



PROFESSORIAL INAUGURAL LECTURE

PROFESSOR RONEL NEL

Topic:

**SEA TURTLES AS OCEAN AMBASSADORS: OPPORTUNITIES AND CHALLENGES**

Faculty of Science

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**SEA TURTLES AS OCEAN AMBASSADORS:  
OPPORTUNITIES AND CHALLENGES**

INAUGURAL LECTURE

By

Professor Ronel Nel (PhD)

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## Abstract

Sea turtles are ocean migrants that nest on the same beaches where they were born but forage on reefs and oceanic waters great distances away. Movement between these locations is sometimes years or even decades apart. Because of these broad-ranging movements and the many countries, they visit throughout their lives, effective conservation can only be achieved through international cooperation. However, wherever and whenever sea turtles come ashore, they fascinate people. Watching a sea turtle nest is like looking back through a window into deep time. This appearance and disappearing act of sea turtles create an enigma that elicits a multitude of disciplinary, inter-, and intradisciplinary teaching, research and engagement opportunities ranging from archaeology to social sciences, including tourism, biology and ecology, conservation and policy. In these different spheres, I operated over the last two decades to understand sea turtles, their biology and behaviour to affect their conservation.

The biggest question I have pursued in my research career is to understand why the leatherback sea turtle population (*Dermochelys coriacea*) nesting in the iSimangaliso Wetland Park, South Africa, has not increased despite decades of protection. Another sea turtle species, namely loggerheads (*Caretta caretta*) nesting in the same area, experiencing similar conditions, has responded positively to conservation.

Through two decades of research evaluating the intrinsic and extrinsic population drivers, such as reproductive output, age to maturity, natality and mortality, it seems evident that the population dynamics of sea turtles is much more complicated than what a simple population model would predict. From the literature, it is clear that other species, like the Mediterranean monk seal, red knot (a sandpiper) and other coastal species, are suffering a similar fate, i.e., lack of recovery despite conservation. These trends suggest that these species have become refugees in their own habitat. Marine habitats are transformed through human activities and may now be unsuitable to support larger populations under the current climate for these complex species.

Current research is aimed to disentangle past and present distributions to assess if these species have responded by using alternative habitats over time or if there are body condition parameters (such as individual size, offspring size or survivorship, or metabolomics) that will point us in the direction to grow these endangered populations. Our research suggests that sea turtles, with their very complex life history facing multiple threats, live at the edge of success and extinction. Understanding and managing their path to success is a delicate balance with many aspects that need consideration.

[Full text: Sea turtles as ocean ambassadors](#)

## **Introduction**

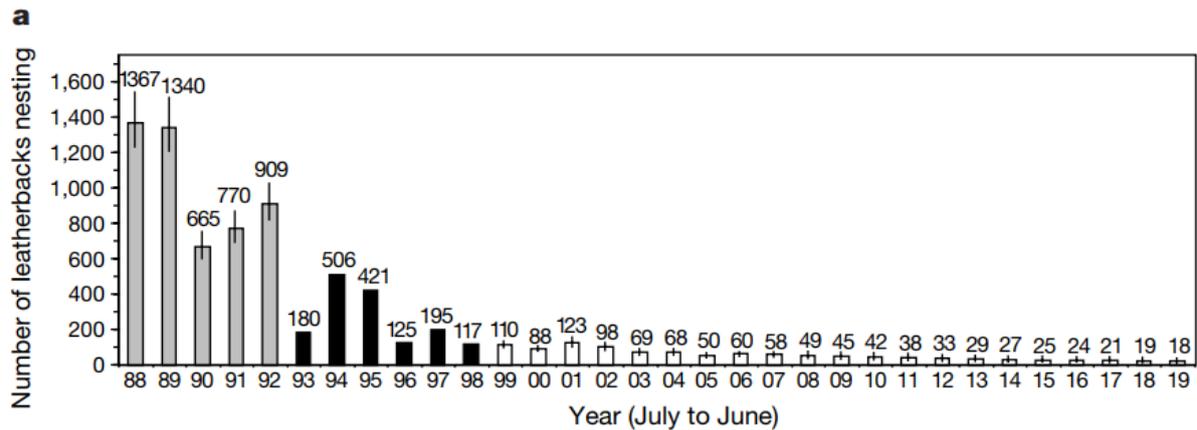
I am delighted to present to you my inaugural lecture entitled sea turtles as ocean migrants. Most of us would say that we are familiar with sea turtles but have only interacted with them in aquaria or got an idea of the size in displays. But it is when you first see them in the field that you really get to appreciate what they are about. You can admire the dexterity with which a female digs a hole for her eggs or see the beastliness of them close up. Then there is the fragility and chaos of a nest hatching. It was the same for me when I saw my first leatherback female. I am not a small girl and neither was she. But this is where my story starts...



**Ronel Nel with the first leatherback she ever saw. (Photo Credit: Paulo Luschi)**

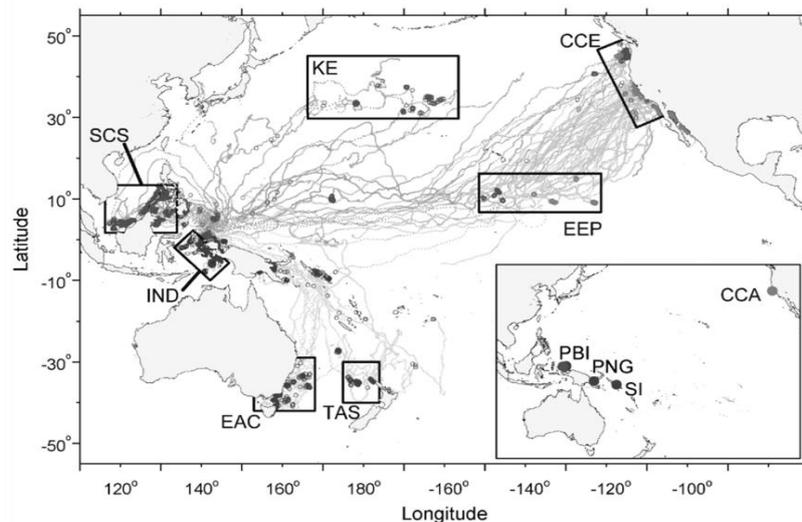
## **Pacific leatherbacks**

Just a year or two before I started working on sea turtles that this nature publication (Spotila et al 2000) indicated that leatherback turtles in the Pacific Ocean faces extinction and implying that this was partly driven by interactions with fisheries. The Playa Grande population declined from about 1500 individuals to less than a 150 individuals in a decade. They also predicted that once the population have declined that much that it is much more vulnerable and will take much longer to recover. And their prediction became true. The numbers nesting currently on this beach is less than 30 per year with the population listed as Critically Endangered.



Population decline in leatherback sea turtle population in the Pacific Ocean (from Spotila et al 2000).

A decade later Benson et al (Benson et al 2011) published a paper that reported on the transoceanic migrations of Western Pacific leatherbacks. Individuals migrate from the beaches in Indonesia and Malaysia to multiple locations in the Pacific Ocean but most striking is the transoceanic movements from nesting grounds in the west to, across the entire Pacific which is about half the surface area of the globe, to the foraging ground in the east. This is the first point I want to make – sea turtles require international cooperation for conservation. So, nations get together regularly to discuss common conservation issues even if they are at odds on economic affairs or policy. Sea turtles facilitates common ground.



Transoceanic movements of Western Pacific leatherback turtles (from Benson et al 2011).

### Opportunities

Sea turtles are however not the only species that have these massive transoceanic migrations. There are dozens of species including fish, marine mammals, and sea birds (Block et al 2011). The difference however is that sea turtles use a variety of different habitats in the process, including crawling out on the beach where females lay their nests. It is here where they enamour people, irrespective of age, culture, or creed. It is impossible to be unaffected watching these charismatic beasts. It is also here where opportunity presents itself!



**Collage of pictures of people admiring nesting sea turtles at different rookeries across the Indian Ocean.** (Photo credits left to right: Stephanie Ciccione, Douglas Hykle, Diane Le Gouvello, Jason Boswell, Welly Qwabe – centre photo)

Because of the charismatic nature, the wide-ranging distribution, the complicated life history and the bridge between nature and people over time it is a most ideal study animal. It allows for disciplinary studies as well as inter- and transdisciplinary collaborations. For example, these are species that fossilised reasonably well which give us a glimpse into evolutionary time. Some cultures, for example the Iroquois people believe that North America was formed on the back of a sea turtle and the indigenous people of Australia believe that “the Great Mother Turtle” will guide her hatchlings safely at sea. Turtle shell, fisheries and farming was at the heart of many island economies but that has now been replaced with tourism and advertisement, allowing for a range of interdisciplinary opportunities. The biology and ecology are obvious themes and where most of tonight’s presentation will centre, along with conservation and management, including spatial planning, and naturally, law, policy and multilateral environmental agreements. In fact, we can clearly see all three university spheres of Teaching and Learning, Research and Engagement and internationalization in these domains. For example, I have to date graduated 17 M and D students, and 26 Hons students, more than 60 publications or technical reports on sea turtles. Five of the students graduated or studying with us are international students and I have participated in an abundance of national meetings, including 22 international meetings negotiating on behalf of the country or providing decision support to governments in the Indian Ocean. However, these very same attributes that make sea turtles such ideal study animals also come with an abundance of challenges. This is what the rest of the presentation will be about.

## Challenges

Few people know that South Africa, and particularly the Natal Parks Board, now Ezemvelo KZN Wildlife, is a global pioneer in sea turtle conservation. We have the longest quantitative monitoring program in the world on leatherback sea turtles, and second longest on loggerheads. This all started in 1963 when they knew very little about these critters and no “best practice protocols” yet established. However, I got my first job at Ezemvelo where I was introduced to turtles and the general interpretation was the turtle conservation program a success. However, my interpretation was different and found it necessary to start a more rigorous research program that provides more in-depth understanding of the population dynamics.



**Photos of early pioneer-conservationists in South Africa developing best practice approaches to monitor sea turtles (Photo credits: George Hughes).**

The characters for the rest of my story are thus the Leatherback turtle (*Dermochelys coriacea*) and the Loggerhead turtle (*Caretta caretta*), and in particular the isolated South West Indian Ocean populations. These populations were first recognised as genetically isolated and individual management units (Wallace et al. 2010) with ~ 70% of the turtle nesting located in the iSimangaliso Wetland Park, a UNESCO world heritage site. The one single question that has driven most of the research of my career is to investigate why this leatherback population is not increasing despite the significant conservation effort?

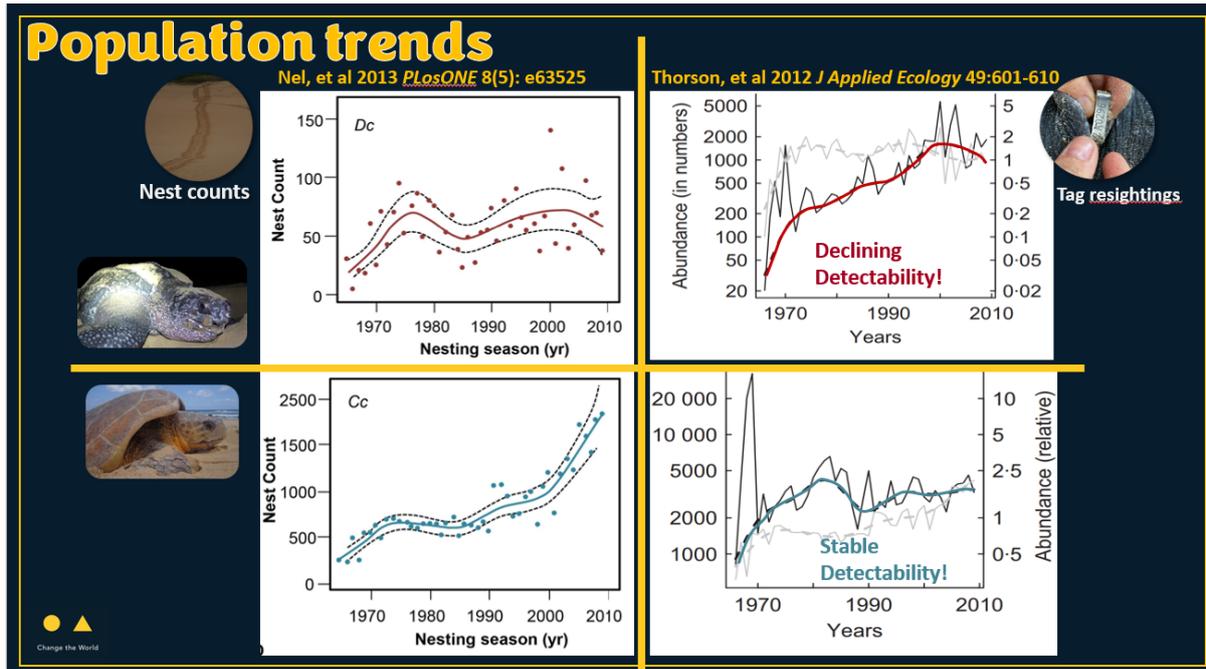


**Two nesting sea turtles from iSimangaliso Wetland Park South Africa. On the left, a leatherback, *Dermochelys coriacea* and the right, a loggerhead turtle, *Caretta caretta*. (Photo credits: Ronel Nel and Linda Harris)**

### **Population modelling**

With my first sabbatical I headed off to the Pacific North West to consult with the world's leading population modellers at the University of Washington. We ran two different population models; the first was based on the number of tracks counted in the monitoring area (Nel et al 2013). The advantage is that this approach is fairly robust and does not require the individual animal to be seen, but only the tracks. And by using the same index we can compare trends over time of the same species or between two species. The first model confirmed my hypothesis that loggerhead abundance was growing rapidly but leatherback abundances were at best stable. The second model, based on individual tag sightings gave a contradictory answer. It appeared as if the number of leatherbacks were increasing whereas loggerheads were stable (Thorson et al 2012). The interpretation was due to a declining detectability of individual leatherback tags which suggested either an increase in tag loss or wider use of the nesting area. The stable detectability in the loggerhead number gave us greater confidence in the other metrics that we derived from this same model.

# Population trends

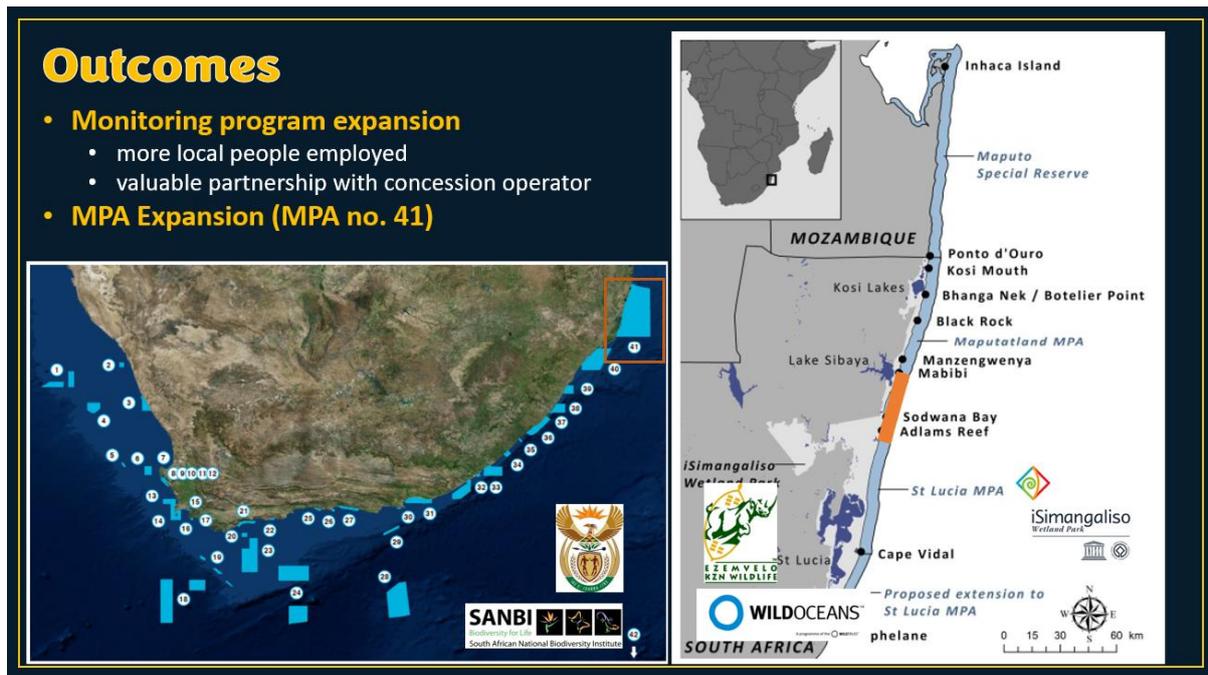


Population trends from two different models applied. On the left it is a GAM based on track counts (by Nel et al 2013) and on the right a mark-recapture model based on flipper tag resightings (by Thorson et al 2012). Population patterns for leatherback turtles are in the top panels and the loggerhead trends on the bottom panels.

## Spatial distribution

To investigate these contradictions, and understand interesting behaviour, we applied several satellite tags. In the case of loggerheads, it was 24 and 17 on leatherbacks sea turtles (Harris et al. 2015). The results from these tags clearly indicated incredible nest site fidelity by loggerhead turtles which nested almost exclusively in the high-density area in the north of the park. In the case of leatherbacks, the picture was much more complicated. The interesting loops were massively long distances outside of the world heritage site with less than half of the nesting events taking place in the monitoring area. In total, 12 % of the loggerhead nesting events are not captured while less than 40 % of the leatherback nesting events are recorded. The conclusion is thus that we have much more confidence in the conservation status of loggerheads than leatherbacks, but no explanation yet for the lack of recovery.

Two positive outcomes came from the satellite tagging study though. Firstly, an expansion of the monitoring area to include more community monitors and a valuable partnership with a concession operator that record tags numbers in an area where no one monitors (so expanded effort). And a sea-ward expansion of the iSimangaliso Marine Protected area to protect a larger proportion of leatherbacks while at the nesting ground.



Two outcomes from the satellite tagging study was an expanded monitoring program as well as an expansion of the iSimangaliso MPA.

### Drivers of patterns

One very important contribution from our research to the conservation and monitoring of these protected species is to investigate the potential reasons for this apparent lack of increase. To understand the rest of the talk we need to recap on a basic population model which is a function of the intrinsic growth rate ( $r$ ), the population size ( $N$ ), and the environmental carrying capacity ( $K$ ). We have seen in the last two years exactly how this plays out in the spread of COVID. Initially there is a small number of individuals which rapidly increases, unless there is an intervention to flatten the curve, or to reduce population size in the case of an animal population, which will lead to a slower increase. Finally, the population will increase to a level that is sustainable by the environment and will fluctuate around that level depending on local conditions.

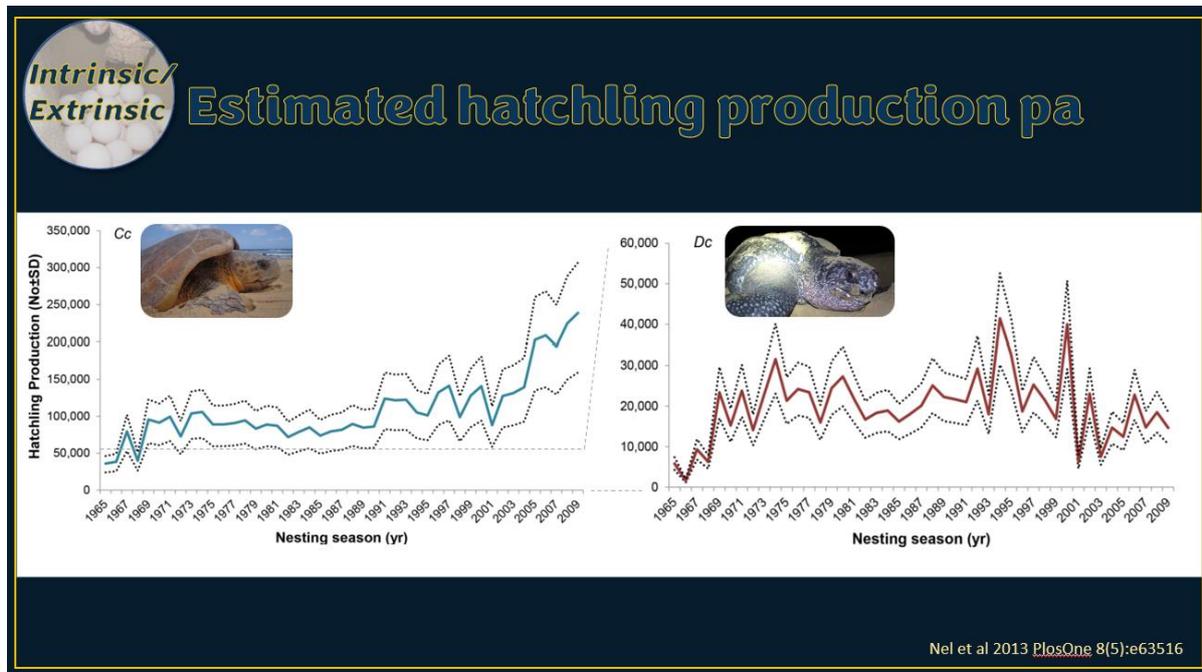
The individual drivers of each of these metrics can be described as follows. Intrinsic growth rate is dependent on, for example, fecundity (in the case of sea turtles that means the number of eggs produced per female per year), and the age to maturity. In other words, how long it will take for her offspring to come back to breed themselves. Population size ( $N$ ) is a function of the intrinsic environment, that will determine how many of these eggs/hatchlings will survive (i.e., natality) or the number of breeding individuals that will be killed in each year. In the case of sea turtles, immigration and emigration is largely ignored because they are a closed population coming back to the beaches where they were born and therefore not changing populations. The carrying capacity is a function of the habitat. In the case of sea turtles that is across multiple life stages so difficult to pin down, but still affected by the amount of space available, the quality of the habitat available, and how that will be affected over time by climate (and climate change).

#### 1. Fecundity

So, for loggerheads and leatherbacks we investigate these metrics starting with fecundity. For more than a decade now we have been counting the number of eggs laid by female turtles as they come ashore. The mean number of eggs per loggerhead is 106 eggs and slightly lower for leatherbacks at an average of 96 per individual. However, leatherbacks nest 6 – 8 times per season (and can be up to 10 times) while loggerheads only nest 3 – 5 times. Of these eggs about 78% of the loggerhead eggs will produce emerging hatchlings and about 70% for

leatherbacks. In total we see that the number of hatchlings produced per loggerhead female per season is ~305 and ~445 hatchlings per leatherback female. So contrary to expectations, leatherbacks have the higher reproductive output per female (Nel, Unpublished data, Hughes 1974, Nel et al 2013).

At a population level though, loggerheads still win as they have a much larger population size than leatherbacks. The annual hatchling production for the population of loggerheads exceed 100 thousand hatchlings per year and is now estimated to be close to 250 thousand hatchlings per year whereas the total leatherback production is one tenth that, ranging between 20 – 40 thousand hatchlings emerging per year (Nel et al 2013).

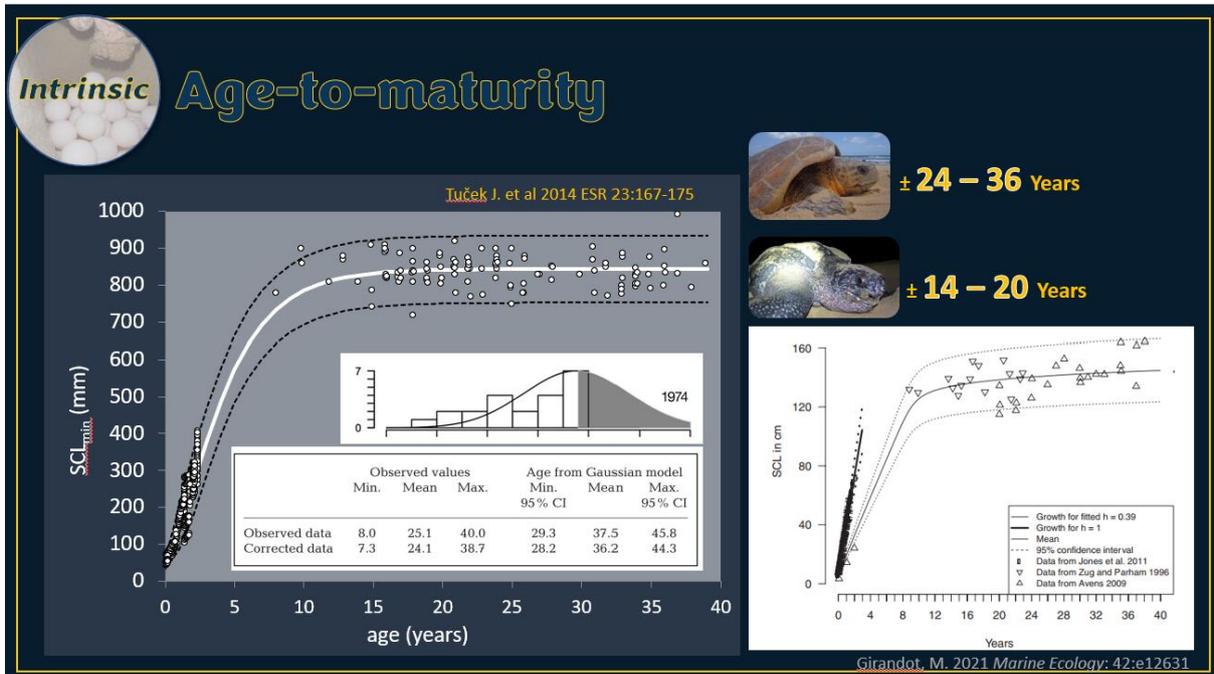


Estimated annual hatchling production over time per species based on the estimates of fecundity, hatching and emergence rate and female population size over time (Nel et al 2013).

## 2. Age-to-maturity

The next factor to investigate is age to maturity. For loggerheads a mutilation tagging experiment was done where more than 10 thousand hatchlings per year were notched with a specific year code. That is a permanent tag scar but allows for returning females to be identified to the year in which they were born. This was only conducted on loggerhead hatchlings as the morphology of leatherbacks did not allow for it.

Based on the number of individuals that came back by the time we did this paper the mean age of returning loggerheads was ~ 24 years. However, we recognised that it was only the early part of the notched population and with some population modelling it was estimated that the true age at maturity is most likely closer to 36 years of age (Tucěk et al. 2014). No such direct measurements for leatherbacks and the current estimates, although wide ranging, is converging on 14 – 20 years of age (Girondot et al 2021).

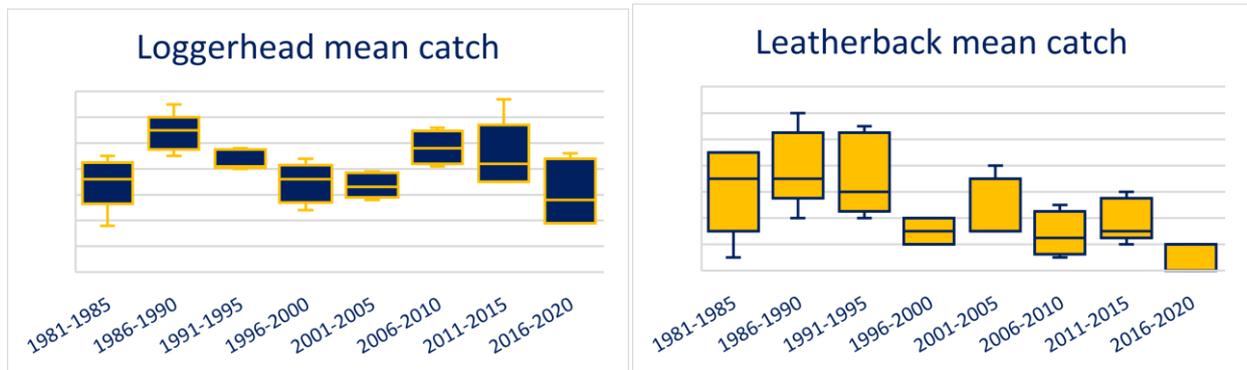


Two graphs summarising the growth rate and estimates of age to maturity of two sea turtle species. Loggerheads (left from Tucek et al 2014) and the current best estimates for leatherbacks (right; Girardot et al 2021).

To summarise the intrinsic factors, we can say that leatherbacks have a higher individual productivity and they come back sooner to breed but at least part of the large current population size of loggerheads is facilitating the population growth suggesting that the two populations may be at two different stages of the population curve.

### 3. Mortality

There are multiple sources of mortality to sea turtles both on the beach and in the open ocean. Given that nesting females and their brood is fully protected from anthropogenic threats in South Africa, there are only natural threats affecting them on the beaches. However, that is already considered in the population model. Once hatchlings enter the water there is a whole suite of man-made and natural threats for which we do not have very good estimates. However, there are two that I do want to single out. Firstly, plastic pollution. A varying number of hatchlings strand every year along our shores mostly depending on the climate and body conditions. However, what we have seen in recent years is that a large proportion of those that strand have a significant amount of plastic in the gut, particularly hard plastics. Even if this is not the primary reason for stranding, it is most likely a contributing factor, making for inefficient digestion or disease causing. The other very important threat to sea turtles is fisheries – both on the coast and offshore. Coastal fisheries in South African waters is well-managed (as far as sea turtles are concerned) with the largest known catch in the KZN bather protection nets. However, the Sharks board is monitoring this fishery very diligently with a reduction in effort over time, and if anything, its effect is much greater on loggerhead sea turtles than leatherbacks which has a median annual catch of three or less, of which the majority of these are male turtles.



**Trends of sea turtle catches in bather protection nets confirming that many more loggerhead than leatherback sea turtles are caught annually (Unpublished data KZN Sharks board).**

Offshore fisheries are more difficult to manage but there are observers on a large proportion of our tuna and sword fishing longlining fleet. It provides an idea of the number of turtles caught per set per species. Monitoring impacts directly is difficult because of the large variation and the enormous amount of uncertainty in the data. However, if we go back to the analysis by Thorson where we have two long-term data sets, there is no explanatory power in either data set (for both loggerheads and leatherbacks) in terms of mortality. It does not mean that fisheries are not a contributing factor, but there it is not the single explanation as many conservationists make it out to be.

#### Sea turtles as potential refugee species

So now, after a decade of research we have a good idea what are *not* the causes in the lack of recovery. So, it led me to go back to the literature and investigate if there are other marine species that are suffering the same fate... so failing to recover despite conservation. Four case studies got my attention. Mediterranean monk seal, *Monachus monachus*, were excessively hunted for hundreds of years for their skin, meat and oil or killed because of being in competition with fishers leaving only relict populations in the most inaccessible locations (to humans) (according to Gonzales 2015). The extant Mediterranean monk seal have only two relict populations left, with only a few hundred individuals left. Historically, they used a variety of different habitat types but are now restricted to a few coastal caves as haul-out or pupping grounds with lower survival rates. The story is similar for the southern sea otter *Enhydra lutris*. These species were harvested by traditional means for 7000 years but escalated in the last two centuries until only about 2000 individuals remained. The species has recovered well in Washington and Alaska (*E. lutris kenyoni*) but (*E. lutris nereis*) is still doing poorly in California. Hughes et al (2019) argued that habitat complexity may be partly responsible for this differential recovery. The rocky habitat available to them seems to suboptimal and that larger sheltered bays and estuaries, like San Francisco Bay, would be better suited with a greater abundance of food and a higher carrying capacity. Coho salmon (*Oncorhynchus kisutch*) is a migratory fish that spawns in cold water lakes during late fall and early winter. However, freshwater abstraction in spring and summer preceding this spawning migration drops the water levels so that the lakes and rivers become fragmented and the temperatures fluctuate hugely (Jeffres and Moyle 2012). Restoration projects attempted to rehabilitate gravel spawning beds that were physically successful but not thermally successful. the last example is a migratory sandpiper, the Red Knot (*Calidris canutus*). These migratory birds are on their way north this time of the year for their breeding in northern Canada, and use Delaware Bay as a staging site to fatten up on horseshoe crab eggs (Gillings et al 2009). However, as horseshoe crabs are declining (because their blood is used in the pharmaceutical industry) there is less and less food available at this site. There is now a substantial decline of this species and is likely to be listed as a threatened species on the next evaluation. These species have been proposed as candidate refugee species.

Refugee species principle are those species that are conserved in suboptimal habitat. This notion is based on the declining population paradigm proposed by Caughley (1994). He stated that populations, even small ones, in stable environments will persist whereas even large populations in highly stochastic or suboptimal environments will decline. Traditionally we think of marine systems as stable however, in recent years that is no longer the

case. Climate change is adding to the unpredictability of marine ecosystems and habitats are no longer suitable as they have become degraded, or species are displaced.

### **Terrestrial example of a refugee species**

The sentinel example of refugee species is the European Bison (proposed by Kerley et al 2012). This species was broadly distributed over the plains of Europe and populations have shrunk and distribution changed until only two relict populations remained. Despite 100 years of conservation these populations did not recover, until the realization that these forest habitats where they remained was the only habitat where they could hide from hunters but is suboptimal foraging habitat. Since this realisation and adjustment in management regime the species has bounced back. These authors also proposed three conditions for species to be listed as candidate refugee species; that is range contraction, population decline (or at least lack of recovery) despite conservation, and anomalous habitat use.

### **Current research**

That brings me to my current research and Pew Fellowship project. The questions that I am investigating are: firstly, to establish if marine (migratory) species can be refugee species? Secondly, if so, would it be the same three criteria or are there different criteria for marine species (like having to face serial ecological traps). And thirdly, is the South Western Indian Ocean leatherback population such a species, that is being protected, but with only suboptimal habitat left? To be a refugee species it must meet the three criteria proposed by Kerley et al (2012). I have already made a case for lack of recovery despite protection, but we need to review past and current distribution and we need to assess if there are current habitat anomalies. So, let's look at what we know on these two matters.

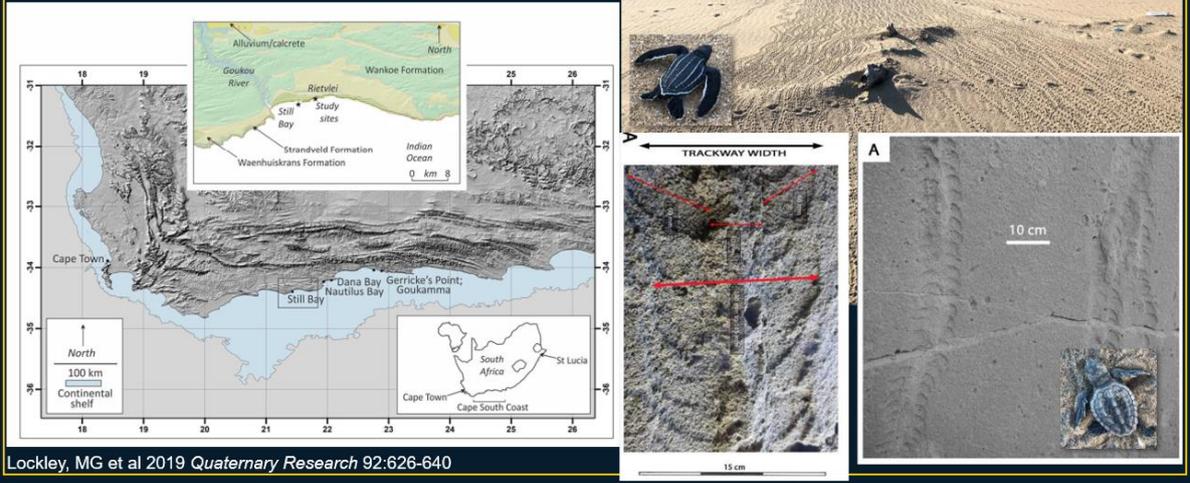
#### Space

##### *Past distributions*

The historic distribution of sea turtles is hard to infer unless it is in the written record somewhere. However, fortuitously, our Paleosciences Unit stumbled onto some really well-preserved animal tracks from the Pleistocene. Among these tracks were these peculiar tracks and on interrogation we realised that they matched turtle hatchling tracks (Lockley et al 2019). More interestingly, they matched the sizes of the two species that we currently have nesting in the country. What you do have to realise is that the period we are talking about is ~ 100 thousand years ago, so we cannot say that it is the same species. What it does tell us though, is that the climate was suitable along the south coast of the continent for successful sea turtle nesting and hatching.

# 1. New fossil sea turtle trackway from the Pleistocene

90-130 K ya



Lockley, MG et al 2019 *Quaternary Research* 92:626-640

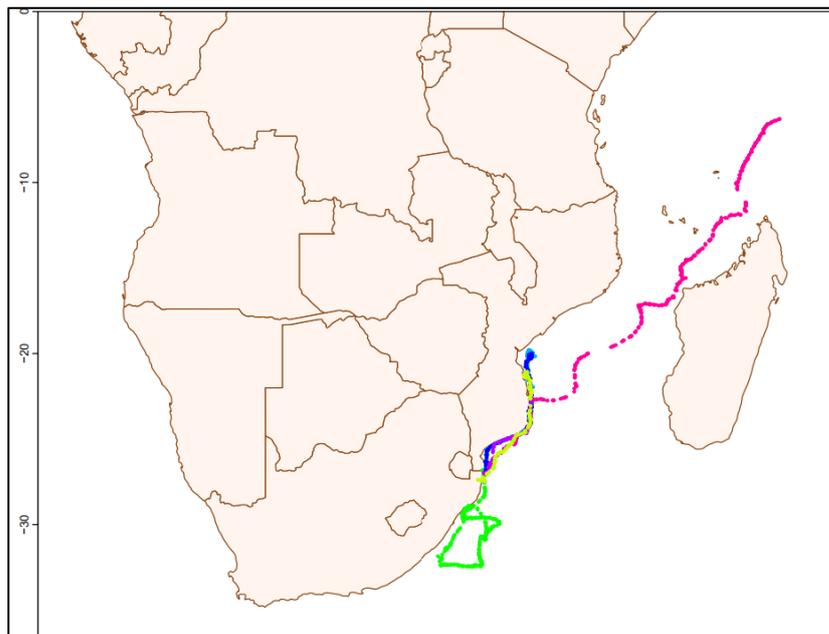
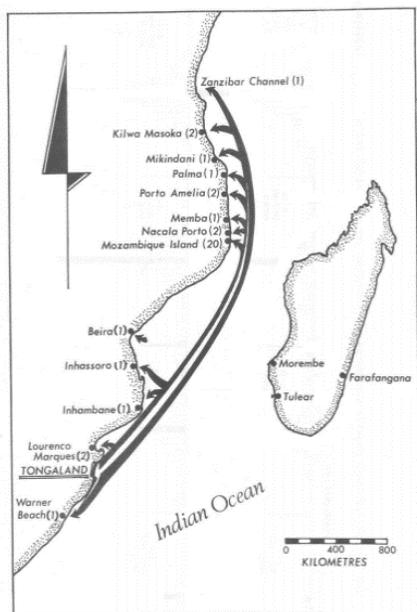
Evidence from the Pleistocene suggesting that the climate was much different a 100k years ago and the south coast of the African continent could have supported sea turtle nesting populations (Lockley et al 2019).

## Contemporary distribution

Coming more into contemporary times, we have more of a written record in the colonial history. The writings of the natural historian, Rose Montero, report of large turtles of “good quality” in the Bay. This bay being Delagoa Bay (or Maputo of today). The letters of Sydney Turner, in 1961, report on the large number of turtles caught in nets in estuaries. In this case the Mzimkhulu river, which is on the lower south coast of KwaZulu-Natal. Inferring from the size information he provides (5 hundred-weight) or 500 pounds/250 kgs, suggest that these would be mature green turtles or possibly loggerheads but not leatherback turtles. He also continues to comment on how tough these individuals are that they can be left on the lawn for weeks without any harm. My I sidestep for the moment and confirm that all research that I have spoken about under our program has been with the appropriate permit and ethics consent.

The writings of Dr George Hughes have suggested that the motivation for the South African turtle monitoring program was the recognised threat of turtle harvesting on the beaches of northern KZN. The outcome of this investigation is that we can't report on changes in distribution but there is definitely a case of past abundances of sea turtles that seem to exceed the numbers we see today.

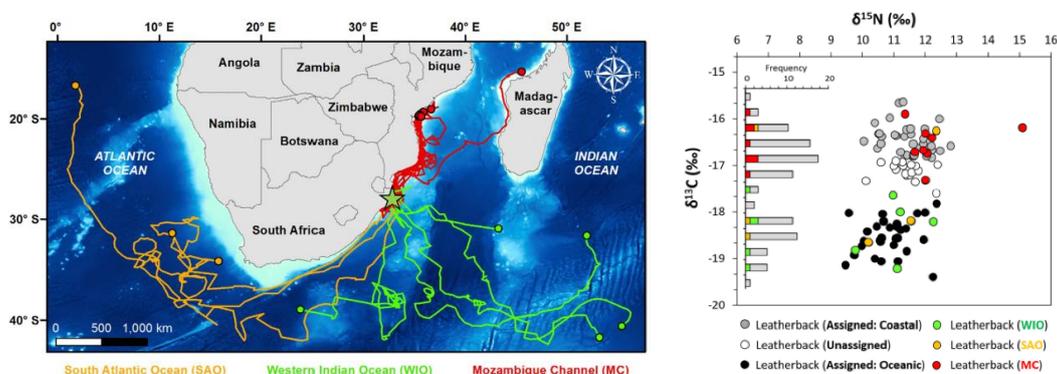
If we can't pinpoint the distributions of the past then we can, at least, describe the contemporary distribution. The first post nesting descriptions of loggerheads came from flipper tag returns from Dr Hughes' work (Hughes 1974). His collaborators later deployed satellite tags and mapped a similar distribution – or at least to central Mozambique on the Sofala Bank off the Zambezi delta. These distributions have been matched by the SA government's sponsored satellite tagging program and the current collaborative Pew and STORM projects.



Historic distribution as described from flipper tag returns (Hughes 1974, left) and the current distributions from satellite tags deployed under a STORM/Pew/NMU collaboration (Nel unpublished data).

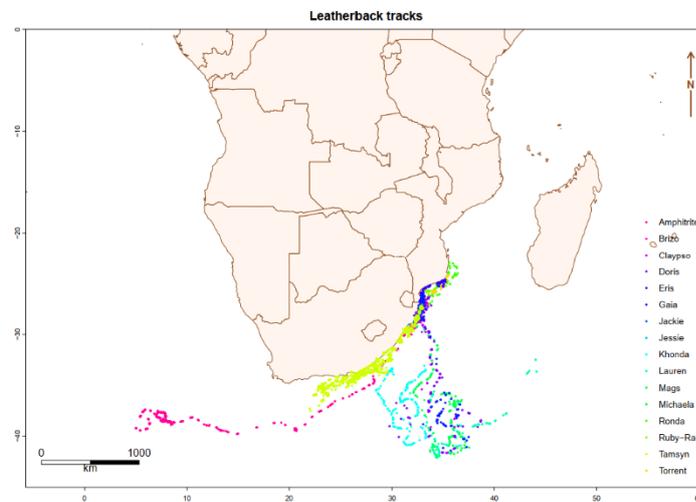
The leatherback tracks are a little bit more interesting. The first satellite tags deployed by our Italian colleagues, using back packs, drifted southwards with the Agulhas current and individuals ended along the south coast of the continent or off the west coast of South Africa (Luschi et al 2006). More recent satellite tagging in collaboration with some US scientists suggested that there is a strong northerly movement of leatherbacks not previously noted. In fact, half of the tags deployed moved north into the Mozambique channel. It was not sure if this was a change in methodology or a real migration route, so alternative distribution, not yet recorded.

Among all of the South African partners (Ezemvelo, DFFE and NMU) we scraped money together and deployed another 17 satellite tags on leatherbacks with very similar outcomes (Harris et al. 2018). What was more interesting than confirming the post nesting migrations was the notable novel behaviour that left a clear isotopic signature suggesting that these individuals show fidelity to the habitat, and that there is a clear split in leatherback individuals foraging on the coast versus those feeding offshore (Robins et al 2016). Harris et al 2015 also reported of this same clinger and rover behaviour that were present in the interesting distribution of these individuals.



Migration routes (left) and the isotopic signature (right) of leatherback turtles that are foraging along the coast (in red) and in the open ocean (green and yellow) with a clear split in the values (Robinson et al 2012).

The latest distributions of leatherbacks currently at large are matching these very same patterns of coastal clinging behaviour and ocean roavers, although for the first time we see individuals hugging the coast, going south.



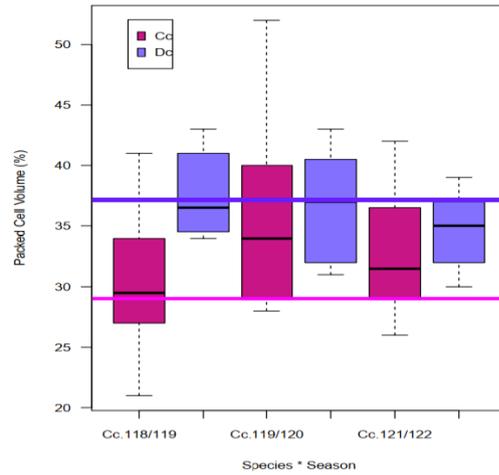
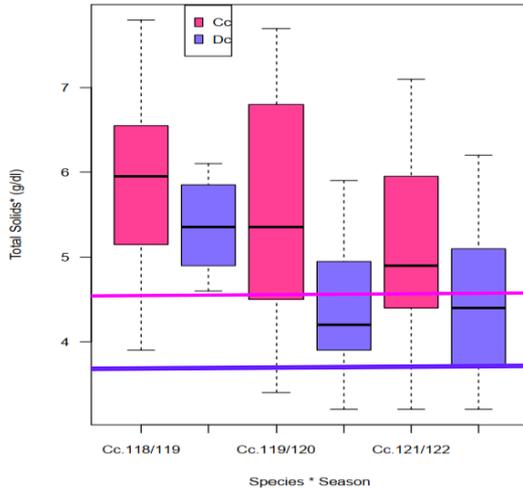
Current distribution of leatherbacks equipped with satellite tags swimming in the Indian Ocean. The tags are deployed under a STORM/Pew/NMU collaboration (Nel unpublished data).

## Habitat Quality

### *Habitat anomalies*

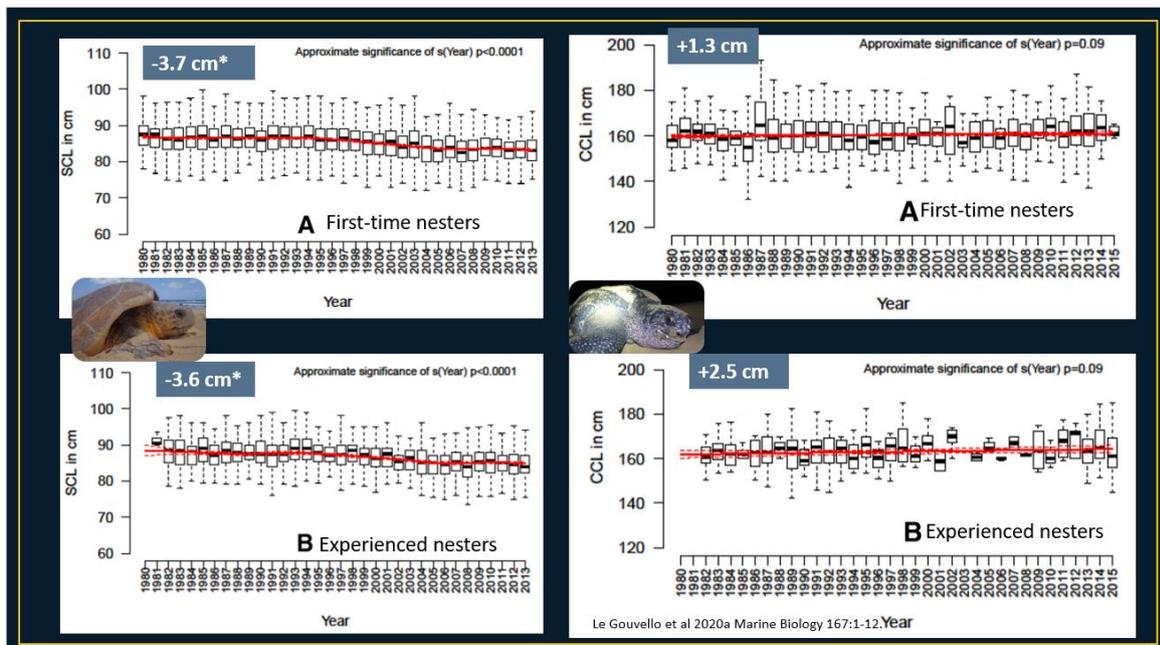
The last factor we need to investigate is habitat anomalies, but that is very difficult to do in the marine environment which is constantly changing. The principles we use to evaluate these patterns must hold across nesting and foraging habitats as well as along the migration routes. It is important that connectivity is maintained over thousands of kilometres and decades apart in time. Ironically, even a small amount of habitat loss may lead to rapid extinction, and it is the survivorship of a small critical habitat patch that will dictate success, like we see from the example of the red knot in its staging area in Delaware Bay feeding on horseshoe crab eggs.

It is however very difficult to isolate these patches for marine migrants like sea turtles. The question is if we can use body condition metrics to assist. So, we used blood metrics on the nesting ground as indicators over the last three years. If we compare the basic blood metrics, like Total Solids (a proxy for protein levels) against that of reference values (in this case it is a growing population in the North West Atlantic nesting in Florida; Perrault et al 2012) it seems like both our leatherbacks and loggerheads are in great body condition when they arrive on the nesting ground. It is similar for Packed Cell Volume (or PCV) which is a gradient between anaemic at the lower end and dehydrated at the top end of the scale. Again, the values for South African turtles is within a range suggesting good body condition.



Blood parameters, Total solids (left) and Packed Cell Volume (right), for loggerhead and leatherback females measure on the nesting grounds over three seasons. All values are in the range or above of published reference values for comparable conditions (from Perrault et al 2012).

A longer-term indicator would be body size. It is expected that mean body size will decline if there are more younger (so smaller) individuals in the population. However, we evaluated the body size for both species, for two size classes; those are first time nesters (or neophytes) and experienced nesters. Surprisingly, the body size of loggerhead turtles of both young and experienced nesters has declined significantly by almost 4 cm in 30 years (Le Gouvello et al 2020a). I anticipated that we would see the same in leatherbacks. However, the opposite was true. Leatherback turtles have increased in size over time.



Change in individual size of loggerheads (left) and leatherbacks (right) for both first-time nesters (top) and experienced nesters (bottom). (From Le Gouvello et al 2020a.)

This is important as the reproductive output of females is a function of size. Smaller females are therefore expected to have reduced output (so fewer eggs) or less competitive offspring (so smaller eggs). In the case of South African loggerheads, the relationships do indeed hold for loggerheads. So larger females lay more eggs so a reduction in size should lead to fewer eggs. This is also the case for leatherbacks. So, because the females tend to be larger we expect more eggs. However, when we compare the size and number of eggs of both species with those of other sea turtle rookeries across the world, all of the loggerhead values tend to be average. The leatherbacks are however large in size, with large clutches but smallish eggs (Table 1).

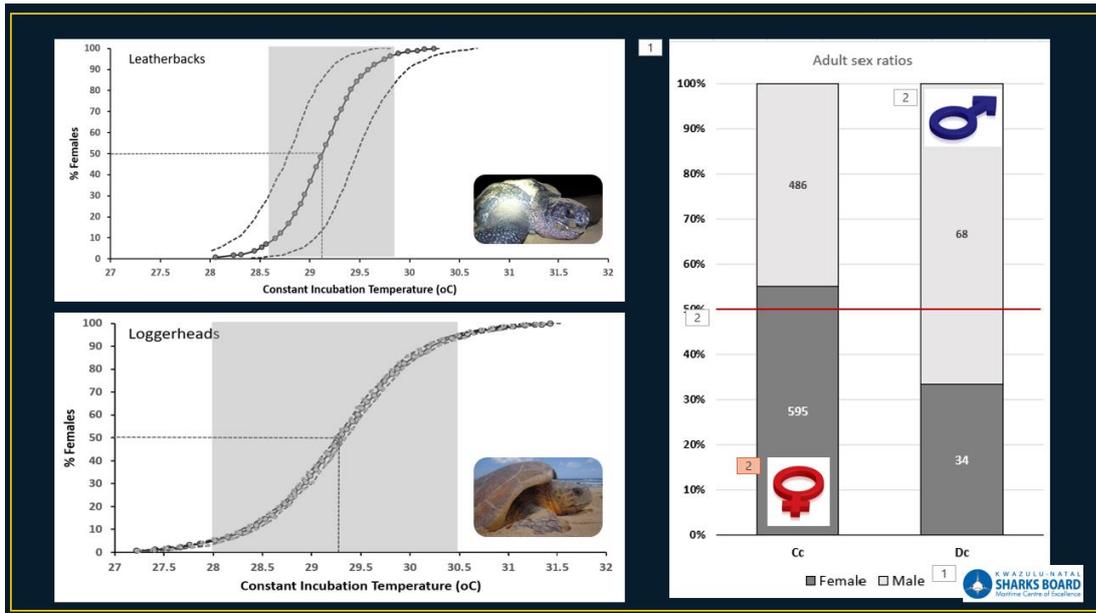
TABLE 1: Comparison of female sizes and egg sizes from the South African rookery to that of other sea turtle rookeries around the world. (From Le Gouvello et al 2020b.)

	<b>This study</b> Mean $\pm$ SE (n)	Range of mean measurements worldwide (n)
<b>Loggerhead</b>		
Maternal length (SCL, mm)	<b>835.4</b> $\pm$ 39.31 (265)	668.6 (11) – 970.9 (25)
Clutch size	113.5 $\pm$ 19.23 (265)	70.4 (128) – 149 (26)
Egg size (mm)	<b>39.9</b> $\pm$ 1.44 (2650)	37.6 (23) – 49.9 (260)
Hatchling length (SCL, mm)	43.9 $\pm$ 0.08 (412)	40.0 (221) – 45.8 (60)
Hatchling mass (g)	19.0 $\pm$ 0.09 (412)	18.7 (28) – 22.0 (58)
<b>Leatherback</b>		
Maternal length (CCL, mm)	<b>1633.6</b> $\pm$ 104.58 (24)	1438.0–1695.0 (25)
Clutch size	101.0 $\pm$ 26.24 (24)	61.8–104.0 (34)
Egg size (mm)	<b>50.8</b> $\pm$ 2.00 (240)	51.0–55.4 (17)
Hatchling length (SCL, mm)	56.3 $\pm$ 0.29 (48)	53.5–65.0 (13)
Hatchling mass (g)	38.8 $\pm$ 0.26 (48)	37.3–52.6 (12)

## Climate

### *Sex ratios*

The last factor to investigate is the effect of climate, and that is now in a changing climate extremely important. Sea turtles undergo environmental sex determination, so they do not have male and female genes, but the environmental cues during a specific part of the incubation period will trigger them to be male or female depending on cold or warm conditions. Cooler temperatures produce males and warmer temperatures females. We have done some work incubation sex ratios and determined the approximate pivotal temperatures for the two sea turtle species. Tucěk (2015) approximated the pivotal temperatures, so where we get a 50:50 sex ration to be very similar for the two species around 29.2 – 29.3 °C. However, these relationships are much more complicated than what a single graph can predict since the curve moves to the left or right depending on the moisture level in the sand. What we can measure however is the ration of adult turtles that we get. The most reliable and informative sample is from the bather protection nets. These samples suggest that we have a balanced loggerhead production or slightly female biased which is aiding recovery, whereas we have a strong male bias in leatherbacks with a 2: 1 male to female ratio.



Comparison of incubation curves of two sea turtles indicating similar pivotal temperatures but different transition ranges (grey). When we investigate the adult sex ratios (as they are captured in the bather protection nets) it suggest that South Africa's rookery has a female biased loggerhead population but a male biased leatherback population.

### In summary

Even though individual reproductive output is higher in leatherbacks and they replace themselves sooner by maturing at a younger age, and the different behavioural adaptations (i.e. clingers and rovers) and changed distribution (in addition to nesting outside of the monitoring area) that we see, the small eggs and apparent male bias underpins the lack of female recovery on the beach. The reproductive output by loggerheads, in addition to the large population size and female bias is enough to boost the population productivity.

The next step in my research is to complete the question on refugee species, and how that fits in with marine migrants. This will be completed with a thorough genetic investigation to assess current and past population structure. To rerun the abundance models with increased tagging and sampling effort. To complete a niche modelling exercise that reviews both thermal and ecological niches for hatchlings and adults, and finally to assess if the body condition is as good as we think it is from the simple blood parameters presented here.

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