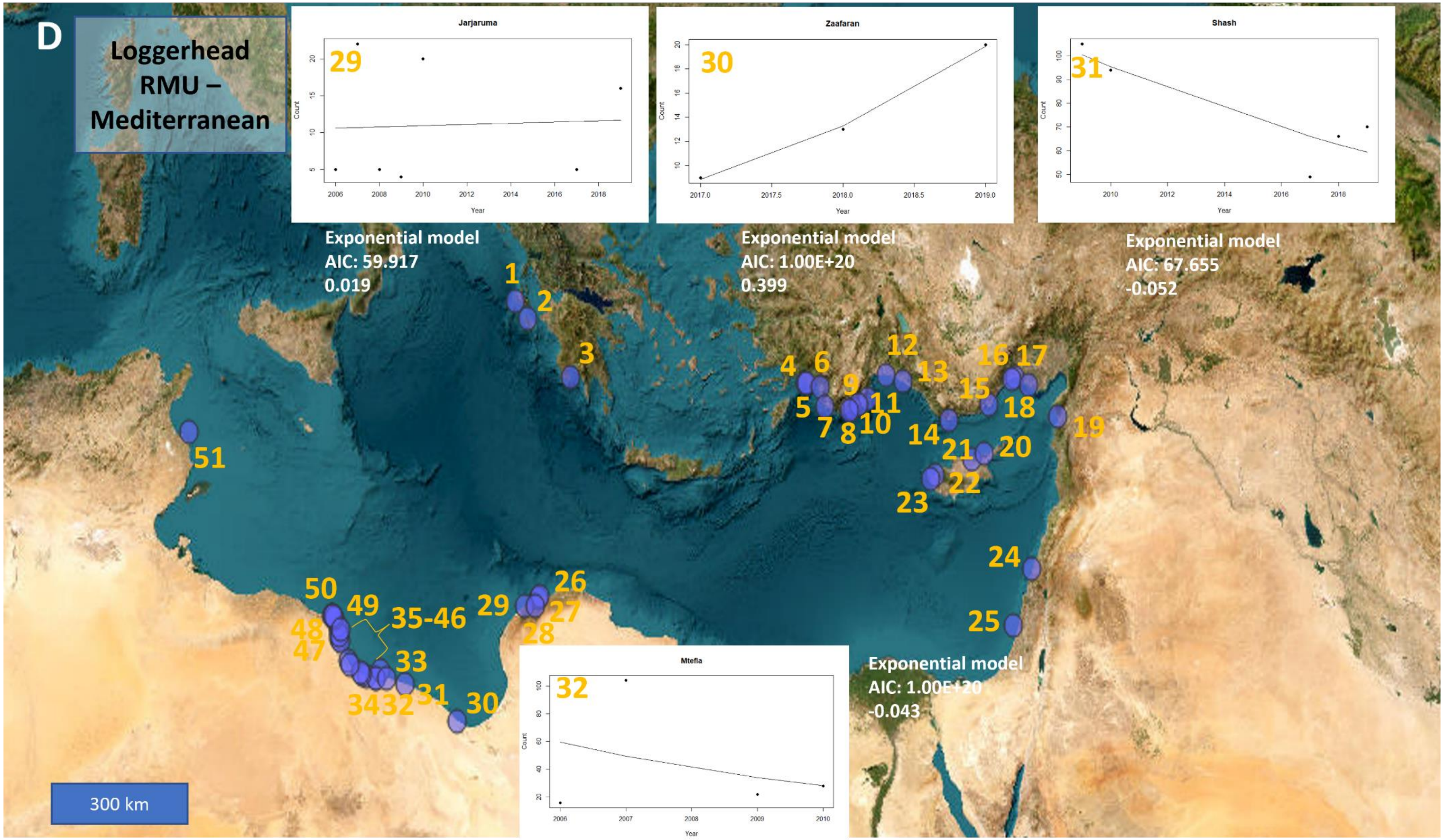


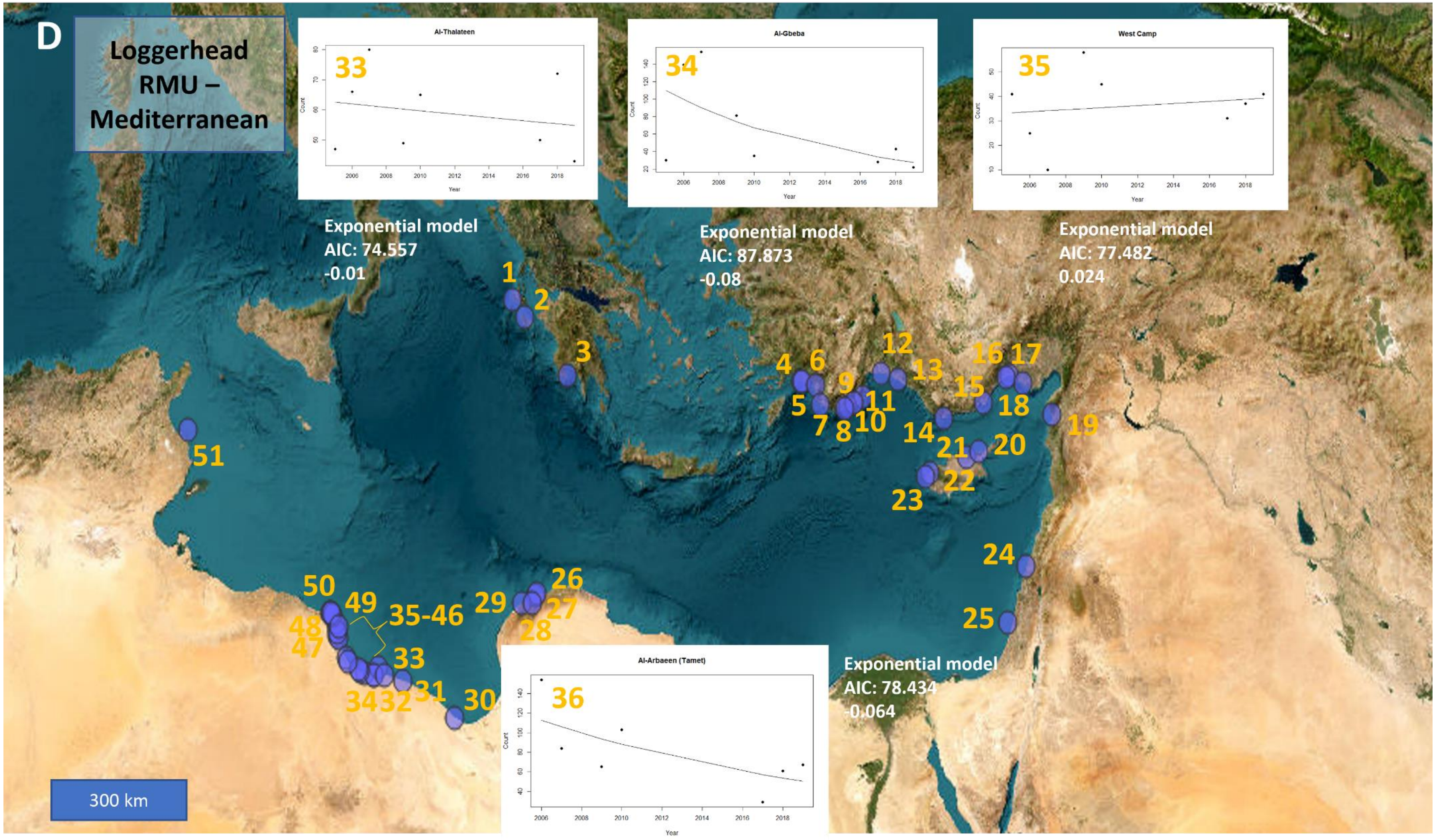
Exponential model
AIC: 196.089
0.113

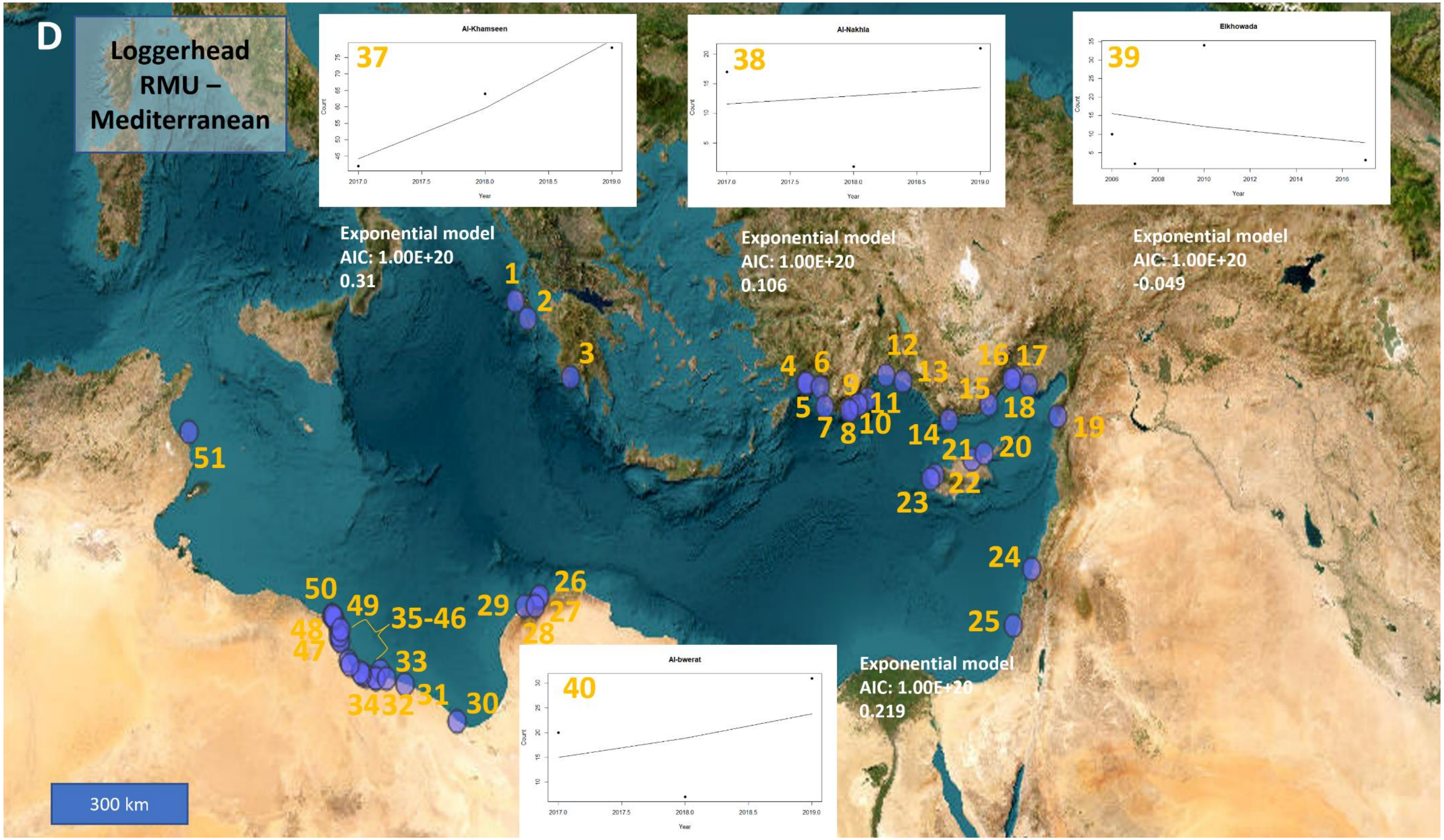
Exponential model
AIC: 52.349
-0.114

Exponential model
AIC: 56.521
0.065

Exponential model
AIC: 1.00E+20
-0.09


D
Loggerhead RMU – Mediterranean
Jarjaruma
29
Count
Year
5
10
15
20
2006
2008
2010
2012
2014
2016
2018
Exponential model
AIC: 59.917
0.019
Zaafaran
30
10
12
14
16
18
20
2017.0
2017.5
2018.0
2018.5
2019.0
Exponential model
AIC: 1.00E+20
0.399
Shash
31
50
60
70
80
90
100
2010
2012
2014
2016
2018
Exponential model
AIC: 67.655
-0.052
Mtefla
32
20
40
60
80
100
2006
2007
2008
2009
2010
Exponential model
AIC: 1.00E+20
-0.043
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35-46
47
48
49
50
51
300 km


D
Loggerhead RMU – Mediterranean
Al-Thalateen
33
Count
80
70
60
50
2006
2008
2010
2012
2014
2016
2018
Year
Exponential model
AIC: 74.557
-0.01
Al-Gbeba
34
Count
140
120
100
80
60
40
20
2006
2008
2010
2012
2014
2016
2018
Year
Exponential model
AIC: 87.873
-0.08
West Camp
35
Count
50
40
30
20
10
2006
2008
2010
2012
2014
2016
2018
Year
Exponential model
AIC: 77.482
0.024
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35-46
47
48
49
50
51
Al-Arbaeen (Tamet)
36
Count
140
120
100
80
60
40
2006
2008
2010
2012
2014
2016
2018
Year
Exponential model
AIC: 78.434
-0.064
300 km



D

Loggerhead RMU – Mediterranean

Al-Khamseen

Exponential model
AIC: 1.00E+20
0.31

Al-Nakhla

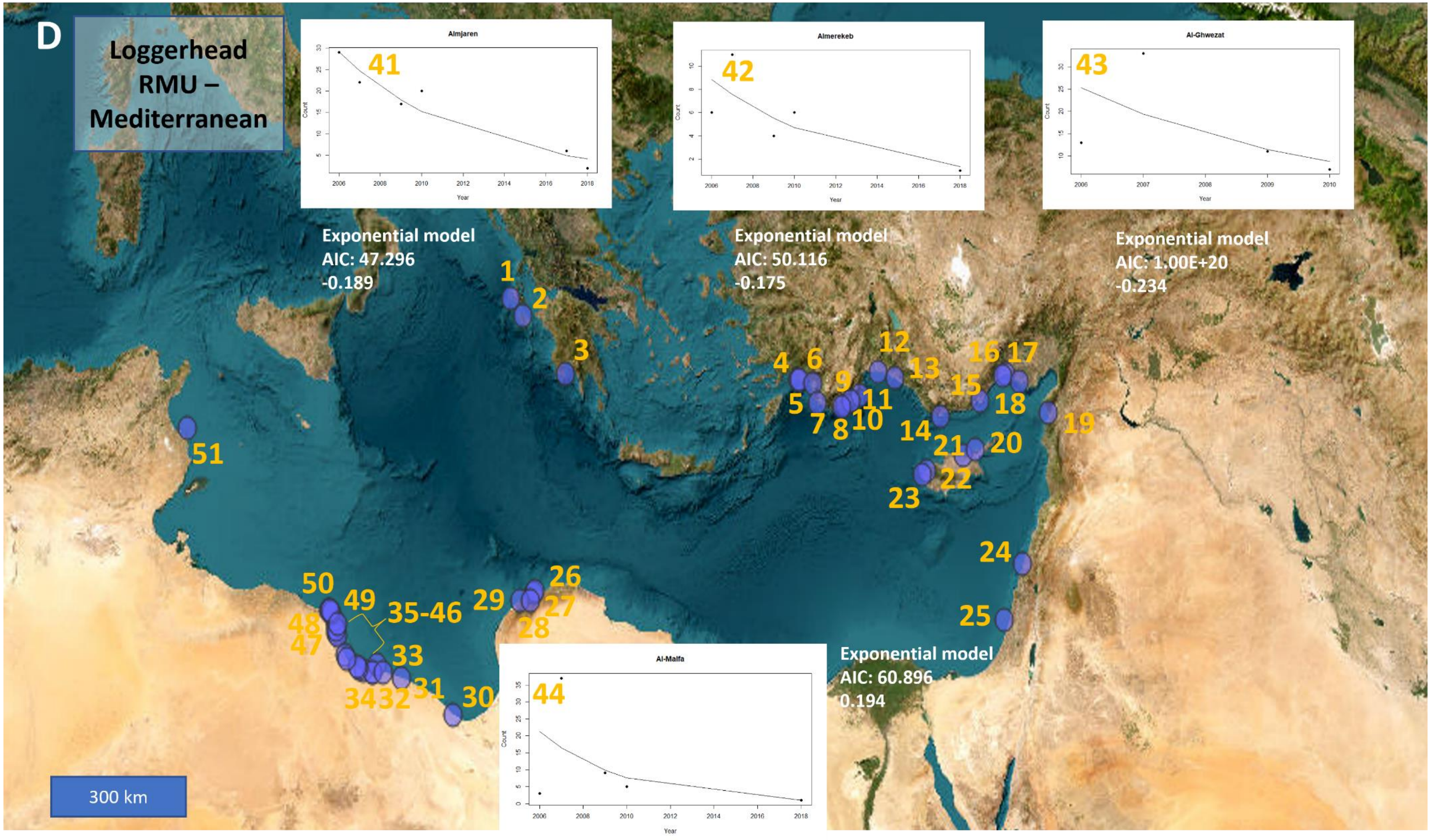
Exponential model
AIC: 1.00E+20
0.106

Elkhowada

Exponential model
AIC: 1.00E+20
-0.049

Al-bwerat

Exponential model
AIC: 1.00E+20
0.219

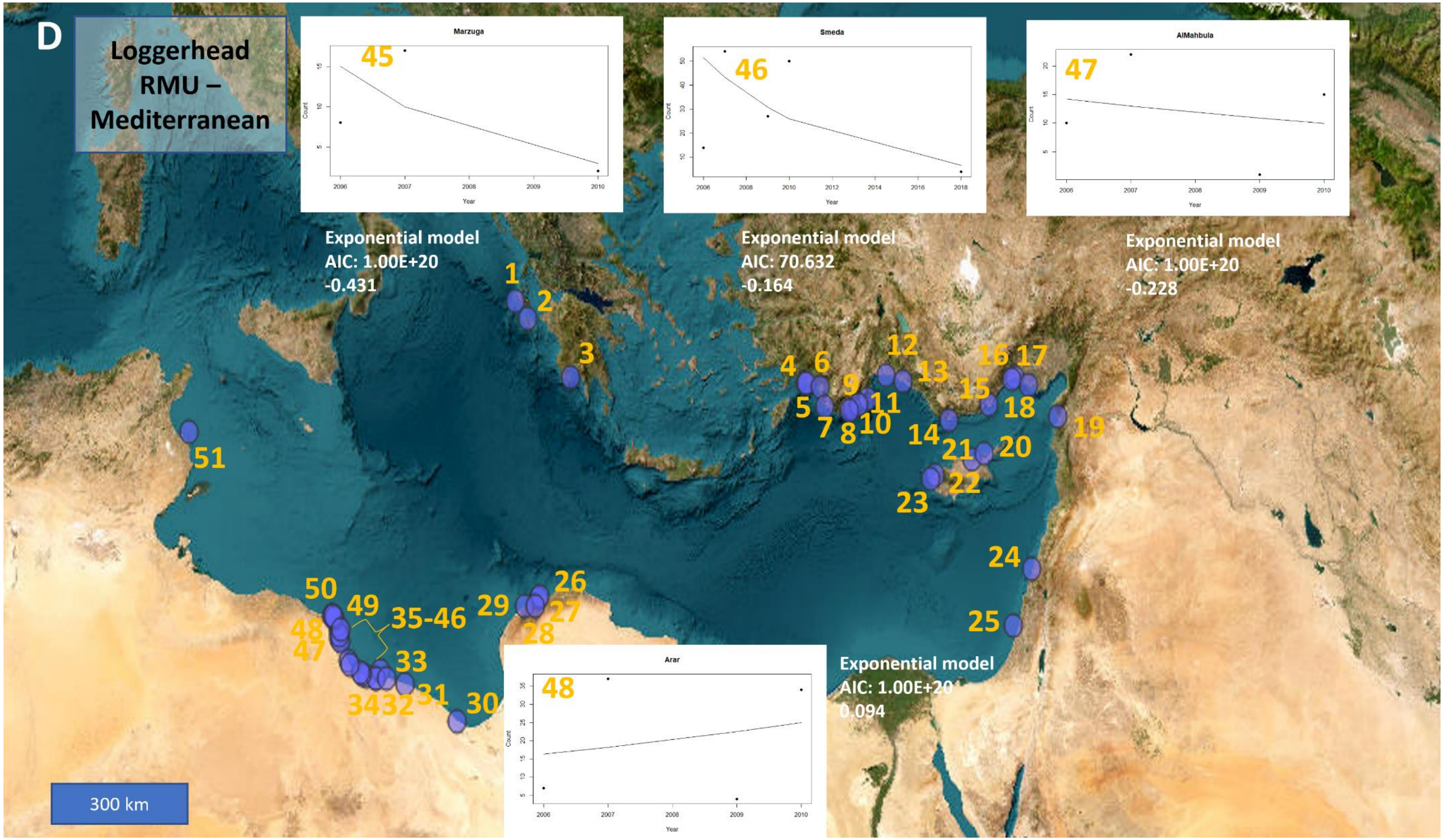


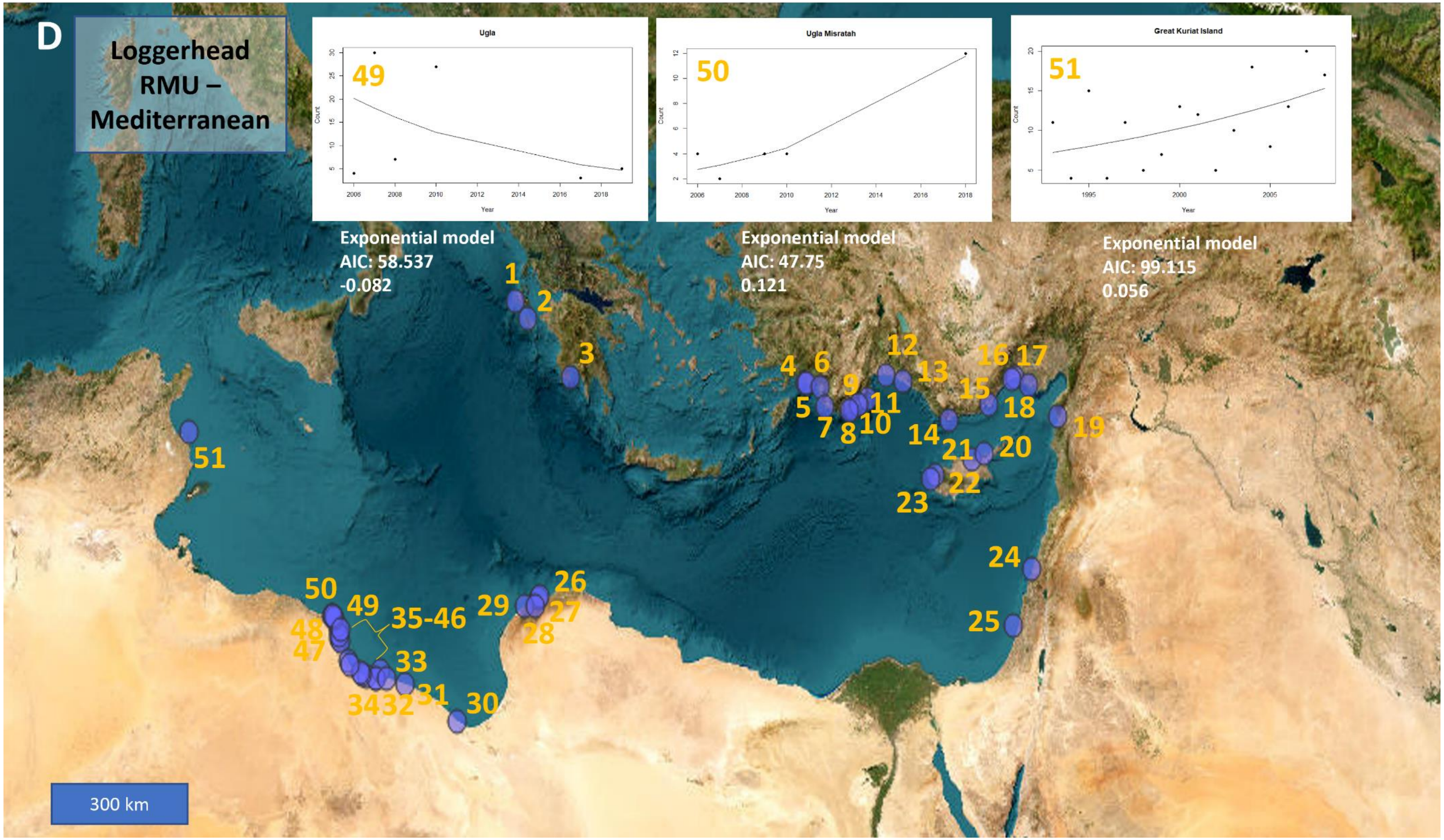
Exponential model
AIC: 47.296
-0.189

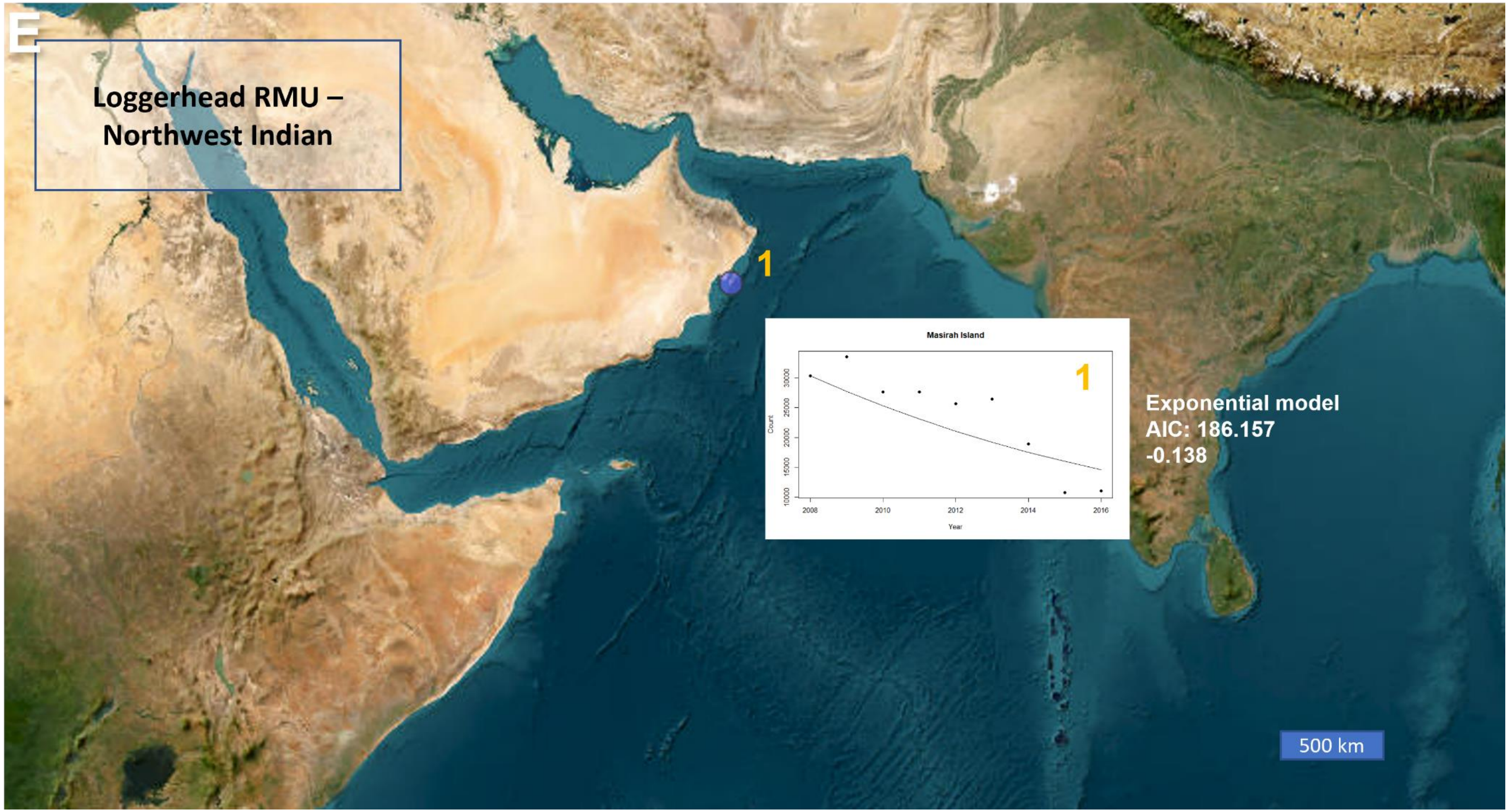
Exponential model
AIC: 50.116
-0.175

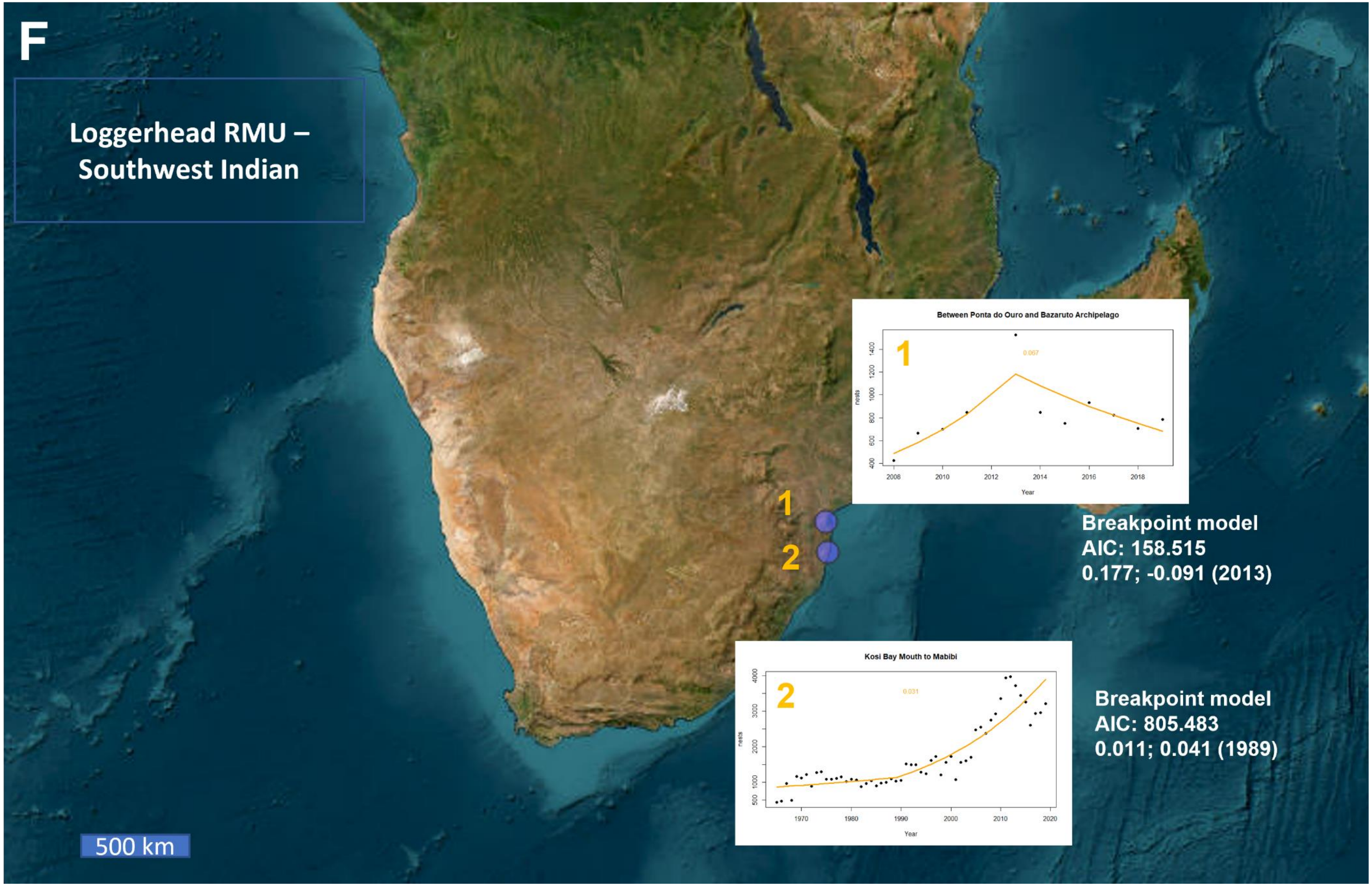
Exponential model
AIC: 1.00E+20
-0.234

Exponential model
AIC: 60.896
0.194


D
Loggerhead RMU – Mediterranean
Marzuga
45
Count
15
10
5
2006
2007
2008
2009
2010
Year
Exponential model
AIC: 1.00E+20
-0.431
Smeda
46
Count
50
40
30
20
10
2006
2008
2010
2012
2014
2016
2018
Year
Exponential model
AIC: 70.632
-0.164
AlMahbula
47
Count
20
15
10
5
2006
2007
2008
2009
2010
Year
Exponential model
AIC: 1.00E+20
-0.228
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35-46
47
48
49
50
51
Arar
48
Count
35
30
25
20
15
10
5
2006
2007
2008
2009
2010
Year
Exponential model
AIC: 1.00E+20
0.094
300 km


D
Loggerhead RMU – Mediterranean
Ugla
49
Count
Year
2006
2008
2010
2012
2014
2016
2018
5
10
15
20
25
30
Exponential model
AIC: 58.537
-0.082
Ugla Misratah
50
Count
Year
2006
2008
2010
2012
2014
2016
2018
2
4
6
8
10
12
Exponential model
AIC: 47.75
0.121
Great Kuriat Island
51
Count
Year
1995
2000
2005
5
10
15
20
Exponential model
AIC: 99.115
0.056
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35-46
47
48
49
50
51
300 km

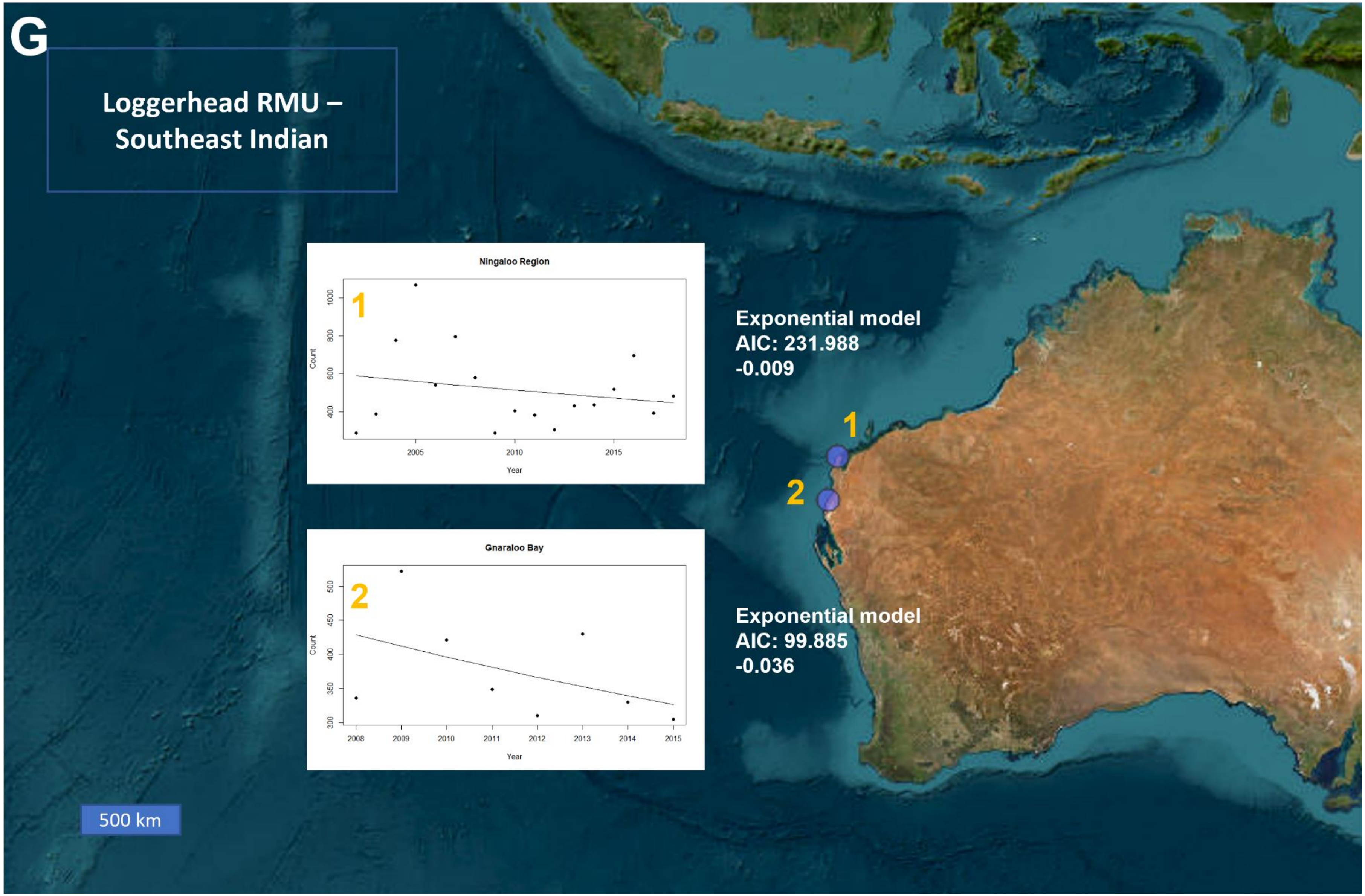

E
Loggerhead RMU –
Northwest Indian
1
Masirah Island
1
Count
10000
15000
20000
25000
30000
2008
2010
2012
2014
2016
Year
Exponential model
AIC: 186.157
-0.138
500 km



Loggerhead RMU – Southwest Indian

Breakpoint model
AIC: 158.515
0.177; -0.091 (2013)

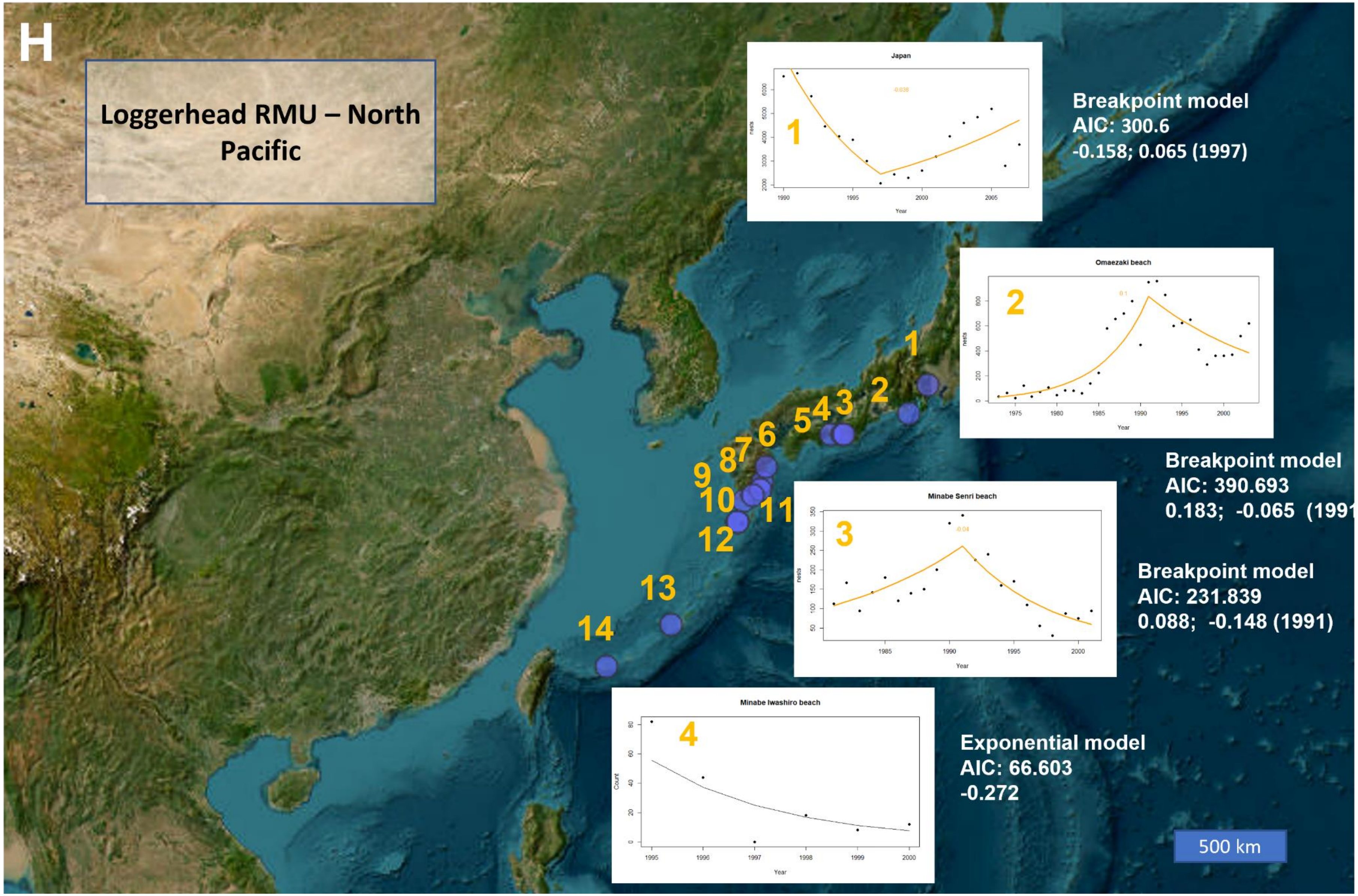
Breakpoint model
AIC: 805.483
0.011; 0.041 (1989)



Loggerhead RMU – Southeast Indian

Exponential model
AIC: 231.988
-0.009

Exponential model
AIC: 99.885
-0.036



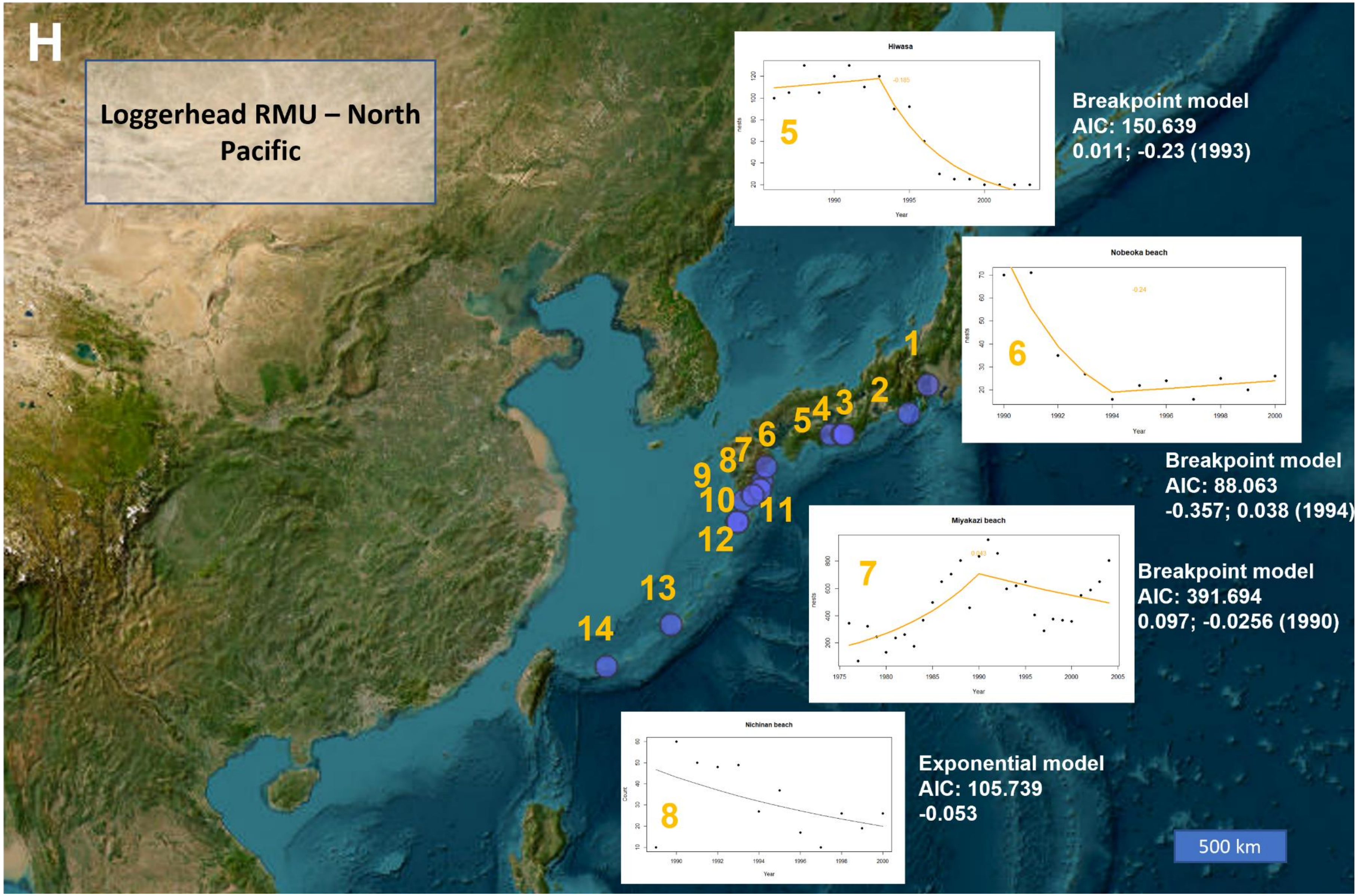
Loggerhead RMU – North Pacific

Breakpoint model
AIC: 300.6
-0.158; 0.065 (1997)

Breakpoint model
AIC: 390.693
0.183; -0.065 (1991

Breakpoint model
AIC: 231.839
0.088; -0.148 (1991)

Exponential model
AIC: 66.603
-0.272



Loggerhead RMU – North Pacific

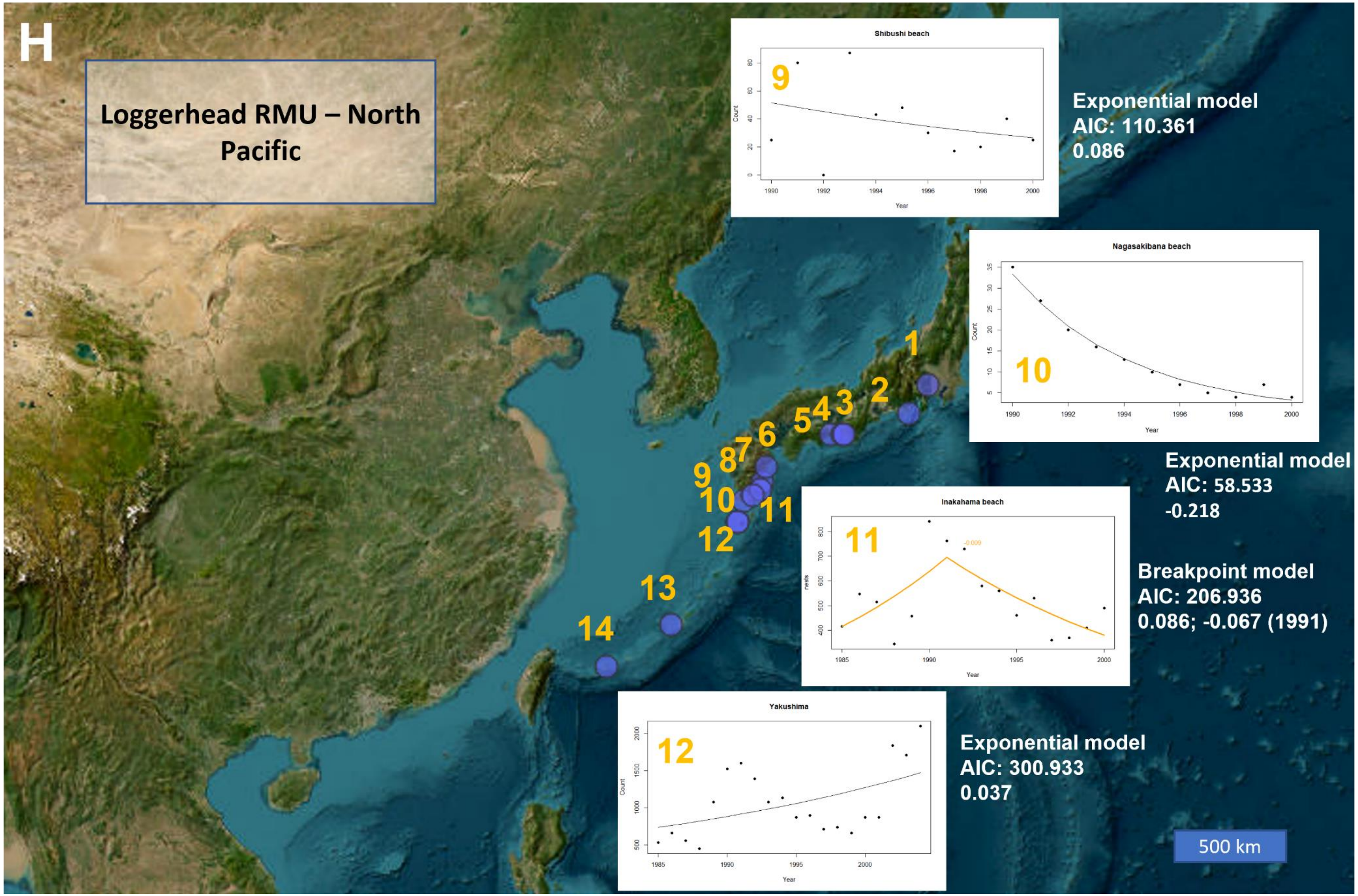
Breakpoint model
AIC: 150.639
0.011; -0.23 (1993)

Breakpoint model
AIC: 88.063
-0.357; 0.038 (1994)

Breakpoint model
AIC: 391.694
0.097; -0.0256 (1990)

Exponential model
AIC: 105.739
-0.053

500 km



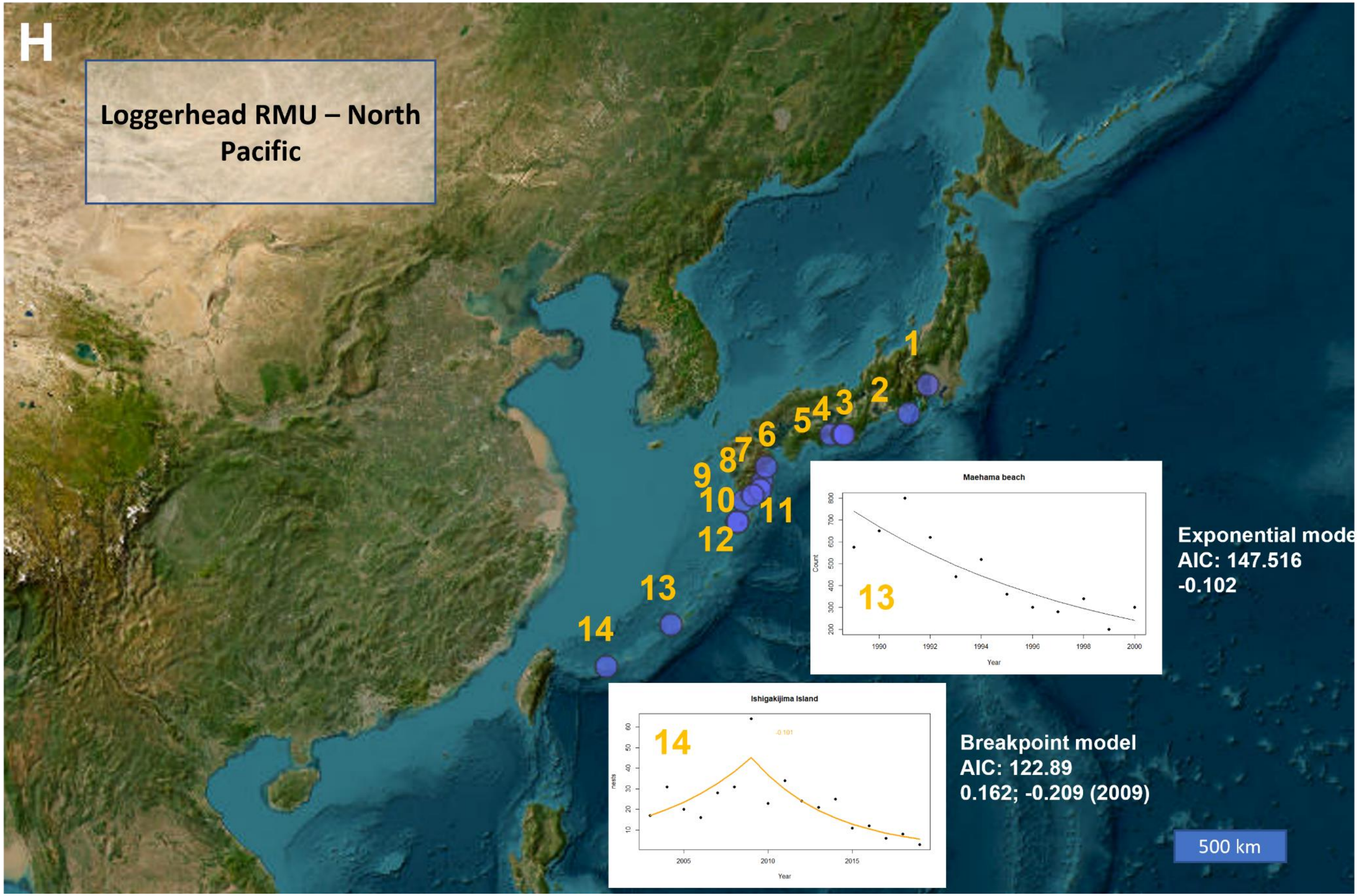
Loggerhead RMU – North Pacific

Exponential model
AIC: 110.361
0.086

Exponential model
AIC: 58.533
-0.218

Breakpoint model
AIC: 206.936
0.086; -0.067 (1991)

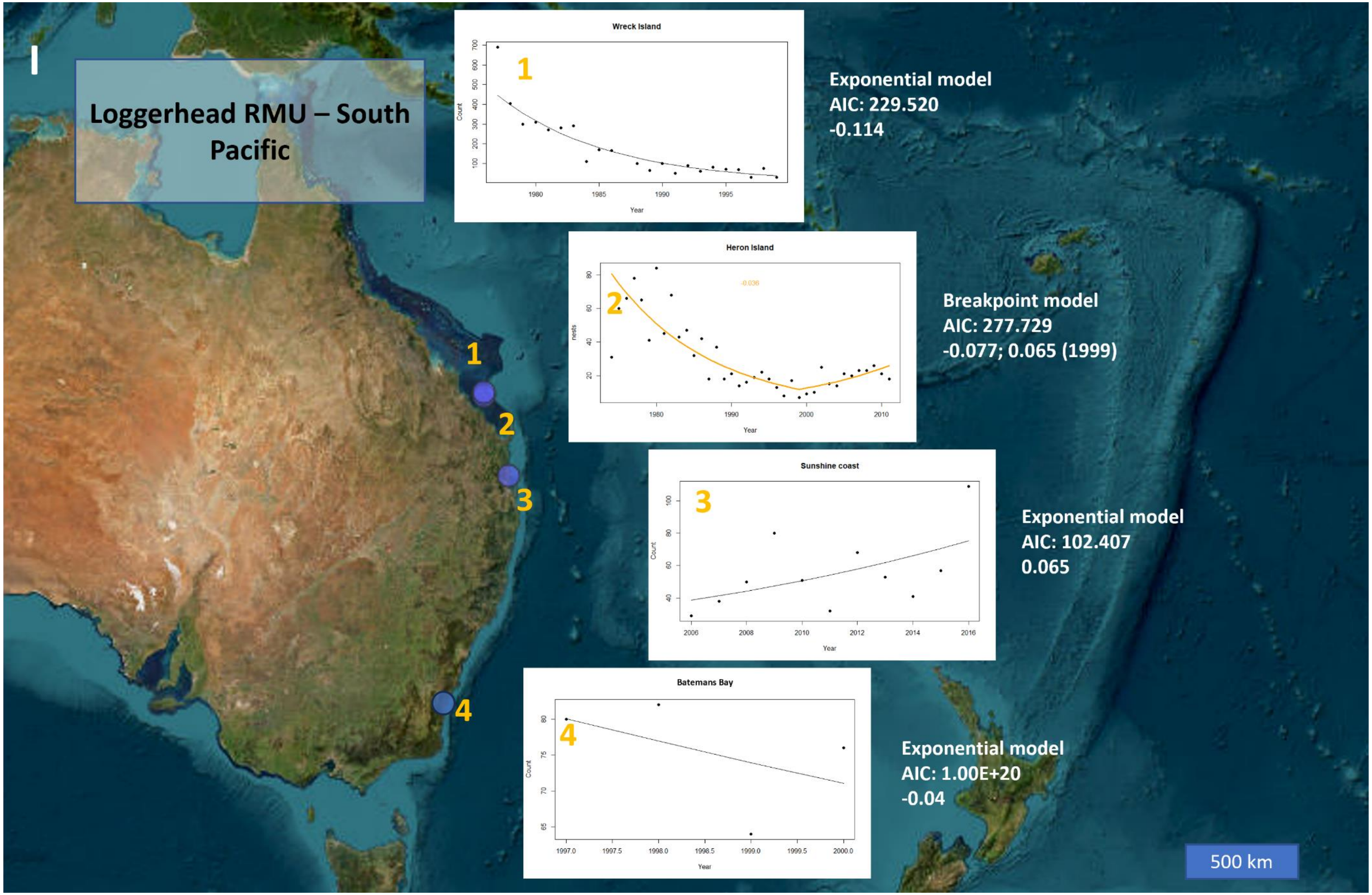
Exponential model
AIC: 300.933
0.037



Loggerhead RMU – North Pacific

Exponential mode
AIC: 147.516
-0.102

Breakpoint model
AIC: 122.89
0.162; -0.209 (2009)



Loggerhead RMU – South Pacific

Exponential model
AIC: 229.520
-0.114

Breakpoint model
AIC: 277.729
-0.077; 0.065 (1999)

Exponential model
AIC: 102.407
0.065

Exponential model
AIC: 1.00E+20
-0.04

Supplementary Figure 2.3: Loggerhead sea turtle RMU and species-level trends in abundance over time: (A) Northwest Atlantic, (B) Southwest Atlantic, (C) Northeast Atlantic, (D) Mediterranean, (E) Northwest Indian, (F) Southwest Indian, (G) Southeast Indian, (H) North Pacific and (I) South Pacific

Supplementary Table 2.2: List of loggerhead sea turtle nesting sites within their respective RMUs, data availability and sources of data collection

	Regional Management Unit	Country/Region	Site	Data availability	Source(s)
A	Northwest Atlantic	United States	North Carolina beaches	2015-2021	North Carolina Wildlife Resources Commission. n.d. North Carolina WRC Sea Turtle Project. Available at http://seaturtle.org/nestdb/index.shtml?view=1&year=2018 [accessed 7 April 2022].
		United States	Northern Recovery Unit (North Carolina, South Carolina and Georgia)	1989-2014	Ceriani SA, Casale P, Brost M, Leone EH, Witherington BE. 2019. Conservation implications of sea turtle nesting trends: elusive recovery of a globally important loggerhead population. *Ecosphere*, 10: e02936. Valdivia A, Wolf S, Suckling K. 2019. Marine mammals and sea turtles listed under the U.S. Endangered Species Act are recovering. *PLoS ONE*, 14: e0210164.
		United States	Peninsular Florida	1989-2020	Ceriani SA, Casale P, Brost M, Leone EH, Witherington BE. 2019. Conservation implications of sea turtle nesting trends: elusive recovery of a globally important loggerhead population. *Ecosphere*, 10: e02936. Florida Fish and Wildlife Conservation Commission. 2022. Index nesting beach survey totals (1989-2021). Available at https://myfwc.com/research/wildlife/sea-turtles/nesting/beach-survey-totals/ [accessed 7 April 2022]. Valdivia A, Wolf S, Suckling K. 2019. Marine mammals and sea turtles listed under the U.S. Endangered Species Act are recovering. *PLoS ONE*, 14: e0210164.

		United States	Dry Tortugas National Park	2001-2010	Richards P, Epperly SP, Heppell S, King R, Sasso CR, Moncada F, Nodarse G, Shaver D, Medina Y, Zurita J. 2011. Sea turtle population estimates incorporating uncertainty: A new approach applied to western North Atlantic loggerheads Caretta caretta. *Endangered Species Research*, 15: 151-158. Valdivia A, Wolf S, Suckling K. 2019. Marine mammals and sea turtles listed under the U.S. Endangered Species Act are recovering. *PLoS ONE*, 14: e0210164.
		United States	NW Management Unit of Florida	1997-2021	Ceriani SA, Casale P, Brost M, Leone EH, Witherington BE. 2019. Conservation implications of sea turtle nesting trends: elusive recovery of a globally important loggerhead population. *Ecosphere*, 10: e02936. Valdivia A, Wolf S, Suckling K. 2019. Marine mammals and sea turtles listed under the U.S. Endangered Species Act are recovering. *PLoS ONE*, 14: e0210164.
		United States	Northern Gulf of Mexico	1995-2007	Ceriani SA, Casale P, Brost M, Leone EH, Witherington BE. 2019. Conservation implications of sea turtle nesting trends: elusive recovery of a globally important loggerhead population. *Ecosphere*, 10: e02936. Valdivia A, Wolf S, Suckling K. 2019. Marine mammals and sea turtles listed under the U.S. Endangered Species Act are recovering. *PLoS ONE*, 14: e0210164.
		Mexico	Half Moon Bay, Akumal Bay, Jade Bay, and South Akumal Bay	1995-2018	González JM, Anastácio R, Lizárraga-Cubedo HA, Pereira MJ. 2020. *Caretta caretta* nesting activity on Akumal Beaches, Mexico. *Scientific Reports*, 10.
		Mexico	Quintana Roo, Paarmul,	1989-2006; 2011-2015	IAC Scientific Committee. 2016. *Status of Loggerhead Turtles (Caretta caretta) within Nations of the Inter-American Convention for the Protection and Conservation of Sea Turtles*. Report No. CIT-CC13-2016-Tec.13.

			Kanzul, San Juan, Xel Ha		Turtle Expert Working Group. 2009. *An assessment of the loggerhead turtle population in the western northern Atlantic ocean*. U.S. Department of Commerce Report No. NOAA Technical Memorandum NMFS-SEFSC-575. Miami, Florida.
		Cuba	Guanahacabibes Peninsula	1999-2015	Azanza-Ricardo J, Martín M, Gonzalez-Sanson G, Harrison E, Cruz Y, Bretos F. 2017. Possible effect of global climate change on *Caretta caretta* (Testudines, Cheloniidae) nesting ecology at Guanahacabibes Peninsula, Cuba. *Chelonian Conservation and Biology*, 16.
		Cuba	Guanahacabibes NP, San Felipe NP, Sur de la Isla PAMR, Jardines de la Reina NP	2001-2015	Azanza-Ricardo J, Gerhartz JL, Martín-Viaña YF, Gavilán FM, Bretos F, Cruz Y, Andreu GN, Martín RP, Alfonso EG. 2018. Achievements and challenges of marine turtle conservation in Cuba. *Bulletin of Marine Science*, 94.
		Cayman Islands	Little Cayman	2014-2019	Blumenthal JM, Hardwick JL, Austin TJ, Broderick AC, Chin P, Collyer L, Ebanks-Petrie G, Grant L, Lamb LD, Olynik J*,* Omeyer LCM, Prat-Varela A, Godley BJ. 2021. Cayman Islands sea turtle nesting population increases over 22 years of monitoring. *Frontiers in Marine Science*, 8.
		Cayman Islands	Cayman Brac	2012-2019	Blumenthal JM, Hardwick JL, Austin TJ, Broderick AC, Chin P, Collyer L, Ebanks-Petrie G, Grant L, Lamb LD, Olynik J*,* Omeyer LCM, Prat-Varela A, Godley BJ. 2021. Cayman Islands sea turtle nesting population increases over 22 years of monitoring. *Frontiers in Marine Science*, 8.
		Cayman Islands	Grand Cayman	1999-2019	Blumenthal JM, Hardwick JL, Austin TJ, Broderick AC, Chin P, Collyer L, Ebanks-Petrie G, Grant L, Lamb LD, Olynik J*,* Omeyer LCM, Prat-Varela A, Godley BJ. 2021. Cayman Islands sea turtle nesting population increases over 22 years of monitoring. *Frontiers in Marine Science*, 8.
		Aruba	Aruba	2002-2017	van der Wal S. 2018. *Aruba Update: Monitoring, Research and Telemetry*. WIDECAST Annual Meeting.

		Bonaire	Klein Bonaire	2004-2020	Sea Turtle Conservation Bonaire. 2020. *Bonaire Turtles: Navigational masters.* STCB Year Report 2020.
		Venezuela	Querepare, Cipara, Parguito Beach, and between Moron and Yaracuy	2009-2015	IAC Scientific Committee. 2016. *Status of Loggerhead Turtles (Caretta caretta) within Nations of the Inter-American Convention for the Protection and Conservation of Sea Turtles*. Report No. CIT-CC13-2016-Tec.13.
B	Southwest Atlantic	Brazil	Farol, Comboios, Povoação, Interlagos, Guarajuba, and Praia do Forte	2014-2019	IAC Scientific Committee. 2016. *Status of Loggerhead Turtles (Caretta caretta) within Nations of the Inter-American Convention for the Protection and Conservation of Sea Turtles*. Report No. CIT-CC13-2016-Tec.13. Reports available at http://www.iacseaturtle.org/informes.htm
		Brazil	Bahia	1988-2003	Marcovaldi M, Chaloupka M. 2007. Conservation status of the loggerhead sea turtle in Brazil: an encouraging outlook. *Endangered Species Research*, 3: 133-143.
		Brazil	Espirito Santo	1988-2003	Marcovaldi M, Chaloupka M. 2007. Conservation status of the loggerhead sea turtle in Brazil: an encouraging outlook. *Endangered Species Research*, 3: 133-143.
		Brazil	Rio de Janeiro	1993-2011	Lima EPe, Wanderlinde J, de Almeida DT, Lopez G, Goldberg DW. 2012. Nesting ecology and conservation of the loggerhead sea turtle (*Caretta caretta*) in Rio de Janeiro, Brazil. *Chelonian Conservation and Biology*, 11: 249-254.
C	Northeast Atlantic	Cape Verde	Santa Luzia	2011-2013	Rocha P, Melo T, Rebelo R, Catry P. 2015. A Significant Nesting Population of Loggerhead Turtles at the Nature Reserve of Santa Luzia, Cabo Verde. *Chelonian Conservation and Biology*, 14: 161-166.

		Cape Verde	Sal	2008-2017	Laloë J-O, Cozem J, Renom B, Taxonera A, Hays GC. 2020. Conservation importance of previously undescribed abundance trends: increase in loggerhead turtle numbers nesting on an Atlantic island. *Oryx*, 54: 315-322.
		Cape Verde	Boa Vista Island	2007-2009; 2013-2018	Marco A, Abella Pérez E, Liria Loza A, Tavares Martins S, López López Ó, Jiménez-Bordón S, Medina M, Oujo C, Gaona P, Godley B, López-Jurado L. 2012. Abundance and exploitation of loggerhead turtles nesting in Boa Vista island, Cape Verde: the only substantial rookery in the eastern Atlantic. *Animal Conservation*, 15: 351-360. Marco A, Tavares Martins S, Abella Pérez E, Patino-Martinez J. 2018. Potential causes for an important and hopeful increase in sea turtle nesting in Cabo Verde in 2018. *African Sea Turtle Newsletter*, 10: 1-6.
		Cape Verde	Maio Island	2016-2019	Patino-Martinez J, Passos L, Afonso I, Teixidor A, Tiwari M, Székely T, Moreno R. 2021. Globally important refuge for the loggerhead sea turtle: Maio Island, Cabo Verde. *Oryx*, 56: 1-9.
D	Mediterranean	Greece	Kyparissia Bay	1984-2000;2019	Margaritoulis D and Rees AF. 2001. The loggerhead turtle, *Caretta caretta*, population nesting in Kyparissia Bay, Peloponnesus, Greece: results of beach surveys over seventeen seasons and determination of the core nesting habitat. *Zoology in the Middle East*, 24: 75-90. ARCHELON. 2019. Conservation efforts during 2019 at the nesting habitat of *Caretta caretta* in Kyparissia Bay (Natura 2000 - GR2550005 “Thines Kyparissias”)

		Greece	Zakynthos	1984-2009; 2012; 2017-2018; 2020-2021	ARCHELON. 2012. Sea turtle monitoring and conservation in Laganas Bay, Zakynthos, Greece, during 2012. Short report submitted to the European Commission, and the Bern Convention (Council of Europe) ARCHELON. 2017. Concerning decrease of the nest numbers in Zakynthos this year. Available at https://www.archelon.gr/eng/ourdeltia.php?mid=&screen=4&nid=939 [accessed 4 April 2022]. ARCHELON. 2019. A high number of loggerhead nests on Zakynthos island in 2018: what else is needed to achieve good conservation status for the species in Laganas bay? Available at https://www.archelon.gr/eng/ourdeltia.php?mid=6&mid2=17&nid=1035 [accessed 4 April 2022]. ARCHELON. 2020. Sea turtle monitoring and conservation in Laganas Bay, Zakynthos, Greece, during 2020. Short report submitted to the European Commission, and the Bern Convention (Council of Europe). pp. 17. ARCHELON. 2021. Sea turtle monitoring and conservation in Laganas Bay, Zakynthos, Greece, during 2021. Short report submitted to the European Commission, and the Bern Convention (Council of Europe). pp. 18. Camiñas J. 2004. Sea turtles of the Mediterranean Sea: population dynamics, sources of mortality and relative importance of fisheries impacts. *FAO Fisheries Report.* Margaritoulis D. 2005. Nesting activity and reproductive output of loggerhead sea turtles, *Caretta caretta*, over 19 seasons (1984-2002) at Laganas Bay, Zakynthos, Greece: the largest rookery in the Mediterranean. *Chelonian Conservation and Biology*, 4: 916-929.

					Margaritoulis D, Rees A, Dean C, Riggall T. 2011. Reproductive data of loggerhead turtles in Laganas Bay, Zakynthos Island, Greece, 2003-2009.
		Greece	Keroni	1995-2002	Margaritoulis D, Rees AF. n.d. Loggerhead nesting in Koroni, southern Peloponnesus, Greece: nesting data 1995-2002. Proceedings of the Twenty Third International Sea Turtle Symposium. 17 - 21 March 2003, Kuala Lumpur, Malaysia. Margaritoulis D, Rees AF. 2003. Loggerhead nesting effort and conservation initiatives at the monitored beaches of Greece during 2002. *Marine Turtle Newsletter*, 102.
		Turkey	Dalaman beach	1988-1989; 1994; 1998; 2002-2006	Canbolat A. 2004. A review of sea turtle nesting activity along the Mediterranean coast of Turkey. *Biological Conservation*, 116: 81-91. Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp.
		Turkey	Dalyan Beach	1979; 1982; 1987-2006	Canbolat A. 2004. A review of sea turtle nesting activity along the Mediterranean coast of Turkey. *Biological Conservation*, 116: 81-91. Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp. Turkozan O, Taskavak E, Ilgaz C. 2003. A review of the biology of the loggerhead turtle, *Caretta caretta*, at five major nesting beaches on the south-western Mediterranean coast of Turkey. *Herpetological Journal*, 13: 27-33. Türkozan O, Yilmaz C. 2008. Loggerhead Turtles, *Caretta caretta*, at Dalyan Beach, Turkey: nesting activity (2004–2005) and 19-year abundance trend (1987–2005). *Chelonian Conservation and Biology*, 7: 178-187.

		Turkey	Fethiye Bay	1993-2006; 2011-2013; 2019	Başkale E, Katılmış Y, Tataroğlu M, Sözbilen D, Polat F, Lambropoulos M, Fellhofer-Mıhcıoğlu C, Stachowitsch M, Kaska Y. 2016. Monitoring and conservation of loggerhead turtle's nests on Fethiye beaches, Turkey. *Biharean Biologist*, 10: 20-23. Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp. Ilgaz Ç, Türkozan Ou, Özdemir A, Kaska Y, Stachowitsch M. 2007. Population decline of loggerhead turtles: two potential scenarios for Fethiye Beach, Turkey. *Biodiversity and Conservation*, 16: 1027-1037. Kesler M. 2019. 115,000 baby *Caretta caretta*s make it to sea in Turkey: Report. Available at https://www.hurriyetdailynews.com/115-000-baby-caretta-carettas-make-it-to-sea-in-turkey-report-148181#:~:text=%E2%80%9COf%20these%20babies%20%5Bthat%20hatched,mother%20in%2025%20years'%20time. [accessed 5 April 2022]. Sak S, Baran I. 2001. Research on the sea turtle population of Belek Beach. *Turkish Journal of Zoology*, 25: 361-367. Turkozan O, Taskavak E, Ilgaz C. 2003. A review of the biology of the loggerhead turtle, *Caretta caretta*, at five major nesting beaches on the south-western Mediterranean coast of Turkey. *Herpetological Journal*, 13: 27-33.
		Turkey	Patara beach	1989-1990; 1992-1994; 1996-2002;	Canbolat A. 2004. A review of sea turtle nesting activity along the Mediterranean coast of Turkey. *Biological Conservation*, 116: 81-91. Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp.

				2004-2020	Kesler M. 2019. 115,000 baby *Caretta caretta*s make it to sea in Turkey: Report. Available at https://www.hurriyetdailynews.com/115-000-baby-caretta-carettas-make-it-to-sea-in-turkey-report-148181#:~:text=%E2%80%9COf%20these%20babies%20%5Bthat%20hatched,mother%20in%2025%20years'%20time. [accessed 5 April 2022]. Mediterranean Association to Save the Sea Turtles. 2021. Follow-up of recommendations nos. 182 and 183 (2015) on presumed degradation of nesting beaches in Fethiye and Patara SPAs (Turkey) Report Turkozan O, Taskavak E, Ilgaz C. 2003. A review of the biology of the loggerhead turtle, *Caretta caretta*, at five major nesting beaches on the south-western Mediterranean coast of Turkey. *Herpetological Journal*, 13: 27-33.
		Turkey	Kale beach	1995; 1998; 2006	Canbolat A. 2004. A review of sea turtle nesting activity along the Mediterranean coast of Turkey. *Biological Conservation*, 116: 81-91. Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp.
		Turkey	Demre coast	1994; 1998; 2003; 2006; 2020	Altın A, Ayyildiz H, Maden M. 2021. Conservation and monitoring of marine turtle (*Caretta caretta*) population in the Demre (Kale) beach region of Antalya province. *Marine and Life Sciences*, 3: 80-87.
		Turkey	Finike-Kumluca	1979; 1988; 1994; 1998; 2003	Canbolat A. 2004. A review of sea turtle nesting activity along the Mediterranean coast of Turkey. *Biological Conservation*, 116: 81-91. Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp.

		Turkey	Cirali beach	1994-2006; 2013-2020	Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp. Sönmez B, Elginöz E, Ilgaz M, Altınkaya H. 2021. Nesting activity of loggerhead turtles (2013–2020) and 20 years abundance trend (2001–2020) on Çıralı Beach, Turkey. *Regional Studies in Marine Science*, 44: 101758.
		Turkey	Belek beach	1979; 1994-2006; 2016; 2019-2020	Antalya. 2020. *Caretta caretta* record on Belek beach. Available at https://www.hurriyetdailynews.com/caretta-caretta-record-on-belek-beach-158160 [accessed 5 April 2022]. Canbolat A. 2004. A review of sea turtle nesting activity along the Mediterranean coast of Turkey. *Biological Conservation*, 116: 81-91. Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp. Kesler M. 2019. 115,000 baby *Caretta caretta*s make it to sea in Turkey: Report. Available at https://www.hurriyetdailynews.com/115-000-baby-caretta-carettas-make-it-to-sea-in-turkey-report-148181#:~:text=%E2%80%9COf%20these%20babies%20%5Bthat%20hatched,mother%20in%2025%20years'%20time. [accessed 5 April 2022]. Sak S, Baran I. 2001. Research on the sea turtle population of Belek Beach. *Turkish Journal of Zoology*, 25: 361-367. Tükozan O, Taskavak E, Ilgaz Ç. 2003. A review of the biology of the loggerhead turtle, *Caretta caretta*, at five major nesting beaches on the south-western Mediterranean coast of Turkey. *Herpetological Journal*, 13: 27-33.

		Turkey	Kizilot beach	1990; 1994; 1996-1998	Canbolat A. 2004. A review of sea turtle nesting activity along the Mediterranean coast of Turkey. *Biological Conservation*, 116: 81-91. Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp. Turkozan O, Taskavak E, Ilgaz C. 2003. A review of the biology of the loggerhead turtle, *Caretta caretta*, at five major nesting beaches on the south-western Mediterranean coast of Turkey. *Herpetological Journal*, 13: 27-33.
		Turkey	Anamur beach	1990; 1994; 1996; 2006	Canbolat A. 2004. A review of sea turtle nesting activity along the Mediterranean coast of Turkey. *Biological Conservation*, 116: 81-91. Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp.
		Turkey	Goksu Delta	1988; 1991-1992; 1994; 1996; 1998; 2004-2006; 2019	Glen F, Godley BJ, Kelly A, Broderick AC. 1997. Marine turtle nesting in the Göksu Delta, Turkey, 1996. *Marine Turtle Newsletter*, 77: 17-19. Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp. Kesler M. 2019. 115,000 baby *Caretta carettas* make it to sea in Turkey: Report. Available at https://www.hurriyetdailynews.com/115-000-baby-caretta-carettas-make-it-to-sea-in-turkey-report-148181#:~:text=%E2%80%9COf%20these%20babies%20%5Bthat%20hatched,mother%20in%2025%20years'%20time. [accessed 5 April 2022].
		Turkey	Alata beach	2002-2003; 2005-2006	Canbolat A. 2004. A review of sea turtle nesting activity along the Mediterranean coast of Turkey. *Biological Conservation*, 116: 81-91.

					Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp.
		Turkey	Kazanli beach	1990; 1996; 2001-2002; 2004; 2006	Canbolat A. 2004. A review of sea turtle nesting activity along the Mediterranean coast of Turkey. *Biological Conservation*, 116: 81-91. Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp.
		Turkey	Akyatan beach	1992; 1994; 2006	Canbolat A. 2004. A review of sea turtle nesting activity along the Mediterranean coast of Turkey. *Biological Conservation*, 116: 81-91. Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp.
		Turkey	Samandag beach	1996; 2001-2006	Canbolat A. 2004. A review of sea turtle nesting activity along the Mediterranean coast of Turkey. *Biological Conservation*, 116: 81-91. Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp.
		Cyprus	Northern Cyprus	1993-2019	Casale P, Hochscheid S, Kaska Y, Panagopoulou A. 2020. Sea turtles in the Mediterranean Region: MTSG Annual Regional Report 2020
		Cyprus	Alagadi beach	1993-2019	Broderick AC, Glen F, Godley BJ, Hays GC. 2002. Estimating the number of green and loggerhead turtles nesting annually in the Mediterranean. *Oryx*, 36: 227-235. Omeyer LCM, Stokes KL, Beton D, Çiçek BA, Davey S, Fuller WJ, Godley BJ, Sherley RB, Snape RTE, Broderick AC. 2021. Investigating differences in population recovery rates of two sympatrically nesting sea turtle species. *Animal Conservation*, 24: 832-846.
		Cyprus	Chrysochou Bay	1999-2015	Casale P, Hochscheid S, Kaska Y, Panagopoulou A. 2020. Sea turtles in the Mediterranean Region: MTSG Annual Regional Report 2020
		Cyprus	West coast	1989-2008	Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp.

		Lebanon	El Mansouri beach	2002-2007	Khalil M., Syed H, Aureggi M. 2009. Impact of war on the South Lebanon sea turtle nesting population. *Testudo: The Journal of the British Chelonia Group*, 7, 71.
		Israel	Israeli coast	1984-2007	Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp. Silbersteinand D, Dmi'el R. 1991. Loggerhead sea turtle nesting in Israel. *Marine Turtle Newsletter*, 53: 17-18.
		Libya	Bananes	2006-2010; 2019	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Al-Hasi	2006-2010; 2017; 2019	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Ain Ghazala	2007-2010	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Jarjaruma	2006-2010; 2017; 2019	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Zaafaran	2017-2019	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Shash	2009-2010; 2017-2019	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.

		Libya	Mtefla	2006-2007; 2009-2010	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Al-Thalateen	2005-2007; 2009-2010; 2017-2019	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Al-Gbeba	2005-2007; 2009-2010; 2017-2019	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	West Camp	2005-2007; 2009-2010; 2017-2019	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Al-Arbaeen (Tamet)	2006-2007; 2009-2010; 2017-2019	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.

		Libya	Al-Khamseen	2017-2019	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Al-Nakhla	2017-2019	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Elkhowada	2006-2007; 2010; 2017	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Al-bwerat	2017-2019	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Almjaren	2006-2007; 2009-2010; 2017-2018	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Almerekeb	2006-2007; 2009-2010; 2018	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Al-Ghwezat	2006-2007; 2009-2010	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.

		Libya	Al-Malfa	2006-2007; 2009-2010; 2018	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Marzuga	2006-2007; 2010	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Smeda	2006-2007; 2009-2010; 2018	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	AlMahbula	2006-2007; 2009-2010	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Arar	2006-2007; 2009-2010	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Ugla	2006-2008; 2010; 2017; 2019	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.
		Libya	Ugla Misratah	2006-2007; 2009-	SPA/RAC-UNEP/MAP. 2021. Marine turtle research and conservation in Libya: a contribution to safeguarding Mediterranean biodiversity. By Hamza A. (Ed). SPA/RAC, Tunis: pp. 77.

				2010; 2018	
		Tunisia	Great Kuriat Island	1993-2008	Casale P, Margaritoulis D. 2010. Sea turtles in the Mediterranean: distribution, threats and conservation priorities. Gland, Switzerland: IUCN. 294 pp.
E	Northwest Indian Ocean	Oman	Masirah Island	2008-2016	Willson A, Witherington B, Baldwin R, Tiwari M, Al Sariri T, Al Kiyumi A, Al Harthi S, Willson MS, Al Bulushi A, Al Farsi G, Al Humaidy J, Al Araimi J, Daar LA, Schroeder B, Ross JP, Possardt E. 2020. Evaluating the long-term trend and management of a globally important loggerhead population nesting on Masirah Island, sultanate of Oman. *Frontiers in Marine Science*, 7.
F	Southwest Indian Ocean	Mozambique	Ponta do Ouro to Bazaruto Archipelago	2008-2011; 2013-2019	Fernandes RS, Inteca GE, Williams JL, Muaves L, Xavier M. 2020. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2019/20. Maputo, CTV, pp. 61 Fernandes RS, Inteca GE, Williams JL, Taju A, Muaves L, Pereira MAM. 2019. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2018/19. Maputo, CTV, pp. 47 Fernandes RS, Williams JL, Gonzalez-Valladolid S, Muaves L, Pereira MAM. 2018. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2017/18. Maputo, CTV, pp. 45 Fernandes RS, Williams J, Louro CMM, Pereira MAM. 2014. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2013/14. Maputo, CTV, pp. 6. Fernandes RS, Williams JL, Trindade J. 2016. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2015/16. Maputo, CTV, pp. 26

					Fernandes RS, Williams JL, Trindade J, Pereira MAM. 2015. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2014/15. Maputo, CTV, pp. 25 Fernandes RS, Williams JL, Valladolid SG, Muaves L, Louro CMM, Pereira MAM. 2017. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2016/17. Maputo, CTV, pp. 31 Louro C, Videira EJ, Pereira MA, Fernandes R. 2012. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2011/12. Maputo. CTV/AICM, pp. 10 Pereira M, Videira E, Narane D. 2009. Monitoring, tagging and conservation of marine turtles in Mozambique: 2008/09 annual report. Maputo, AICM/GTT, pp. 4. Videira EJS, Pereira MAM, Louro CMM. 2011. Monitoring, tagging and conservation of marine turtles in Mozambique: Annual Report 2010/11. Maputo, AICM/GTT, pp. 10 Videira EJS, Pereira MAM, Narane DA, Louro CMM. 2010. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2009/10. Maputo, AICM/GTT., pp. 7
		South Africa	Kosi Bay Mouth to Mabibi	1965-2019	Bachoo S. n.d. Unpublished data. Ezemvelo KZN Wildlife. Nel R, Punt AE, Hughes GR. 2013. Are coastal protected areas always effective in achieving population recovery for nesting sea turtles? *PLoS ONE*, 8: e63525.
G	Southeast Indian Ocean	Australia	Ningaloo Region	2002-2018	DBCA (ed). 2020. *Ningaloo Turtle Program Annual Report 2018-2019*. Department of Biodiversity, Conservation and Attractions and the Ningaloo Turtle Program. Exmouth, Western Australia.

		Australia	Gnaraloo Bay	2008-2015	Hattingh K, Thomson J, Goldsmith N, Nielsen K, Green A, Do M (eds). 2016. *Gnaraloo Turtle Conservation Program (GTCP). Gnaraloo Bay Rookery and Gnaraloo Cape Farquhar Rookery, Report 2015/16*. Gnaraloo Wilderness Foundation. Western Australia.
H	North Pacific	Japan	Japan	1990-2000; 2002-2007	Rexstad R, Buckland ST (eds). n.d. *Center for Independent Experts (CIE) review on sea turtle impacts from Hawaiian longline fisheries*. Snover ML (ed). 2008. *Assessment of the population-level impacts of potential increases in marine turtle interactions resulting from a Hawaii Longline Association proposal to expand the Hawaii-based shallow-set fishery*. NOAA/NMFS/Pacific Islands Fisheries Science Center Report No. PIFSC Internal Report IR-08-010. Honolulu, Hawaii.
		Japan	Omaezaki beach	1973-2000; 2002-2003	Kamezaki N, Matsuzawa Y, Abe O, Asakawa H, Fujii T, Goto K, Hagino S, Hayami M, Ishii M, Iwamoto T, Kamata T, Kato H, Kodama J, Kondo Y, Miyawaki I, Mizobuchi K, Nakamura Y, Nakashima Y, Naruse H, Omuta K, Samejima M, Suganuma H, Takeshita H, Tanaka T, Toji T, Uematsu M, Yamamoto A, Yamato T, Wakabayashi I. 2003. Loggerhead turtles nesting in Japan. In: Bolten AB, Witherington BE editors. *Loggerhead Sea Turtles*. Washington: Smithsonian Books. pp. 210-217. Sea Turtle Association of Japan. n.d. Available at http://www.umigame.org/E1/turtlepowerstyle2.html [accessed 6 April 2022].
		Japan	Minabe Senri beach	1981-2000	Hatase H, Kinoshita M, Bando T, Kamezaki N, Sato K, Matsuzawa Y, Goto K, Omuta K, Nakashima Y, Takeshita H, Sakamoto W. 2002. Population structure of loggerhead turtles, *Caretta caretta*, nesting in Japan: bottlenecks on the Pacific population. *Marine Biology*, 141: 299-305. Kamezaki N, Matsuzawa Y, Abe O, Asakawa H, Fujii T, Goto K, Hagino S, Hayami M, Ishii M, Iwamoto T, Kamata T, Kato H, Kodama J, Kondo Y, Miyawaki I, Mizobuchi K,

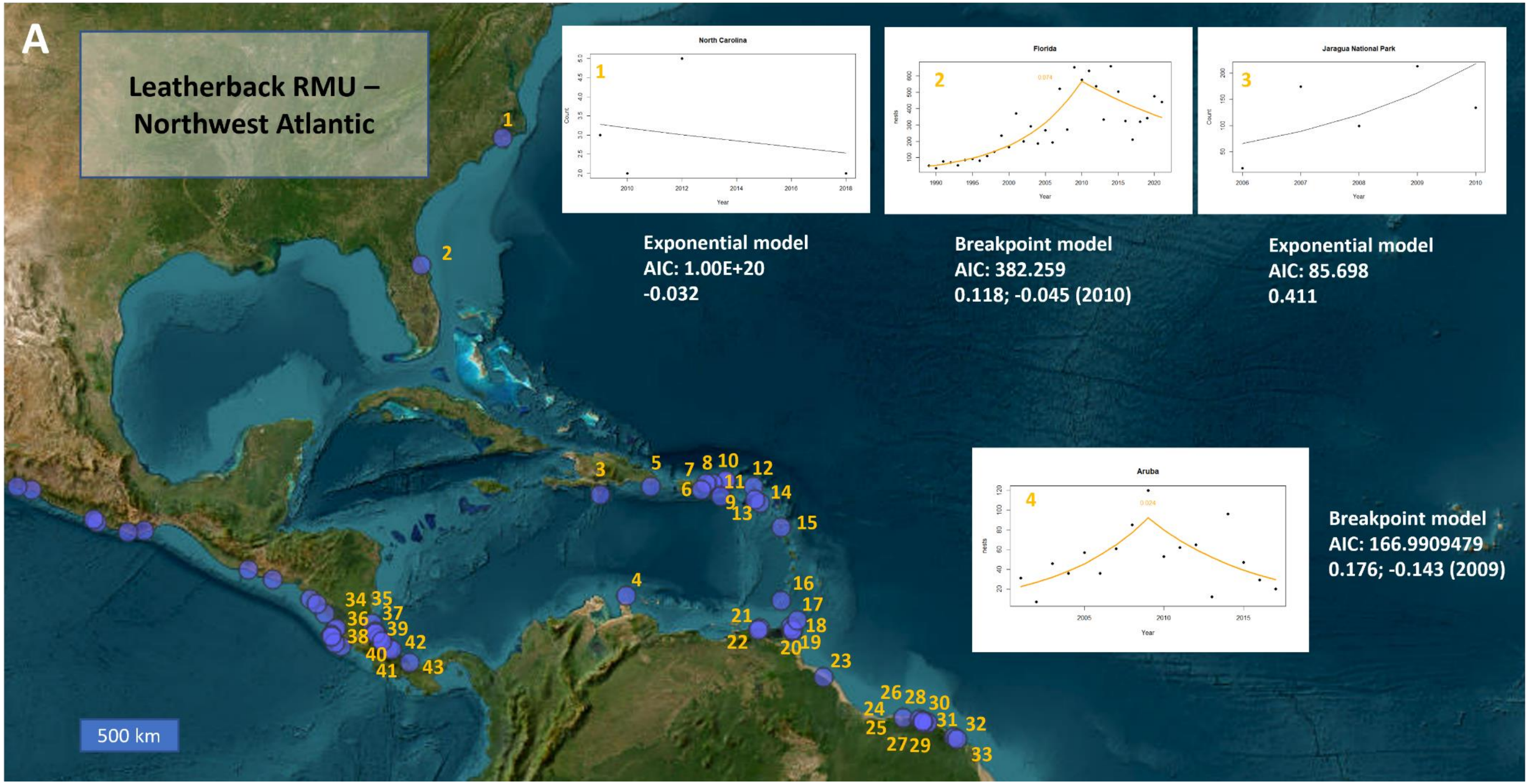
					Nakamura Y, Nakashima Y, Naruse H, Omuta K, Samejima M, Suganuma H, Takeshita H, Tanaka T, Toji T, Uematsu M, Yamamoto A, Yamato T, Wakabayashi I. 2003. Loggerhead turtles nesting in Japan. In: Bolten AB, Witherington BE editors. *Loggerhead Sea Turtles*. Washington: Smithsonian Books. pp. 210-217.
		Japan	Minabe Iwashiro beach	1995-2000	Kamezaki N, Matsuzawa Y, Abe O, Asakawa H, Fujii T, Goto K, Hagino S, Hayami M, Ishii M, Iwamoto T, Kamata T, Kato H, Kodama J, Kondo Y, Miyawaki I, Mizobuchi K, Nakamura Y, Nakashima Y, Naruse H, Omuta K, Samejima M, Suganuma H, Takeshita H, Tanaka T, Toji T, Uematsu M, Yamamoto A, Yamato T, Wakabayashi I. 2003. Loggerhead turtles nesting in Japan. In: Bolten AB, Witherington BE editors. *Loggerhead Sea Turtles*. Washington: Smithsonian Books. pp. 210-217.
		Japan	Hiwasa	1986-2003	Sea Turtle Association of Japan. n.d. Available at http://www.umigame.org/E1/turtlepowerstyle2.html [accessed 6 April 2022].
		Japan	Nobeoka beach	1990-2000	Kamezaki N, Matsuzawa Y, Abe O, Asakawa H, Fujii T, Goto K, Hagino S, Hayami M, Ishii M, Iwamoto T, Kamata T, Kato H, Kodama J, Kondo Y, Miyawaki I, Mizobuchi K, Nakamura Y, Nakashima Y, Naruse H, Omuta K, Samejima M, Suganuma H, Takeshita H, Tanaka T, Toji T, Uematsu M, Yamamoto A, Yamato T, Wakabayashi I. 2003. Loggerhead turtles nesting in Japan. In: Bolten AB, Witherington BE editors. *Loggerhead Sea Turtles*. Washington: Smithsonian Books. pp. 210-217.
		Japan	Miyakazi beach	1976-2000; 2002-2004	Kinan I. 2006. *Proceedings of the second western pacific sea turtle cooperative research and management workshop. Volume II: North Pacific loggerhead sea turtles.* Western Pacific Regional Fishery Management Council. Honolulu, HI, USA.
		Japan	Nichinan beach	1989-2000	Kamezaki N, Matsuzawa Y, Abe O, Asakawa H, Fujii T, Goto K, Hagino S, Hayami M, Ishii M, Iwamoto T, Kamata T, Kato H, Kodama J, Kondo Y, Miyawaki I, Mizobuchi K, Nakamura Y, Nakashima Y, Naruse H, Omuta K, Samejima M, Suganuma H, Takeshita H, Tanaka T, Toji T, Uematsu M, Yamamoto A, Yamato T, Wakabayashi I. 2003. Loggerhead turtles nesting in Japan. In: Bolten AB, Witherington BE editors. *Loggerhead Sea Turtles*. Washington: Smithsonian Books. pp. 210-217.
		Japan	Shibushi beach	1990-2000	Kamezaki N, Matsuzawa Y, Abe O, Asakawa H, Fujii T, Goto K, Hagino S, Hayami M, Ishii M, Iwamoto T, Kamata T, Kato H, Kodama J, Kondo Y, Miyawaki I, Mizobuchi K,

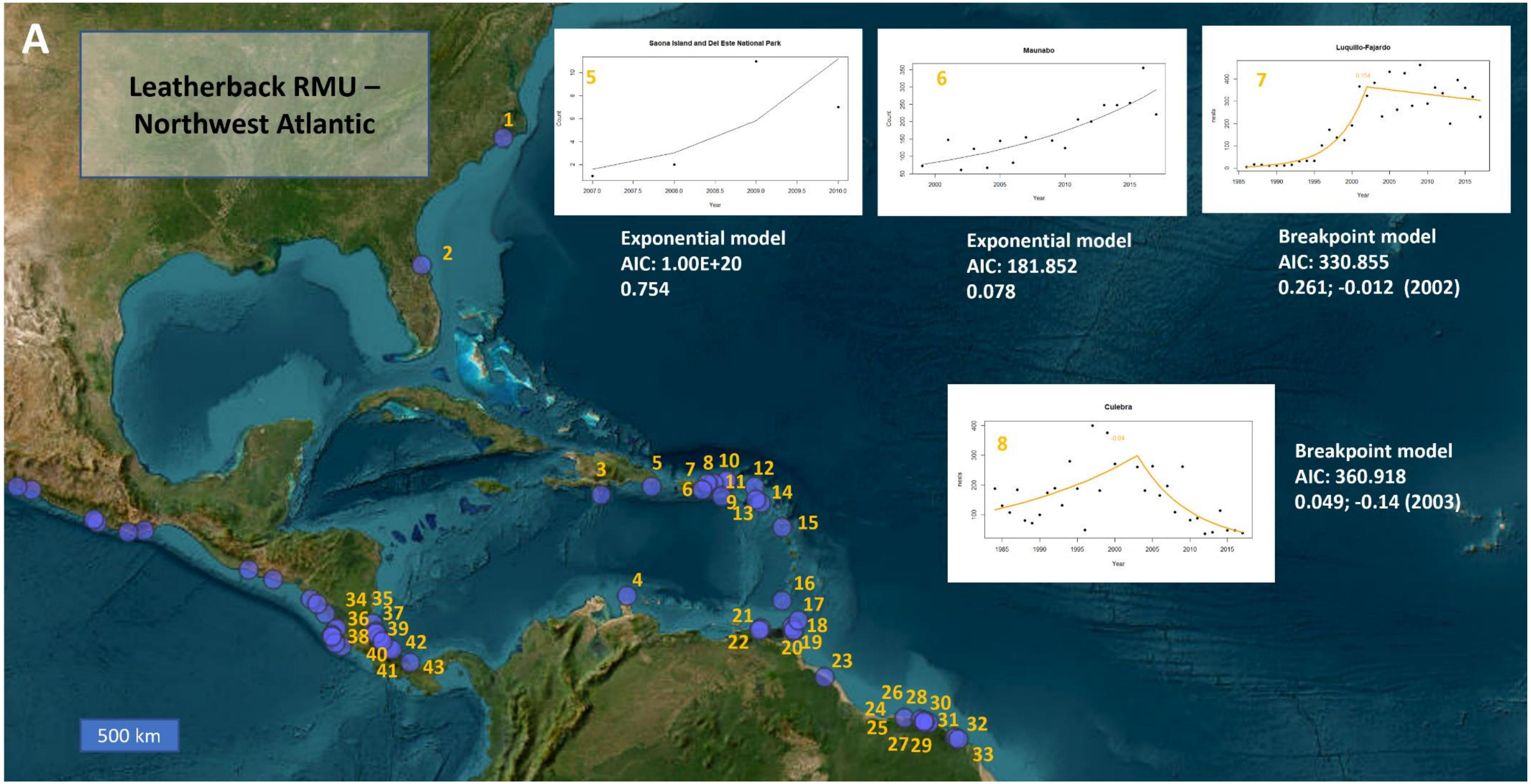
					Nakamura Y, Nakashima Y, Naruse H, Omuta K, Samejima M, Suganuma H, Takeshita H, Tanaka T, Toji T, Uematsu M, Yamamoto A, Yamato T, Wakabayashi I. 2003. Loggerhead turtles nesting in Japan. In: Bolten AB, Witherington BE editors. *Loggerhead Sea Turtles*. Washington: Smithsonian Books. pp. 210-217.
		Japan	Nagasakibana beach	1990-2000	Kamezaki N, Matsuzawa Y, Abe O, Asakawa H, Fujii T, Goto K, Hagino S, Hayami M, Ishii M, Iwamoto T, Kamata T, Kato H, Kodama J, Kondo Y, Miyawaki I, Mizobuchi K, Nakamura Y, Nakashima Y, Naruse H, Omuta K, Samejima M, Suganuma H, Takeshita H, Tanaka T, Toji T, Uematsu M, Yamamoto A, Yamato T, Wakabayashi I. 2003. Loggerhead turtles nesting in Japan. In: Bolten AB, Witherington BE editors. *Loggerhead Sea Turtles*. Washington: Smithsonian Books. pp. 210-217.
		Japan	Inakahama beach	1985-2000	Kamezaki N, Matsuzawa Y, Abe O, Asakawa H, Fujii T, Goto K, Hagino S, Hayami M, Ishii M, Iwamoto T, Kamata T, Kato H, Kodama J, Kondo Y, Miyawaki I, Mizobuchi K, Nakamura Y, Nakashima Y, Naruse H, Omuta K, Samejima M, Suganuma H, Takeshita H, Tanaka T, Toji T, Uematsu M, Yamamoto A, Yamato T, Wakabayashi I. 2003. Loggerhead turtles nesting in Japan. In: Bolten AB, Witherington BE editors. *Loggerhead Sea Turtles*. Washington: Smithsonian Books. pp. 210-217.
		Japan	Yakushima	1985-2004	Kinan I. 2006. *Proceedings of the second western pacific sea turtle cooperative research and management workshop. Volume II: North Pacific loggerhead sea turtles.* Western Pacific Regional Fishery Management Council. Honolulu, HI, USA.
		Japan	Maehama beach	1989-2000	Kamezaki N, Matsuzawa Y, Abe O, Asakawa H, Fujii T, Goto K, Hagino S, Hayami M, Ishii M, Iwamoto T, Kamata T, Kato H, Kodama J, Kondo Y, Miyawaki I, Mizobuchi K, Nakamura Y, Nakashima Y, Naruse H, Omuta K, Samejima M, Suganuma H, Takeshita H, Tanaka T, Toji T, Uematsu M, Yamamoto A, Yamato T, Wakabayashi I. 2003. Loggerhead turtles nesting in Japan. In: Bolten AB, Witherington BE editors. *Loggerhead Sea Turtles*. Washington: Smithsonian Books. pp. 210-217.
		Japan	Ishigakijima Island	2003-2015	Okuyama J, Ishii H, Tanizaki S, Suzuki T, Abe O, Nishizawa H, Yano A, Tsujimura M, Ishigaki T, Ishigaki T, Kobayashi M, Yanagida H. 2020. Quarter-century (1993–2018) nesting trends in the peripheral populations of three sea turtle species at Ishigakijima Island, Japan. *Chelonian Conservation and Biology*, 19: 101.

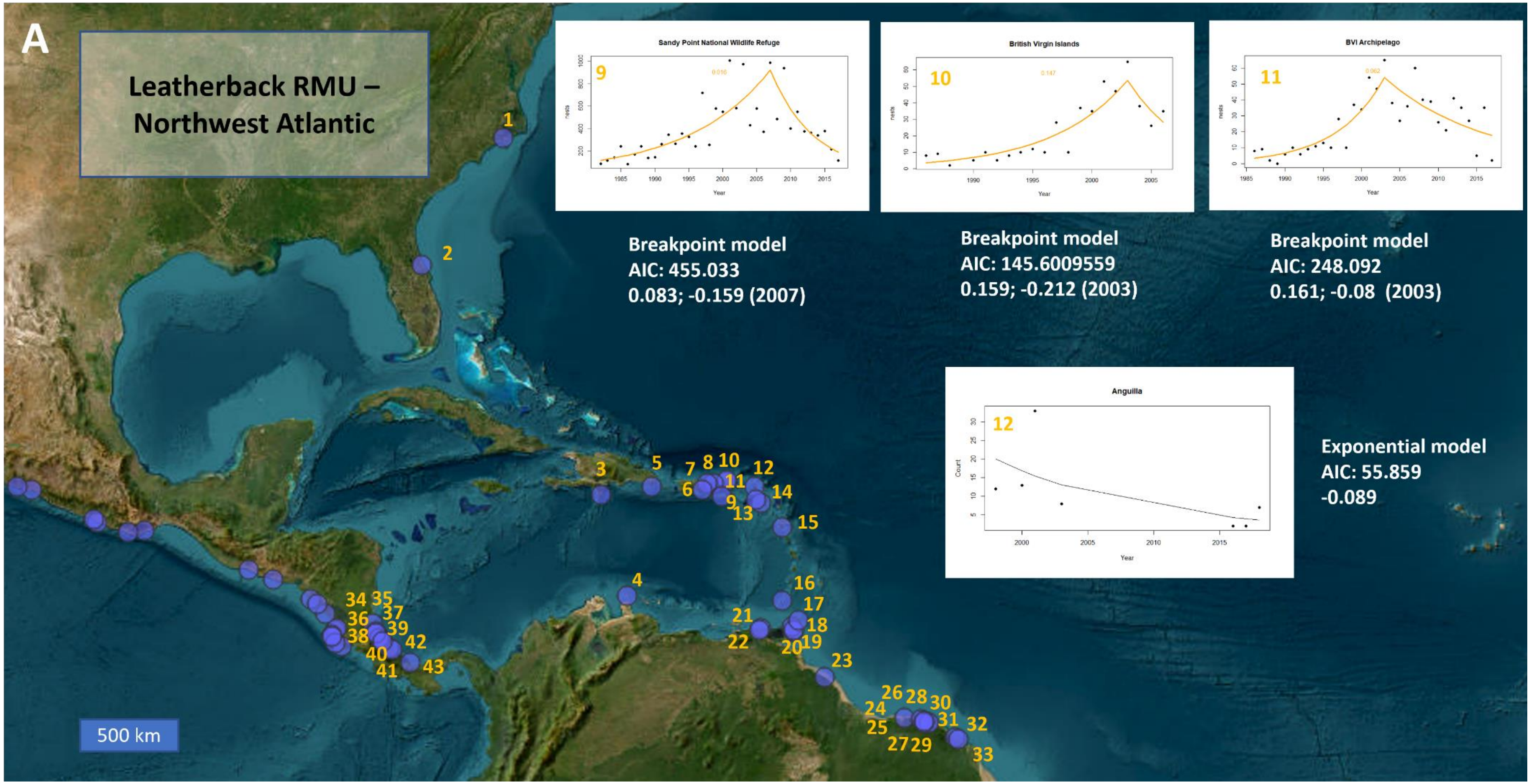
I	South Pacific	Australia	Wreck Island	1977-1986; 1988-1999	Shanker K. 2004. *Marine turtle status and conservation in the Indian Ocean*. FAO Fisheries Report No. 738 supplement. Rome, Italy.
		Australia	Heron Island	1974-2011	Limpus CJ, Parmenter CJ, Chaloupka M (eds). 2013. *Monitoring of Coastal Sea Turtles: Gap Analysis 1. Loggerhead turtles, Caretta caretta, in the Port Curtis and Port Alma Region*. Report produced for the Ecosystem Research and Monitoring Program Advisory Panel as part of Gladstone Ports Corporation's Ecosystem Research and Monitoring Program.
		Australia	Sunshine coast	2006-2016	Golder Associates. 2017. *Turtle Impact Assessment Yaroomba Beach*. Report No. 1414745-002-R-Rev2. Hofmeister K, Twaddle H, O'Connor J, Limpus CJ, TurtleCare Sunshine Coast Volunteers, Coolum and North Shore Coast Care Volunteers. 2019. *Marine Turtle Nesting Populations: Sunshine Coast Region 2005 – 2016.* Caloundra: Sunshine Coast Council.
		Australia	Batemans Bay	1997-2000	Limpus CJ. 2008. *A biological review of Australian marine turtles. 1. Loggerhead turtle, Caretta caretta (Linneaus).* Queensland Environmental Protection Agency. Queensland, Australia.

Supplementary Table 2.3: Leatherback sea turtle Regional Management Units (Wallace et al. 2023)

Number	Regional Management Unit
A	Northwest Atlantic
B	Southwest Atlantic
C	Southeast Atlantic
D	Southwest Indian
E	Northeast Indian
F	West Pacific
G	East Pacific


A
Leatherback RMU –
Northwest Atlantic
North Carolina
1
Count
Year
Exponential model
AIC: 1.00E+20
-0.032
Florida
2
nests
Year
0.074
Breakpoint model
AIC: 382.259
0.118; -0.045 (2010)
Jaragua National Park
3
Count
Year
Exponential model
AIC: 85.698
0.411
Aruba
4
nests
Year
0.024
Breakpoint model
AIC: 166.9909479
0.176; -0.143 (2009)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
500 km


A
Leatherback RMU – Northwest Atlantic
Saona Island and Del Este National Park
5
Count
Year
Exponential model
AIC: 1.00E+20
0.754
Maunabo
6
Count
Year
Exponential model
AIC: 181.852
0.078
Luquillo-Fajardo
7
nests
Year
0.154
Breakpoint model
AIC: 330.855
0.261; -0.012 (2002)
Culebra
8
nests
Year
-0.04
Breakpoint model
AIC: 360.918
0.049; -0.14 (2003)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
500 km



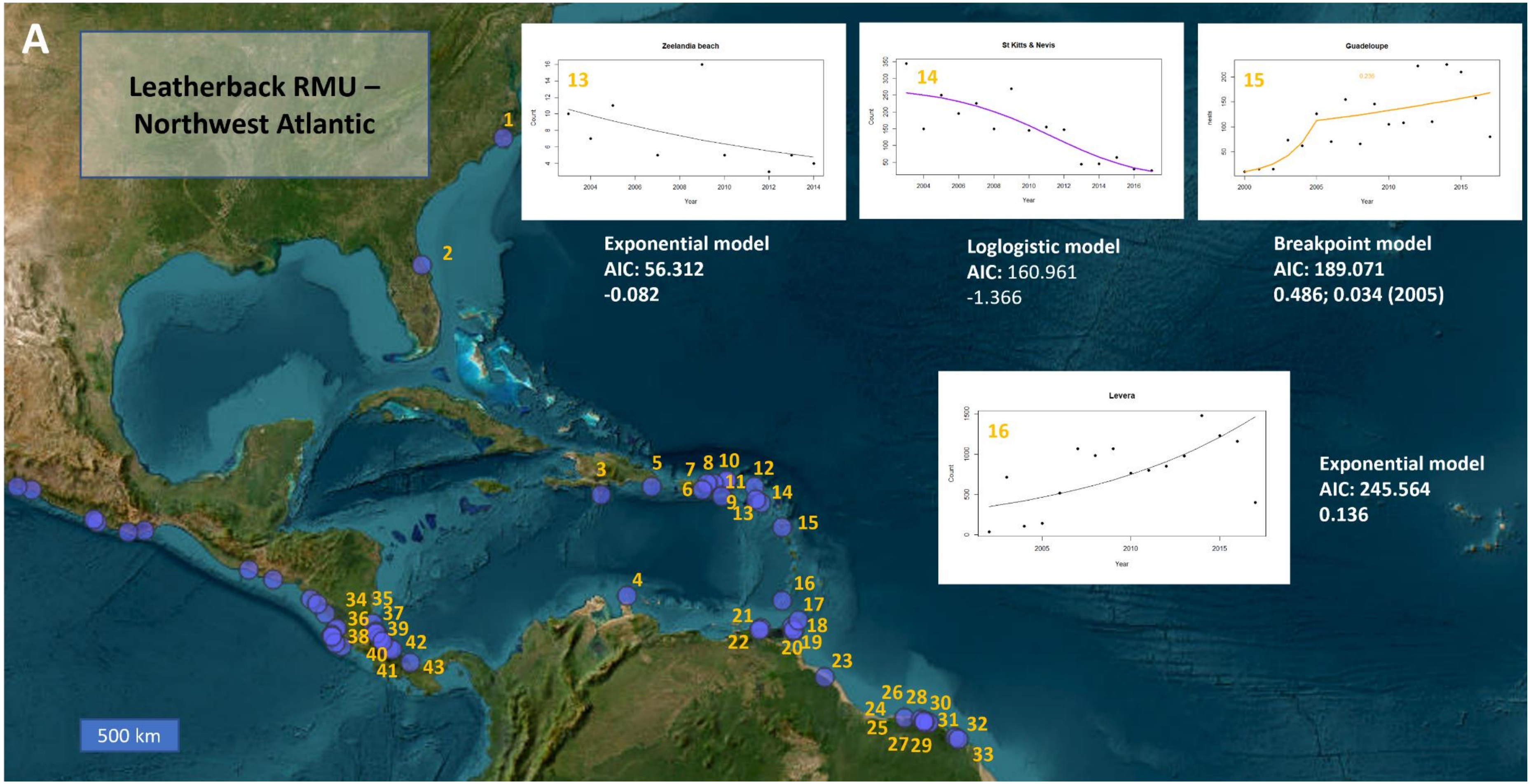
Leatherback RMU – Northwest Atlantic

Breakpoint model
AIC: 455.033
0.083; -0.159 (2007)

Breakpoint model
AIC: 145.6009559
0.159; -0.212 (2003)

Breakpoint model
AIC: 248.092
0.161; -0.08 (2003)

Exponential model
AIC: 55.859
-0.089



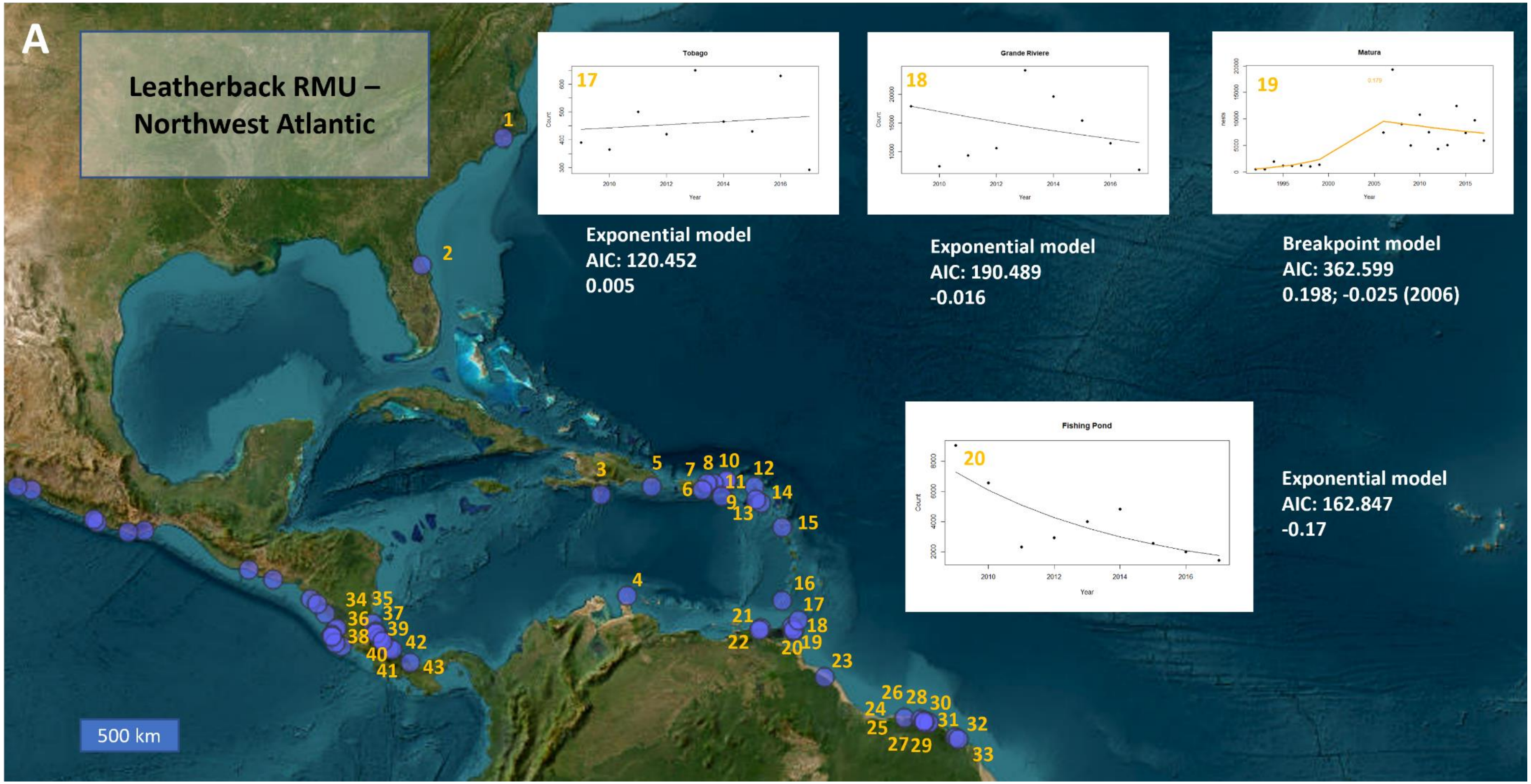
Leatherback RMU – Northwest Atlantic

Exponential model
AIC: 56.312
-0.082

Loglogistic model
AIC: 160.961
-1.366

Breakpoint model
AIC: 189.071
0.486; 0.034 (2005)

Exponential model
AIC: 245.564
0.136



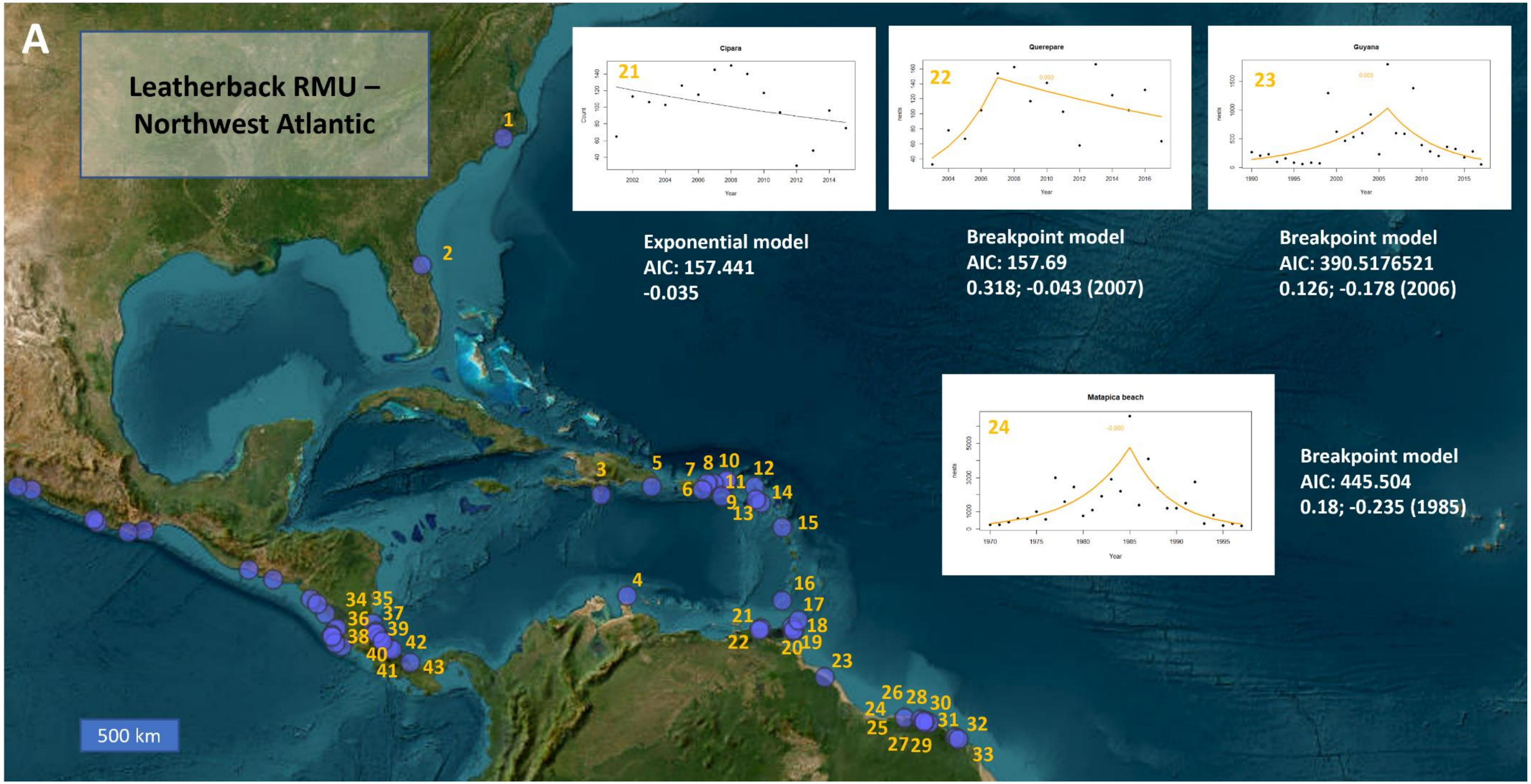
Leatherback RMU – Northwest Atlantic

Exponential model
AIC: 120.452
0.005

Exponential model
AIC: 190.489
-0.016

Breakpoint model
AIC: 362.599
0.198; -0.025 (2006)

Exponential model
AIC: 162.847
-0.17

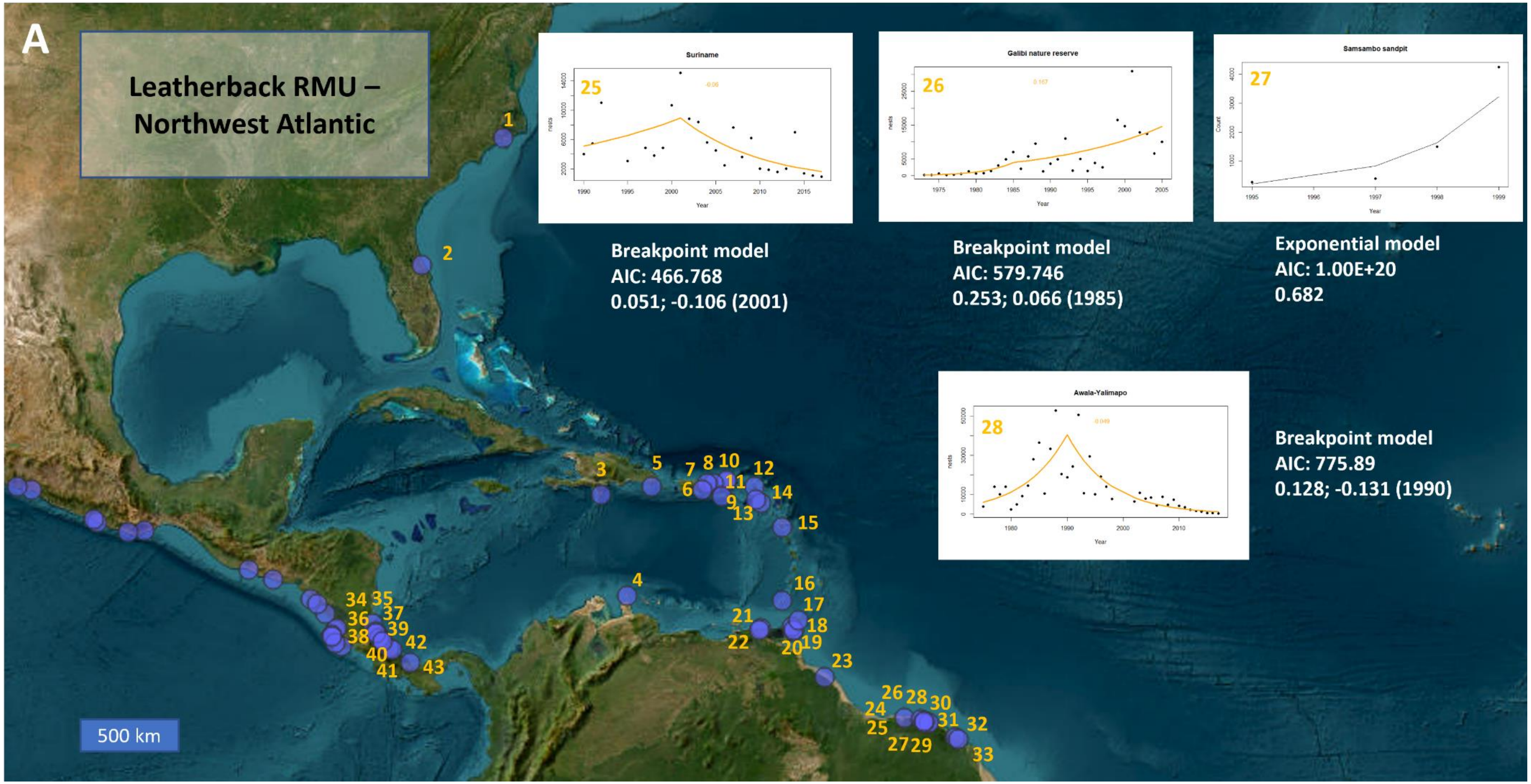


Exponential model
AIC: 157.441
-0.035

Breakpoint model
AIC: 157.69
0.318; -0.043 (2007)

Breakpoint model
AIC: 390.5176521
0.126; -0.178 (2006)

Breakpoint model
AIC: 445.504
0.18; -0.235 (1985)



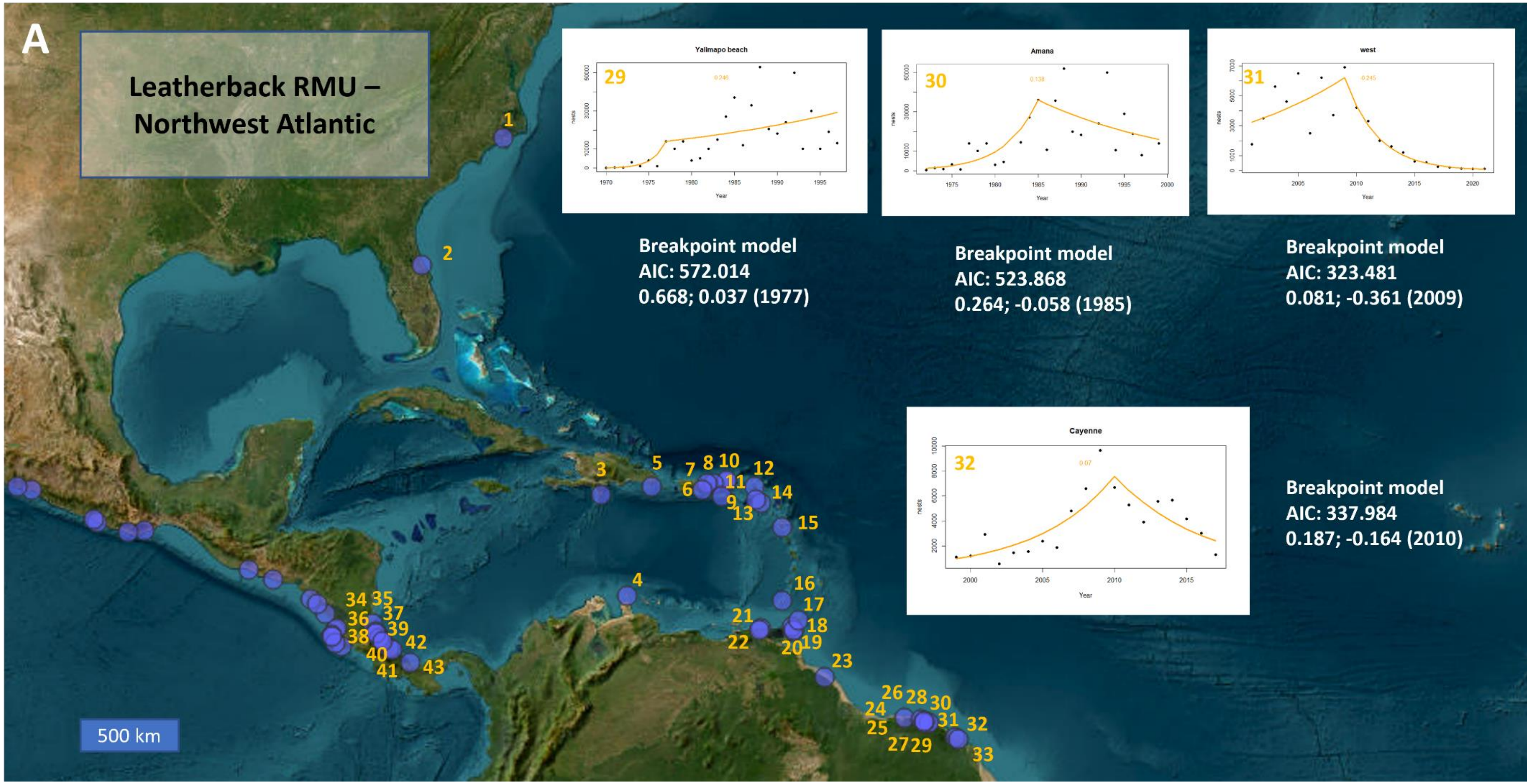
Leatherback RMU – Northwest Atlantic

Breakpoint model
AIC: 466.768
0.051; -0.106 (2001)

Breakpoint model
AIC: 579.746
0.253; 0.066 (1985)

Exponential model
AIC: 1.00E+20
0.682

Breakpoint model
AIC: 775.89
0.128; -0.131 (1990)

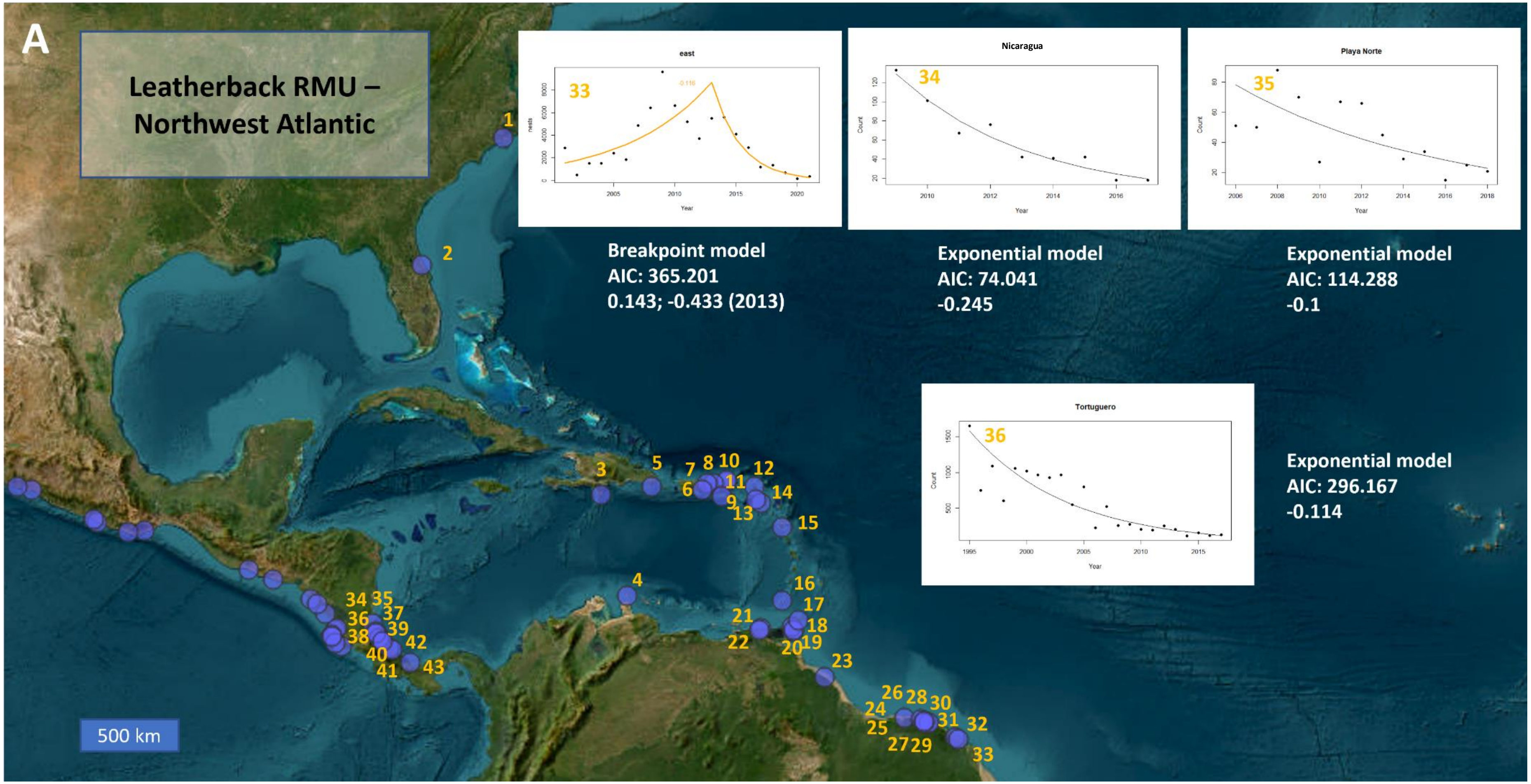


Breakpoint model
AIC: 572.014
0.668; 0.037 (1977)

Breakpoint model
AIC: 523.868
0.264; -0.058 (1985)

Breakpoint model
AIC: 323.481
0.081; -0.361 (2009)

Breakpoint model
AIC: 337.984
0.187; -0.164 (2010)



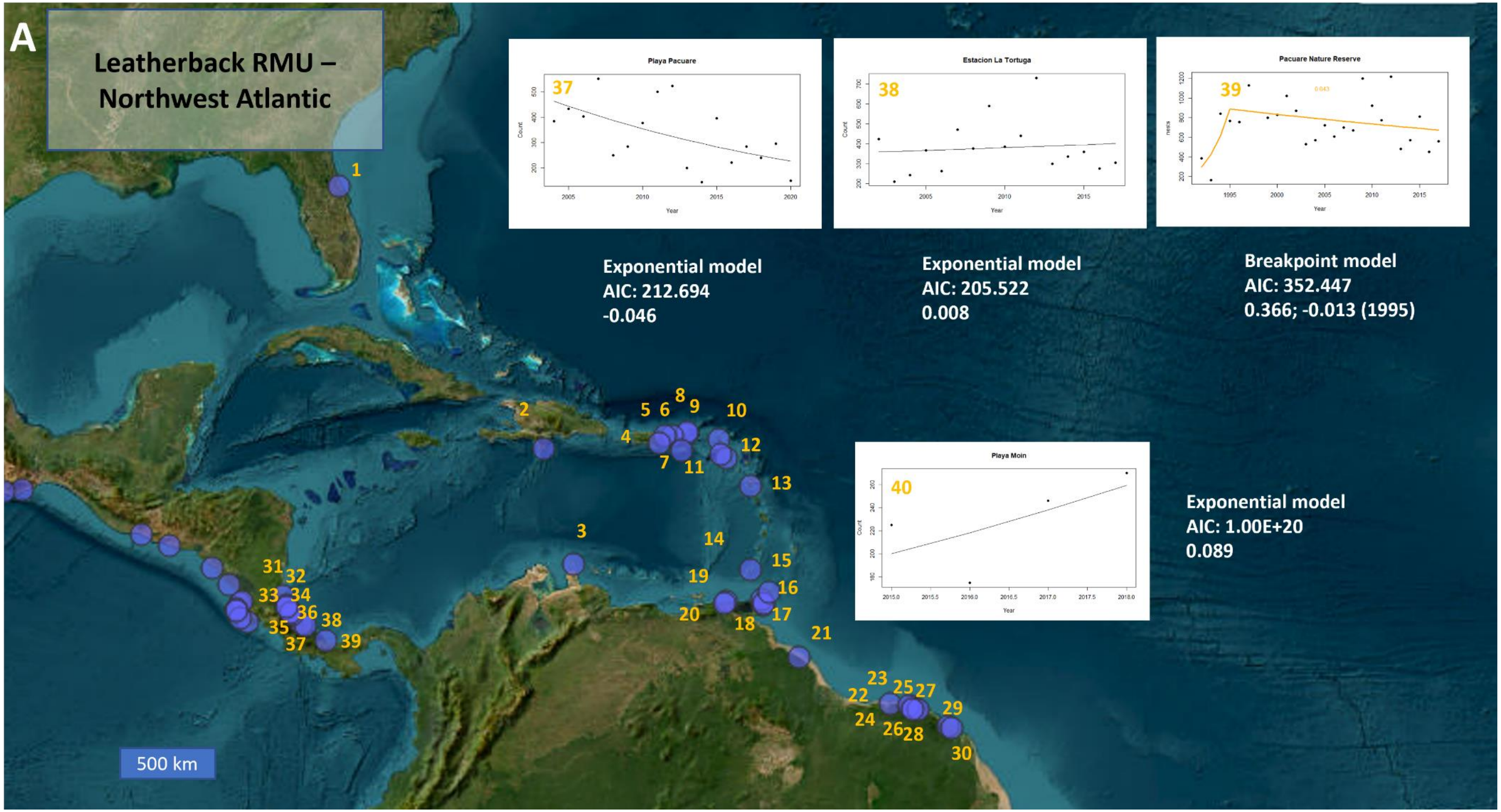
Leatherback RMU – Northwest Atlantic

Breakpoint model
AIC: 365.201
0.143; -0.433 (2013)

Exponential model
AIC: 74.041
-0.245

Exponential model
AIC: 114.288
-0.1

Exponential model
AIC: 296.167
-0.114

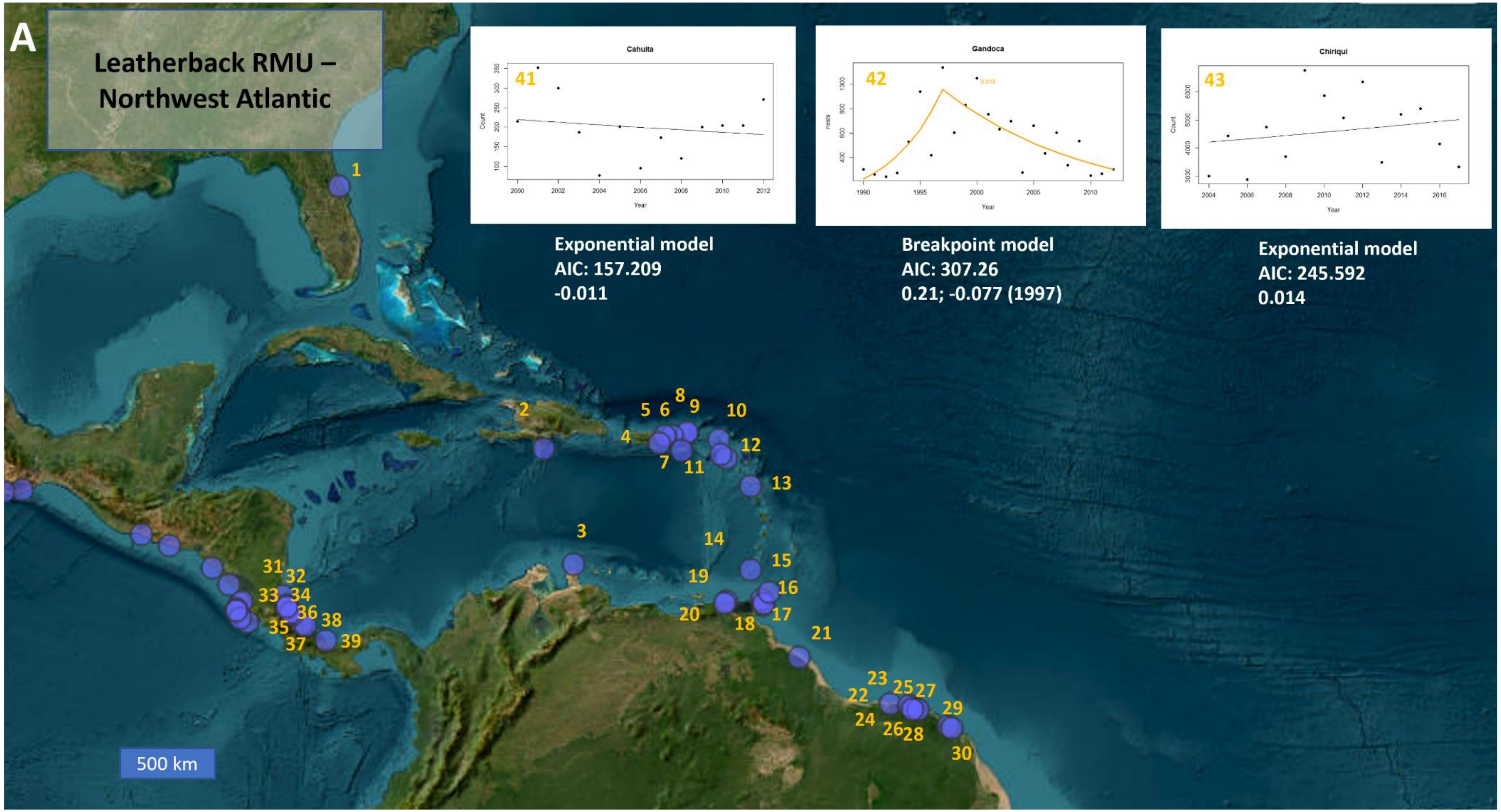


Exponential model
AIC: 212.694
-0.046

Exponential model
AIC: 205.522
0.008

Breakpoint model
AIC: 352.447
0.366; -0.013 (1995)

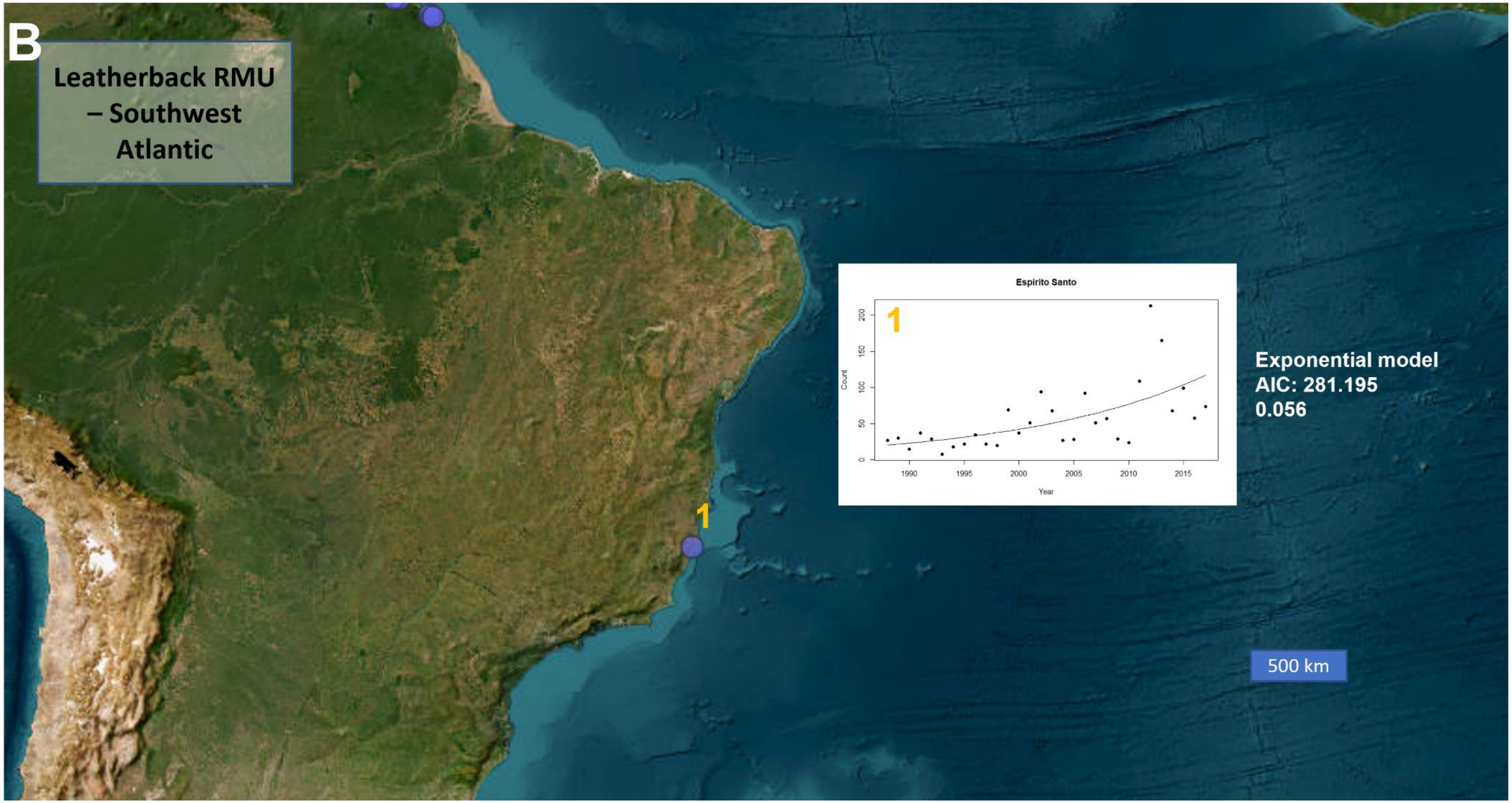
Exponential model
AIC: 1.00E+20
0.089

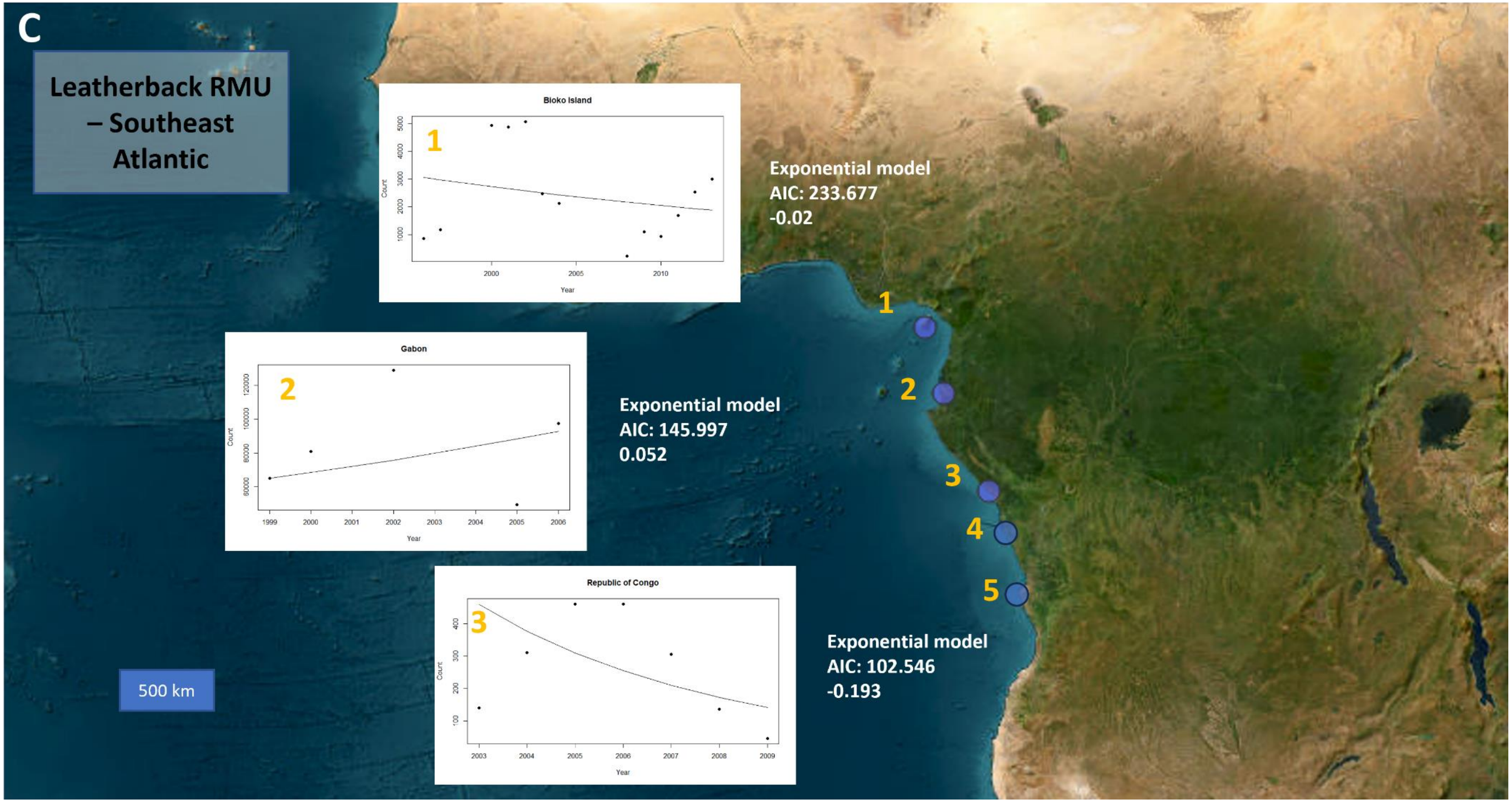


Exponential model
AIC: 157.209
-0.011

Breakpoint model
AIC: 307.26
0.21; -0.077 (1997)

Exponential model
AIC: 245.592
0.014


B
Leatherback RMU – Southwest Atlantic
1
Espirito Santo
1
0
50
100
150
200
Count
1990
1995
2000
2005
2010
2015
Year
Exponential model
AIC: 281.195
0.056
500 km

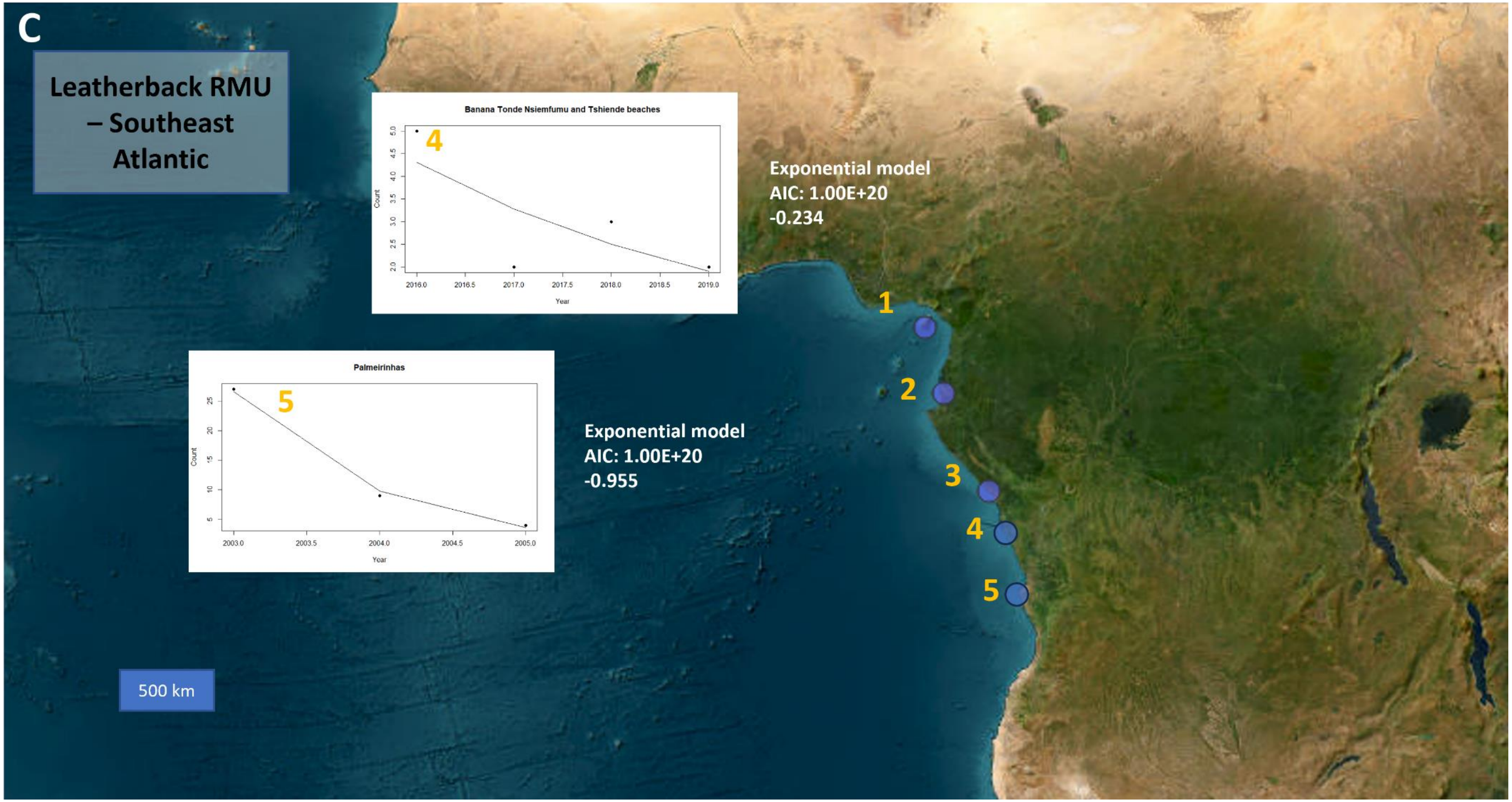


Leatherback RMU – Southeast Atlantic

Exponential model
AIC: 233.677
-0.02

Exponential model
AIC: 145.997
0.052

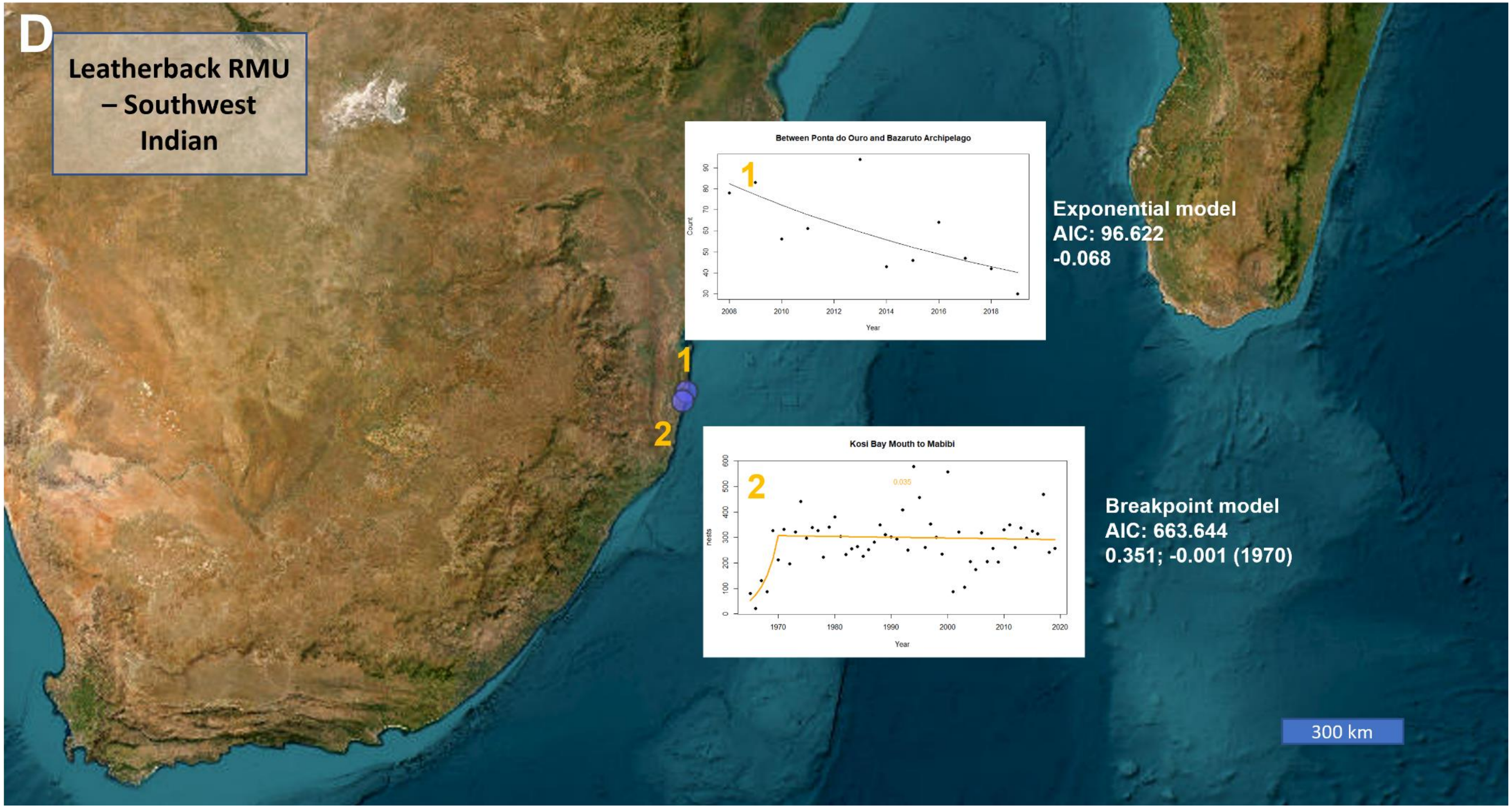
Exponential model
AIC: 102.546
-0.193

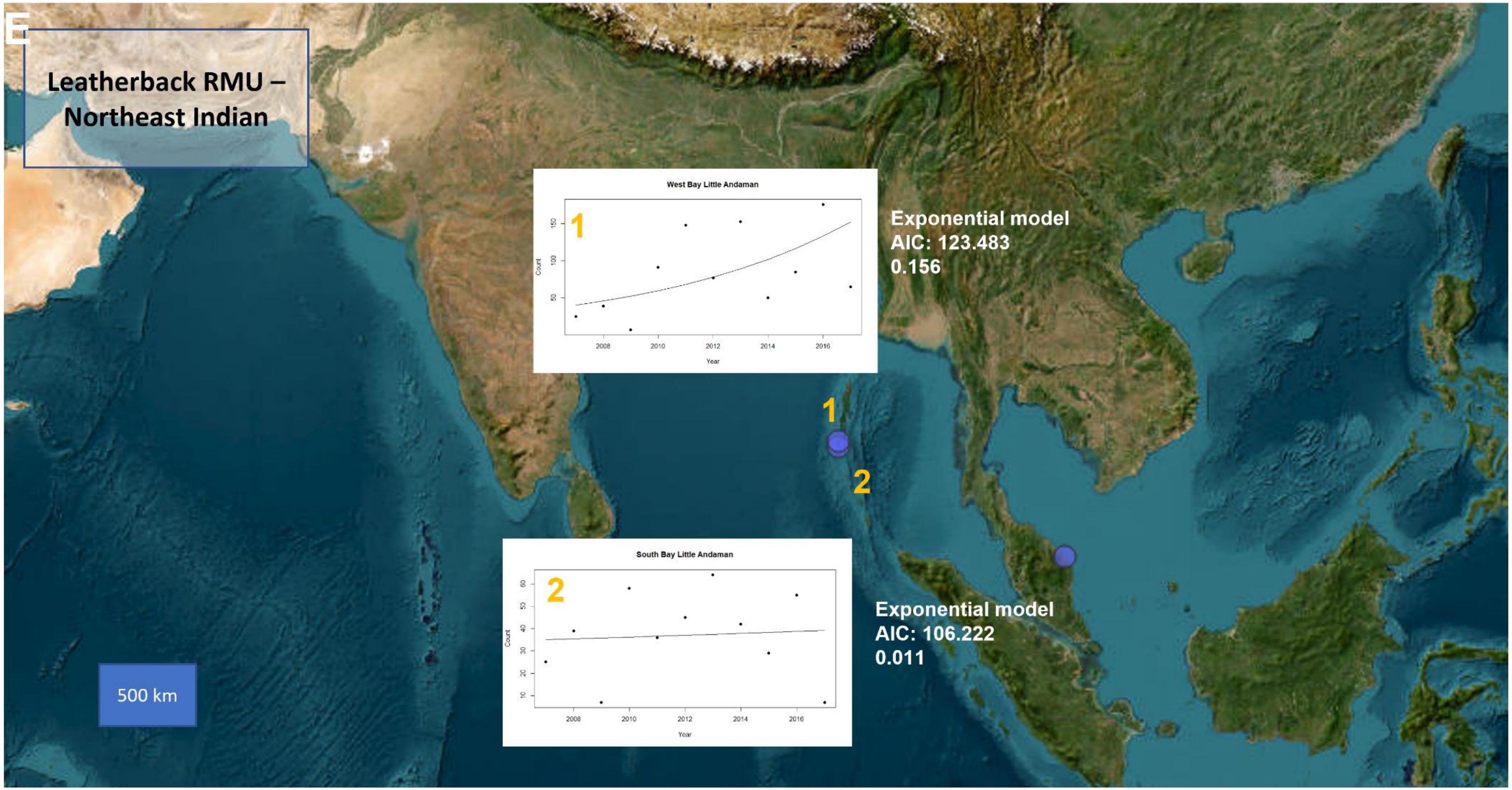


Leatherback RMU – Southeast Atlantic

Exponential model
AIC: 1.00E+20
-0.234

Exponential model
AIC: 1.00E+20
-0.955

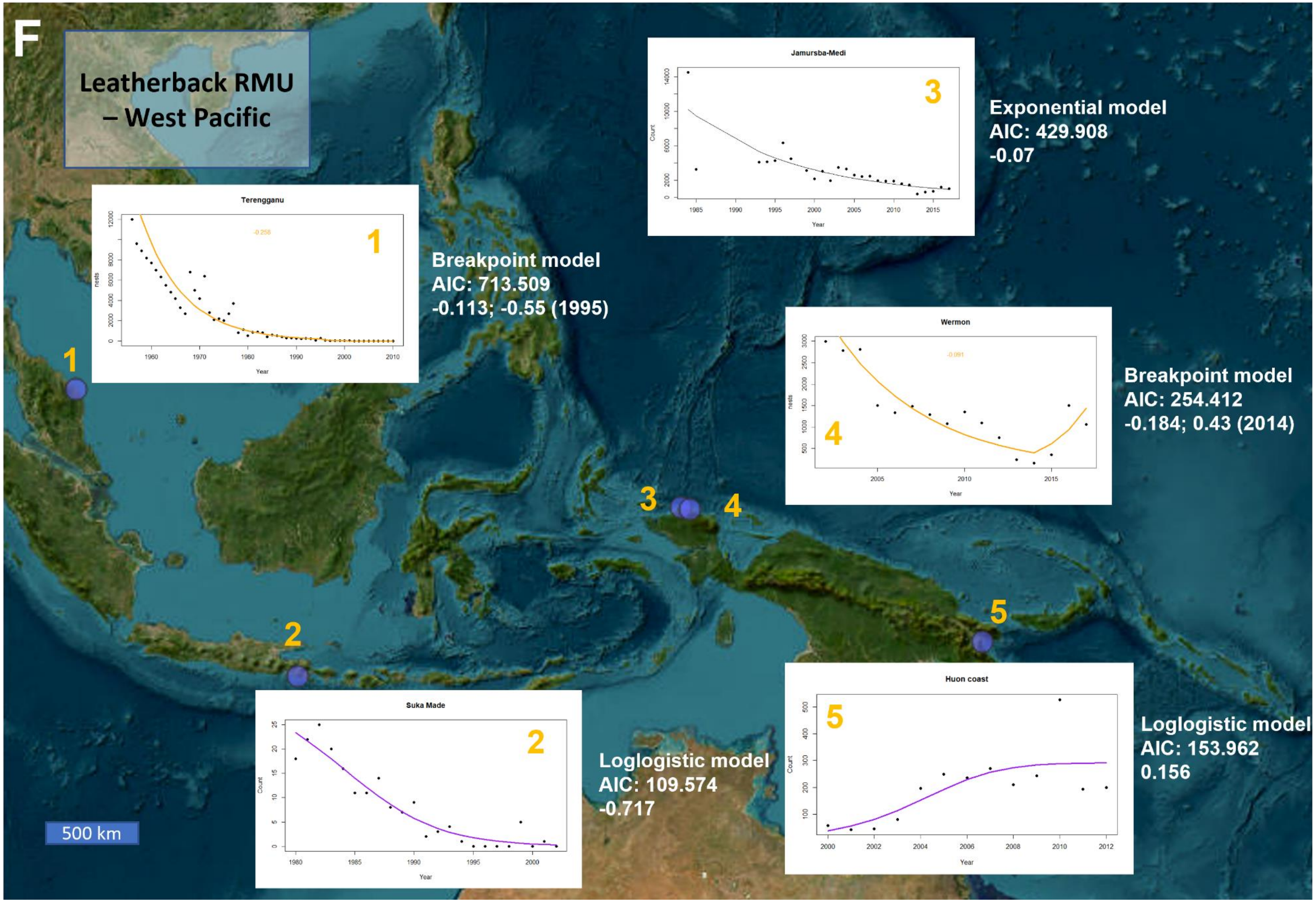
D
Leatherback RMU – Southwest Indian
Between Ponta do Ouro and Bazaruto Archipelago
1
Count
30
40
50
60
70
80
90
2008
2010
2012
2014
2016
2018
Year
Exponential model
AIC: 96.622
-0.068
1
2
Kosi Bay Mouth to Mabibi
2
0.035
nests
0
100
200
300
400
500
600
1970
1980
1990
2000
2010
2020
Year
Breakpoint model
AIC: 663.644
0.351; -0.001 (1970)
300 km

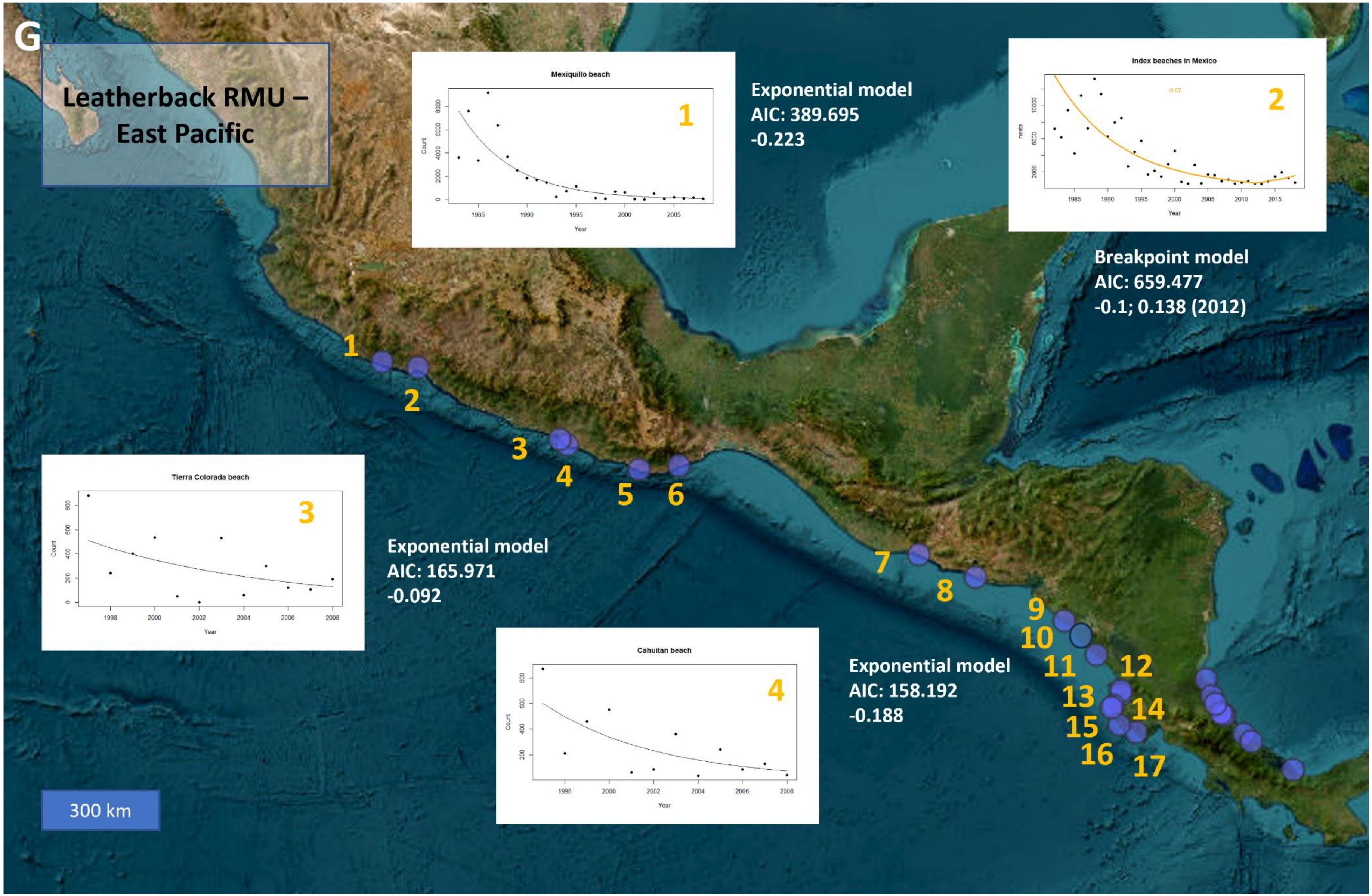


Leatherback RMU – Northeast Indian

Exponential model
AIC: 123.483
0.156

Exponential model
AIC: 106.222
0.011


F
Leatherback RMU – West Pacific
1
2
3
4
5
500 km
Terengganu
nests
Year
-0.258
1
Breakpoint model
AIC: 713.509
-0.113; -0.55 (1995)
Jamursba-Medi
Count
Year
3
Exponential model
AIC: 429.908
-0.07
Wermon
nests
Year
-0.091
4
Breakpoint model
AIC: 254.412
-0.184; 0.43 (2014)
Suka Made
Count
Year
2
Loglogistic model
AIC: 109.574
-0.717
Huon coast
Count
Year
5
Loglogistic model
AIC: 153.962
0.156



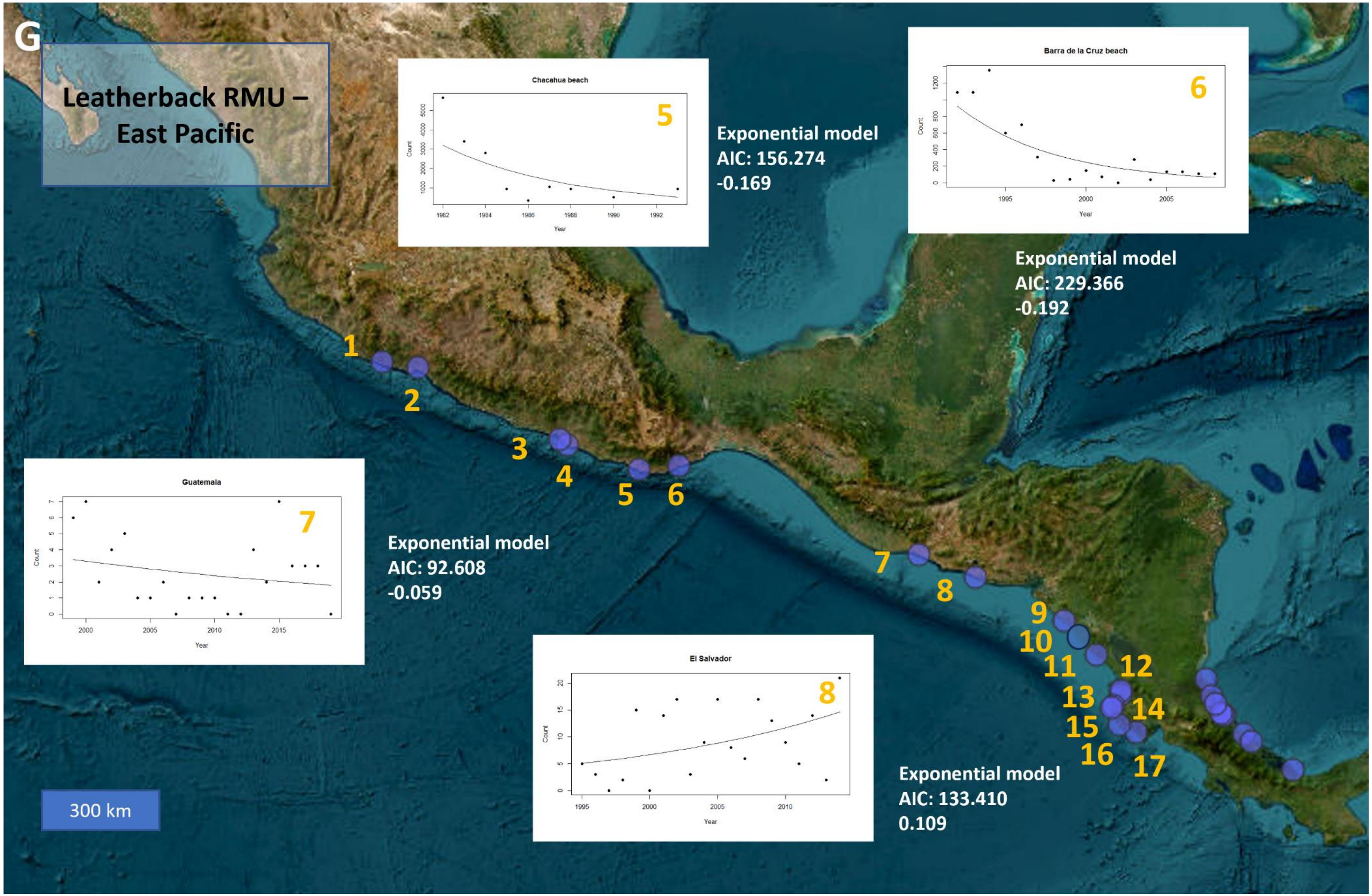
Leatherback RMU – East Pacific

Exponential model
AIC: 389.695
-0.223

Breakpoint model
AIC: 659.477
-0.1; 0.138 (2012)

Exponential model
AIC: 165.971
-0.092

Exponential model
AIC: 158.192
-0.188



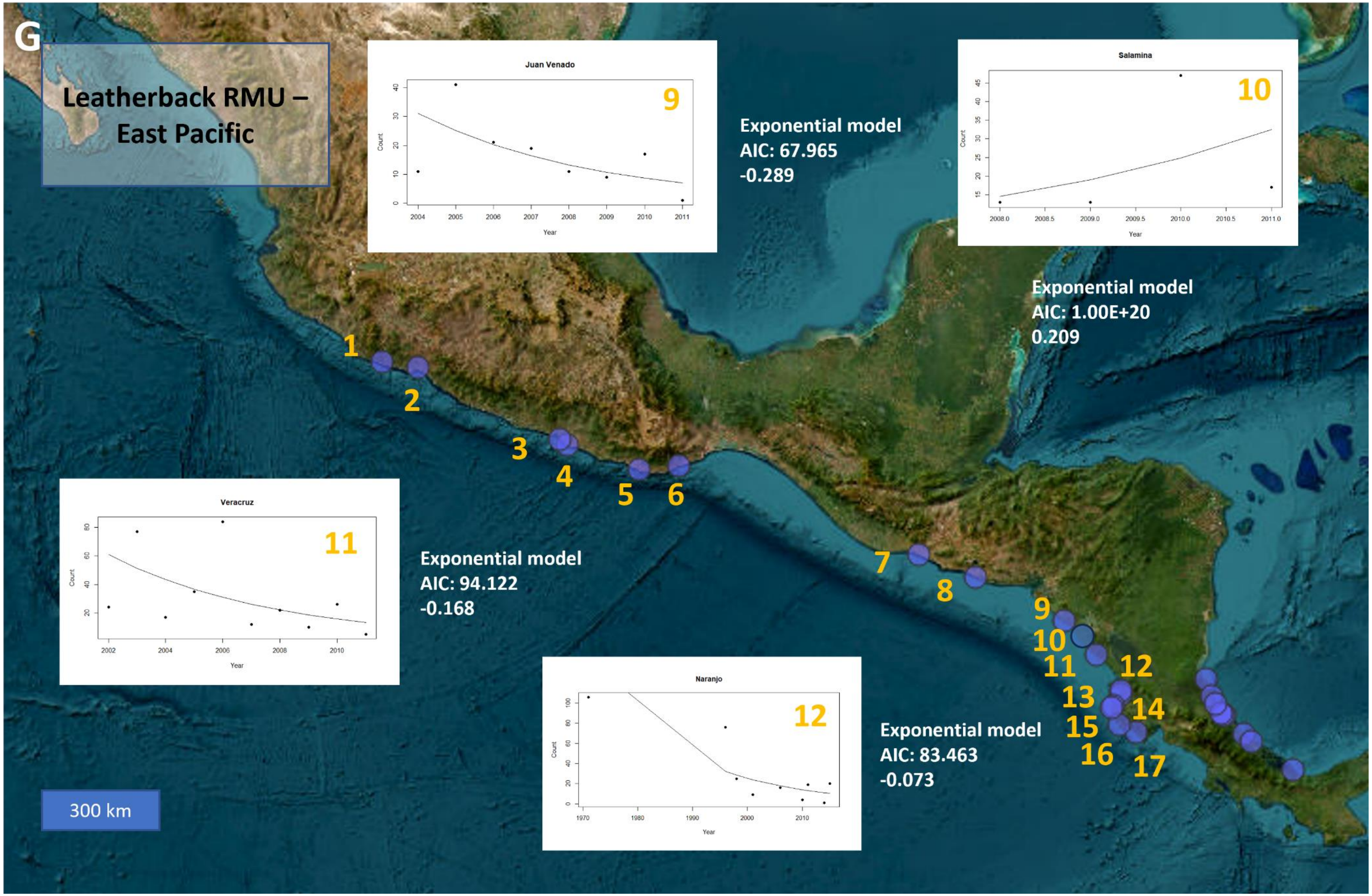
Leatherback RMU – East Pacific

Exponential model
AIC: 156.274
-0.169

Exponential model
AIC: 229.366
-0.192

Exponential model
AIC: 92.608
-0.059

Exponential model
AIC: 133.410
0.109



G

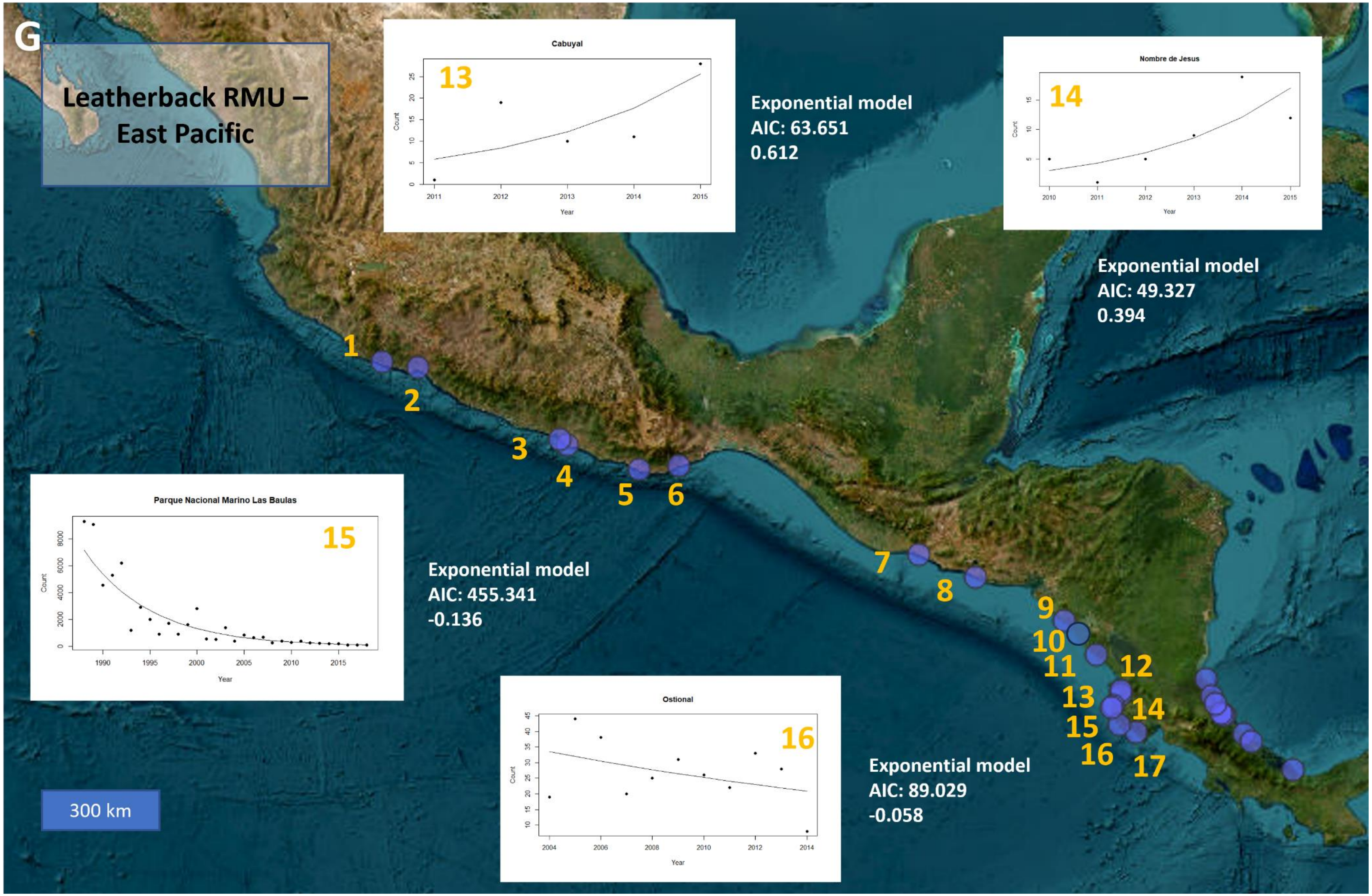
Leatherback RMU – East Pacific

Exponential model
AIC: 67.965
-0.289

Exponential model
AIC: 1.00E+20
0.209

Exponential model
AIC: 94.122
-0.168

Exponential model
AIC: 83.463
-0.073

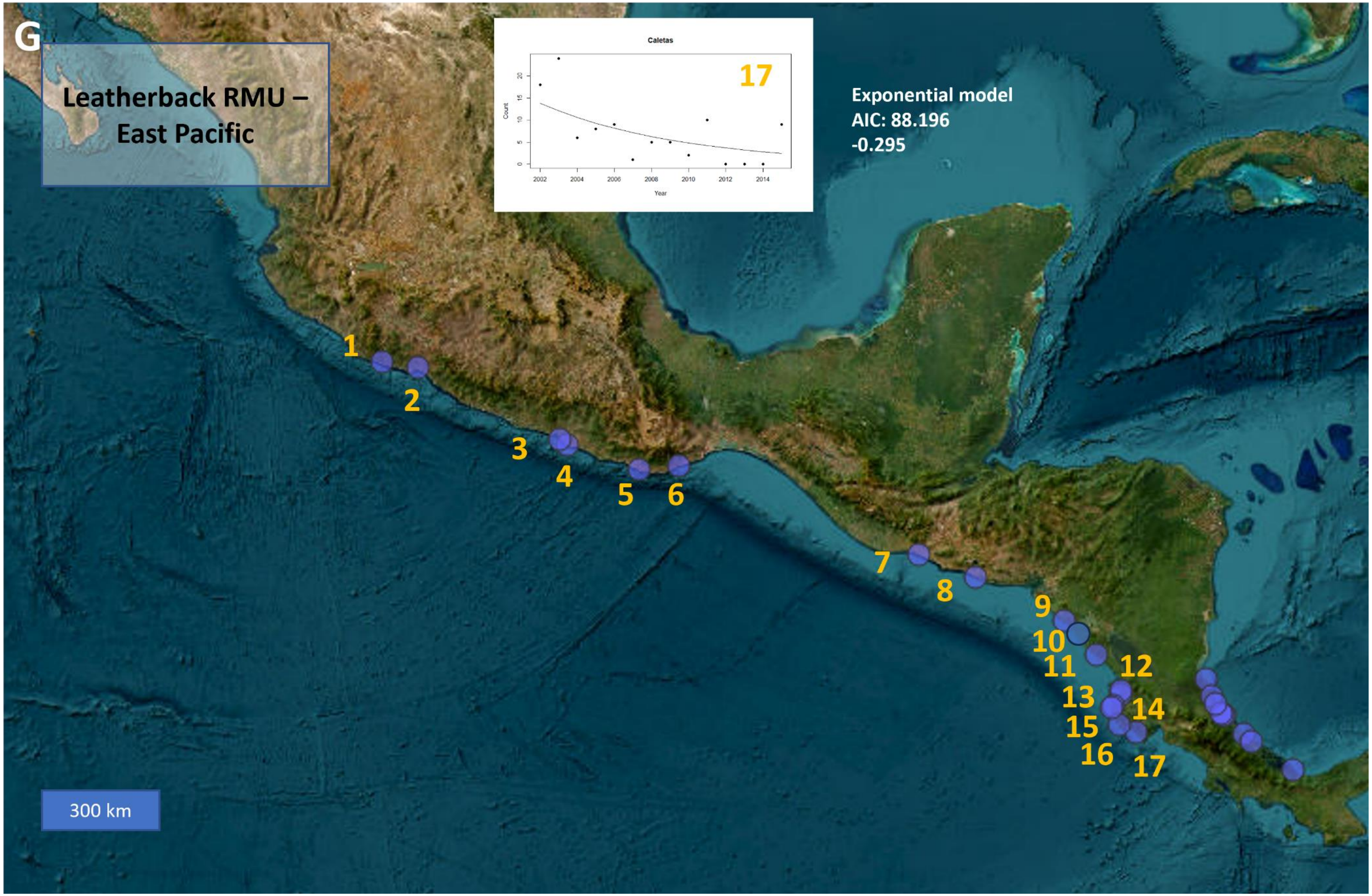


Exponential model
AIC: 63.651
0.612

Exponential model
AIC: 49.327
0.394

Exponential model
AIC: 455.341
-0.136

Exponential model
AIC: 89.029
-0.058


G
Leatherback RMU – East Pacific
Caletas
17
Count
0
5
10
15
20
2002
2004
2006
2008
2010
2012
2014
Year
Exponential model
AIC: 88.196
-0.295
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
300 km

Supplementary Figure 2.4: Leatherback sea turtle RMU and species-level trends in abundance over time: (A) Northwest Atlantic, (B) Southwest Atlantic, (C) Southeast Atlantic, (D) Southwest Indian, (E) Northeast Indian, (F) West Pacific and (G) East Pacific

Supplementary Table 2.4: List of leatherback sea turtle nesting sites within their respective RMUs, data availability and sources of data collection

	Regional Management Unit	Country/Region	Site	Data availability	Source(s)
A	Northwest Atlantic	United States	North Carolina	2009-2010; 2012; 2018	North Carolina WRC Sea Turtle Project. n.d. Sea turtle nest monitoring system. Available at http://seaturtle.org/nestdb/index.shtml?view=1&year=2018. [accessed 6 June 2022].
		United States	Florida	1989-2021	Florida Fish and Wildlife Conservation Commission. 2022. Index nesting beach survey totals (1989-2021). Available at https://myfwc.com/research/wildlife/sea-turtles/nesting/beach-survey-totals/#:~:text=Surveyors%20counted%20435%20leatherback%20nests,during%20the%202009%2D2015%20period. [accessed 6 June 2022]. Valdivia A, Wolf S, Suckling K. 2019. Marine mammals and sea turtles listed under the U.S. Endangered Species Act are recovering. *PLoS ONE*, 14: e0210164.
		Dominican Republic	Jaragua National Park	2006-2010	Revuelta O, León Y, Feliz P, Godley B, Raga J, Tomás J. 2012. Protected areas host important remnants of marine turtle nesting stocks in the Dominican Republic. *Oryx*, 46: 348-358.
		Aruba	Aruba	2001-2017	van der Wal S. 2018. *Aruba Update: Monitoring, Research and Telemetry*. WIDECAST Annual Meeting
		Dominican Republic	Saona Island and Del Este	2007-2010	Revuelta O, León Y, Feliz P, Godley B, Raga J, Tomás J. 2012. Protected areas host important remnants of marine turtle nesting stocks in the Dominican Republic. *Oryx*, 46: 348-358.

			National Park		
		Puerto Rico	Maunabo	1999; 2001-2007; 2009-2017	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle (Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Puerto Rico	Luquillo-Fajardo	1986-2017	Diez CE, Soler R, Olivera G, White A, Tallevast T, Young N, van Dam RP. 2010. Caribbean leatherbacks: results of nesting seasons from 1984-2008 at Culebra Island, Puerto Rico. *Marine Turtle Newsletter*, 127: 22-23. Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle (Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Puerto Rico	Culebra	1984-2000; 2003-2017	Diez CE, Soler R, Olivera G, White A, Tallevast T, Young N, van Dam RP. 2010. Caribbean leatherbacks: results of nesting seasons from 1984-2008 at Culebra Island, Puerto Rico. *Marine Turtle Newsletter*, 127: 22-23. Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle (Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		United States	Sandy Point National Wildlife Refuge	1982-2017	Valdivia A, Wolf S, Suckling K. 2019. Marine mammals and sea turtles listed under the U.S. Endangered Species Act are recovering. *PLoS ONE*, 14: e0210164.

		British Virgin Islands	British Virgin Islands	1986-1988; 1990-2006	McGowan A, Broderick AC, Frett G, Gore S, Hastings M, Pickering A, Wheatley D, White J, Witt M, Godley B. 2008. Down but not out: marine turtles of the British Virgin Islands. *Animal Conservation*, 11: 92-103.
		British Virgin Islands	BVI Archipelago	1986-2017	McGowan A, Broderick AC, Frett G, Gore S, Hastings M, Pickering A, Wheatley D, White J, Witt M, Godley B. 2008. Down but not out: marine turtles of the British Virgin Islands. *Animal Conservation*, 11: 92-103. Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle (Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Anguilla	Anguilla	1998; 2000-2001; 2003; 2016-2018	Godley B, Broderick A, Campbell L, Ranger S, Richardson P (eds). 2004. *An Assessment of the Status and Exploitation of Marine Turtles in Anguilla*. Final Project Report for the Department of Environment, Food and Rural Affairs and the Foreign and Commonwealth Office. Soanes LM, Johnson J, Eckert K, Gumbs K, Halsey LG, Hughes G, Levasseur K, Quattro J, Richardson R, Skinner JP, Wynne S, Mukhida F. 2022. Saving the sea turtles of Anguilla: combining scientific data with community perspectives to inform policy decisions. *Biological Conservation*, 268: 109493.
		St. Eustatius	Zeelandia beach	2003-2005; 2007; 2009-2010; 2012-2014	Berkel J (ed). 2009. *St. Eustatius National Parks Foundation Sea Turtle Conservation Program Annual Report 2009*. St Eustatius National Parks Foundation (STENAPA) Gallows Bay, St Eustatius, Netherlands Antilles Berkel J (ed). 2010. St. Eustatius National Parks Foundation Sea Turtle Conservation Program Annual Report 2010. St Eustatius National Parks Foundation (STENAPA) Gallows Bay, St Eustatius, Netherlands Antilles

					Berkel J (ed). 2012. St. Eustatius National Parks Foundation Sea Turtle Conservation Program Annual Report 2012. St Eustatius National Parks Foundation (STENAPA) Gallows Bay, St Eustatius, Netherlands Antilles Berkel J (ed). 2013. St. Eustatius National Parks Foundation Sea Turtle Conservation Program Annual Report 2013. St Eustatius National Parks Foundation (STENAPA) Gallows Bay, St Eustatius, Netherlands Antilles Berkel J (ed). 2014. St. Eustatius National Parks Foundation Sea Turtle Conservation Program Annual Report 2014. St Eustatius National Parks Foundation (STENAPA) Gallows Bay, St Eustatius, Netherlands Antilles Harrison E (ed). 2005. St Eustatius Sea Turtle Conservation Programme Annual Report 2005. St Eustatius National Parks Foundation (STENAPA) Gallows Bay, St Eustatius, Netherlands Antilles Herrera A (ed). 2007. St Eustatius Sea Turtle Conservation Programme Annual Report 2007. St Eustatius National Parks Foundation (STENAPA) Gallows Bay, St Eustatius, Netherlands Antilles Le scao R, Esteban N (eds). 2003. *St Eustatius Sea Turtle Monitoring Programme Annual Report, 2003*. St Eustatius National Parks Foundation (STENAPA) Gallows Bay, St Eustatius, Netherlands Antilles. Le scao R, Esteban N (eds). 2004. *St Eustatius Sea Turtle Monitoring Programme Annual Report, 2004*. St Eustatius National Parks Foundation (STENAPA) Gallows Bay, St Eustatius, Netherlands Antilles.
		St Kitts	St Kitts & Nevis	2003-2017	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle*

					(Dermochelys coriacea) Status Assessment. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Guadeloupe	Guadeloupe	2000-2017	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle* *(Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Grenada	Levera	2002-2017	Buckmire T, Spirits O, Foundation Y-K (eds). 2012. *Sea Turtle Conservation in Grenada*. WIDECAST Annual General Meeting. Yucatan, Mexico. Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle* *(Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Tobago	Tobago	2009-2017	United States National Marine Fisheries Service, U.S. Fish and Wildlife Service. 2020. Endangered Species Act status review of the leatherback turtle (*Dermochelys coriacea*) 2020. Available at https://repository.library.noaa.gov/view/noaa/25629 [accessed 5 June 2022].
		Trinidad and Tobago	Grande Riviere	2009-2017	United States National Marine Fisheries Service, U.S. Fish and Wildlife Service. 2020. Endangered Species Act status review of the leatherback turtle (*Dermochelys coriacea*) 2020. Available at https://repository.library.noaa.gov/view/noaa/25629 [accessed 5 June 2022].
		Trinidad and Tobago	Matura	1992-1999; 2006-2017	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle*

					(Dermochelys coriacea) Status Assessment. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois. Turtle Expert Working Group (ed). 2007. *An assessment of the leatherback turtle population in the Atlantic ocean*. NOAA Technical Memorandum NMFS-SEFSC-555. Miami, Florida.
		Trinidad and Tobago	Fishing Pond	2009-2017	United States National Marine Fisheries Service, U.S. Fish and Wildlife Service. 2020. Endangered Species Act status review of the leatherback turtle (*Dermochelys coriacea*) 2020. Available at https://repository.library.noaa.gov/view/noaa/25629 [accessed 5 June 2022].
		Venezuela	Cipara	2001-2015	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle (Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Venezuela	Querepare	2003-2017	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle (Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Guyana	Guyana	1990-2017	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle (Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Suriname	Matapica beach	1970-1997	Chevalier J, Girondot M (eds). 1998. *Marine turtles identification in French Guiana : why, where and how ?*
		Guianas/Trinidad	Suriname	1990-1992;	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle*

				1995; 1997-2017	*(Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Suriname	Galibi nature reserve	1973-1997; 1999-2005	Chevalier J, Girondot M (eds). 1998. *Marine turtles identification in French Guiana : why, where and how ?* Hilterman M, Goverse E. 2007. Nesting and nest success of the leatherback turtle (*Dermochelys coriacea*) in Suriname, 1999-2005. *Chelonian Conservation and Biology*, 6: 87-100.
		Suriname	Samsambo sandpit	1995; 1997-1999	Hilterman ML. 2001. *The sea turtles of Suriname, 2000*. Guianas Forests and Environmental Conservation Project (GFECP). World Wildlife Fund Guianas/Biotopic Foundation Technical Report. Amsterdam, Netherlands. Hilterman ML and Goverse E. 2002. *Aspects of nesting and nest success of the leatherback turtle (Dermochelys coriacea) in Suriname, 2001*. Guianas Forests and Environmental Conservation Project (GFECP). World Wildlife Fund Guianas/Biotopic Foundation Technical Report. Amsterdam, Netherlands. Hilterman ML and Goverse E. 2003. *Aspects of nesting and nest success of the leatherback turtle (Dermochelys coriacea) in Suriname, 2002*. Guianas Forests and Environmental Conservation Project (GFECP). World Wildlife Fund Guianas/Biotopic Foundation Technical Report. Amsterdam, Netherlands. Hilterman ML and Goverse E. 2004. *Annual report on the 2003 leatherback turtle research and monitoring project in Suriname*. World Wildlife Fund - Guianas Forests and Environmental Conservation Project (WWF-GFECP). Netherlands Committee for IUCN (NC-IUCN) Technical Report. Amsterdam, Netherlands.

					Hilterman ML and Goverse E. 2005. *Annual report on the 2004 leatherback turtle research and monitoring project in Suriname*. World Wildlife Fund - Guianas Forests and Environmental Conservation Project (WWF-GFECP). Netherlands Committee for IUCN (NC-IUCN) Technical Report. Amsterdam, Netherlands. Hilterman ML and Goverse E. 2006. *Annual report on the 2005 leatherback turtle research and monitoring project in Suriname*. World Wildlife Fund - Guianas Forests and Environmental Conservation Project (WWF-GFECP). Netherlands Committee for IUCN (NC-IUCN) Technical Report. Amsterdam, Netherlands. Hilterman ML and Goverse E. 2007. Nesting and nest success of the leatherback turtle (Dermochelys coriacea) in Suriname, 1999-2005. *Chelonian Conservation and Biology*, 6: 87-100. Turtle Expert Working Group (ed). 2007. *An assessment of the leatherback turtle population in the Atlantic ocean*. NOAA Technical Memorandum NMFS-SEFSC-555. Miami, Florida.
		French Guiana	Awala-Yalimapo	1975; 1977-1998; 2002-2017	Chevalier J, Girondot M (eds). 1998. *Marine turtles identification in French Guiana : why, where and how ?* Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle (Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		French Guiana	Yalimapo beach	1970-1997	Chevalier J, Girondot M (eds). 1998. *Marine turtles identification in french guiana : why, where and how ?*
		French Guiana	Amana	1972-1981; 1983-	

				1990; 1992-1997; 1999	Hilterman ML, Swinkels JL, Hoekert WEJ, van Teinen LHG. 2002. *The leatherback on the move? Promising news from Suriname*. NOAA Technical Memorandum NMFS-SEFSC 477: 138-139. Orlando, Florida. Hilterman ML. 2001. *The sea turtles of Suriname, 2000*. Guianas Forests and Environmental Conservation Project (GFECP). World Wildlife Fund Guianas/Biotopic Foundation Technical Report. Amsterdam, Netherlands. Hilterman ML and Goverse E. 2002. *Aspects of nesting and nest success of the leatherback turtle (Dermochelys coriacea) in Suriname, 2001*. Guianas Forests and Environmental Conservation Project (GFECP). World Wildlife Fund Guianas/Biotopic Foundation Technical Report. Amsterdam, Netherlands. Hilterman ML and Goverse E. 2003. *Aspects of nesting and nest success of the leatherback turtle (Dermochelys coriacea) in Suriname, 2002*. Guianas Forests and Environmental Conservation Project (GFECP). World Wildlife Fund Guianas/Biotopic Foundation Technical Report. Amsterdam, Netherlands. Hilterman ML and Goverse E. 2004. *Annual report on the 2003 leatherback turtle research and monitoring project in Suriname*. World Wildlife Fund - Guianas Forests and Environmental Conservation Project (WWF-GFECP). Netherlands Committee for IUCN (NC-IUCN) Technical Report. Amsterdam, Netherlands. Hilterman ML and Goverse E. 2005. *Annual report on the 2004 leatherback turtle research and monitoring project in Suriname*. World Wildlife Fund - Guianas Forests and Environmental Conservation Project (WWF-GFECP). Netherlands Committee for IUCN (NC-IUCN) Technical Report. Amsterdam, Netherlands. Hilterman ML and Goverse E. 2006. *Annual report on the 2005 leatherback turtle research and monitoring project in Suriname*. World Wildlife Fund - Guianas Forests

					and Environmental Conservation Project (WWF-GFECP). Netherlands Committee for IUCN (NC-IUCN) Technical Report. Amsterdam, Netherlands. Hilterman ML and Goverse E. 2007. Nesting and nest success of the leatherback turtle (Dermochelys coriacea) in Suriname, 1999-2005. *Chelonian Conservation and Biology*, 6: 87-100. Turtle Expert Working Group (ed). 2007. *An assessment of the leatherback turtle population in the Atlantic ocean*. NOAA Technical Memorandum NMFS-SEFSC-555. Miami, Florida.
		French Guiana	Western beaches	2001-2021	Nalovic MA, Kelle L, Chevalier A, de Thoisy B, Lasfargue M, Wongsopawiro R, Chevallier D (eds). 2022. *Why are French Guiana leatherbacks declining?* SWOT The State of the World’s Sea Turtles report. Ross, California, United States.
		French Guiana	Cayenne	1999-2017	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle (Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		French Guiana	Eastern beaches	2001-2021	Nalovic MA, Kelle L, Chevalier A, de Thoisy B, Lasfargue M, Wongsopawiro R, Chevallier D (eds). 2022. *Why are French Guiana leatherbacks declining?* SWOT The State of the World’s Sea Turtles report. Ross, California, United States.
		Nicaragua	Nicaragua	2009-2017	United States National Marine Fisheries Service, U.S. Fish and Wildlife Service. 2020. Endangered Species Act status review of the leatherback turtle (*Dermochelys coriacea*) 2020. Available at https://repository.library.noaa.gov/view/noaa/25629 [accessed 5 June 2022].
		Mexico	Playa Norte	2006-2018	Allison N (ed). 2018. *Marine Turtle Monitoring and Tagging Program Leatherback Season Report*. Caño Palma Biological Station. Canadian Organisation for Tropical Education and Rainforest Conservation. Playa Norte, Costa Rica.
		Costa Rica	Tortuguero	1995-2017	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle*

					(Dermochelys coriacea) Status Assessment. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Costa Rica	Playa Pacuare	2004-2020	Altamirano Urbina E, Chacón-Chaverri D (eds). 2020. *Anidación de tortugas marinasBarra Norte de Pacuare, Costa RicaInforme Final*. Tibás, San José, Costa Rica. Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle (Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Costa Rica	Estacion La Tortuga	2002-2017	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle (Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Costa Rica	Pacuare Nature Reserve	1992-1997; 1999-2017	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle (Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois. United States National Marine Fisheries Service, U.S. Fish and Wildlife Service. 2020. Endangered Species Act status review of the leatherback turtle (*Dermochelys coriacea*) 2020. Available at https://repository.library.noaa.gov/view/noaa/25629 [accessed 5 June 2022].
		Costa Rica	Playa Moin	2015-2018	Anon. 2018. *Informe de la anidacion de tortugas marinas en Playa Moin, Costa Rica (Temporada 2018)*.
		Costa Rica	Cahuita	2000-2012	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle*

					(Dermochelys coriacea) Status Assessment. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Costa Rica	Gandoca	1990-2012	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle* *(Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
		Panama	Chiriqui	2004-2017	Northwest Atlantic Leatherback Working Group (ed). 2018. *Northwest Atlantic Leatherback Turtle* *(Dermochelys coriacea) Status Assessment*. Conservation Science Partners and the Wider Caribbean Sea Turtle Conservation Network (WIDECAST). WIDECAST Technical Report No. 16. Godfrey, Illinois.
B	Southwest Atlantic	Brazil	Espirito Santo	1988-2017	Colman L, Thomé J, Almeida A, Baptistotte C, Barata PCR, Broderick AC, Ribeiro FA, Vila-Verde L, Godley B. 2019. Thirty years of leatherback turtle *Dermochelys coriacea* nesting in Espírito Santo, Brazil, 1988–2017: reproductive biology and conservation. *Endangered Species Research*, 39: 147-158. Thomé J, Baptistotte C, Moreira L, Scalfoni J, Almeida A, Rieth D, Barata P. 2009. Nesting biology and conservation of the leatherback sea turtle (*Dermochelys coriacea*) in the State of Espírito Santo, Brazil, 1988–1989 to 2003–2004. *Chelonian Conservation and Biology*, 6: 15-27.
C	Southeast Atlantic	Equatorial Guinea	Bioko Island	1996-1997; 2000-2004; 2008-2013	Honarvar S, Fitzgerald DB, Weitzman CL, Sinclair EM, Echube JME, O'Connor M, Hearn GW. 2016. Assessment of important marine turtle nesting populations on the southern coast of Bioko Island, Equatorial Guinea. *Chelonian Conservation and Biology*, 15: 79-89, 11. Rader H, Mba MAE, Morra W, Hearn G. Marine turtles on the southern coast of Bioko Island (Gulf of Guinea, Africa), 2001-2005. *Marine Turtle Newsletter*, 111: 8-10.

					Tomás J, Castroviejo J, Raga JA. 1999. Sea turtles in the south of Bioko Island (Equatorial Guinea). *Marine Turtle Newsletter*, 84: 4-6.
		Gabon	Gabon	1999-2000; 2002; 2005-2006	Witt MJ, Baert B, Broderick AC, Formia A, Fretey J, Gibudi A, Mounguengui GAM, Moussounda C, Ngouessono S, Parnell RJ, Roumet D, Sounguet G-P, Verhage B, Zogo A, Godley BJ. 2009. Aerial surveying of the world's largest leatherback turtle rookery: a more effective methodology for large-scale monitoring. *Biological Conservation*, 142: 1719-1727.
		Congo	Republic of Congo	2003-2009	Doyle TK, Georges J-Y, Houghton JDR. 2013. A leatherback turtle's guide to jellyfish in the North East Atlantic. *Munibe Monographs. Nature Series*, 1: 15-21. Girard A, Breheret N. 2013. The Renatura sea turtle conservation program in Congo. *Munibe Monographs, Nature Series*, 1: 65-69. Zaldua-Mendizabal N, Egaña-Callejo A. 2012. *Marine turtles of the North East Atlantic. Contributions for the First Regional Conference. Munibe Monographs*. Nature Series 1. Aranzadi Society of Sciences. San Sebastian.
		Congo	Banana, Tonde, Nsiemfumu and Tshiende beaches	2016-2019	Kouerey Oliwina CK, Honarvar S, Girard A, Casale P (eds). 2020. *Sea Turtles in the West Africa/East Atlantic Region. MTSG Annual Regional Report 2020*. Report of the IUCN-SSC Marine Turtle Specialist Group, 2020.
		Angola	Palmeirinhas	2003-2005	Weir CR, Ron T, Morais M, Duarte ADC. 2007. Nesting and at-sea distribution of marine turtles in Angola, West Africa, 2000–2006: occurrence, threats and conservation implications. *Oryx*, 41: 224-231.

D	Southwest Indian	Mozambique	Ponta do Ouro to Bazaruto Archipelago	2008-2011; 2013-2019	Fernandes RS, Inteca GE, Williams JL, Muaves L, Xavier M. 2020. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2019/20. Maputo, CTV, pp. 61 Fernandes RS, Inteca GE, Williams JL, Taju A, Muaves L, Pereira MAM. 2019. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2018/19. Maputo, CTV, pp. 47 Fernandes RS, Williams JL, Gonzalez-Valladolid S, Muaves L, Pereira MAM. 2018. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2017/18. Maputo, CTV, pp. 45 Fernandes RS, Williams J, Louro CMM, Pereira MAM. 2014. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2013/14. Maputo, CTV, pp. 6. Fernandes RS, Williams JL, Trindade J. 2016. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2015/16. Maputo, CTV, pp. 26 Fernandes RS, Williams JL, Trindade J, Pereira MAM. 2015. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2014/15. Maputo, CTV, pp. 25 Fernandes RS, Williams JL, Valladolid SG, Muaves L, Louro CMM, Pereira MAM. 2017. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2016/17. Maputo, CTV, pp. 31 Louro C, Videira EJ, Pereira MA, Fernandes R. 2012. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2011/12. Maputo. CTV/AICM, pp. 10

					Pereira M, Videira E, Narane D. 2009. Monitoring, tagging and conservation of marine turtles in Mozambique: 2008/09 annual report. Maputo, AICM/GTT, pp. 4. Videira EJS, Pereira MAM, Louro CMM. 2011. Monitoring, tagging and conservation of marine turtles in Mozambique: Annual Report 2010/11. Maputo, AICM/GTT, pp. 10 Videira EJS, Pereira MAM, Narane DA, Louro CMM. 2010. Monitoring, tagging and conservation of marine turtles in Mozambique: annual report 2009/10. Maputo, AICM/GTT., pp. 7
		South Africa	Kosi Bay Mouth to Mabibi	1965-2019	Bachoo S n.d. Unpublished data. Ezemvelo KZN Wildlife. Nel R, Punt AE, Hughes GR. 2013. Are Coastal Protected Areas Always Effective in Achieving Population Recovery for Nesting Sea Turtles? *PLoS ONE*, 8: e63525.
E	Northeast Indian	India	West Bay Little Andaman	2007-2017	United States National Marine Fisheries Service, U.S. Fish and Wildlife Service. 2020. Endangered Species Act status review of the leatherback turtle (*Dermochelys coriacea*) 2020. Available at https://repository.library.noaa.gov/view/noaa/25629 [accessed 5 June 2022].
		India	South Bay Little Andaman	2007-2017	United States National Marine Fisheries Service, U.S. Fish and Wildlife Service. 2020. Endangered Species Act status review of the leatherback turtle (*Dermochelys coriacea*) 2020. Available at https://repository.library.noaa.gov/view/noaa/25629 [accessed 5 June 2022].
F	West Pacific	Malaysia	Terengganu	1956-2010	Chan E-H and Liew HC. 1996. Decline of the leatherback population in Terengganu, Malaysia, 1956-1995. *Chelonian Conservation and Biology*, 2: 196-203. Chan E-H. 2006. Marine turtles in Malaysia: on the verge of extinction? *Aquatic Ecosystem Health & Management*, 9: 175-184.

					Liew HC. 2011. Tragedy of the Malaysian leatherback population. what went wrong. In: Dutton PH, Squires D, Ahmed M editors. *Conservation of Pacific Sea Turtles*. Hawaii: University of Hawaii Press. p. 97-107. United States National Marine Fisheries Service, U.S. Fish and Wildlife Service. 2020. Endangered Species Act status review of the leatherback turtle (*Dermochelys coriacea*) 2020. Available at https://repository.library.noaa.gov/view/noaa/25629 [accessed 5 June 2022].
		Indonesia	Suka Made	1980-2002	Adnyana W (ed). 2006. *Status of leatherback turtles in Indonesia*. Indian Ocean & SE Asian Leatherback-Tsunami Assessment.
		Indonesia	Jamursba-Medi	1984-1985; 1993-1997; 1999-2017	Martin S, Siders Z, Eguchi T, Langseth B, Yau A, Baker J, Ahrens R, Jones T (eds). 2020. *Assessing the population-level impacts of North Pacific loggerhead and western Pacific leatherback turtle interactions in the Hawaii-based shallow-set longline fishery*. U.S. Dept. of Commerce, NOAA Technical Memorandum NOAA-TM-NMFS-PIFSC-95. Tapilatu RF. 2014. The conservation of the Western Pacific leatherback sea turtle (*Dermochelys coriacea*) at Bird's Head Peninsula, Papua Barat, Indonesia. Doctor of Philosophy, The University of Alabama, Birmingham, Alabama. Tapilatu RF, Dutton PH, Tiwari M, Wibbels T, Ferdinandus HV, Iwanggin WG, Nugroho BH. 2013. Long-term decline of the western Pacific leatherback, *Dermochelys coriacea*: a globally important sea turtle population. *Ecosphere*, 4: art25.
		Indonesia	Wermon	2002-2017	Martin S, Siders Z, Eguchi T, Langseth B, Yau A, Baker J, Ahrens R, Jones T (eds). 2020. *Assessing the population-level impacts of North Pacific loggerhead and western Pacific leatherback turtle interactions in the Hawaii-based shallow-set longline fishery*. U.S. Dept. of Commerce, NOAA Technical Memorandum NOAA-TM-NMFS-PIFSC-95.

					Tapilatu RF. 2014. The conservation of the Western Pacific leatherback sea turtle (*Dermochelys coriacea*) at Bird’s Head Peninsula, Papua Barat, Indonesia. Doctor of Philosophy, The University of Alabama, Birmingham, Alabama.
		Papua New Guinea	Huon coast	2000-2012	Ishizaki A (ed). 2015. *Protected Species Conservation by the Western Pacific Regional Fishery Management Council*. Pacific Islands Fishery Monographs. A Publication of the Western Pacific Regional Fishery Management Council. Pilcher NJ (ed). 2011. *Community-based conservation of leatherback turtles along the Huon coast, Papua New Guinea*. Project final report.
G	East Pacific	Mexico	Mexiquillo beach	1983-1995; 1997-2008	Barragán A, Zenteno M, Sarti L (eds). 2010. *Conservation of leatherback turtles in the Mexican Pacific. Executive Summary for nesting season 2008-2009. Final Technical Report*. Kutzari AC / Programa Nacional para la Conservación de las Tortugas Marinas, CONANP. pp 10 Martínez LS, Barragán AR, Muñoz DG, García N, Huerta P, Vargas F. 2007. Conservation and biology of the leatherback turtle in the Mexican Pacific. *Chelonian Conservation and Biology*, 6: 70-78, 79.
		Mexico	Index beaches in Mexico	1982-2018	The Laúd OPO Network. 2020. Enhanced, coordinated conservation efforts required to avoid extinction of critically endangered Eastern Pacific leatherback turtles. *Scientific Reports*, 10: 4772.
		Mexico	Tierra Colorada beach	1997-2008	Barragán A, Zenteno M, Sarti L (eds). 2010. *Conservation of leatherback turtles in the Mexican Pacific. Executive Summary for nesting season 2008-2009. Final Technical Report*. Kutzari AC / Programa Nacional para la Conservación de las Tortugas Marinas, CONANP. pp 10
		Mexico	Cahuitan beach	1997-2008	Barragán A, Zenteno M, Sarti L (eds). 2010. *Conservation of leatherback turtles in the Mexican Pacific. Executive Summary for nesting season 2008-2009. Final Technical Report*. Kutzari AC / Programa Nacional para la Conservación de las Tortugas Marinas, CONANP. pp 10

		Mexico	Chachahua beach	1982-1988; 1990; 1993	Martínez LS, Barragán AR, Muñoz DG, García N, Huerta P, Vargas F. 2007. Conservation and biology of the leatherback turtle in the Mexican Pacific. *Chelonian Conservation and Biology*, 6: 70-78, 79.
		Mexico	Barra de la Cruz beach	1992-2008	Barragán A, Zenteno M, Sarti L (eds). 2010. *Conservation of leatherback turtles in the Mexican Pacific. Executive Summary for nesting season 2008-2009. Final Technical Report*. Kutzari AC / Programa Nacional para la Conservación de las Tortugas Marinas, CONANP. pp 10 Martínez LS, Barragán AR, Muñoz DG, García N, Huerta P, Vargas F. 2007. Conservation and biology of the leatherback turtle in the Mexican Pacific. *Chelonian Conservation and Biology*, 6: 70-78, 79.
		Guatemala	Guatemala	1999-2019	Rguez-Baron JM, Kelez S, Lilies M, Zavala-Norzagaray A, Amorocho D, Gaos A (eds). 2021. *Sea Turtles in the Eastern Pacific Region. MTSG Annual Regional Report 2021.* Draft Report to the IUCN-SSC Marine Turtle Specialist Group.
		El Salvador	El Salvador	1995-2014	Herrera N. 2017. *Estado de conservación de la tortuga baule (Dermochelys coriacea) en El Salvador*.
		Nicaragua	Juan Venado	2004-2011	Paso Pacifico. n.d. Leatherback nesting assessment in the Pacific coast of Nicaragua. National Fish and Wildlife Foundation. Available at https://pasopacifico.org/leatherback-conservation-on-the-pacific-coast-of-nicaragua/ [accessed 9 April 2022].
		Nicaragua	Salamina	2008-2011	Paso Pacifico. n.d. Leatherback nesting assessment in the Pacific coast of Nicaragua. National Fish and Wildlife Foundation. Available at https://pasopacifico.org/leatherback-conservation-on-the-pacific-coast-of-nicaragua/ [accessed 9 April 2022].
		Nicaragua	Veracruz	2002-2011	Paso Pacifico. n.d. Leatherback nesting assessment in the Pacific coast of Nicaragua. National Fish and Wildlife Foundation. Available at https://pasopacifico.org/leatherback-conservation-on-the-pacific-coast-of-nicaragua/ [accessed 9 April 2022].

		Costa Rica	Naranjo	1971; 1996; 1998; 2001; 2006; 2010-2011; 2014-2015	Santidrian P, Robinson NJ, Fonseca L, Quiros W, Arauz R, Beange M, Piedra R, Velez E, Paladino FV, Spotila JR, Wallace BP. 2017. Secondary nesting beaches for leatherback turtles on the Pacific coast of Costa Rica. *Latin American Journal of Aquatic Research*, 45: 563-571.
		Costa Rica	Cabuyal	2011-2015	Santidrian P, Robinson NJ, Fonseca L, Quiros W, Arauz R, Beange M, Piedra R, Velez E, Paladino FV, Spotila JR, Wallace BP. 2017. Secondary nesting beaches for leatherback turtles on the Pacific coast of Costa Rica. *Latin American Journal of Aquatic Research*, 45: 563-571.
		Costa Rica	Nombre de Jesus	2010-2015	Santidrian P, Robinson NJ, Fonseca L, Quiros W, Arauz R, Beange M, Piedra R, Velez E, Paladino FV, Spotila JR, Wallace BP. 2017. Secondary nesting beaches for leatherback turtles on the Pacific coast of Costa Rica. *Latin American Journal of Aquatic Research*, 45: 563-571.
		Costa Rica	Parque Nacional Marino Las Baulas	1988-2018	Santidrian P, Robinson NJ, Fonseca L, Quiros W, Arauz R, Beange M, Piedra R, Velez E, Paladino FV, Spotila JR, Wallace BP. 2017. Secondary nesting beaches for leatherback turtles on the Pacific coast of Costa Rica. *Latin American Journal of Aquatic Research*, 45: 563-571. The Laúd OPO Network. 2020. Enhanced, coordinated conservation efforts required to avoid extinction of critically endangered Eastern Pacific leatherback turtles. *Scientific Reports*, 10: 4772.
		Costa Rica	Ostional	2004-2014	Santidrian P, Robinson NJ, Fonseca L, Quiros W, Arauz R, Beange M, Piedra R, Velez E, Paladino FV, Spotila JR, Wallace BP. 2017. Secondary nesting beaches for leatherback turtles on the Pacific coast of Costa Rica. *Latin American Journal of Aquatic Research*, 45: 563-571.

		Costa Rica	Caletas	2002-2015	Santidrian P, Robinson NJ, Fonseca L, Quiros W, Arauz R, Beange M, Piedra R, Velez E, Paladino FV, Spotila JR, Wallace BP. 2017. Secondary nesting beaches for leatherback turtles on the Pacific coast of Costa Rica. *Latin American Journal of Aquatic Research*, 45: 563-571.

Supplementary Tables 2.5 and 2.6 indicate details regarding the extraction of the loggerhead and leatherback RMU sizes respectively using QGIS. All RMU shapefiles were reprojected and assigned a new coordinate reference system (EPSG: 4326 – WGS 84). The *field calculator* was then used to calculate the true areas (in km²) using the expression "*$area/1000000*".

Supplementary Table 2.5: Assigned coordinate system used to extract loggerhead RMU sizes.

Regional Management Unit	Assigned coordinate reference system
Northwest Atlantic	EPSG: 4326 - WGS 84
Southwest Atlantic	EPSG: 4326 - WGS 84
Northeast Atlantic	EPSG: 4326 - WGS 84
Mediterranean	EPSG: 4326 - WGS 84
Northwest Indian	EPSG: 4326 - WGS 84
Southwest Indian	EPSG: 4326 - WGS 84
Southeast Indian	EPSG: 4326 - WGS 84
North Pacific	EPSG: 4326 - WGS 84
South Pacific	EPSG: 4326 - WGS 84

Supplementary Table 2.6: Assigned coordinate system used to extract leatherback RMU sizes.

Regional Management Unit	Assigned coordinate reference system
Northwest Atlantic	EPSG: 4326 - WGS 84
Southwest Atlantic	EPSG: 4326 - WGS 84
Southeast Atlantic	EPSG: 4326 - WGS 84
Southwest Indian	EPSG: 4326 - WGS 84
Northeast Indian	EPSG: 4326 - WGS 84
West Pacific	EPSG: 4326 - WGS 84
East Pacific	EPSG: 4326 - WGS 84

Supplementary Material II:

Chapter 2 | The portfolio effect and persistence of sea turtle species and populations

Loggerhead RMUs

Northwest Atlantic

The majority of loggerhead sea turtle rookeries within the **Northwest Atlantic** RMU display clear increases in the number of nests over time (Table 2.1), which is also evident when viewed at the RMU-level (Figure 2.1A). This RMU contains one of the largest loggerhead sea turtle nesting rookeries globally, where thousands of nests are laid annually along the coastline of Florida, USA (Casale and Tucker 2017). Similar to other locations, countries within the Northwest Atlantic region comply with the international conventions for the conservation of species, including the loggerhead sea turtles. Major loggerhead sea turtle nesting sites have been subject to protection and monitoring by government and non-governmental organisations (Ceriani and Meylan 2017), which has contributed to the success of Northwest Atlantic loggerhead sea turtles.

In addition, various conservation efforts have been implemented by various organisations and individuals within the United States to protect loggerhead sea turtles. These protective measures include the purchase of critical sea turtle nesting habitat in an attempt to limit anthropogenic development (e.g. Archie Carr refuge), actions to limit artificial lighting on nesting beaches, which could otherwise negatively impact the movement of sea turtles (National Marine Fisheries Service and US Fish and Wildlife Service 2008; Hu et al. 2018), efforts to reduce sea turtle nest predation (Engeman et al. 2010; Engeman et al. 2016; Butler et al. 2020), reducing bycatch (Gilman et al. 2006; Swimmer et al. 2017), acting on the impacts of dredging (Dickerson et al. n.d.; Sundin 2007; National Marine Fisheries Service and US Fish and Wildlife Service 2008), in-water sea turtle abundance and behaviour monitoring projects (Eaton et al. 2008), the use of sea turtle rescue, rehabilitation and release operations (Baker et al. 2015; Innis et al. 2019) and a wide range of other additional strategies in an attempt to allow loggerhead sea turtles to thrive within the Northwest Atlantic region (National Marine Fisheries Service and US Fish and Wildlife Service 2008).

These effective conservation protocols have contributed to the increase in loggerhead sea turtle abundances within the Northwest Atlantic. Despite four of the rookeries experiencing a decline in abundance over time (Table 2.1), the RMU-level trend in abundance continues to increase (Figure 2.1A) as the remaining rookeries (n=12) show increasing patterns (Table 2.1). The fact that the level of protection, type and intensity of threats faced by sea turtles could change in the future, it remains essential that a diversity of sea turtle rookeries and/or populations are conserved in an attempt to retain a large, diversified and “complex” portfolio.

Southwest Atlantic

In the **Southwest Atlantic** RMU, three loggerhead sea turtle rookeries appear to be increasing in the number of nests deposited per nesting season, while the remaining nesting beach shows an opposite trend (Table 2.1). The overall RMU-level trend within the Southwest Atlantic, however, shows an increasing trend in loggerhead sea turtle abundance over time (Figure 2.1B). Regardless of whether the weighted or unweighted RMU-level trend is investigated, the pattern remains the same (Figure 2.1B).

Nesting along the Brazilian coastline, various conservative actions have been put in place to allow the Southwest Atlantic subpopulation to experience an increase in the annual number of nests. In the early 1980s, it became illegal to harvest and consume sea turtles occurring in the region (Law on Environmental Crimes No 9605; Marcovaldi et al. 2005; de Vasconcellos Pegas and Stronza 2010). In 1980, the Brazilian Sea Turtle Conservation Program (project TAMAR) was implemented as a strategy to protect (e.g. from poaching, predation, beach destruction) and monitor all sea turtles species occupying the area (Marcovaldi et al. 1998; Baptistotte et al. 2003; Marcovaldi et al. 2005). Another project that has contributed to the success of the Southwest Atlantic loggerhead sea turtles is the Santos Basin Beach Monitoring Project, which aims to determine the effects of several anthropogenic activities on the health and status of sea turtles (as well as other marine fauna; Werneck et al. 2018).

These conservation projects and initiatives has potentially solely been responsible for the increase in sea turtle nests within the Southwest Atlantic region. Despite the increases at the RMU-level (Figure 2.1H) and within three of the four rookeries (Table 2.1), the remaining rookery experienced a decline. One of the potential threats facing loggerhead sea turtles nesting in Brazil include the accidental capture of sea turtles in the form of bycatch (Pinedo and Polacheck 2004; Marcovaldi et al. 2006; Nogueira and Alves 2016; Barreto et al. 2021). Due to the presence (and possible intensification) of bycatch as a threat facing Southwest Atlantic sea turtles, protecting a diversity of sea turtle rookeries becomes important to ensure the continued persistence of loggerheads within the region as a whole.

As the environmental conditions, level of protection and types and/or extent of threats faced by sea turtles can change rapidly over space and time, maintaining a larger portfolio of individual rookeries becomes essential. The three rookeries experiencing increases in the number of nests over time did buffer the effect of the largest, yet declining sea turtle rookery within the Southwest Atlantic (Table 2.1; Figure 2.1B), suggesting that smaller sea turtle rookeries are equally as important as larger sea turtle rookeries. The absence of one (or more) of the smaller rookeries along the coastline of Brazil may have resulted in a decline in loggerhead abundance within the Southwest Atlantic Ocean region. The maintenance and protection of a diverse range of rookeries within the Southwest Atlantic Ocean has thus enabled the region to experience an increase in abundance over time, even though the larger rookery experienced an exponential rate of decline over time (Table 2.1).

Northeast Atlantic

In the **Northeast Atlantic** RMU, loggerhead sea turtles appear to be increasing over time (Figure 2.1C). Data for only four nesting sites were collected for the Northeast Atlantic RMU, namely Santa Luzia, Sal, Boa Vista Island and Maio Island (Table 2.1). The larger rookery, in terms of average annual number of nests, appears to be declining at an exponential rate (Boa Vista Island). However, even though the remaining rookeries have lower mean annual number of nests over time (Table 2.1), the occurrence of these rookeries shift the Northeast Atlantic RMU's abundance trend from declining to increasing over time. Despite Cape Verde housing one of the largest aggregations of nesting loggerhead sea turtles worldwide (Marco et al. 2012; West Africa Biodiversity and Climate Change (WA BiCC) Program 2020; Ferreira et al. 2022; Patino-Martinez et al. 2022), a major gap in information and research regarding the behaviour and status of loggerhead sea turtles within the Northeast Atlantic exists (West Africa Biodiversity and Climate Change (WA BiCC) Program 2020; Hays et al. 2022; Ferreira et al. 2022).

However, appropriate conservation actions have potentially resulted in an increase in loggerhead sea turtles associated with the Northeast Atlantic RMU. Regulations, beach patrolling and protection as well as awareness programs has potentially contributed greatly to the success of loggerheads situated in the Northeast Atlantic (Marco et al. 2012; Marco et al. 2018; Martins et al. 2021). Despite the Northeast Atlantic loggerhead sea turtles experiencing an increase in abundance over time (Figure 2.1C), the notion regarding a lack of information (Ferreira et al. 2022) is a cause of concern.

There are various threats that could potentially reverse the contemporary upward trend in abundance, such as the illegal harvesting, trade and killing of sea turtles as a source of meat (Hancock et al. 2017), destruction of critical sea turtle nesting habitats due to coastal development (Marco et al. 2011; Abella Perez et al. 2016) and bycatch (Freire Lopes et al. 2016; Martins et al. 2022). Considering the lack of comprehensive information regarding the dynamics of loggerhead sea turtles in the Northeast Atlantic RMU, as well as the possible intensification of contemporary threats, it becomes essential that a diversity of rookeries within the Northeast Atlantic RMU is appropriately monitored and protected. The Northeast Atlantic loggerhead sea turtle RMU exemplifies the importance of having additional rookeries to buffer declines in abundance evident at other rookeries situated within the same RMU.

Mediterranean

Most loggerhead sea turtle rookeries within the **Mediterranean** RMU display increasing nest numbers over time (Table 2.1), while the RMU-level trend seems to also exhibit an increase over time (Figure 2.1D). There are various conservation actions in place within and surrounding countries situated in the Mediterranean region to protect sea turtles. One of the main reasons why the Mediterranean loggerhead sea turtles appears to be increasing is that the main threat has possibly be identified and the successful recognition of the problem has the potential to alleviate the threat through appropriate actions.

Bycatch has been suggested to be one of the main threats facing sea turtles in the Mediterranean sea (Casale 2011; Lucchetti et al. 2019). It has been predicted that approximately 124 000 - 150 000 sea turtles are caught as bycatch within the Mediterranean Sea on an annual basis, while a great proportion of these sea turtles may fail to recover (Carpentieri et al. 2021). It has, however, been recognised that bycatch is a serious issue that needs to be addressed to conserve Mediterranean sea turtles, which can be accomplished by testing and implementing bycatch mitigation procedures, as well as to monitor and reduce fisheries bycatch (Camiñas et al. 2020). In addition to identifying the main threat facing Mediterranean Sea turtles, local committees and non-profit groups have taken the responsibility of protecting the major nesting sites of sea turtles within Mediterranean countries (Camiñas et al. 2020).

Sea turtle rescue and rehabilitation centres are also situated within various countries, providing veterinary care and support to injured sea turtles and/or individuals that have an illness (Camiñas et al. 2020). Sea turtle rescue centres, informal rescue organisations and first-aid stations contribute to the success of loggerhead sea turtles in the Mediterranean by providing scientific information, raising public awareness and mitigating the negative impacts of bycatch (Ullmann and Stachowitsch 2015). There are also some non-governmental organisations (NGOs) involved in the conservation of Mediterranean sea turtles, such as ARCHELON and MEDASSET that have been operational since the 1980s.

National and international legislation has also played a massive role in the protection of sea turtles. Some of these conventions, agreements and international treaties include Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), Convention on the Conservation of European Wildlife and Natural Habitats (BCCEW/Bern Convention), Convention for the Protection of Migratory Species of Wild Animals (CMS/Bonn Convention), Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean (Barcelona Convention), Mediterranean Action Plan (MAP), General Fisheries Commission for the Mediterranean (GFCM) of the Food and Agriculture Organisation of the United Nations (FAO), Habitats Directive, Convention on Biological Diversity (CBD), International Commission for the Conservation of Atlantic Tunas (ICCAT) on bycatch in tuna fisheries, etc. (Casale and Margaritoulis 2010; Camiñas et al. 2020).

Based on the wide range of the abovementioned actions and regulations implemented to protect the Mediterranean RMU's loggerhead sea turtles, it becomes clear as to why the number of loggerhead sea turtles have experienced an increase in abundance over time within this "complex" RMU. Despite some rookeries experiencing a decline in abundance over time, the diversity of rookeries has resulted in the RMU-level trend to be increasing. This pattern exemplifies the importance of having a greater diversity of rookeries (i.e. having a greater portfolio) to mitigate declining abundance trends evident at some rookeries.

Northwest Indian

The **Northwest Indian** loggerhead sea turtle population situated at Masirah Island, Oman, has recently experienced a devastating decline in the number of nests per nesting season (Willson et al. 2020; Table 2.1; Figure 2.1E). This RMU can be described as a "simple RMU", as very few individual rookeries comprise the entire Northwest Indian loggerhead sea turtle RMU. Some of the major threats facing Omani sea turtles include bycatch (Hamann et al. 2013; Willson et al. 2020), coastal developments and other anthropogenic structures (e.g. artisanal skiff vessels), and the predicted growth in the human population along the coastline of Oman (Al-Awadhi et al. 2016). All of these factors have had (or will potentially have) a negative impact on the status of loggerhead sea turtles situated in the Northwest Indian Ocean (Willson et al. 2020).

The reason why portfolio or “buffering” effects are not evident within the Northwest Indian loggerhead RMU is because a sufficient number of individual rookeries comprising the particular RMU are non-existent. If this “simple RMU” had a greater diversity of rookeries, and thus have had a greater portfolio, the current trend in loggerhead abundance may have been reversed by other rookeries that may have experienced an increase in size over time. In this case, it becomes essential that other sea turtle populations and/or RMUs display increasing trends in abundance to mitigate the current decline in population size evident within the Northwest Indian.

Southwest Indian

The **Southwest Indian** loggerhead sea turtle RMU-level trend displays an increasing pattern as a result of an increase in the annual number of nests deposited along the coastlines of both South Africa and Mozambique (Table 2.1; Figure 2.1F). In the Southwest Indian Ocean loggerhead sea turtle RMU, approximately 80% of nesting occurs along the South African coastline and the remainder of nests are deposited in Mozambique (Nel and Casale 2015), with few nesting events (although largely unquantified) occurring along the coastline of Madagascar.

South African female loggerhead and leatherback sea turtles nest along the north-eastern coastline of KwaZulu-Natal and have been protected, monitored and studied since 1963 in a series of coastal and marine protected areas (Nel et al. 2013; Nel and Casale 2015), which has potentially contributed greatly towards the increase in loggerhead abundance within the Southwest Indian Ocean. In Mozambique, similar sea turtle conservation efforts (as in South Africa) have been implemented since 1996 (Nel and Casale 2015).

Despite the protection of nesting loggerhead sea turtles in the terrestrial environment, the influence of onshore and offshore anthropogenic activities can be detrimental. Illegal harvesting of sea turtles for the trade industry remains an issue, with reports suggesting products being sold to Asian markets (IOSEA 2014; Riskas et al. 2018). Sea turtle eggs, for example, continue to be harvested along the Mozambique coastline (Williams et al. 2016; Pilcher and Williams 2018). In addition, other major threats facing loggerhead sea turtles within the region may include the effects of fisheries bycatch (Petersen et al. 2009; Pilcher and Williams 2018, but see Nel et al. 2013), the influence of shark nets (Brazier et al. 2012), the potential loss of sea turtle nests (eggs) and/or hatchlings due to the driving of offroad vehicles at nesting sites (Lucrezi et al. 2014) and the occurrence of plastics and other anthropogenic debris/material (Ryan et al. 2016; Schuyler et al. 2016; Williams et al. 2019). As a range of these threats has the potential to become more detrimental in the near future (e.g. Béné et al. 2015; Lebreton and Andrady 2019; Patrício et al. 2021; Barrowclough and Birkbeck 2022), it is possible that the current RMU-level trend may be reversed if proactive measures are not implemented.

This RMU can, however, be defined as a “simple RMU” due to the limited number of rookeries constituting the entire RMU. As a result, a sudden change in the rate of increase/decline in abundance within one rookery can have severe effects on the RMU-level trend. In Mozambique, it appears that a sudden decline in the number of nests deposited annually from 2013 has caused the RMU-level trend in abundance to experience a similar decline when the trend is unweighted by rookery size (Table 2.1; Figure 2.1F). If the RMU-level trend is weighted by mean size, however, the trend in abundance appears to neither increase or decrease (Figure 2.1F). Nonetheless, whether the weighted or unweighted growth rates are taken into account, the impact of a decline in the number of nests within a single rookery (i.e. Mozambique) can have detrimental effects on the RMU-level trend in abundance.

The increase in the number of nests deposited annually along the South African coastline, which constitutes the largest rookery in the Southwest Indian Ocean RMU, has allowed the Southwest Indian Ocean loggerhead population to experience an increase over time. The annual increase in loggerhead sea turtle nests in Kosi Bay has buffered the decline experienced from Ponta do Ouro to Bazaruto Archipelago. The absence of the nesting South African loggerhead sea turtle population may thus have resulted in a decline in loggerhead abundance at the RMU-level. Although limited, the occurrence of two independent rookeries has created a small, yet significant “portfolio effect”, allowing the Southwest Indian Ocean loggerhead sea turtle RMU to increase in abundance over time.

Southeast Indian

Both loggerhead sea turtle rookeries situated within the **Southeast Indian** RMU display declining trends in abundance over time (Table 2.1), which is also evident at the RMU-level (Figure 2.1G). In the most recent IUCN Red List assessment for the Southeast Indian loggerhead sea turtle subpopulation, the population trend over time was reported as being unknown (Casale et al. 2015). Our results, however, suggest that the number of nests deposited annually along the western coastline of Australia has declined over time (Table 2.1; Figure 2.1G). Unfortunately, despite the Southeast Indian Ocean loggerhead subpopulations containing a large number of sea turtles, the availability of long-term monitoring datasets remains lacking (Casale et al. 2015).

Predation on eggs and hatchlings is one of the contributors to the decrease in loggerheads within the RMU. Various native as well as introduced predators are responsible for this decline in loggerhead abundance, such as ghost crabs, birds and feral cats (Hilmer et al. 2010; DBCA 2022). Aerial and ground baiting and trapping methods have, however, reduced the negative impact of nest predation by introduced predators (e.g. foxes and/or dogs; DBCA 2022). Off-road vehicles traveling on nesting beaches or in the coastal environment near rookeries is another threat that has the potential to decrease the survivorship of eggs as well as newly-emerged hatchlings (Hamann et al. 2013). Light pollution, which has the potential to increase the mortality rate of hatchlings through disorientation, dehydration and/or starvation, as well as the ability to refrain adult females from laying eggs (Silva et al. 2017; Cruz et al. 2018; Vandersteen et al. 2020), may also have had a detrimental effect on the abundance trends of loggerhead sea turtles occupying the Southeast Indian Ocean (Kamrowski et al. 2012; Hamann et al. 2013).

Along the coastline of western Australia, it has been found that light pollution has caused approximately 90% of green sea turtle (*Chelonia mydas*) hatchlings to become disorientated, which ultimately had a negative impact on their survivorship (Thumbs et al. 2016). The influence of artificial lighting on green sea turtles in the Southeast Indian Ocean would either have a similar or an identical effect on loggerhead sea turtles. It therefore becomes prominent that light pollution could have had a detrimental effect on the number of nests deposited annually along the western Australian coastline. The absence of portfolio effects at the RMU-level within the Southeast Indian Ocean occurs due to the limited number of individual (or independent) rookeries constituting this “simple RMU”. Both rookeries for which data was collected also display declines in abundance over time (Table 2.1). Reversing either one of the two trends by either increasing conservation efforts or eliminating threats may shift the contemporary declining RMU-level trend to an increasing trend. Therefore, it becomes essential that the importance of the occurrence of nesting loggerhead sea turtles within other RMUs are recognised as a supplement to restrict a potential decline in loggerhead sea turtles worldwide.

North Pacific

The **North Pacific** loggerhead sea turtle RMU seems to experience a decline in the number of loggerhead sea turtle nests over time (Figure 2.1H), with the majority of individual rookeries within the RMU displaying similar trends (Table 2.1). Within this RMU, loggerhead sea turtles solely nest in Japan (Kamezaki et al. 2003). Loggerhead sea turtles have started experiencing a rapid decline since the 1990s, which was then followed by a period of brief recovery (Kamezaki et al. 2003; Biodiversity Center of Japan, Ministry of the Environment 2016; Biodiversity Center of Japan, Ministry of the Environment 2020). The recovery of the North Pacific loggerhead sea turtle population was short-lived, as populations across Japan started experiencing declining patterns once again (e.g. Martin et al. 2020; Okuyama et al. 2020).

There are various reasons as to why loggerhead sea turtles may be experiencing declines in this region. Pelagic (e.g. longlines, driftnets) and coastal (e.g. fish weirs, pound nets, coastal longlines) fisheries have primarily been responsible for the unintentional capture (and in some cases, mortality) of thousands of loggerhead sea turtles annually (Gilman et al. 2006; Lewison and Crowder 2007; Peckham et al. 2007; Peckham et al. 2017). In recent years, actions have been undertaken to try and reduce the impacts of fisheries on loggerhead sea turtles roaming the North Pacific (e.g. Ishihara et al. 2011; Peckham et al. 2017). Even though some of the larger rookeries situated in the North Pacific have experienced an increase in loggerhead abundance (e.g. Yakushima, Miyakazi beach and Omaezaki beach; Table 2.1), the declines evident at 10 of the 14 rookeries have resulted in a declining RMU-level trend.

The rate of decline was, however, greatly buffered by the rookeries experiencing increasing patterns in abundance. Rookeries at which the annual number of nests are increasing have counteracted the rapid exponential declines in rookery sizes experienced at, for example, Minabe Iwashiro and Nagasakibana beaches (Table 2.1). If the four nesting locations at which the number of nests is increasing were non-existent, the North Pacific subpopulation may possibly have ceased to exist in the very near future. Even though portfolio effects are evident within the "complex" North Pacific RMU, the increase in abundances within the four rookeries were not strong enough to reverse the RMU-level decline.

South Pacific

The majority of rookeries within the **South Pacific** loggerhead sea turtle RMU displayed declines in the annual number of nests over time, where only a single rookery has experienced an increase in abundance (Table 2.1). The RMU-level trend, however, appears to be decreasing over time (Figure 2.1I). The rate of increase in loggerhead abundance along the Sunshine Coast was not sufficient to reverse the declining trend evident at the RMU-level (Table 2.1; Figure 2.1I), despite an increase in abundance at Heron Island from 1999. The larger sea turtle rookery, Wreck Island, experienced an exponential rate of decline over time (Table 2.1).

At the RMU-level, however, various threats may have contributed to the decline in loggerhead nests over time. Coastal development and the use of artificial lights has the potential to greatly affect loggerhead sea turtle survivorship (Salmon 2003; Silva et al. 2017), which has also been observed along the east coast of Australia (Berry et al. 2013). The impact of anthropogenically-induced light pollution has the potential to disorientate both hatchling and adult sea turtles (Silva et al. 2017), which may potentially lead to the death of individuals through dehydration and/or predation (Witherington and Martin 1996; Thums et al. 2016).

Marine turtle bycatch is another issue faced by loggerhead sea turtles roaming the oceanic waters of the South Pacific (Limpus 2008; Wallace et al. 2013a; Riskas et al. 2016), especially in longline fisheries (Alfaro-Shigueto et al. 2011; Mangel et al. 2011). In addition to the accidental capture of sea turtles by fishing crafts, boat strikes from passing marine vessels includes another cause for concern (Limpus 2008). In addition, anthropogenically-induced debris has also shown to have a negative impact on loggerhead sea turtles resident within South Pacific waters. The accidental ingestion of plastics has also increased the rate of loggerhead sea turtle mortality (Duncan et al. 2021), while other sources of anthropogenic pollution has also contributed to the decline in South Pacific loggerhead sea turtles through entanglement (Limpus 2008; Hamann et al. 2013; United Nations Environment Programme and Convention on Migratory Species 2014).

Another threat faced by loggerhead sea turtles includes nest loss, which has been shown to be intensified through continued predator activity (Madden Hof et al. 2020). For example, it was found that yellow-spotted goannas (*Varanus panoptes*) appeared more frequently at loggerhead sea turtle nests compared to other predators in the Wreck Rock beach area situated along the east coast of Australia (Lei and Booth 2017). It was found that lace monitors (*V. varius*) are also a major threat to loggerhead sea turtles within the region (Madden Hof et al. 2020). Given the wide range of threats faced by the South Pacific loggerhead sea turtles, it becomes clear that the rookeries experiencing an increase in growth are critical to reverse the declining RMU-level trend. The increase in loggerhead sea turtle nests along the Sunshine Coast has greatly reduced the rate at which the population size of loggerhead sea turtles is declining at the RMU-level.

Leatherback RMUs

Northwest Atlantic

The majority of leatherback sea turtle rookeries situated in the **Northwest Atlantic** display increasing trends in the number of nests over time (Table 2.2), which is supported the overall RMU-level trend (Figure 2.2A). Our results do, however, contradict the findings from other publications. A recently published report illustrated that a great proportion of rookeries (as well as regionwide areas) experienced a decline in leatherback abundances over time (The Northwest Atlantic Leatherback Working Group 2018). The abundance trends reported by the Northwest Atlantic Leatherback Working Group only included long-term data starting from 1990, while this particular analysis includes data entries as early as 1970 (Supplementary Table 2.4). It is therefore possible that a positive RMU-level trend, within this particular analysis and when weighted trends are investigated, was acquired as a result of an increase in the abundance of leatherback sea turtles up to the 1990s.

In the most recent IUCN Red List Assessment for the Northwest Atlantic leatherback sea turtle subpopulation, it was also reported that the abundance of leatherback sea turtles are currently in decline (The Northwest Atlantic Leatherback Working Group 2019). Based on the RMU-level trajectory (Figure 2.2A), it appears as if the abundance of leatherback sea turtles have been increasing up to 1990 and 2010 for weighted and unweighted trends respectively, while the declining patterns are evident from the start of the 2010s (regardless of whether the weighted or unweighted trajectory over time is considered). This observation is supported by additional results obtained in this particular investigation.

In the majority of rookeries situated in the Northwest Atlantic for which breakpoint models were the best-fit model, a positive growth rate in abundance was followed by a pattern of decline following the breakpoint year (Table 2.2). In addition, a previous IUCN Red List assessment found that leatherback sea turtles occupied a stable yet increasing trend in abundance over time (Tiwari et al. 2013a). Despite obtaining an overall increasing growth rate for the Northwest Atlantic subpopulation within this particular analysis, it becomes evident that leatherback sea turtles may have increased in abundance in the past, but currently face a season of declining at various rookeries situated within the region.

There are various potential causes for the decline in leatherbacks in recent decades within the Northwest Atlantic region. Bycatch is potentially one of the main threats facing leatherback sea turtles (Wallace et al. 2013a). In the Northwest Atlantic region, leatherback sea turtles have been reported as being caught within fisheries occurring both near major nesting beaches (Eckert 2013; Connor Blades et al. 2019) as well as in oceanic waters exhibiting important foraging habitats for sea turtles (Stewart et al. 2013; Hamelin et al. 2017; Swimmer et al. 2017; Hurtubise et al. 2020). The declines across the different rookeries are, however, widespread (Table 2.2). This suggests that other threats have also potentially contributed towards the decline in Northwest Atlantic leatherback sea turtles.

Another threat facing leatherback sea turtles is the loss of suitable nesting habitat and/or nests due to beach erosion (Barragan et al. 2022). Since the 1990s, for example, beach erosion has been proposed as one of the major contributing factors to the approximate 99% decline in leatherback nesting along the coastline of Awala-Yalimapo (The Northwest Atlantic Leatherback Working Group 2018). Vessel strikes is another threat faced by leatherback sea turtles roaming the oceanic waters of the Northwest Atlantic Ocean (Moore Dourdeville et al. 2018). Another threat includes the effects of plastic waste on the survivorship of leatherback sea turtles. Since the diet of leatherbacks primarily includes gelatinous organisms (i.e. jellyfish; Estrades et al. 2007; Heaslip et al. 2012; Jones et al. 2012), individuals may mistakenly ingest plastic wastes due to the resemblance such pollutants have towards their main prey item (Mrosovsky et al. 2009).

In the Northwest Atlantic region, the occurrence of plastic waste has the potential to have adverse effects on leatherback sea turtles roaming the oceanic environment through both accidental ingestion and entanglement (Blais and Wells 2022). As global plastic production will most likely continue to increase in the future (Lebreton and Andrady 2019; Walker and Fequet 2023), the severity of plastic waste as a threat facing sea turtles may intensify.

As a result of the substantial decline in leatherback abundances across the vast majority of rookeries situated within the Northwest Atlantic in recent decades, portfolio effects were not strong enough to reverse such declines. Portfolio effects may be more evident if few rookeries start experiencing an increase in abundance over time. Based on the observation that the majority of rookeries displayed a decline in abundance after a breakpoint year occurring during a similar time period (Table 2.2), it appears that the Northwest Atlantic subpopulation is faced by regional-level threat(s) that are influencing leatherback sea turtles situated in multiple rookeries in a similar/identical manner, reducing the strength, degree and prevalence of potential portfolio effects.

Southwest Atlantic

The **Southwest Atlantic** RMU displays an increasing trend in terms of leatherback abundance (Figure 2.2B), which is attributable to the single rookery (i.e. Espirito Santo, Brazil) experiencing an increase in the number of annual nests deposited for which data was available (Table 2.2). According to the latest IUCN Red List Assessment concerning the Southwest Atlantic leatherback subpopulation, the number of leatherbacks appeared to be increasing (Tiwari et al. 2013c), which is similar to the results from this investigation (Figure 2.2B). The Southwest Atlantic leatherback sea turtle population is relatively small in size compared to other locations around the globe, where the majority of nests are laid along the coastline of Espirito Santo in Brazil (occasional nesting events may occur along the coastline of Brazil; Thomé et al. 2007; Colman 2019).

It has recently been reported that the leatherback sea turtles comprising the Southwest Atlantic RMU have increased in population size in recent decades (Colman et al. 2019). The leatherback sea turtles nesting along the Brazilian coastline have received the same protective measures as the loggerhead sea turtle. Legislative procedures put in place to reduce the harvesting and subsequent use (e.g. consumption) of sea turtle products potentially contributed to the current increase in population size within the Southwest Atlantic (Law on Environmental Crimes No 9605; Marcovaldi et al. 2005; de Vasconcellos Pegas and Stronza 2010). In addition, in 1980, the Brazilian Sea Turtle Conservation Program (project TAMAR) was implemented as a strategy to protect (e.g. from poaching, predation, beach destruction) and monitor all sea turtle species occupying the area (Marcovaldi et al. 1998; Baptistotte et al. 2003; Marcovaldi et al. 2005).

Despite the current increase in leatherback sea turtle nests within the region, the occurrence of threats to sea turtles has the potential to reverse contemporary trends. Leatherback sea turtles are, for example, commonly caught as bycatch within Brazilian waters. It was found that leatherback sea turtles (along with loggerhead sea turtles) constituted one of the most common sea turtle species caught as bycatch in various small-scale fisheries situated in southeastern Brazil (Bugoni et al. 2008). An increase in fishing efforts within Brazilian waters could potentially cause the leatherback sea turtle abundance trend to experience a decline in the near future. In addition, the lack of additional leatherback sea turtle rookeries situated in the "simple" Southeast Atlantic RMU makes this population prone to great fluctuations in abundance if environmental conditions and/or threats change. This population therefore does not exhibit any portfolio effects, which makes this population vulnerable to extirpation if current protective and monitoring efforts are neglected.

Southeast Atlantic

Apart from a single rookery, all leatherback rookeries situated within the **Southeast Atlantic** display decreasing trends in the number of nests deposited annually (Table 2.2), resulting in a subsequent decline in abundance over time at the RMU-level (Figure 2.2C). This decline at the RMU-level is only evident when the individual rookeries comprising the RMU are unweighted according to their average size. If mean rookery size is considered, the RMU-level trend appears to neither be increasing nor decreasing. This difference between the weighted and unweighted growth rates is due to the increase in leatherback abundance along the coastline of Gabon, where the largest proportion of leatherback sea turtles within the Southeast Atlantic nest (Table 2.2; Fretey 1984; Fretey et al. 2007; Fossette et al. 2008). The most recent

IUCN Red List Assessment for the Southeast Atlantic leatherback sea turtles remain data deficient (Tiwari et al. 2013b).

There exist various reasons as to why leatherbacks may be decreasing in the Southeast Atlantic RMU (based on the unweighted RMU-level trend, Figure 2.2C). As within the vast majority of other RMUs, bycatch is a prevalent threat facing leatherback sea turtles situated within the region (Witt et al. 2011; Riskas and Tiwari 2013). In the Gabonese trawl fishery, for example, a range of sea turtle species (including leatherbacks) are commonly caught as bycatch (Casale et al. 2017). In addition, the occurrence of artificial lighting has previously resulted in the mortality of adult leatherback sea turtles in Gabon (Deem et al. 2007). Commercial logging is a common practice taking place in Gabon (White 1994; Abebe and Holm 2003; Laurance et al. 2006; Legault and Cochrane 2021). Adult leatherback sea turtles could become entrapped, disorientated and/or damaged by these logs (Pikesley et al. 2013), as well as potentially reduce the number of clutches laid by causing adults to abort nesting attempts if their access to suitable nesting grounds is limited or as a result of disrupted nesting activities (Laurence et al. 2008).

Due to the prevalence of current threats and the possibility of emerging threats in the near future, it becomes essential that leatherback sea turtle rookeries situated within the Southeast Atlantic region are continuously monitored and protected. The results obtained for the Southeast Atlantic subpopulation displays how the occurrence of multiple rookeries can result in portfolio effects being evident at the RMU-level. Even though declines in abundance were evident at four out of five rookeries (Table 2.2), the RMU-level trend has remained stabilised due to an increase in abundance at a single rookery (Table 2.2; Figure 2.2C). The portfolio effect is clearly evident within the Southeast Atlantic leatherback RMU, where a diverse portfolio (i.e. a range of independent rookeries experiencing different rates of increase/declines) has a resulted in a stabilised trend in abundance at the RMU-level.

Southwest Indian

The **Southwest Indian** leatherback sea turtle RMU shows a slight decrease in the abundance of leatherback sea turtle nests over time when rookeries (regardless of size) are given equal weight to the RMU-level trend (Figure 2.2D). If individual rookeries with larger annual number of nests have a greater influence on the RMU-level trend compared to smaller rookeries, then the Southwest Indian leatherback sea turtle population appears to show an overall increase in abundance over time. It does, however, appear that leatherbacks situated within the Southwest Indian Ocean region have been declining in numbers since the late 2000s (Figure 2.2D). In the latest IUCN Red List Assessment, it was reported that leatherback sea turtles were decreasing in population size within the Southwest Indian region (Wallace et al. 2013b).

Similar to the loggerhead sea turtles nesting along the coastline of Southeast Africa, approximately 80% of nesting occurs along the South African coastline and the remainder of nests are mostly deposited in Mozambique (Nel and Casale 2015). South African leatherback sea turtles nest along the north-eastern coastline of KwaZulu-Natal and have been protected, monitored and studied since 1963 in a series of coastal and marine protected areas (Nel et al. 2013; Nel and Casale 2015), while similar sea turtle conservation efforts (as in South Africa) have been implemented since 1996 along Mozambique (Nel et al. 2013; Nel and Casale 2015).

Based on the results obtained (Table 2.2; Figure 2.2D), it appears that an overall increase in the number of leatherback sea turtle nests along the coastline of South Africa has counteracted the effect of a decline in nests observed along the Mozambique coastline (i.e. if rookery size is taken into account; weighted trends). In this case, it would suggest that there are some portfolio effects evident in the Southwest Indian leatherback sea turtle RMU. Nevertheless, in recent years, it appears as if leatherback sea turtles within the region have experienced an overall decline in abundance (Figure 2.2D; Nel et al. 2013; Wallace et al. 2013b).

Leatherback sea turtles face various threats in both the onshore and offshore environment of Mozambique. The illegal harvesting of sea turtles remains an issue that needs to be addressed (Williams 2017; Pilcher and Williams 2018), as well as the damaging and/or killing of mobile leatherbacks through spearfishing (Pilcher and Williams 2018; Williams et al. 2019). The harvest of sea turtle eggs remains a problem along the Mozambique coast (Pilcher and Williams 2018). The most prevalent threat facing leatherback sea turtles in the Southwest Indian Ocean region is potentially the effects of bycatch on the nesting population. It has been reported that potentially over 100 000 sea turtles (which includes leatherbacks) are caught as bycatch annually within Mozambique waters (Williams 2017; Pilcher and Williams 2018).

In South Africa, the industrial longlining industry is potentially responsible for the lack of rapid recovery rates in leatherbacks nesting along the coastline (Grantham et al. 2008; Petersen et al. 2009; Nel et al. 2013; Harris et al. 2018). Other threats have also been linked as possible causes for the recent observed decline in leatherbacks nesting in South Africa, such as the use of motor vehicles on nesting beaches, artificial lighting, and coastal erosion (Nel 2006; additional suggestions as to why South African leatherback sea turtles may not be recovering as well as their loggerhead sea turtle counterparts are outlined in Nel et al. 2013).

Given these threats and the current concern regarding the recent decline in leatherback nest numbers, maintaining the contemporary portfolio effect evident at the RMU-level is important to this population's continued persistence. Due to the fact that there are only a limited number of rookeries situated within the Southwest Indian Ocean region, the overall population becomes prone to high variability in abundance over time. A similar response (e.g. decline) in abundance within rookeries may result in an absence of portfolio effects at the RMU-level. The larger size of the South African rookery has had a buffering effect on the decline in leatherback sea turtle abundance in Mozambique, which exemplifies the importance of maintaining a diversity of rookeries within larger regions.

Northeast Indian

Both leatherback sea turtle rookeries situated within the **Northeast Indian** RMU have experienced an increase in abundance over time (Table 2.2), while the annual number of nests at the RMU-level has also increased (Figure 2.2E). The increase in the annual number of nests at the RMU-level is as a result of an increased growth rate in the annual number of nests deposited along the coastline of the Little Andaman Island (Table 2.2).

In 2004, one of the most devastating tsunamis in modern times caused extensive damage to both anthropogenic and natural environments of countries and/or islands situated in the Indian Ocean (Ramalanjaona 2011; Suppasri et al. 2015). The nesting beaches along the coastlines as well as surrounding coral reefs of the Andaman and Nicobar Islands were greatly altered (i.e. reduced in size) and damaged as a result of the tsunami (Murugan 2005; Kumar et al. 2007; Bahuguna et al. 2008). This catastrophic event resulted in the loss of many leatherback sea turtles and has also potentially had a negative impact on their reproductive potential due to the loss of nesting beaches (Murugan 2005; Andrews et al. 2006). To record the post-tsunami recovery of leatherback sea turtles nesting along the Little Andaman Island, a long-term annual monitoring program was implemented in 2008 on the South Bay beach of the island, while the West Bay beach also received attention in 2010 (Swaminathan et al. 2011). Despite the negative impact of the tsunami on India's nesting sea turtles, the major nesting beaches have been restored and leatherbacks have appeared to undergo a period of population recovery (Swaminathan et al. 2011; Swaminathan et al. 2017; Swaminathan et al. 2019), which is also supported by the findings of this investigation.

Various other investigations have also allowed scientists to effectively monitor the status and behaviour of leatherbacks situated within the region, such as tracking the movement of sea turtles and increasing our knowledge regarding their migratory routes (Namboothri et al. 2012; Swaminathan et al. 2019). The increase in monitoring efforts has contributed to the success of leatherbacks nesting within the Northeast Indian RMU. The occurrence of an independent leatherback sea turtle rookery in the Northeast Indian Ocean, which has experienced a positive growth rate in the annual number of nests deposited over time, thus broadens the portfolio of the leatherback sea turtle population at the global scale. This population may therefore potentially act as a buffer against declining leatherback populations comprising other RMUs.

The occurrence of relatively few rookeries within the Northeast Indian RMU does, however, make the population prone to fluctuations in abundance over time. The RMU itself does not exhibit a broad portfolio, suggesting that the occurrence of a stochastic event at a single rookery can influence the leatherback population size at the RMU-level. It therefore becomes essential that all rookeries within this particular RMU are exposed to ongoing monitoring efforts to possibly limit and predict future perturbations.

West Pacific

In the **West Pacific** leatherback sea turtle RMU, leatherback sea turtle numbers appear to be declining despite a single rookery displaying an increase in nest numbers over time (Table 2.2). Regardless of whether rookery size is considered (i.e. weighted or unweighted), leatherback sea turtles situated in the West Pacific appears to be declining tremendously since the 1950s (Figure 2.2F). The results obtained for this particular RMU is consistent with the conclusions from previously published literature (e.g. Tapilatu et al. 2013; Benson et al. 2020).

West Pacific leatherback sea turtles have been exposed to a number of perturbations that have threatened their persistence for decades. One of the greatest challenges facing West Pacific leatherback sea turtles include the impact of fisheries. It was found that leatherbacks are at risk of being subject to bycatch within the longline fishing industry occurring within north and central Pacific, as well as near principal nesting beaches of the Indo-Pacific Islands (Roe et al. 2014). The overharvesting of sea turtle adults and/or eggs and anthropogenic development on nesting beaches are also considered to be major contributors to observed declines in West Pacific leatherbacks (Bailey et al. 2012; Tapilatu et al. 2013). Predation is another factor contributing to the demise of West Pacific leatherback sea turtles (Adnyana 2006). For example, pigs and dogs have been found to consume sea turtle eggs from learherback sea turtle nests located in Wermon, Indonesia (Thebu and Hitipeuw 2005). The factor that has been suggested as being primarily responsible for the decline in leatherback sea turtles in the West Pacific is, however, poaching of adults and eggs (Adnyana 2006).

All the abovementioned threats have contributed, in varying degrees, to the rapid decline of West Pacific leatherback sea turtles, making the population prone to extirpation. The absence of strong portfolio effects to reverse declining patterns in abundance at the RMU-level is possibly attributable to the low number of rookeries experiencing an increase in the number of annual nests over time. In this case, the increase in nests along the Huon coast has mitigated the rapid declines evident in Suka Made (Indonesia) and Terengganu (Malaysia). Unfortunately, since the rookery along the Huon coastline is not very large compared to other rookeries within the region (Table 2.2), as well as the remaining rookeries experiencing a decline in sea turtle nests over time (Table 2.2), the RMU-level trend in abundance has remained in decline for decades.

Nevertheless, despite most rookeries experiencing declines in abundance, it does not suggest that conservation and monitoring efforts should solely be focused at rookeries experiencing an increase in the number of nests. As environmental conditions and associated threats to sea turtles can shift in a short period of time, so can sea turtle abundance trends. It is therefore possible that the rookery experiencing a contemporary increase in abundance (i.e. Huon coast) may experience a decline in abundance in the near future, while the opposite may be true for rookeries that are currently experiencing a decline in sea turtle nests over time. It becomes essential that a diversity of rookeries are monitored and protected, as having a diversity of rookeries may ultimately promote stability in terms of nest numbers.

East Pacific

When investigating leatherback sea turtles nesting along coastlines situated in the **East Pacific** RMU, most rookeries display declines in the number of nests deposited every nesting season (Table 2.2). These patterns complement the RMU-level trend (weighted and unweighted; Figure 2.2G). Leatherback sea turtles occupying the East Pacific have experienced a substantial decline in population size over the last few decades (Spotila et al. 2000; Martínez et al. 2007).

It has long been recognised that East Pacific leatherback sea turtle mortality is primarily caused by human fishing activities (i.e. bycatch, Spotila et al. 2000; Martínez et al. 2007; Alfaro Shigueto et al. 2007; Wallace et al. 2011; Wallace et al. 2013a; Roe et al. 2014) as well as egg harvesting for consumption (Eckert 1997; Tomillo et al. 2008; Urteaga et al. 2012). In addition, as with sea turtles occupying other RMUs, climate change remains a threat and can have detrimental effects on the hatching success and hatchling emergence rates on nesting beaches (Saba et al. 2012; Santidrián Tomillo et al. 2015), as well as on the availability of important pelagic habitats (Willis-Norton et al. 2015).

The major threat facing East Pacific leatherback sea turtles is, however, the negative impacts of bycatch on the abundance of adult sea turtles and (subsequently) associated annual nest deposits (Wallace and Saba 2009; Hamann et al. 2010). During the 1990s, thousands of leatherback sea turtles were caught as bycatch in human fisheries, which contributed greatly to the ongoing decline in population size (Frazier and Montero 1990; Spotila et al. 1996). Gillnets and longlines are the primary fishing activities having a negative impact on East Pacific leatherbacks (Wallace et al. 2013a). In addition, leatherback sea turtles are caught within the gillnets and/or longlines of fishing vessels originating from a range of countries, such as from Mexico, Panama, Colombia, Costa Rica and Nicaragua (Ortiz-Alvarez et al. 2020).

The threats facing leatherback sea turtles within the East Pacific is so detrimental that, if left unaddressed, the entire population will continuously become prone to regional extinction (Ábrego et al. 2020). The absence of portfolio effects at the RMU-level is likely due to the declines in the annual number of nests at 13 out of 17 rookeries. The increase in the abundance of nests at four rookeries was not sufficient enough to buffer declines evident at the remaining rookeries situated in the “complex” East Pacific RMU. In addition, the rookeries that experienced an increase in the annual number of nests deposited include some of the smaller rookeries with a low average annual number of nests (Table 2.2). As a result, this population may continue to experience an overall decline in the coming decades.

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