Reproductive biology, morphology and diet of *Raja straeleni* (spotted skate) in South Africa

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Dedication and acknowledgements

I would like to give special thanks to my supervisor, Colin Attwood, for offering me a project that I have grown a passion for, sharing his expertise with me and for teaching me every step of the way.

Thank you to the people at Capfish and Birdlife for providing me with my samples from the trawl industry to complete my study.

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Declaration

I, **Alexandra M. Azevedo,** hereby declare that the work on which this thesis is based on my original work (except where acknowledgements indicate otherwise) and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other university. Furthermore, I authorize the University of Cape Town to reproduce, for the purpose of research, either the whole or any portion of the contents of this thesis in any manner whatsoever.

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Abstract

The spotted skate, *Raja straeleni,* is the most abundant and frequently caught skate in the waters of southern Africa. This study aims to add information on the morphology, reproductive biology and feeding habits of *R. straeleni* in southern Africa to better manage the species and to understand its role in the ecosystem. Samples were obtained from trawlers operating on the west and south coasts of South Africa during 2020. A total of 72 skates ranging in total length (L_T) from 392 to 695 mm were examined. The 19 males ranged from 437 to 630 mm and the 53 females ranged from 392 to 695 mm. The following relationships were quantified (1) disk width (D)$=0.77L_T-11.96$, (2) $D=0.94$*Length to first dorsal*-14.66, (3) male weight $W_{male}= 3.61L_T-22.74$, (4) $W_{female}= 3.32L_T-20.85$. The length-at-50% maturity (L50) of the males was estimated at 57.1 cm (95% confidence interval: 54.2-59.4 cm), or 91% of the maximum male length recorded in this study. The total length-at-50% maturity (L50) of the females was estimated at 62.5 cm (95% confidence interval: 57.0-64.0 cm), or 90% of the maximum female length recorded in this study. Adult skates were collected during a period of sexual dormancy, as deduced from the low sperm presence and lack of oocytes. The diet of 57 skates were examined of which four had empty stomachs two contained only unidentifiable remains. Prey items spanning six phyla were recorded. In terms of %frequency they were Arthropoda (17%), Chordata, (8.2%), Mollusca (4.5%), Echinodermata (1.9%), Annelida (1.9%), and Nemertea (1.9%). The trophic level of *R. straeleni* was 3.98 ±0.05 SE. The trophic level was previously calculated as 3.74 ($n = 421$) (Ebert and Bazzarro 2007). The difference in findings is a result of a higher incidence of squid in the diet of skates examined in this study. The average trophic level of *Raja* species is 3.76 ($n = 12$, 95% Cl = 3.71 to 3.80), and for all skates it is estimated at 3.78 ±0.05 SE ($n = 60$) (Ebert and Bazzarro 2007). The diet of *R. straeleni* is very similar to that of other skates. Approximately

1000 t are landed per annum, predominantly from the inshore Agulhas Bank, which suggests a standing biomass at least ten times this amount (Attwood et al. 2011). *R. straeleni*, like other skates, is an important generalist carnivore in the Benguela system.

Keywords: Length-at-50% maturity, batoid, Rajiformes, southern Africa

Introduction

Batoids (Superorder: Batoidea) include the skates (Order: Rajiformes : Rajoidei), from the squalomorph shark group, form the second-most diverse chondrichthyan order, compromising 25% of the described chondrichthyan species (Fowler et al. 2005). The skates are still under phylogenetic review, and there is some inconsistency among recent taxonomic classification and grouping. Heemstra and Heemstra (2004) reported that there were more than 220 species and nine genera, Compagno and Ebert (2007) reported that were 245 species and 27 genera, and the most recent report from Seret et al. (2016) described 574 valid species and 17 genera. The 17 genera most recently described are *Amblyraja, Beringraja, Breviraja, Dactylobatus, Dentiraja, Dipturus, Hongeo, Leucoraja, Malacoraja, Neoraja, Okamejei, Orbiraja, Raja, Rajella, Rostroraja, Spiniraja,* and *Zearaja* (Seret et al. 2016).

Morphology and anatomy

Skates in the family *Rajidae* are a morphologically group characterized by a dorsoventrally flattened shape, depressed body, a pointed snout, wing-like pectoral fins, a tail that's long and thin, two small dorsal fins near the tip of the tail, well-developed spiracles, pelvic fins divided into posterior and anterior lobes, five pairs of gills on the underside, a medial row of thorns or denticles, and a small mouth with powerful jaws and numerous teeth (Heemstra and Heemstra 2004).

Skates' anatomy provides a good indicator of the species' environment, ecological role, and life history. Their shape can range from being round to angular, and soft to hard depending on their geographic environments. For example, skates living on sandy or muddy bottoms have transparent, delicate skin on their head and belly. Skates living on rocky substrate have a thicker protective skin with dermal denticles on their ventral surface. Their disk can be soft and flexible to move freely in caves and crevices, or strongly flattened to live in sandy environments (Last et al. 2016). Their disk shape can vary dependent on their developmental stage and sex. For example, young skates have a rounder shape and become more angular with age, and male adults tend to have a longer rostrum and a curvier disk shape than females. Due to these differences, skates have a history of misidentification (Last et al. 2016).

There are macro-ecologic correlations with body size of skates such as trophic level, geographic range size and niche breadth. Many skates feed on a great variety of prey species as they grow, leading to a positive correlation between niche breadth and body size (Barbini et al. 2018). Large-bodied skates (>100 cm) tend to occupy a larger niche breath and high trophic levels like marine mammals, seabirds, and sharks (Ebert and Bazzarro 2007). Skates with large bodies tend to have a larger geographic size range, which increase their chances of survival (Dulvy and Reynolds 2002).

Reproductive biology

All skates are fertilised internally, the claspers of male's channel semen into the female's cloaca during copulation (Last et al. 2016). The males have enlarged, hooked spines on the dorsal surface, used for holding the females during copulation (Heemstra and Heemstra 2004). The skates are oviparous, and the females lay their egg cases in a dark brown, tough keratinous case on the seafloor or attached to a structure (Heemstra and Heemstra 2004). The young hatch, depending on the temperature of their environment, after a few months to more than 2 years.

Some cold and deep-water skates may only reproduce every two years. Age at maturity has been examined in skates varies from 5 to 17 years (Last et al. 2016).

Skates aggregate to spawn. Skates have minimal reproductive activity for the remainder of the year. This could be due to them struggling to find mates in dark deep water, or that they spawn with multiple partners, or that their eggs need to be put in a certain location. After reproducing, skates disperse, lessening the competition among individuals for food (Last et al. 2016).

Skates' distribution, characteristics and life-history

Rajiformes are a 'shelf overlap' species meaning that they occupy a wide range of environments, and they are found from the poles to the tropics in all oceans (Compagno 2005; Ebert et al. 2008). Skates are marine, with the exception of one species found in Tasmanian estuaries. Similar to most batoids, they occupy sandy or muddy benthic habitats (Compagno and Ebert 2007; Last and Yearsley 2002; Ebert et al. 1991). Skates prefer cold waters and are found from shallow coastal shelves to beyond the continental shelves, covering a depth range from 5 to 3000 m (Compagno and Ebert 2007; Heemstra and Heemstra 2004). Skates' diversity is greatest on continental shelves between 100 and 500 m (Compagno and Ebert 2007). In low and mid latitudes, skates are in deeper waters and are replaced with stingrays (*Myliobatiformes)* in the warm shallow waters. As they move towards the poles, skates occupy shallower water (Compagno and Ebert 2007).

Skates are predisposed to a high rate of speciation due to their bottom-dwelling nature and their flattened body shape. Their benthic environments are highly variable compared to pelagic species. Due to their specialisation, it is difficult for a species to move throughout different geographical areas or environments. For example, one species may be more specialized for rocky environments and their morphology is not as well suited for sandy environments. Eventually, this leads to limited gene exchange and a generation of a new species (Last et al. 2016). Also, the skates need to find localised feeding or spawning habitats to lay their egg-cases, unlike live-bearing species, like rays, that move widely with their unborn pups. Speciation is enhanced by stronger site fidelity leading to faithfulness in spawning or egg laying grounds. These factors contribute to skates having more species, a greater species diversity and smaller geographical ranges compared to other batoids (Last et al. 2016).

The impact skates have on demersal marine communities is not well known, despite their abundance in the demersal communities and in trawl catches around the world (Compagno et al. 1991). Instead of using their vision, they have highly developed electroreception systems. They are used to detect weak electric fields to find their prey and for mate recognition (Pasolini et al. 2011; Tricas et al. 1995). Skates have a diverse carnivorous or scavenger diet and the main prey taxa they consume are invertebrates, cephalopods, bony fish, polychaetae worms and gastropods (Heemstra and Heemstra 2004). These are the same food resources as many upper trophic-level marine predators and due to this, skates are likely to be important ecosystem regulators (Ebert et al. 1991). There are few quantified descriptions of the diet compositions of skates, but the general consensus is that skates occupy high-trophic levels, and their body size has a positive correlation with higher trophic levels (Davenport and Bax 2002). The concern is that the reduction of skates' abundance could influence ecosystem dynamics throughout the oceans (Beddington 1984; Rogers et al. 1999). To better understand skates' role in the ecosystem, their diets need to be described and compared with other species in the ecosystem (Ebert and Bazzarro 2007).

Skates' life-history traits typically include large body size, slow-growth, high longevity and low fecundity, which make them particularly vulnerable to exploitation (Compagno and Cook 2005). Species' life-history characteristics contribute to the resilience of a species to exploitation or other perturbations. Certain life-history features are known to be predictors of low resilience, so knowing where a species lies in the complex spectrum of life-histories will help to provide information on their resilience (Dulvy and Reynolds 2002). Stock assessments now frequently use Bayesian models that require prior information on life history parameters. Such information can be massively informative, particularly for non-target species which tend to be data poor.

Anthropogenic impacts

One of the major sources of direct and indirect anthropogenic impacts on marine ecosystems is capture fisheries that may cause over-harvesting and associated habitat damage (Yemane et al. 2009). Skates' large body size (and associated large offspring size) make them vulnerable, and they can be caught in fishing nets from a young age (Dulvy and Reynolds 2002). Along with this and their other life-history characteristics, skates are poorly suited to withstand fishing pressure. It could take decades for the population to recover compared to more productive teleosts (bony fish) (Camhi et al. 1998; Hoeing and Gruber 1990; Japp et al. 1994). The continued fishing may lead to ecosystem effects such as a cascade effect down the food chain or food chain collapse (Peterson 2008).

In the northwestern and northeastern Atlantic there is evidence of local extinction of four species of skate: *Dipturus laevis, D. batis, D. oxyrhinchu* and *Rostroraja alba* (Dulvy and Reynolds 2002). They are all on the large end of the body spectrum and are characterized with intermediate depth and latitudinal ranges compared to extant species. Dulvy and Reynolds (2002) found that body size is the main predictor of vulnerability particularly where the threat is from fishing.

Rajiformes in southern Africa

In southern Africa (Mozambique, South Africa, Namibia and southern Angola), skates are represented by four genera and ~28 species, approximately half of which are endemic to the region (Compagno and Ebert 2007; Heemstra and Heemstra 2004). Almost all the skates in southern Africa are members of the family *Rajidae*, composed of *Amblyrajini* (9 species), *Rajini* (10 species), *Anacanthobatini* (5 species), and *Gurgesiellini* (3 species) (Compagno and Ebert 2007). Skates comprise between 12.3 and 12.6% of chondrichthyan species in southern African waters (Compagno and Ebert 2007). Skates are predominantly found off the west coast of southern Africa from the intertidal zone to 1200 m deep and become scarer towards tropical waters of the area (Compagno and Ebert 2007).

In the Benguela Upwelling System, in the waters surrounding southern and western South Africa, there is a high degree of endemism amongst skates. Due to their abundance and species diversity, they play an important role in the Benguela ecosystem as a predator of fish and demersal crustaceans (Compagno et al. 1991). The degree of endemism among skates in southern Africa is similar to rates of endemism in other species in geographic regions three to 16 times as large (Compagno and Ebert 2007).

While there have been some studies done on other species in the Rajidae family in southern Africa, they have mostly concentrated on distribution and taxonomy, and to a limited extent, diet (Ebert et al. 2008). There is little known about the reproductive biology and diet of most southern African skates. Ebert and van Hees (2015) conducted a study describing the 'lost sharks' of southern Africa, outlining the lack of information about skates, despite their abundance. The study found that 55% of batoids in southern Africa were data deficient on the International Union for Conservation of Nature (IUCN's) Red List.

The diet of skates in southern Africa needs to be described to understand their importance in their ecosystem. Ebert et al. (1991) published a diet study on a variety of skates of the west coast of southern Africa inclusive of *Cruriraja parcomaculata, Raja alba, R. pullopunctata, R. clavata, Leucoraja wallacei, Bathyraja smithii, Neoraja stehmanni, R. caudaspinosa, R. confundens, R. dissimilis, R. leopardus, R. ravidula, R. spinacidermis and R. springeri.* The study found that the species were important predators on the crustacean and fish fauna in the Benguela ecosystem and to a lesser extent, cephalopods and polychaetes.

Raja straeleni

The spotted skate (previously biscuit skate), *Raja straeleni,* belonging to the family Rajidae, is the most abundant skate found in southern African waters (Compagano *et al.* 1991; Compagno and Ebert 2007). Heemstra and Heemstra (2004) reported a range of *R. straeleni* from East London, South Africa to non-specific West Africa. Compagno and Ebert (2007) reported that they can be found from East London, South Africa to northern Namibia. There have also been dubious (out of range and only once been found) records reporting the presence of *R. straeleni* off the coast of Algoa Bay, Mozambique (Rucabado et al. 1984) and on the Mauritian continental shelf (Jouffre and Inejih 2005). The distribution of *R. straeleni* has moved ~20 km westward and ~12 km southwards over the last 20 years (Currie 2017). Where they are known to be found, they are a benthic species with a depth range of 24 to 820 m and are caught most frequently from 24 to 200 m (Compagno and Ebert 2007; Compagno et al. 1991). The study species occupies a wide range of depths, being the most eurybathic of the southern African skates (Compagno and Ebert 2007; Peterson 2008).

Despite their abundance, there is varying, and questionable data reported on their distribution range due to past misidentification. Specifically, there is confusion about the identification and distribution of *R. straeleni* and the European *Raja clavata.* There is ongoing debate of where *R. clavata's* distribution ends and where *R. straeleni's* begins due to morphological similarities that can only be distinguished by subtle differences in meristic and morphometric characters (Compagno et al. 1991; Pasolini et al. 2011; Capapé and Desoutter 1981). The study conducted by Pasolini et al. (2011) found that the two species are peripatric siblings and estimates suggest they have diverged recently in the Early Pleistocene. Due to a lack of samples from western Africa, the study was unable to determine if there is a co-occurrence of the two species, or a continuum/cline of change along the African coast (Pasolini et al. 2011). Oceanographic discontinuities (e.g., the Angola-Benguela Front and Cape Blanc) may contribute to the low or non-existent gene flow between the siblings (Pasolini et al. 2011; Gasse et al. 2008). Historically, *R. clavata* and *R. straeleni* are listed together in studies, which makes it difficult to determine the actual distribution of *R. straeleni* (Compagno et al. 1991; Smale and Cowley 1992).

R. straeleni are identified by their medium to large size, green-gray-brown coloring with black spots/whirls/blotches, an angular snout, long tail, broad rhombic disk, two small dorsal fins, horns on the upper surface of the disk, small orbital thorns, a gold and black oblong eyespot on the pectoral bases, and a white underside with differing gray markings (Seret et al. 2016; McEachran and Dunn 1998; Heemstra and Heemstra 2004). Their long rostrum is used in deep water to bury and dig in search of prey. *R. straeleni* have protective granular denticles on top of thick skin on their ventral surface, are on the small end of the size spectrum (<100 cm), have a highly variable diet, which all make them well suited for rocky or sandy bottom environments where they reside (Seret et al. 2016). Previous studies on *R. straeleni's* diet have concluded that they play an important role in their ecosystem, commonly preying on invertebrates, cephalopods, bony fish, or fish offal (Ebert et al. 1991; Ebert and Bazzarro 2007; Compagno 2005). Due to the skates' rostrum, small mouth and distensible jaws, they are a specialist in consuming crustaceans (Ebert et al. 1991).

Mixed fisheries, bycatch and fishery threats

R. straeleni are not a primary target of any fishery, but they are recognized as important because they are the most commonly caught skate in southern Africa. The commercial inshore trawl industry catches of *Rajidae* range from 370 t to 1269 t year^{-1}, with an average of 800 t, which is composed of approximately 95% *R. straeleni* (Attwood et al. 2011). Overall, *R. straeleni* accounts for ~1.9% of catch in the hake (*Merluccius capensis*) longline fishery and are caught in 88% of commercial trawl landings (Walmsley-Hart et al. 1999). Bycatch from inshore and deep-sea trawling is often discarded, but in the case of *R. straeleni*, they are a commercially important species with their pectoral fins sold as 'skate wings' for consumption in overseas markets (Ebert et al. 2008; Peterson 2008; da Silva and Burgener 2007). Despite being commercially valuable, they are not reported to species level by inshore trawl fisheries on landing reports and are lumped into the 83 to 400 t of skate wings as reported by the fishery. Thus, making it impossible to estimate the actual landing of *R. straeleni.* Lumping of skates is common globally and compound the threat of fisheries to this group as there are limited data to assess them.

R. straeleni have an enhanced vulnerability of extinction due to their limited dispersal (and other life-history characteristics characterized by Rajiformes) in the waters of southern Africa. There is evidence to support the claim that the probability of extinction in skates increases with body size (Dulvy and Reynolds 2002). Due to these factors, they are a priority for conservation efforts.

Management and protection

Despite large catches, the population status of *R. straeleni* is labeled as data deficient by the IUCN's Red List (Smale 2009). Although, a recent National assessment using the data poor assessment method JARA (Just Another Red List Assessment) on trawl biomass survey data from South Africa indicates that this skate is currently not under threat and has been assessed as

Least Concern (da Silva et al. 2018). Nevertheless, it is vital that these and other chondrichthyans be identified to species level in all fisheries as is required by law (MLRA 1998). Currently, the management of the hake fishery is facilitated by the use of total allowable catch (TAC) and closed areas, which indirectly limits the number of *R. straeleni* caught as bycatch (DEAT 2005).

This minor-dissertation aims to investigate the life history traits of *R. straeleni* in southern African waters by analysing its morphology, reproductive biology and diet. The results will be compared to other studies conducted on *R. straeleni* as a part of multi-species projects, as well compared with other species in southern Africa.

Methods

Study site and sampling methods

Seventy-two *R. straeleni* were collected on 26 September, 24 October, 25 October, 20 November and 14 December 2020. The skates were caught on the continental shelf by the demersal trawlers *Ludwani, Harvest Bounty, Foxglove, Forest Lily* and *Okombahe*. Samples were obtained between 32º00'00"S and 17º00'00"E on the west coast and 36º00'00"S and 20º00'00"E on the south coast (Figure 1). Trawls were conducted at depths between 199 to 483 m. The demersal trawl nets were 39 to 40 m wide with 120 mm stretch mesh. Observers obtained the samples and froze them until collection. The samples were thawed and dissected in the laboratory at the University of Cape Town.

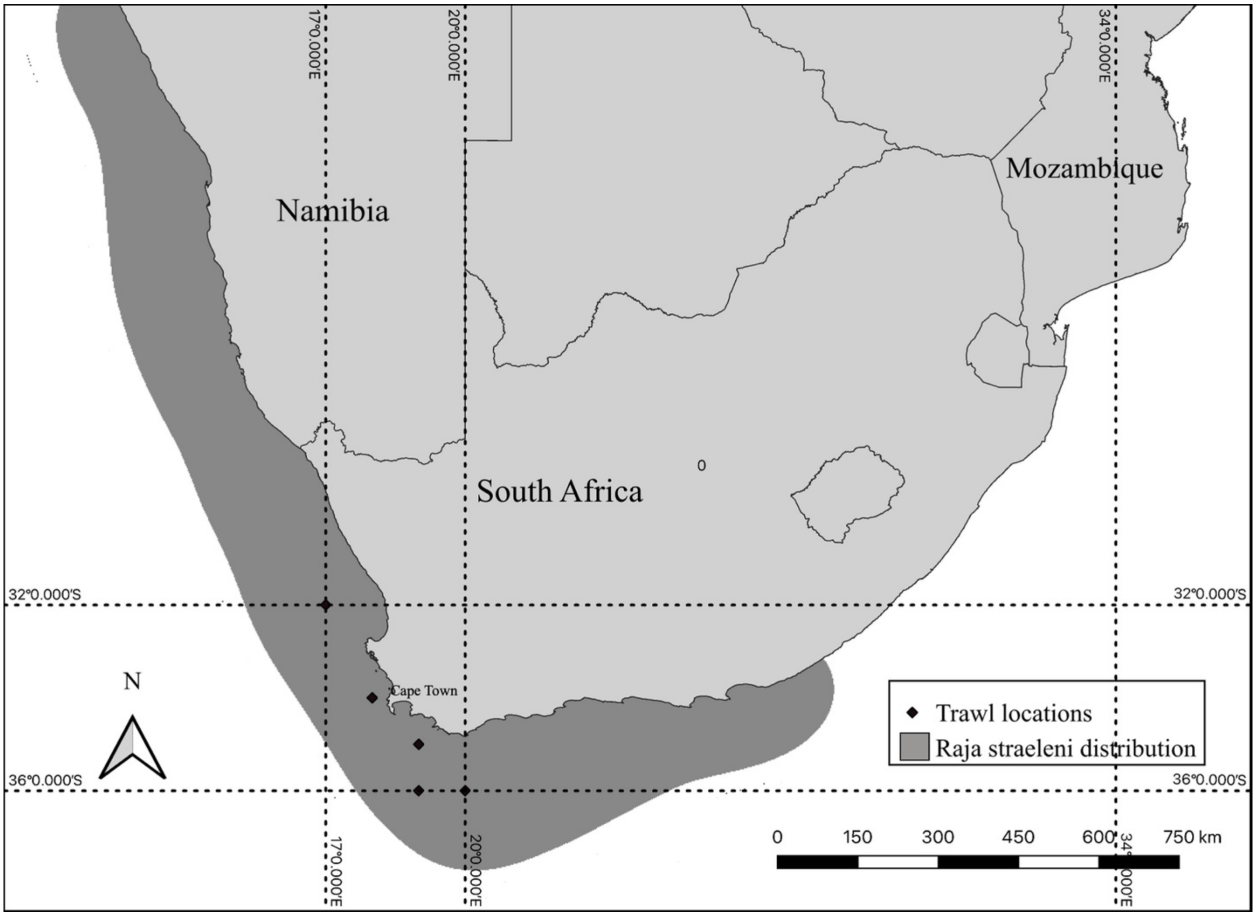

Figure 1: Distribution map of *R. straeleni* in southern Africa and the position of the trawls that yielded the samples used in this study

Morphometric measurements

Morphometric measurements included the total length (L_T), length to first dorsal (*LTD*), and disk width (*D*). L_T, *LTD,* and *D* were measured along the underside of the skate. Each skate was weighed (*W)* on a calibrated electronic balance, accurate to 0.5 g. The sex was determined from each sample by visual inspection of the presence or absence of claspers.

It was assumed that the trawl net was sampled randomly, and that the observer sampled randomly as per their instructions. To test whether the male to female ratio is significantly different than the expected 1:1 ratio, a one-sample two-way *t*-test was done on the Male:Female ratio, using collection dates as replicate samples.

The relationships between total length and disk width and length to first dorsal and disk width were plotted, and linear regressions were used to quantify the relationships. Total length and weight were plotted separately for males and females on a natural logarithmic scale and separate linear regressions were fitted. To test the difference between the slopes of the ln(W) versus ln(L_T), the test statistic was calculated. The t statistic was calculated as follows (Zar 1984):

$$t = \frac{b_1 - b_2}{S_{b1\text{-}b2}}, \qquad \textit{equation 1}$$

where t is the test statistic, b_1-b_2 is the difference between the slopes of each sex-specific regression and $S_{b1\text{-}b2}$ is the standard error of the difference between the slopes. Student's t distribution was used to find the corresponding p-value with 71 degrees of freedom.

The samples were binned into sixteen 20-mm size classes and the frequency of males and females per size class was plotted. A two tailed two sample *t*-test was run to test for significant difference between the sizes of males and females.

Reproductive biology

Visual inspection of the reproductive organs was done to determine the maturity status of the males following Ebert et al. (2008). Males were classed as juvenile, adolescent or mature.

Juvenile males were categorized as having flexible, short claspers that did not extend past the posterior edge of their pelvic fins. Adolescents were defined as those whose claspers were not calcified but extended beyond the posterior edge of the pelvic fins. Males were considered mature when they had elongated and calcified claspers. Internally, development of the testes and coiling of the epididymides were also good indicators for maturity. Externally, if the claspers could articulate and if there was a presence of sperm in the testes that could channel through the claspers, maturation was determined. The point of insertion of the clasper shaft to the clasper tip, or inner clasper length (*ICL)* was recorded to the nearest millimetre using calipers. The *ICL%* was plotted against L_T to assess maturity (Ebert et al. 2008).

For females, visual inspection of the reproductive organs was used to determine maturity. Skates was determined as mature was if there were large, mature oocytes, pendulous posterior portions of the uteri and an oviducal gland that was differentiated from the uteri. Adolescent females were characterized with smaller ovaries, no mature oocytes, undeveloped shell glands and a uteri that was undeveloped. Juveniles were indicated if their shell glands were undifferentiated from the uterus and there was no differentiation from the ovaries (Ebert 2005). The length and width of the oviducal gland were measured to the nearest millimetre using calipers. The uteri and ovaries were removed and weighed, and the number of oocytes in each ovary were counted if they were greater than 5 mm. To test the hypothesis that there is no difference between the mean number of left and right oocytes in adult females, a paired-sample *t*-test was used (Zar 1996). The L_T against the total number of mature oocytes were plotted to visualize the relationship.

A maturity ogive was fitted to estimate the length-at-50% maturity for males and females. The skates were placed into eleven 3-cm size classes and separated by sex. The proportion of skates that were mature were plotted against the mid-point of each eleven 3-cm size class. A logistic curve was fitted to the proportion of mature individuals as a function of length using equation the following equation:

$$P_l = \frac{1}{(1 + e^{a+bl})}, \qquad \textit{equation 2}$$

Where P_l is the proportion of individuals that are mature in length-class I, and a and bl are the coefficients estimated by the fitted model (Roa et al. 1999). The 95% confidence intervals were generated for the parameter estimates by generating 100 random bootstrap samples, 19 for males and 53 for females, each with replacement from the original samples (Jolly et al. 2013). The 100 estimates were ranked from smallest to largest and the 3rd and 97th values in the ranking were taken as the lower and upper confidence limits of the sorted bootstrap estimates (Haddon 2011).

Feeding habits

During the initial dissection process, the skates' stomachs were preserved in 70% ethanol for later analysis. During the stomach analysis, a calibrated scale to the nearest 0.5 g was used. The weight of each entire stomach was recorded. The stomach was laterally cut over a 200 mm sieve and the contents were collected. The empty stomach was weighed and discarded. The stomach contents were separated into piles according to lowest possible taxon. The prey were quantified as the number and weight in each pile, a suitable length measure of the prey item, and the state of decomposition of each item using a 1-4 scale (1=fresh, 2=fragments, 3=decomposed fragments, or 4=highly decomposed). If fragments were found, the smallest number of individuals possible were recorded. The presence and type of parasites were recorded. Squid beaks, invertebrates, and teleost's bones were stored for later inspection.

Stomach contents were analysed for percentage frequency of occurrence (% *F*), percentage by number (% *N*), percentage mass (% *M)* and the index of relative importance (% *IRI)* (Smale and Cowley 1992). The prey condition of each species consumed was represented as percentages of fresh, fragments, decomposed fragments, and highly decomposed material.

A dendrogram representing Bray-Curtis dissimilarity was generated using normalised diet composition data (% per phylum) for each stomach sample. Samples were grouped by maturity stage (juvenile, adolescent, and mature). An analysis of similarities (ANOSIM) test was conducted using 999 permutations to test whether there is a significant difference in the diet among maturity stages.

Prey items were grouped into eight groups representing polychaetes, squids, octopods, amphipods, isopods, decapods, other crustaceans and fish, following Ebert and Bazzarro (2007). The trophic level of each group was multiplied by % mass of the group and summed to find the mean trophic level of *R. straeleni* (Ebert and Bazzarro 2007). Ingested materials such as sediment and related unidentifiable debris were excluded from the analyses.

The cumulative prey curve was calculated to determine if a sufficient number of stomachs had been sampled to adequately describe the diet of *R. straeleni* (Ferry and Calliet 1996).

$$\mathrm{TL_k} = 1 + \left(\sum_{j=1}^{n} \mathrm{P_j} * \mathrm{TL_j}\right), \quad \textit{equation 3}$$

Where TL_k = trophic level of the species, n = total number of prey categories, P_j = proportion of prey category j in the diet and TL_j = trophic level of prey category j (Cortés 1999; Ebert and Bazzarro 2007). The standard deviation was calculated by applying formula (equation 2) to each individual skate to yield 72 trophic level values. The standard error of these values was calculated and then the standard error was calculated by dividing by the square root of 72:

$$\mathrm{SE} = \frac{\sigma}{\sqrt{n}}, \qquad \textit{equation 4}$$

Where SE is the standard error, sigma is the standard deviation, and *n* is the number of samples.

R Core Team (2019) was used for statistical computing.

Results

Distribution

Seventy-two skates were sampled, 53 female and 19 male. The male to female (M:F) sex ratio was 1:2.8. A one sample two-way *t*-test showed that the M:F ratio (Figure 2) was significantly different from the expected 1:1 ratio ($t = -8.1$, df = 4, $p < 0.05$).

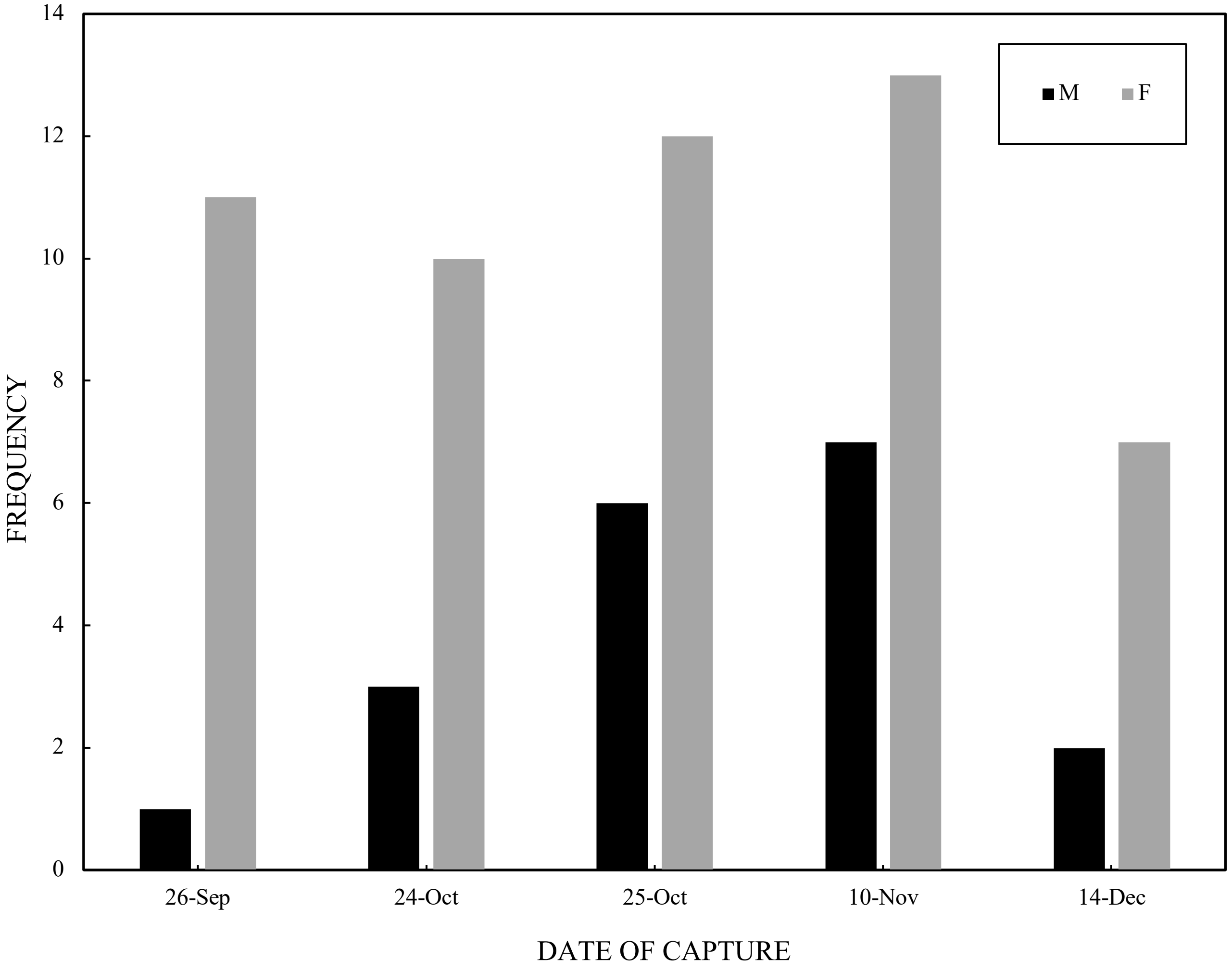

Figure 2: The frequency of males and females *R. straeleni* caught on each date of capture in South African waters in 2020

Morphometric data

Male lengths ranged from 437 mm to 630 mm L_T (mean = 522 mm). Females ranged from 392 mm to 695 mm (mean = 532 mm). There were few males that were <449 mm and few that were >589 mm (Figure 3). A two-sample *t*-test showed no significant difference in the sizes between male and female skates ($t = 0.89$, df = 71, p-value > 0.05).

The relationship between total length and disk width was D=0.77L_T-11.96 ($n = 72$, $r^2 = 0.94$, $p < 0.05$) (Figure 4). The relationship between length to first dorsal and disk width was D=0.94LTD-14.66 ($n = 72$, $r^2 = 0.94$, $p > 0.05$) (Figure 5). The relationship between weight and total length for male *R. straeleni* are $W=3.61L_T-22.74$ (n=19, $r^2 = 0.91$, $p < 0.05$). The relationship between total length and weight for female *R. straeleni* was $W=3.32L_T-20.85$ (n=53, $r^2 = 0.98$, $p < 0.05$). The comparison of the slopes was not significant ($t = 1.56$, $SE = 0.28$, $p > 0.05$), implying that there is no difference in the weight-length relationship between sexes (Figure 6).

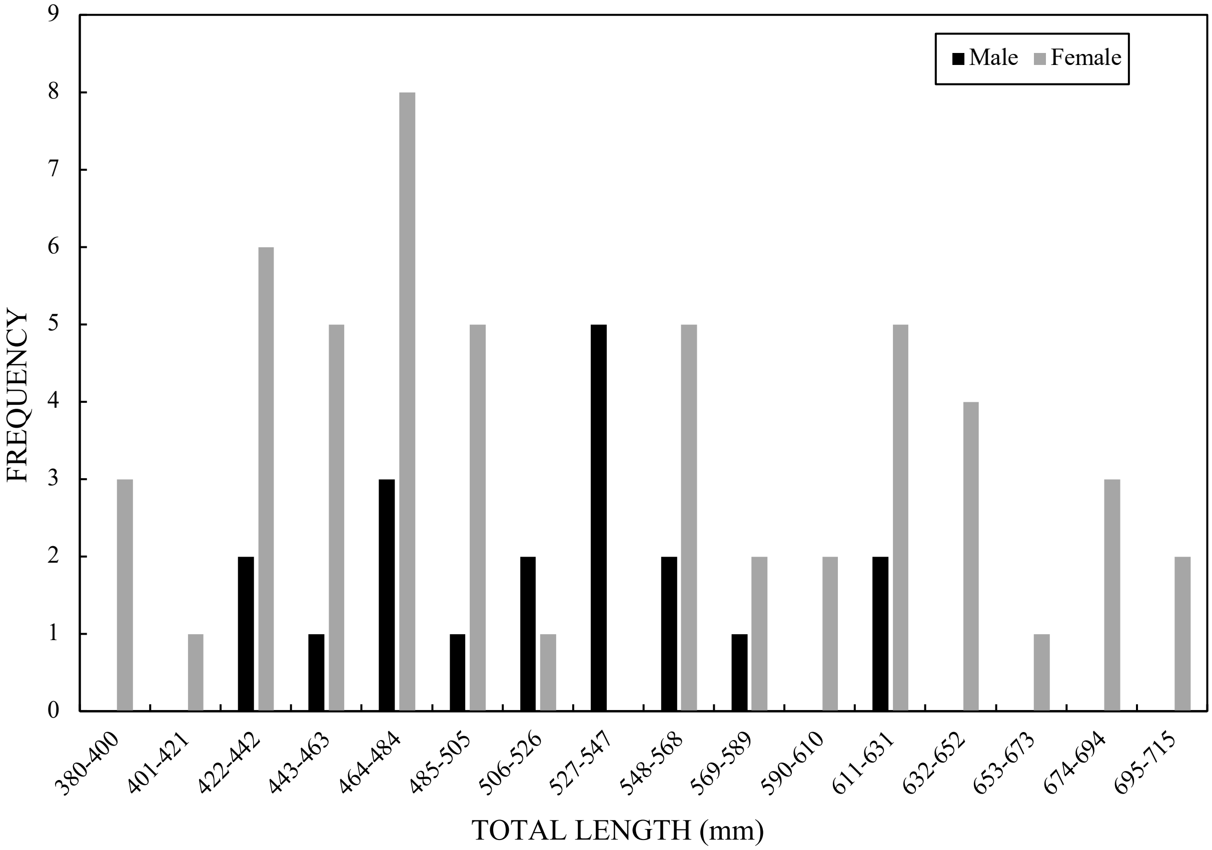

Figure 3: The frequency of males (*n* = 19) and females (*n* = 53) caught per size category of *R. straeleni* examined from South African waters

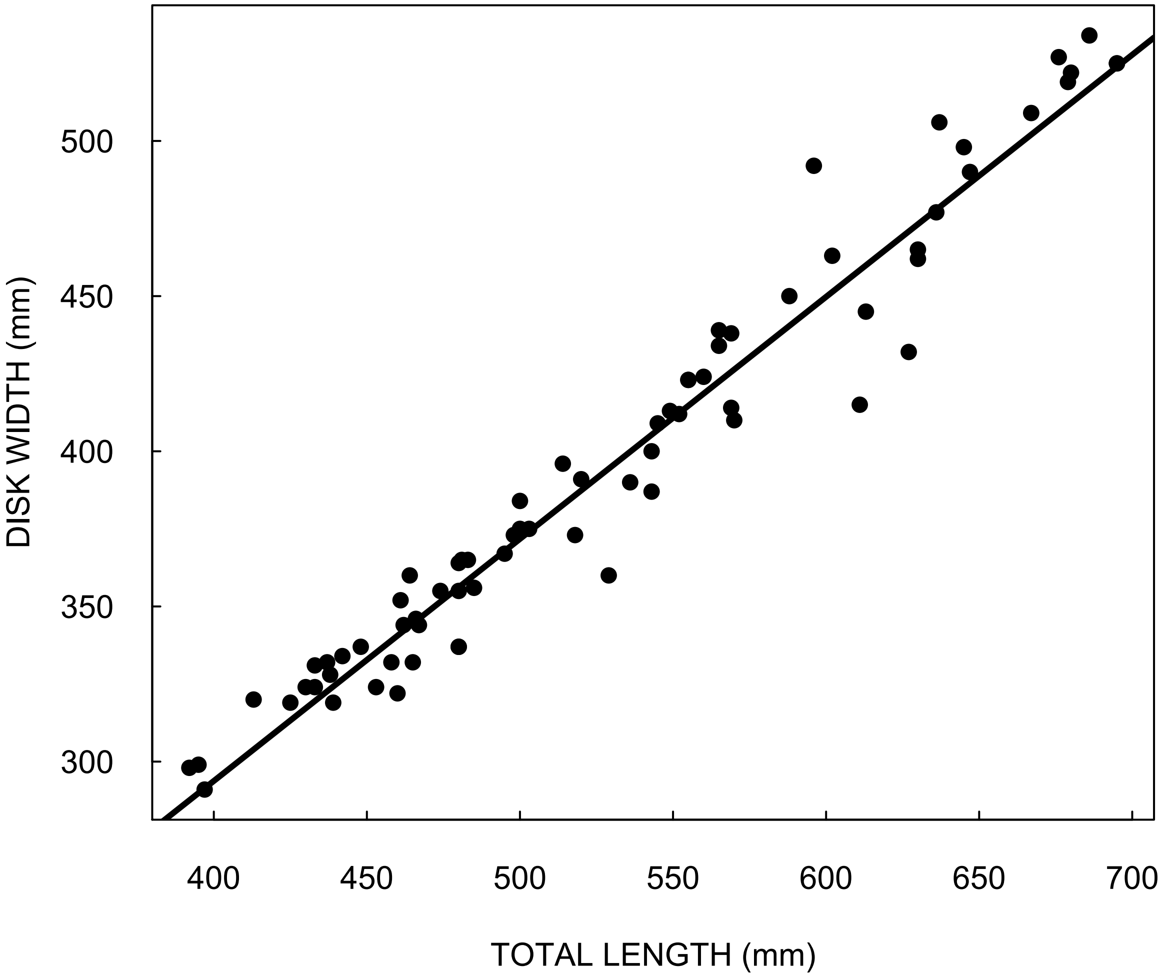

Figure 4: The relationship between disk width and total length for *R. straeleni* in South Africa (n=72)

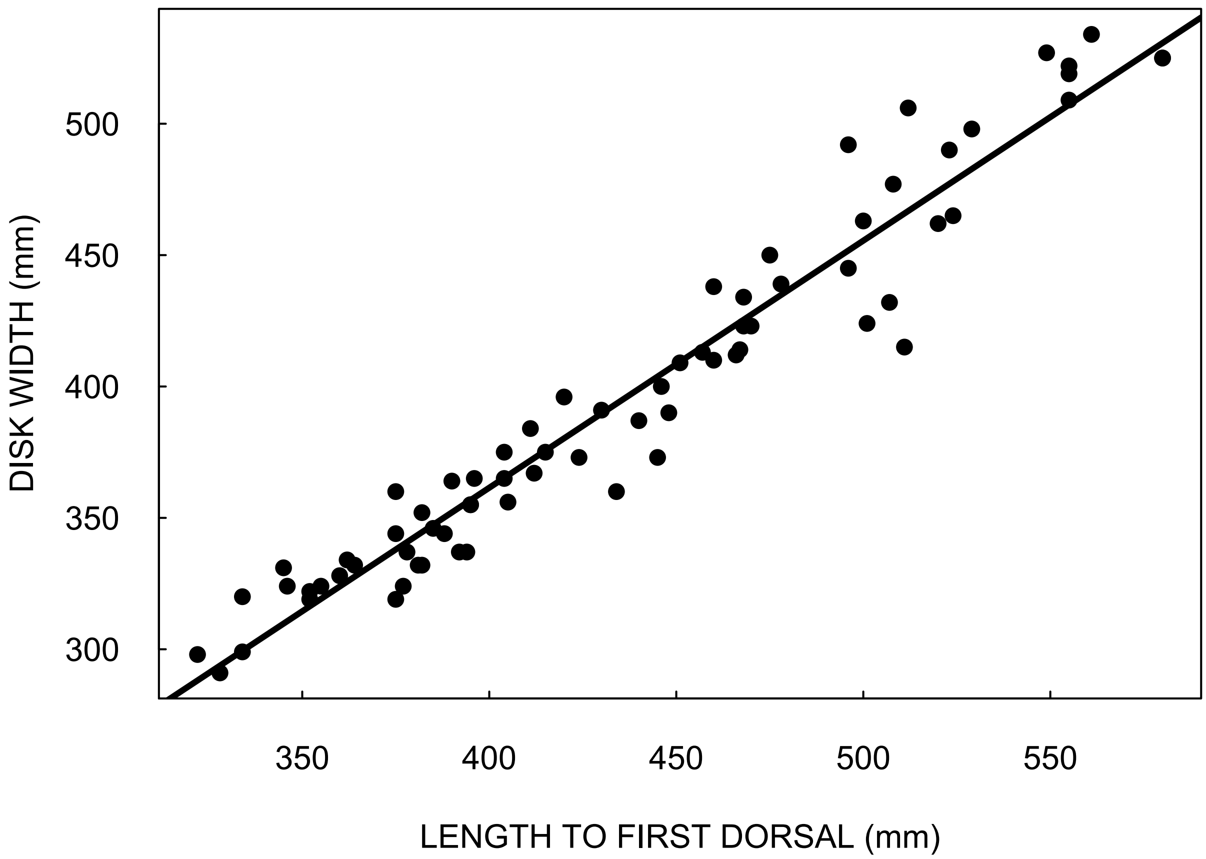

Figure 5: The relationship between disk width and length to first dorsal for *R. straeleni* in South Africa (n=72)

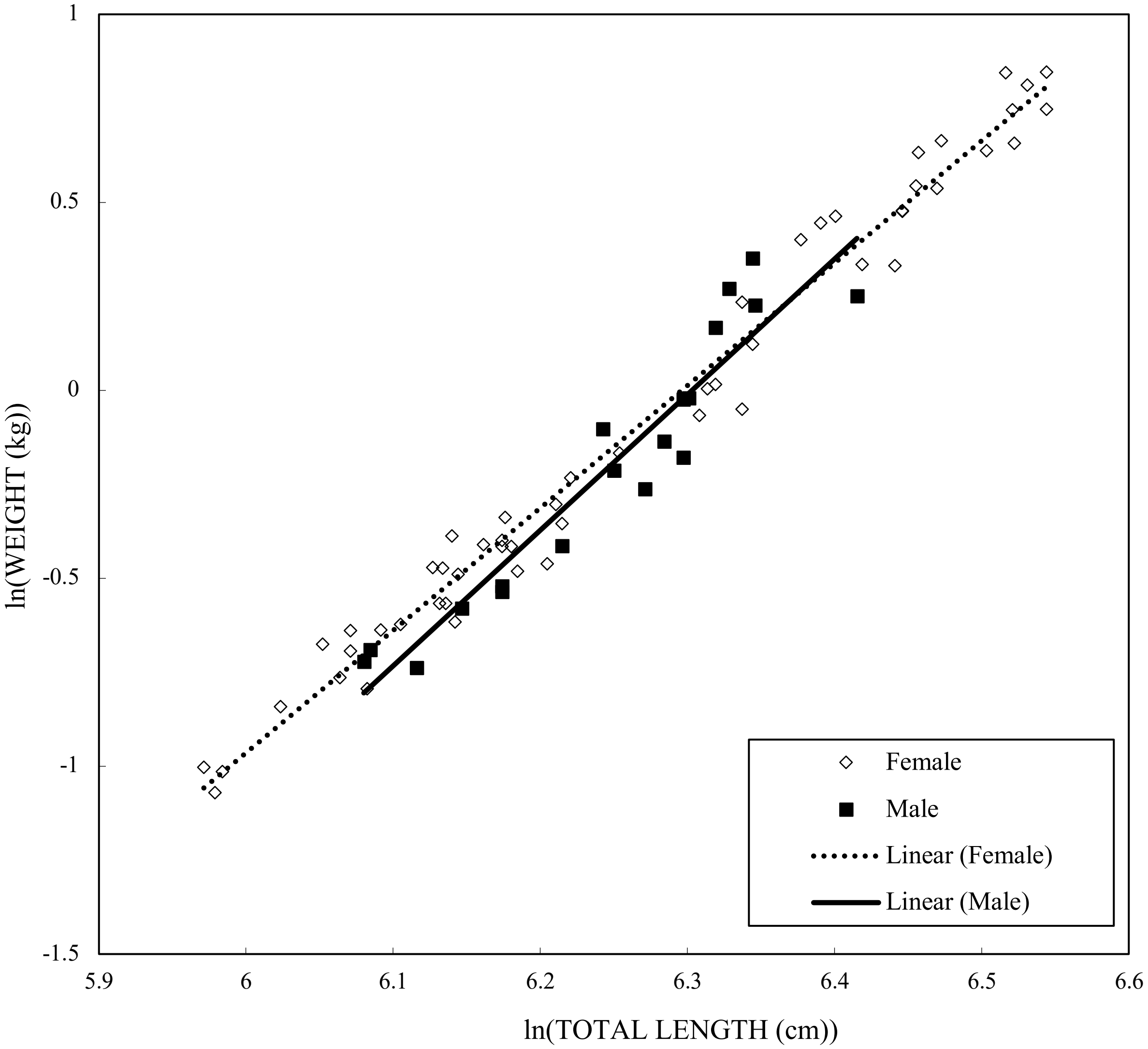

Figure 6: The relationship between natural logarithm of weight and the natural logarithm of total length for *R. straeleni* in South Africa. Female (n=53), male (n=19)

Reproductive biology

Juvenile males ranged between 437 to 543 mm. Adolescent males ranged between 529 to 569 mm. The mature males ranged between 466 to 630 mm. Four of the males were mature with articulating claspers and sperm present (21%). The L_T was compared to clasper length as a percentage (n = 19). Clasper length rapidly increased between L_T of 514 to 630 mm (Figure 7).

The length-at-50% maturity (L50) of the males was estimated at 57.10 cm (95% confidence interval: 54.2-59.4 cm), or 91% of the maximum male length recorded in this study (Figure 8).

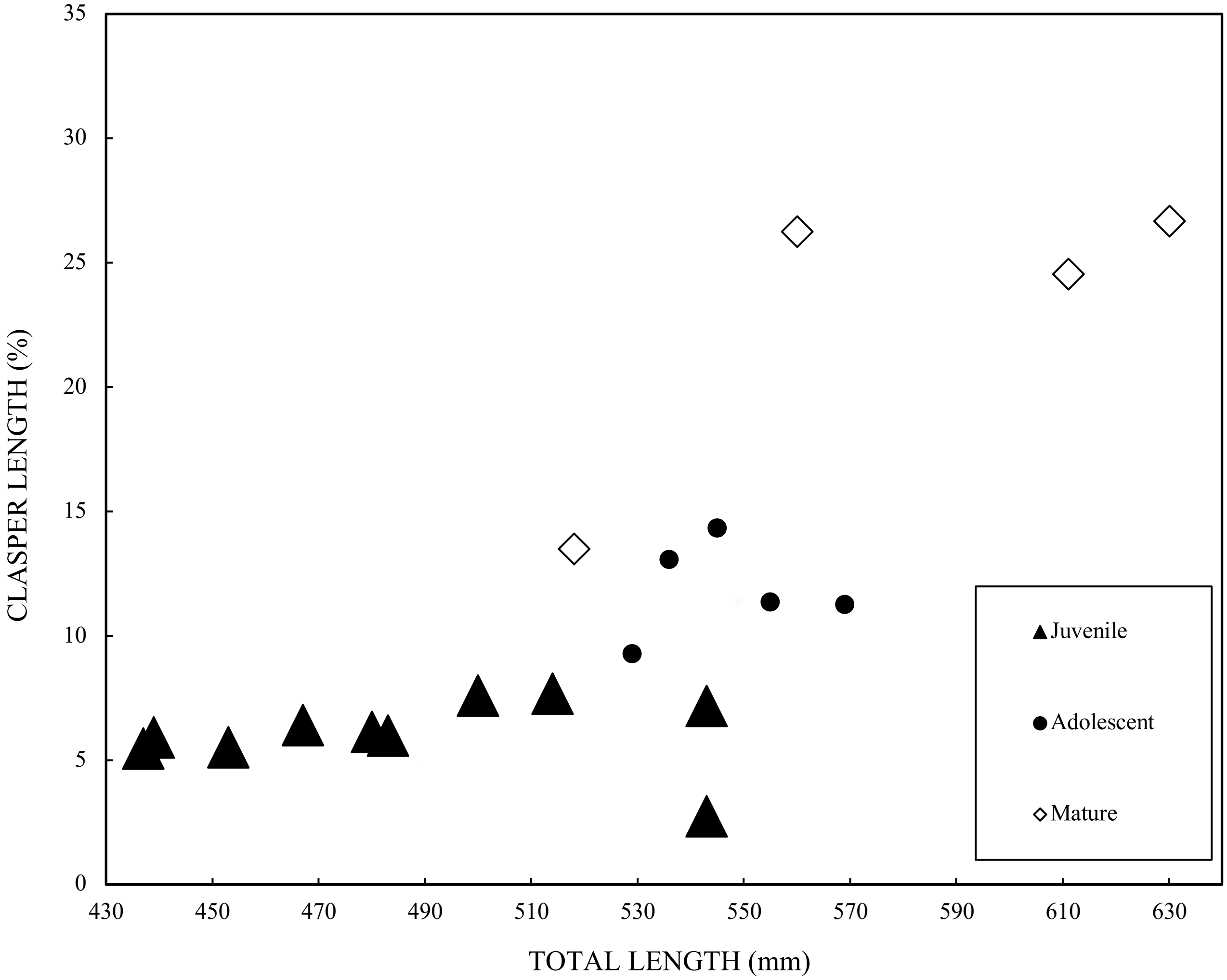

Figure 7: Maturity stages (juvenile, adolescent, and mature) of male *R. straeleni* in South Africa (2020) relative to their total length and percent clasper length

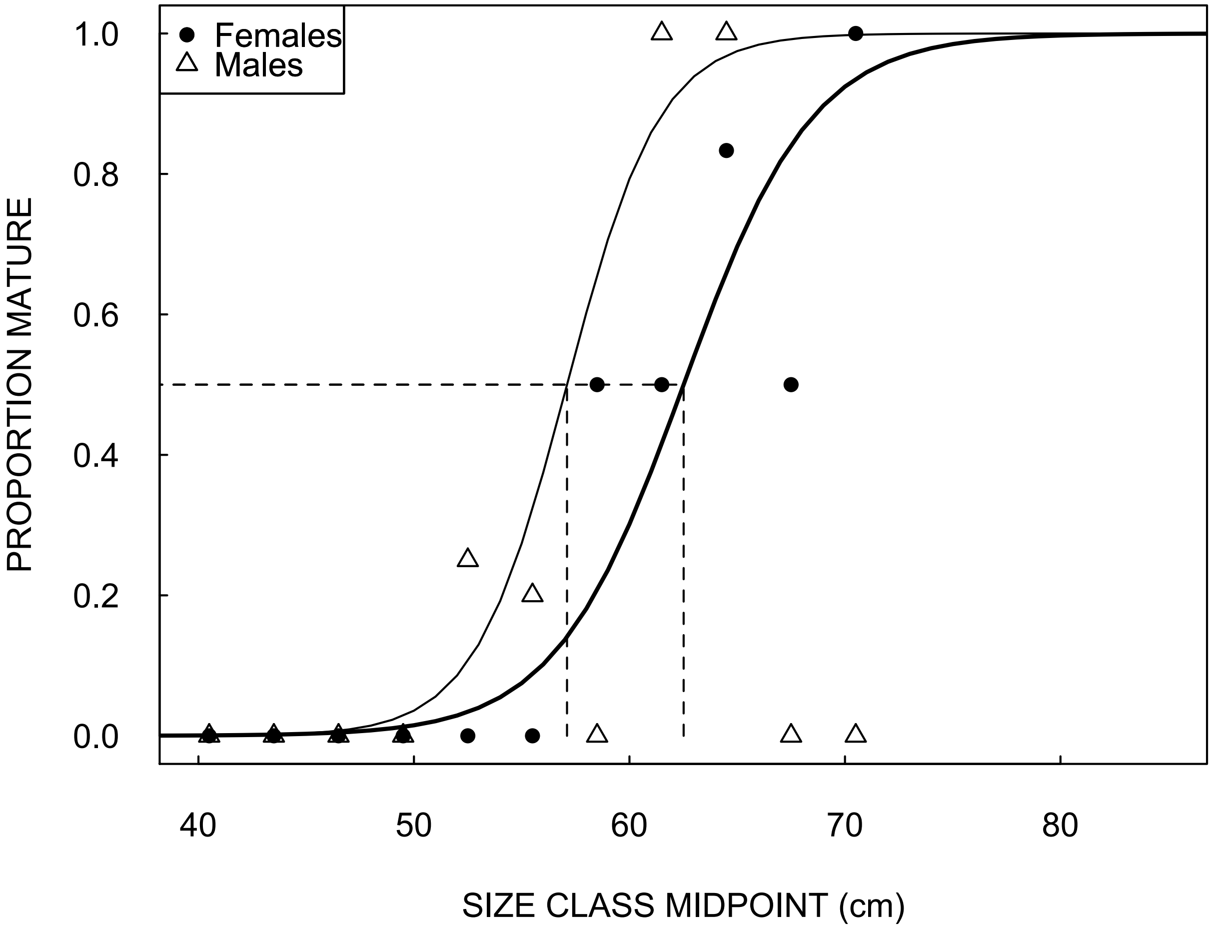

Figure 8: Length-at-50% maturity for female and male *R. straeleni* on the south and west coasts of South Africa

Female juveniles had L_T between 392 to 596 mm. Adolescents ranged between 569 to 680 mm. Mature females ranged between 588 to 695 mm. Twelve (23%) of the females examined were mature. The total length-at-50% maturity (L50) of the females was estimated at 62.51 cm (95% confidence interval: 57.0-64.0 cm), or 90% of the maximum female length recorded in this study. (Figure 8).

The shell glands of juvenile skates were not recorded because they were not differentiated from the uteri. Twenty females (38%) had a widened uterus. All females > 569 had widened uteri. Four of the twelve mature females (33%) were reproductively inactive. Their uteri were pendulous, and they had developed shell glands, but their ovaries appeared atrophied and lacked any oocytes. Both samples were large bodied with L_T values of 630 and 679 mm. The eight females with mature oocytes ranged from two to ten on the right side and from zero to nine on the left side. There was no significance in the number of oocytes on the left versus the right side (Table 1) (*t*-test, d.f. = 7, $p > 0.05$). The total number of oocytes plotted against L_T showed no relationship ($n = 8$) (Figure 9).

Table 1: The number of oocytes (> 5 mm) on the left and right ovaries of mature *R. straeleni*

Sample number	*Right oocytes*	*Left oocytes*
RS001	*7*	*7*
RS003	*3*	*4*
RS009	*8*	*9*
RS033	*2*	*0*
RS034	*2*	*5*
RS035	*10*	*3*
RS046	*4*	*6*
RS069	*3*	*8*

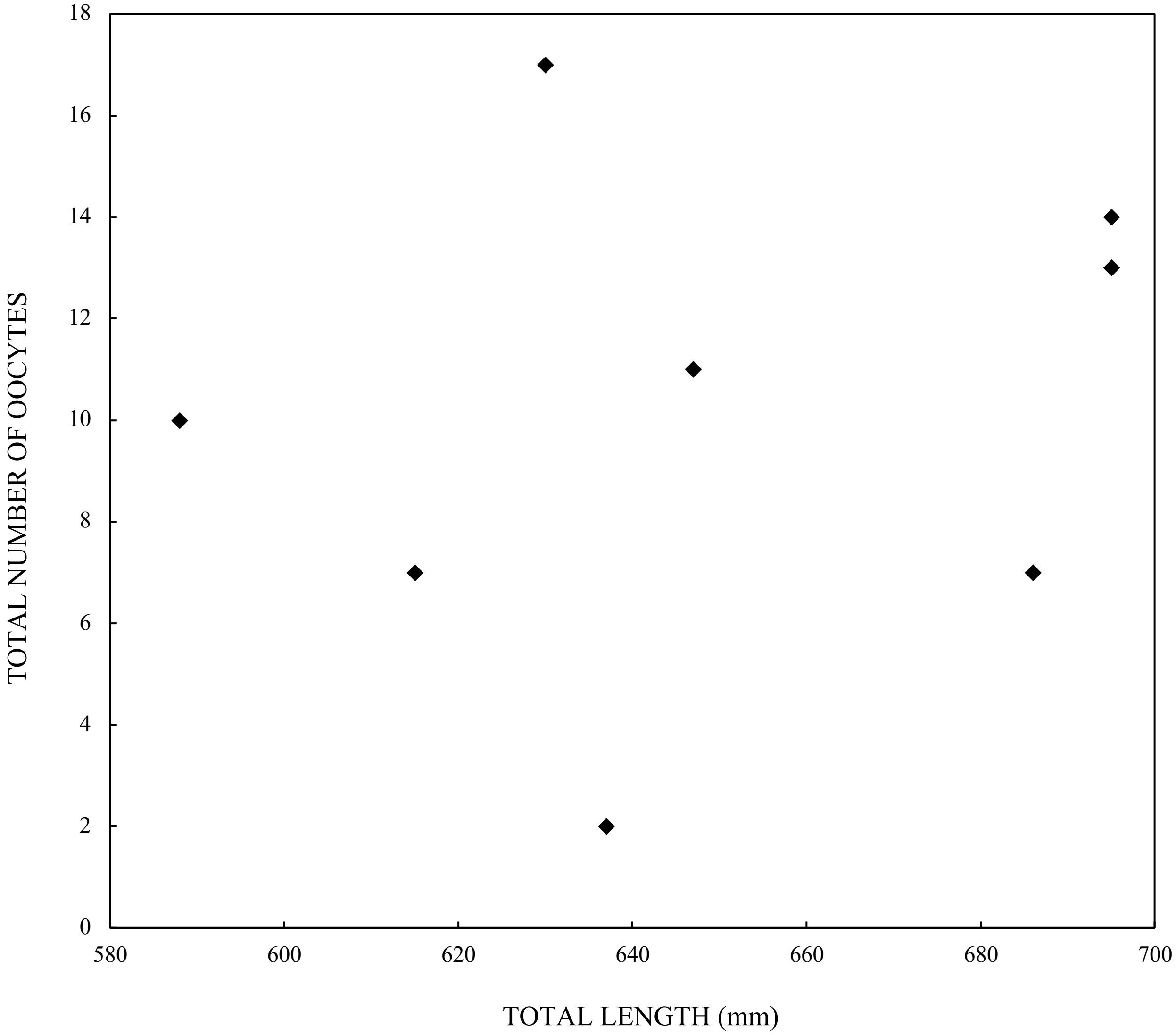

Figure 9: The total number of mature oocytes plotted against L_T for *R. straeleni* in South Africa

Diet analysis

Fifty-seven stomachs were examined from fish ranging from 392 mm to 695 mm $L_{T.}$ Four stomachs were empty (7%), two had unidentifiable remains (3.5%), and 89% had identifiable remains. Debris was found in 16 of the skates, which was composed of sand and completely decomposed material and was not included in the diet analysis. Prey items covered ~25 species in six phyla. The % frequency was highest among Arthropods (77%) and Chordates (42%). To a lesser extent species spanning Mollusca (21%), Echinodermata (4%), Nemertea (2%) and Annelida (2%), were collected (Table 2). 14 Prey species had *decomposed fragments*, 13 were in *fragments*, six were in *fresh* states, and seven prey species that were *highly decomposed*. Arthropod prey condition was dominated by *fragments* (67%) and *highly decomposed* (51%). Chordates were dominated by *decomposed fragments* (63%), with *fragments* and *highly decomposed* compromising 19% of the prey condition. Mollusca was dominated by *fresh* prey items (53%) and *fragments* and *decomposed fragments* compromising 17% and 6%, respectively. Echinoderm prey remains were 50% *fragments* and 50% *highly decomposed*. Nemertea was 100% *fresh*, and Annelida 100% *decomposed fragments* (Table 3). The mean trophic level of *R. straeleni* was 3.98 ±0.05 SE.

The dissimilarity dendrogram shows four groups. One group consists of a single juvenile. The next group has two adolescents and one juvenile which have a dissimilarity of approximately 0.3. The third and fourth groups are clusters of juveniles, adolescents, and mature fish. There is greatest dissimilarity between mature and juvenile fish. There is one group of 18 juveniles, five adolescents and one mature fish (Figure 10). The ANOSIM statistic was 0.074 with a significance of $p > 0.05$. The hypothesis that skates change their diet as they mature was rejected.

Table 2: Summary of the diet contents of *R. straeleni* in South Africa (2020) based on 53 specimens containing identifiable taxonomic prey (Branch and Branch 2017).

Prey items	%F	%N	%M	%IRI	%PSRI	Average length (mm)
Annelida						
Polychaete						
Phyllodocida						
Nereididae	1.9	0.3	0.4	0.0	0.0	

Arthropoda						
Crustacea						
Crustacea unidentified	17.0	1.0	6.8	2.5	0.7	
Decapods						
Mursia cristiata	26.4	10.5	7.9	8.9	2.4	
Brachyura unidentified	20.8	5.7	3.5	3.6	1.0	
Sympagurus dimorphus	7.6	2.7	4.4	1.0	0.3	
Parapaguridae unidentified	17.0	6.1	5.5	3.6	1.0	35.5
Caridea unidentified	52.8	56.4	2.8	57.7	15.0	28.5
Malacostracans						
Anthuridae unidentified	1.9	0.3	0.0	0.0	0.0	
Stomatopoda						
Pterygosquilla capensis	7.6	2.0	2.2	0.6	0.2	
Tanaidacea unidentified	1.9	0.3	0.0	0.0	0.0	36
Chordate						
Ray-finned fishes						
Ray-finned fish unidentified	1.9	0.3	5.5	0.2	0.1	
Aulopiformes						
Synodontidae unidentified	1.9	0.3	0.4	0.0	0.0	
Clupeiformes						
Engraulidae	7.6	2.0	3.4	0.8	0.2	105
Stomiiforme unidentified	1.9	0.3	3.0	0.1	0.0	122
Teleost unidentified	34.0	5.7	19.6	15.9	4.3	224.3
Actinoptergyii						
Clupeiformes						
Sardinops sagax	1.9	0.3	3.1	0.1	0.0	
Echinodermata						
Ophiuroidea unidentified	1.9	0.3	0.0	0.0	0.0	
Sea urchins						
Spatangoida unidentified	1.9	0.3	0.0	0.0	0.0	
Mollusca						
Cephalopoda						
Cephalopoda unidentified	1.9	0.3	0.9	0.0	0.0	
Cuttlefishes						
Sepiidae	1.9	0.3	0.0	0.0	0.0	
Oegopsida						
Oegopsida unidentified	3.8	0.7	1.6	0.2	0.0	
Ommastrephidae						
Ommastrephidae unidentified	11.3	2.4	15.2	3.7	1.0	
Todaropsis eblanae	3.8	0.7	13.9	1.0	0.3	149.3
Nemertea						
Nemertea unidentified	1.9	0.3	0.0	0.0	0.0	

Table 3: The prey items in the stomachs of *R. straeleni* collected in South Africa. Each prey item is listed as percent fresh, fragments, decomposed fragments, and highly decomposed

Prey	% Fresh	% Fragments	% Decomposed fragments	% Highly decomposed
Mursia cristiata	0.0	81.3	18.8	0.0
Unidentified Teleost	0.0	8.0	56.0	36.0
Pterygosquilla capensis	0.0	28.6	71.4	0.0
Unidentified Caridea	1.8	0.6	12.8	84.8
Sympagurus dimorphus	12.5	87.5	0.0	0.0
Unidentified Parapaguridae	0.0	61.1	27.8	11.1
Unidentified Nereididae	0.0	0.0	100.0	0.0
Unidentified Brachyura	0.0	22.2	27.8	50.0
Unidentified Stomiiforme	0.0	100.0	0.0	0.0
Unidentified Tanaidacea	0.0	100.0	0.0	0.0
Unidentified Sepiidae	100.0	0.0	0.0	0.0
Unidenfitied Engraulidae	0.0	66.7	33.3	0.0
Unidentified crustacean	0.0	0.0	44.4	55.6
Unidentified Spatangoida	0.0	0.0	0.0	100.0
Unidentified Ophiuroidea	0.0	100.0	0.0	0.0
Unidentified Anthuridae	0.0	0.0	100.0	0.0
Unidentified Ommastrephidae	33.3	0.0	0.0	66.7
Todaropsis eblanae	50.0	50.0	0.0	0.0
Unidentified Oegopsida	0.0	66.7	33.3	0.0
Coraline structure	0.0	0.0	100.0	0.0
Unidentified Nemertea	100.0	0.0	0.0	0.0
Sardinops sagax	0.0	0.0	100.0	0.0
Unidentified Synodontidae	0.0	0.0	100.0	0.0

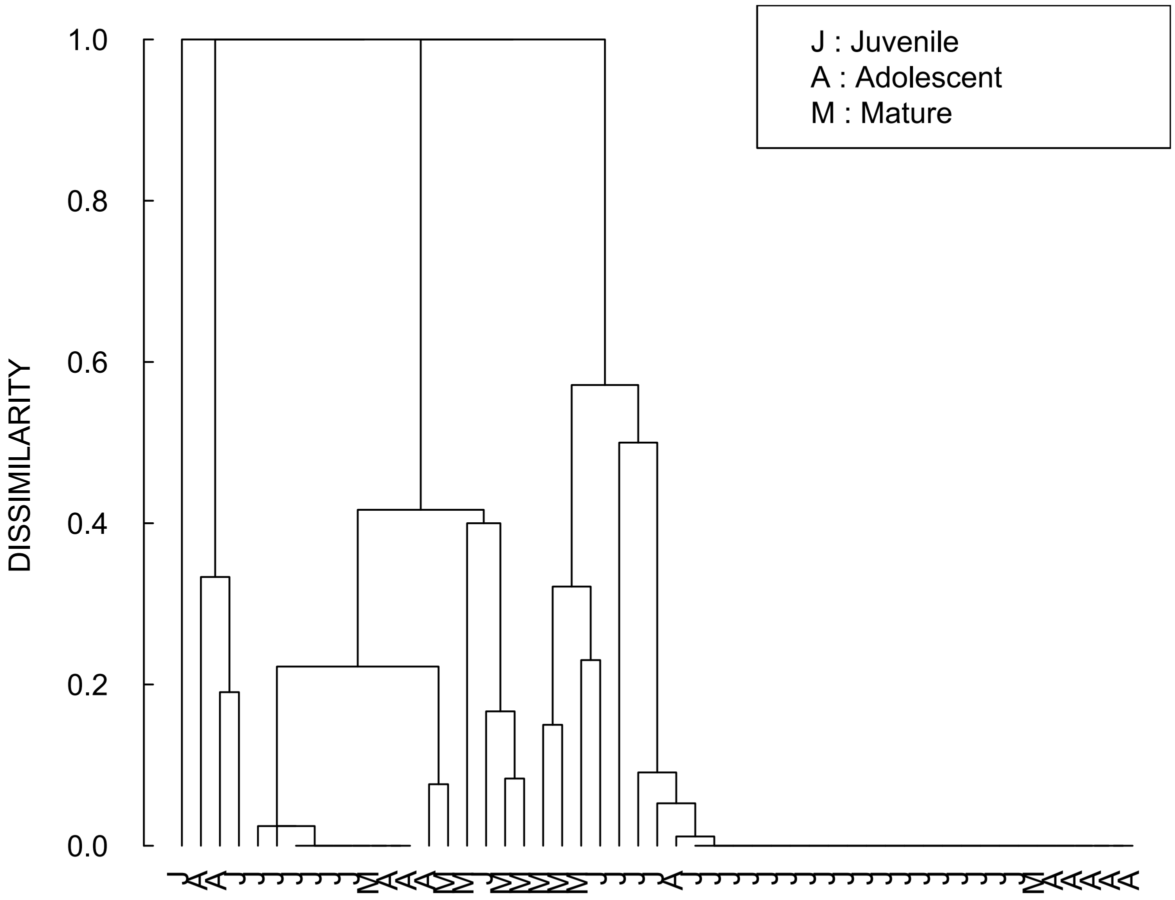

Figure 10: A dendrogram showing the dissimilarity of diet contents based on maturity stage (juvenile, adolescent and mature) of *R. straeleni* in South Africa

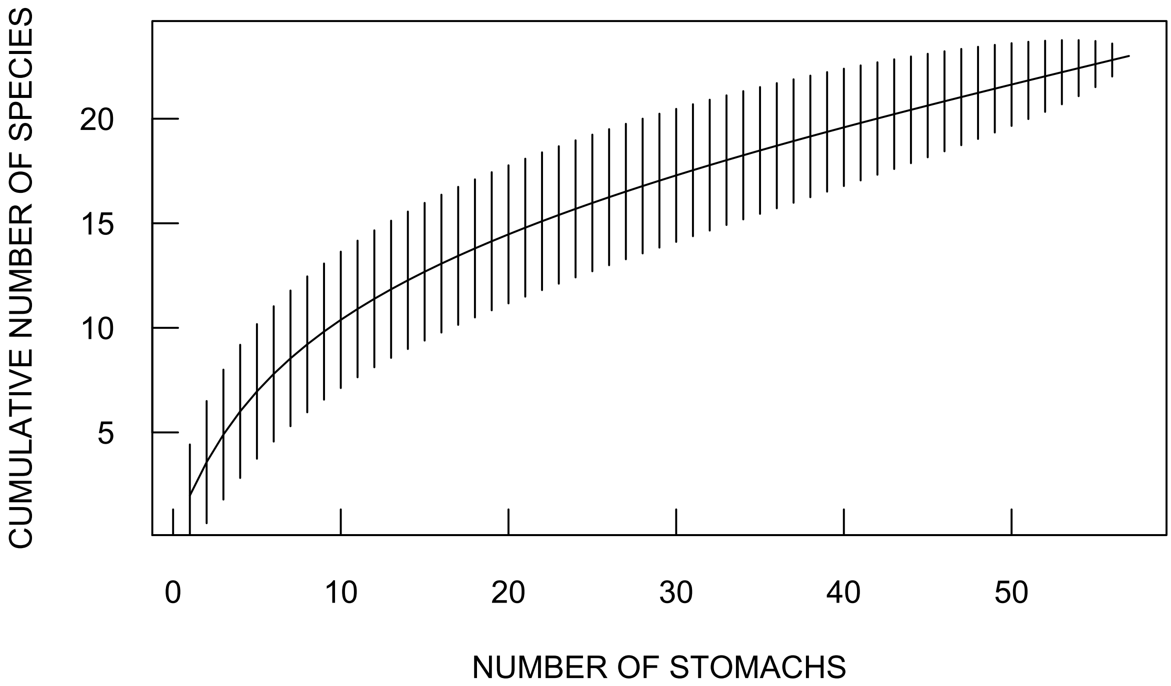

Figure 11: A species accumulation curve showing the expected number of observed species as a function of sampling effort of *R. straeleni* in South Africa

Discussion

This study provides new information based on new and recent samples on the sex ratio, morphometrics, reproductive parameters and feeding habits of *R. straeleni.* The previous assessments were based on data that were more than two decades old. Where appropriate comparisons between my more recent findings and the historical studies have been made. Overall, the new data served to strengthen our knowledge of the most important skates in the demersal trawl fishery, and potentially the most abundant of the southern African skates.

The data presented on *R. straeleni* of the present study has represented the population on the south and west coasts of South Africa but lacks proper temporal replication within the year. An earlier study was conducted on the morphology and reproductive biology of *R. straeleni* by Ebert et al. (2008) on the south and west coasts of South Africa. Their skates were drawn from samples taken on the bi-annual surveys done by the South African government research agency, and therefore also do not represent a complete annual cycle. The diet of *R. straeleni* in South Africa (the southern Benguela and Agulhas Bank) was described from older bi-annual survey samples taken by Ebert et al. (1991), Smale and Cowley (1992) and Ebert and Bazzarro (2007). Macphearson and Roel (1987) also conducted a study on the diet of *R. straeleni* off Namibia. Together these studies provide a comprehensive description of the diet of *R. straeleni*, which is endemic to the Benguela current system, although age and growth estimates are still lacking.

Comparisons with closely related species or sympatric might also be useful. McCully et al. (2012) conducted a study on the age at maturity of the European *R. clavata,* the most closely related to *R. straeleni.* Indeed, these two species have been confused taxonomically. Walmsley-Hart et al. (1999) studied the reproductive biology of *Leuoraja wallacei* and *Dipturus pullopunctatus* and the diet of *L. wallacei.*

Sex Ratio

The present study suggests that females were caught 2.8 times as frequently as males. Ebert et al. (2008) found that female *R. straeleni* were caught 1.3 times as frequently as males. A likely explanation for the skewed sex ratio is that the species population is female dominated. The explanation that females dominate the males numerically is likely because on each capture date, in different locations, using random sampling, females' numbers dominated. Female domination is commonly found among skates. Other examples include, *Dipturus chilensis, Rhynchobatus djiddensis, Rhinobatus granulatus, R. obtusus and R. annandalei* (Paesch and Oddone 2008). Alternatively, another likely explanation for the differences in the skates' sex ratio may be due to the males being in a different location or having a different behavior. Many species of skate segregate by size, sex, and maturity (Fitz and Daiber 1963; Richards et al. 1963).

Morphometrics

The mean total length of females was 10 mm larger than the males, and they were 160 g heavier, but the differences are not sufficient to suggest that females are larger than the males. In order to determine if the sizes of the skates differ between sexes, the study would need to be inclusive of age. Ebert et al. (2008) found that females attain a larger size than males, but they did not test for differences in size. Failure to detect a difference may simply be a problem of low statistical power, as females that are commonly longer and heavier than males in other skates such as the smallnose fanskate (*Sympterygia bonapartii)* (Mabragaňa et al. 2002), zipper sand skate (*Psammobatis extenta)* (Braccini and Chiaramonte 2002), yellow-spotted skate *(Leucoraja wallacei),* slime skate *(Dipturus pullopunctatus)* (Walmsley-Hart et al. 1999) and the shortfin sand skate (*Psammobatis normani)* (Mabragaňa and Cousseau 2004). The reason that females are larger and heavier than males may be due to the production of oocytes and the need to hold egg cases within their body cavities.

I did not find a significant difference in the relationships between disk with and total length between the sexes (Table 4). Likewise, I found no difference in the weight and total length relationships between the sexes (Table 5). Any difference in total size or mass between the sexes would suggests that they females simply get bigger and or older but does not suggest that they have different shapes.

Males and females from the present study were hyperallometric. Statistical analyses provided by Ebert et al. (2008) suggested that west coast males and south coast females were isometric, whereas west coast females and south coast males hyperallometric (Table 5). On balance it would appear that *R. straeleni* is slightly hyperallometric, although this morphological conclusion might only apply to females, and would need to be confirmed by further analyses that take seasonal (reproductive cycle) variation into account. Neither study had adequate seasonal representation for such an analysis.

Ebert et al. (2008) concluded that the disk width versus total length relationships were significantly different between the south and west coasts for each sex, leading them to suggest that there are two populations of *R. straeleni*. No standard error on the slopes of the relationships were provided by Ebert et al. (2008) to statistically compare slopes between our studies. Nevertheless, the slopes of the relationships I found were within two standard errors of those provided by Ebert et al. (2008), which gives no reason to suspect any change in these relationships over the three decades separating these samples (Table 4).

Ebert et al. (2008) stated that the results suggest discrete south and west coast populations. Another explanation is that there are other factors influencing the growth of *R. straeleni* including temperature differences or differences in food availability in each region.

Differences in sizes among geographical locations have been found among other species of skate, such as *R. radiata* (Templeman 1987).

Table 4: Disk width and total length comparisons inclusive of sample size (*n*) for *R. straeleni* on the west and south coasts of South Africa from Ebert et al. (2008) and the present study. The standard error of the slope (SE(b)) is given for each sample from this study

	Ebert et al. (2008)	Present study
West coast males	$n = 238$, $a = 3.08$, $b = 0.66$	$n = 13$, $a = 28.14$, $b = 0.68$ ±0.08 SE(b)
West coast females	$n = 401$, $a = -0.11$, $b = 0.75$	$n = 27$, $a = -14.26$, $b = 0.78$ ±0.02 SE(b)
South coast males	$n = 261$, $a = 2.02$, $b = 0.67$	$n = 6$, $a = -92.62$, $b = 0.89$ ±0.17 SE(b)
South coast females	$n = 237$, $a = -0.54$, $b = 0.75$	$n = 26$, $a = -18.06$, $b = 0.79$ ±0.03 SE(b)

Table 5: Weight versus total length comparisons inclusive of sample size (*n)* for *R. straeleni* on the west and south coasts of South Africa from Ebert et al. (2008) and the present study.

	Ebert et al. (2008)	Present study
West coast males	$W = (9 \text{ x } 10^{-06})L_T^{2.943}$ $n = 238$	$W = (9 \text{ x } 10^{-10})L_T^{3.469}$ $n = 13$
West coast females	$W = (7 \text{ x } 10^{-06})L_T^{3.602}$ $n = 401$	$W = (2 \text{ x } 10^{-9})L_T^{3.210}$ $n = 27$
South coast males	$W = (3 \text{ x } 10^{07})L_T^{3.183}$ $n = 261$	$W = (1 \text{ x } 10^{-12})L_T^{4.359}$ $n = 6$
South coast females	$W = (5 \text{ x } 10^{-06})L_T^{3.053}$ $n = 237$	$W = (10 \text{ x } 10^{-10})L_T^{3.300}$ $n = 26$
Combined male		$W = (1 \text{ x } 10^{-10})L_T^{3.61}$ $n = 19$

Combined female	$W = (9 \times 10^{-10})L_T^{3.32}$ $n = 53$

Reproductive parameters

To assess for maturity in male skates, the presence of sperm, the development of claspers, and the articulation of claspers are considered (Walmsley-Hart et al. 1999). The inspection of reproductive traits internally and externally provides an easy mean for assessing maturity in sampled species. All males with advanced clasper stage had sperm present. There was a distinct transition in the articulation of claspers sized from 518 mm to 630 mm, suggesting a transition to maturity in this size interval. This study estimated male length-at-50% maturity at 571 mm (CI = 542 to 594 mm) (n = 19). Ebert et al. (2008) estimated length-at-50% maturity of west and south coast males at 632 mm (n = 238) and 616 mm (n = 261), respectively. The length-at-50% maturity values for male European *R. clavata* was estimated at 666 mm (n = 5917) (McCully et al. 2012).

To assess for maturity in the female skates, pendulous uteri, developed shell glands, and presence of mature oocytes are taken as signs of maturity (Walmsley-Hart et al. 1999). The skates went through a distinct subadult phase where the skates had a widening uteri and developing ova. Lengths of subadult females were between 520 and 569 mm. The length-at-50% maturity in females was estimated at 595 mm (n = 53). By comparison, to Ebert et al. (2008) estimated length-at-50% maturity of west and south coast females at 658 mm (n = 401) and 625 mm (CI = 570 to 641 mm) (n = 237), respectively.

The length-at-50% maturity values for female European *R. clavata* was estimated at 766 mm (*n* = 3229) (McCully et al. 2012). The differences between length-at-50% maturity for *R. straeleni* and *R. clavata* could be due to the latter's larger size. Samples obtained by McCully et al. (2012) reached 960 mm, whereas this study only found samples with a maximum length of 695 mm. *R. clavata's* population could have different variables affecting them such as greater access to food, or different environmental temperatures, leading them to grow larger in size.

In this study, no uterine wounds were noted, and no egg cases were found. The present study provided indicators that during the period of collection throughout spring and summer, the skates were sexually dormant. Such as, the low number of mature oocytes in the females and the low sperm presence in the males. Ebert et al. (2008) conducted data from bi-annual surveys and out of 198 females, 13 (6.6%) had egg cases in each of their uterus. From the south coast, ten had egg cases *in utero,* two in autumn and eight in spring at depths between 42 and 110 m. Three were caught on the west coast, one in summer and two in winter at depths between 148 and 234 m. The scarcity of year-round data made it difficult to describe the spawning cycle of *R. straeleni.* There is a likelihood that the trawlers from the present study and Ebert et al. (2008) did not collect many samples with egg cases because they lay their eggs outside trawling grounds in shallower waters. Alternatively, *R. straeleni* could spawn infrequently, as some skates are known to reproduce only when conditions are ideal. There is evidence that cold-and deep-water skates only reproduce once every two years, which reduces the likelihood of finding reproductively active skates by 50% (Last et al. 2016).

The male size range of this study was 437 to 630 mm, and the females was 392 to 695 mm. Comparatively, Ebert et al. (2008) had a male sample range of 166 to 805 mm and a female range between 217 to 859 mm. The reason for larger skates and larger lengths-at-50% maturity found by Ebert et al. (2008) could be due a decrease in size due to continued fishing in the three decades separating the collection periods.

The study by Walmsley-Hart et al. (1999), on the reproductive biology of *L. wallacei* and *D. pullopunctatus* estimated a length-at-50% maturity by using their disk width. For the purpose of this comparison, the length-at-50% maturity for *R. straeleni* was converted to disk width. The length-at-50% maturity for *L. wallacei* is 2 mm larger than that of *R. straeleni.* The female *R. straeleni* was found to mature at 95 mm larger than *L. wallacei. D. pullopunctatus* matures at ~255 mm larger than the other male species, and the females mature at more than 186 mm longer than the other species, correlating to their larger body size. All three species have larger females than males at maturity (Table 6).

Table 6: The disk width (*D)* range, length-at-50% maturity (LT_{50}) captured in *D* for each sex, and %max of *D* for each sex of *R. straeleni* (present study)*, Leuoraja wallacei,* and *Dipturus pullopunctatus* (Walmsley-Hart et al. 1999)

	D Range (mm)	LT_{50} Male *D* (mm)	%Max male *D*	LT_{50} Female *D* (mm)	%Max female *D*
Raja straeleni	291 - 534	393	93%	495	93%
L. wallacei	135 - 571	395	77%	400	70%
D. pullopunctatus	177 - 747	641 - 660	93%	681 - 700	92%

Species in which females mature at a larger size than males are common amongst elasmobranchs (Cortés 2000). In the present study, females matured at a size 54 mm larger than the males. Ebert et al. (2008) findings were consistent with this, where *R. straeleni* female length-at-50% maturity on the south coasts were 35 mm larger than the males and 26 mm larger on the west coast. McCully et al. (2012) found that female *R. clavata* mature at 10 mm larger than the males. Walmsley-Hart et al. (1999) found that *L. wallacei* females mature 5 mm larger than the males and *D. pullopunctatus* females mature ~40 mm larger than the males. Males likely mature at a smaller size (and age) to reach maturity faster so they can begin reproducing.

Feeding habits

R. straeleni has thick cartilage in their jaw to crunch hard-bodied prey, mainly crustaceans that bury themselves in the sand and fish that live close to the seabed. Most of the stomach contents were fragments or decomposed fragments, which supports the hypothesis that the skates use their jaws to crush their prey. There are indicators that *R. straeleni's* feeding rate is low, such as the seven percent of the stomachs that were empty, the lack of fresh food present, and high frequency of decomposed prey. Squid comprised a large portion of their diet by mass (30.7%), which suggests that these prey are common on the seabed of the continental shelf between 200 and 500 m, as the skates are not suited to pelagic hunting (Ebert et al. 1991). All other identifiable prey items were benthic in origin. *R. straeleni's* hard, elongated rostrum has been adapted for digging into sand to attain prey that live in the sand, namely crustaceans and small fish. This correlates to the prey found in the stomachs analysed from this study where the highest frequency of occurrence was Caridea, teleosts, and the red-spotted crab (*Mursia cristiata).*

Macpherson and Roel (1987) did not provide a breakdown on the diet of *R. straeleni* in Namibia by mass, but their results showed that the skates collected fed primarily on crustaceans. Smale and Cowley (1992) found that crustaceans comprised 86.33% of their diet by mass and teleosts made up 12.87%. These findings are consistent with the present study in that *R. straeleni* are generalist feeders, taking mostly crustaceans and teleosts.

R. straeleni consume the same prey throughout their lives. These results are born precocial and relatively large-bodied, compared to hatchlings of teleost fish, enabling them to eat the same food as the adults. They live in the same environment throughout their lives, thus having the same access to food.

Ebert and Bazzarro's (2007) study (using data collected from Ebert et al. 1991) was dominated numerically by decapods, fish, and other crustaceans, broadly consistent with the present study. Both studies obtained their samples from trawlers operating at a similar depth of approximately 300 m. Both studies report almost identical findings to the mass of fish found. The differences between the two were that Ebert and Bazzarro (2007) had almost double the weight of decapods and other crustaceans, while the present study had a higher mass of squid. Ebert and Bazzarro (2007) found that squid made up 0.18% by mass whereas the present study found 30.69% (Table 7). The number of squid from Ebert and Bazzarro (2007) is unknown, but for the present study it was 3.8%. The reason the squid take up a large portion of percent mass in the present study is because two fresh specimens were found weighing 79.5 and 72.5 g. Nevertheless, *R. straeleni* were not found to eat squid frequently in either study, compared to crustaceans and teleosts.

Table 7: A diet comparison using percentage by mass of *R. straeleni* between Ebert and Bazzarro (2007) and the present study

	Ebert and Bazzarro (2007)	Present study
Decapods	43.29	24.05
Other crustaceans	20.40	9.01
Fish	33.53	34.93
Euphausiids and mysids	1.11	0.00
Polychaetes and other marine worms	0.55	0.36
Molluscs (excluding cephalopods)	0.55	0.00
Squid	0.18	30.69
Octopods	0.37	0.88
Other invertebrates	0.00	0.06
Amphipods and isopods	0.00	0.02
Undetermined	0.02	0.00

The trophic level of *R. straeleni* examined in this study is 3.98 ±0.05 SE (*n* = 57). The trophic level of *R. straeleni* calculated by Ebert and Bazzarro (2007) was 3.74 (*n* = 421). The differences between the trophic level's estimates are largely because the present study had a larger mass of squid. The present study, along with studies from three decades ago suggest that *R. straeleni* is a benthic, generalist piscivore specializing in small crustaceans and fish. These results means that over the last three decades the diet has not changed, suggesting it is likely there has not been a big shift in the Benguela ecosystem.

The diet study by Walmsley-Hart et al. (1999) found that *L. wallacei* ate similar benthic teleosts and crustaceans to *R. straeleni.* Both *R. straeleni* and *L. wallacei* have a similar body size. *L. wallacei* samples had disk widths 37 mm larger on average than the *R. straeleni* samples in this study. *R. straeleni* has almost nine times the amount of crustacean prey compared to *L. wallacei*. Cephalopods comprised 31.6% of their prey in *R. straeleni,* while no cephalopods were found in *L. wallacei. L. wallacei* had 2.6 times the weight of fish found in *R. straeleni* (Table 8). Ebert and Bazzarro (2007) reported the trophic level of *L. wallacei* and *R. straeleni* to be 3.68 and 3.74, respectively. *L. wallacei* shift their diet to larger species as they increase with size, which is found in other skates in South Africa and worldwide (Macpherson 1986; McEachran et al. 1976). The present study along with Smale and Cowley (1992) found that *R. straeleni* does not change their diet as they mature.

Table 8: A diet comparison (%mass) of *R. straeleni (n* = 53) (present study) and *L. wallacei (n* = 81) (Walmsley-Hart et al. 1999)

	L. wallacei	*R. straeleni*
Decapods	1.46	24.05
Other crustaceans	2.34	9.01
Fish	88.97	34.93
Euphausiids and mysids	1.21	0.00
Polychaetes and other marine worms	0.81	0.36
Molluscs (excluding cephalopods)	1.62	0.00
Squid	0.00	30.69
Octopods	0.00	0.88
Other invertebrates	0.00	0.06
Amphipods and isopods	0.15	0.02
Undetermined	3.44	0.00

The sampling methods shown in the species accumulation curve showed that after dissecting 20 stomachs there was 50% of the prey species found. Every additional skate sample gives a diminishing return.

Skates play an important role as top predators in their demersal marine habitats. It has been hypothesised that skates occupy the same upper-trophic levels as predators such as sharks (Ebert and Bazzarro 2007). Ebert and Bazzarro (2007) estimated that the mean trophic level of skates from the *Rajiformes* order was 3.8 (*n* = 60). Benthic sharks found in the same habitat as *R. straeleni* in the Benguela ecosystem from the orders *Squalidae* and *Scyliorhinidae,* had a mean trophic level of 4.1 (*n* = 38). The similarity between skates and these sharks suggests a degree of competition among the cartilaginous fishes (Ebert and Bazzarro 2007).

Along with the competition of other cartilaginous fish, *R. straeleni* are in competition with teleosts that have similar trophic levels. For example, they live in the Benguela system with jacopever (*Helicolenus dactylopterus)* which has a trophic level of 3.64 (Weston 2021), hake (*Merluccius merluccius*) using the mean of 22 trophic level estimates was 4.09 and the mean of three monkfish (*Lophius budegassa* (2), *Lophius piscatorius* (1) was estimated at 4.2 (Stergiou and Karpouzi 2002). The vast removal of any of these species from commercial fishing could have implications on the others due to their shared diet resources. Multi-species modeling of the target and bycatch species in the trawl fishery should take cognizance of the similarity in diet and trophic position of these economically important species.

Conclusions

The morphology, reproductive biology, and diet of *R. straeleni* had been examined through multi-species collections from three decades ago. The data and analysis that emerged from this study provides additional and current information on *R. straeleni* on the south and west coasts of South Africa.

R. straeleni is a female dominated species, which is common amongst skates. Their morphological features such as their hard, pointed rostrum, helps them to find their main prey namely, crustaceans that live on or in the sediment. Females grow to a larger size than the males to make space for their egg cases. Nevertheless, there was no significant difference in the relationships between disk width and total length or the relationship between weight and total length. *R. straeleni* is slightly hyperallometric.

Females reached maturity 54 mm larger than the males. This is common amongst skates and most likely due to males reaching maturity at a smaller size (and possibly age) to begin reproducing faster. The previous length-at-50% maturity estimate from Ebert et al. (2008) used data from three decades ago. The updated estimated lengths-at-50% maturity generated from this study can be used as a benchmark for monitoring. The closely related and sympatric species, *R. clavata* grew to a larger size and had larger lengths-at-50% maturity.

From this and other studies *R. straeleni* can be described as mid-to-high level generalist carnivores that primarily prey on crustaceans and teleosts. *R. straeleni* occupies the same upper-trophic levels, and compete with, predators such as sharks and other commercially important fishes.

Along with governments needing to authorize species specific catch assessments, there is a need to continue the study of *R. straeleni* to improve our knowledge on the species. Specifically, a study that incorporates age so that there can be accurate parameters created to provide recommendation to government authorities on the size and reproductive parameters of the species. Similar to other studies of skates, this study found that *R. straeleni* are mid-apical predators in South Africa. Due to this, the continued over-fishing of this species may impair benthic food webs.

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