African Journal of Marine Science

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tams20

Movement patterns and catch trends of the diamond ray *Gymnura natalensis* (Dasyatidae) in South African waters

R Daly, GL Jordaan, D Parker, G Cliff, N Nkabi, R Kyle, ST Fennessy & BQ Mann

African Journal of Marine Science 2022: 1–14
Printed in South Africa — All rights reserved

This is the final version of the article that is published ahead of the print and online issue

AFRICAN JOURNAL OF MARINE SCIENCE
ISSN 1814-232X EISSN 1814-2338
https://doi.org/10.2989/1814232X.2022.2032826

Movement patterns and catch trends of the diamond ray *Gymnura natalensis* (Dasyatidae) in South African waters

R Daly[1,2]*, GL Jordaan[1], D Parker[3,4], G Cliff[5,6], N Nkabi[5], R Kyle[7], ST Fennessy[1] and BQ Mann[1]

[1] Oceanographic Research Institute (ORI), Durban, South Africa
[2] South African Institute for Aquatic Biodiversity (SAIAB), Makhanda, South Africa
[3] Department of Forestry, Fisheries and the Environment (DFFE), Cape Town, South Africa
[4] Department of Biological Sciences, University of Cape Town, Cape Town, South Africa
[5] KwaZulu-Natal Sharks Board, Durban, South Africa
[6] School of Life Sciences, University of KwaZulu-Natal, Durban, South Africa
[7] South African Association for Marine Biological Research (SAAMBR), Durban, South Africa
* Corresponding author, e-mail: rdaly@ori.org.za

The diamond ray *Gymnura natalensis* is endemic to southern Africa where its preference for shallow coastal habitats makes it vulnerable to recreational shore-based angling. Although it makes up approximately 1% of the shore-based tag numbers, little is known about its movements, reproduction or population status in South Africa. This study used three independent long-term (34–41 years) datasets, including tagging by recreational anglers, competitive shore angling catches and shark net catches, to investigate the species' movements, catch composition and population status in South Africa. Of the 3 739 individuals tagged (1984–2018), only 30 (1%) were recaptured after an average of 487 days at liberty. The majority (60%) of the recaptures occurred within 10 km of the release site, while 7% had moved more than 1 000 km along the coast. The longest recorded movements (1 577 and 1 756 km) were undertaken by adult rays tagged in the Western Cape Province moving to KwaZulu-Natal Province (KZN). The competitive shore angling catch (1977–2018; *n* = 9 150) from KZN was dominated by adult rays caught north of Durban, while the shark net catch in KZN (1981–2018; *n* = 584) was dominated by juvenile rays primarily from the central beaches of Durban. All the datasets exhibited strong seasonal trends with most catches taking place in summer. A risk assessment confirmed a stable to increasing population trend over four generations, suggesting that the population sampled along the east coast of South Africa should be classified as Least Concern.

Keywords: catch and effort, population status, recapture data, Red List assessment, shore angling, stingray catches, stingray conservation, tagging

Introduction

The diamond ray *Gymnura natalensis* (family Dasyatidae) is an endemic batoid species found from southern Namibia around the entire South African coast to southern Mozambique (Compagno et al. 1989). It inhabits shallow sandy areas from the surf zone to depths of ~75 m and will occasionally enter estuaries (Wallace 1967; Fennessy 1994). It feeds mainly on bony fishes, but will take crustaceans, molluscs and polychaete worms (van der Elst 1993; Smale et al. 2001). Males mature at approximately 100 cm disc width (DW) and females at 150 cm DW (Wallace 1967), sizes that correspond to ages of approximately 2 and 6 years, respectively (van der Elst 1993). Pregnant females have been recorded in the entrance to the Port of Durban and well inside the harbour, known locally as Durban Bay, from January to August (Wallace 1967), and pupping is thought to occur off shallow sandy beaches and bays (Dunlop and Mann 2013). The species exhibits aplacental viviparity, with a 12-month gestation period, and produces between 2 and 9 pups (Compagno et al. 1989; Pollom et al. 2019). It reaches a maximum size of ~250 cm DW and weight of 120 kg (Smith and Heemstra 1991) and maximum age of 24 years (van der Elst 1993). Preliminary tag-recapture results suggest that the species can undertake substantial coastal movements; however, further data are required to quantify the spatial and temporal scales of these coastal movement patterns.

Diamond rays are commonly targeted during recreational shore angling competitions though most are released alive. Large numbers of mature rays are caught every year along the north coast of KwaZulu-Natal Province (KZN) between Richards Bay and the uThukela River during summer, often following a few days of strong northeasterly winds (Pradervand et al. 2007). Historically, diamond rays contributed a large percentage (12.9%) to the elasmobranch component of bycatch taken in the prawn trawl fishery off the uThukela Bank, with a high mortality (Fennessy 1994); in the early 2000s, their contribution was about 16% (Oceanographic Research Institute [ORI], unpubl. data). They are occasionally caught by light-tackle boat anglers fishing in sheltered bays but are seldom kept (S Dunlop, formerly with ORI, pers. comm.). While some are caught incidentally in the shark nets set off certain KZN beaches as part of a bather protection programme, most are released alive (Young 2001). Mature and immature rays are occasionally caught as bycatch in the beach-seine fishery off Durban (Beckley and Fennessy 1996) and in False Bay (Lamberth et al. 1994), but again most are released.

Notwithstanding the amount of information available on the life history of and fishery for *G. natalensis*, there has been no attempt to assess the population status of this species. It has recently been evaluated as Least Concern on the IUCN Red List of Threatened Species (Pollom et al. 2019), albeit in the absence of any population size estimates. Considering this knowledge gap, the current study analysed three long-term datasets, namely the Oceanographic Research Institute's Cooperative Fish Tagging Project (ORI-CFTP) tag and recapture data, the KZN Coastal Anglers Union (KZNCAU) shore angling competition data, and the KZN Sharks Board's (KZNSB) shark net catch data. The aim of the study was to gain a better understanding of the movement patterns of this species and to assess its status using available long-term catch trends. We incorporated both the shore angling and shark net probability-of-encounter (PE) model estimates into the Bayesian state–space framework 'JARA' (Just Another Red-List Assessment) with the aim of quantifying the abundance trend for the population from the east coast of South Africa according to the IUCN Red List criteria (Sherley et al. 2020), thereby providing a regional assessment of its conservation status.

Methods

Tagging study

All tag releases and recaptures for diamond rays *Gymnura natalensis* took place along the South African coastline from Cape Vidal in KZN (28.128588° S, 32.560168° E) to Langebaan Lagoon in the Western Cape Province (WC) (33.143471° S, 18.06054° E) (Figure 1). For graphical representation, all these locations were binned into 100-km zones around the South African coast, extending across KZN, the Eastern Cape Province (EC) and WC, from the Mozambique/South Africa border in the east to Cape Columbine in the west (Figure 1).

All tag-recapture data for diamond rays stored on the ORI-CFTP database between January 1984 and December 2018 were extracted and analysed (see Dunlop et al. [2013] for details of the ORI-CFTP). Most of the tagged rays were caught by rod and line from the shore, although some individuals caught in the KZN shark nets were also tagged and released. Ray disc width (DW) was measured in centimetres and individuals were tagged in the muscle at the base of the tail, although in the early stages of the programme some rays were tagged in the posterior region of the pectoral fin ('wing'). Several types of tags were used, including C-tags (clip-on roto-tags), A-tags (external spaghetti-dart-type tags), D-tags (a smaller version of the A-tag) and B-tags (external spaghetti-dart-type tags with stainless steel heads) (see Dunlop et al. [2013] for details).

To examine the size structure of tagged and recaptured diamond rays, individuals were assigned to one of two size classes: juveniles of 35–125 cm DW, with 35 cm DW being the average size at birth, and adults of >125 cm DW. Unfortunately, sex was not recorded for most of the tagged and recaptured individuals, and thus we used the midpoint at maturity (125 cm DW) for males and females. A monthly comparison of total tag releases and recaptures for these two size classes in each geographic region was performed to detect possible trends in seasonal size distribution.

Movements of recaptured individuals were calculated by measuring the linear distance along the coast in kilometres between the points of tag release and recapture. Dispersal from the release site was assessed by assigning each recapture to a distance bin (0–10, 11–50, 51–100, 101–500, 501–1 000 or >1 000 km). Individuals were assigned to a size class (i.e. juveniles that were immature, or adults presumed to be mature) based on length at recapture.

Competitive shore angling data

Catch data were obtained from the KZNCAU shore angling competition records from 1977 to 2018 (see Pradervand et al. [2007] for more information on the competition format and guidelines). These competitions are held monthly between January and November (11 months) of every year. The data were validated and captured onto the National Marine Linefish System (NMLS) recreational angling database kept at ORI in Durban, South Africa. For this study, competition catch data from the Mozambique border to the Mbhashe River (752-km shore length) on the east coast of South Africa (boundaries of the KZNCAU competitions) were extracted from the database (Figure 1). Catch data included species-specific data on the locality, hours fished, number of anglers, and the length or weight of individual fish caught. The mean annual DW of catches was calculated from available size data. Prior to 1995 all fish caught during competitions were weighed rather than measured. For this reason all earlier individual fish weights were converted to DW using the relationship provided by Dunlop and Mann (2013), as follows:

$$Wt(kg) = 0.0000075 \times DW(cm)^{3.04} \quad (1)$$

KwaZulu-Natal shark net catch data

Shark nets are large-mesh gill nets that have been deployed year-round at popular recreational beaches in KZN since 1952 to reduce the risk of shark injuries to beach users (Cliff and Dudley 1992; Cliff and Dudley 2011) (Figure 1). Most of the nets are 214 m long, 6.3 m deep and are set parallel to and 300–500 m from the shore, in water 10–14 m deep (Cliff and Dudley 2011). Catch data from shark nets conducive for the analysis of long-term population trends were only regarded as sufficiently reliable from the late 1970s for sharks and from the early 1980s for the various bycatch species (such as diamond rays).

Shark net catch data from 1981 to 2018 were analysed for this study. All diamond rays caught in the shark nets were measured (cm DW), except those live individuals that were lost from the net during servicing, and the majority were sexed (84%). Kernel density estimates (KDEs) were used to assess variability in size distributions between competitive shore-angling and shark net data. A KDE estimates the shape of the distribution $\hat{f}(x)$ using:

$$\hat{f}(x) = \frac{1}{nh}\sum_{i=1}^{n} k\left(\frac{\hat{x} - x_i}{h}\right) \quad (2)$$

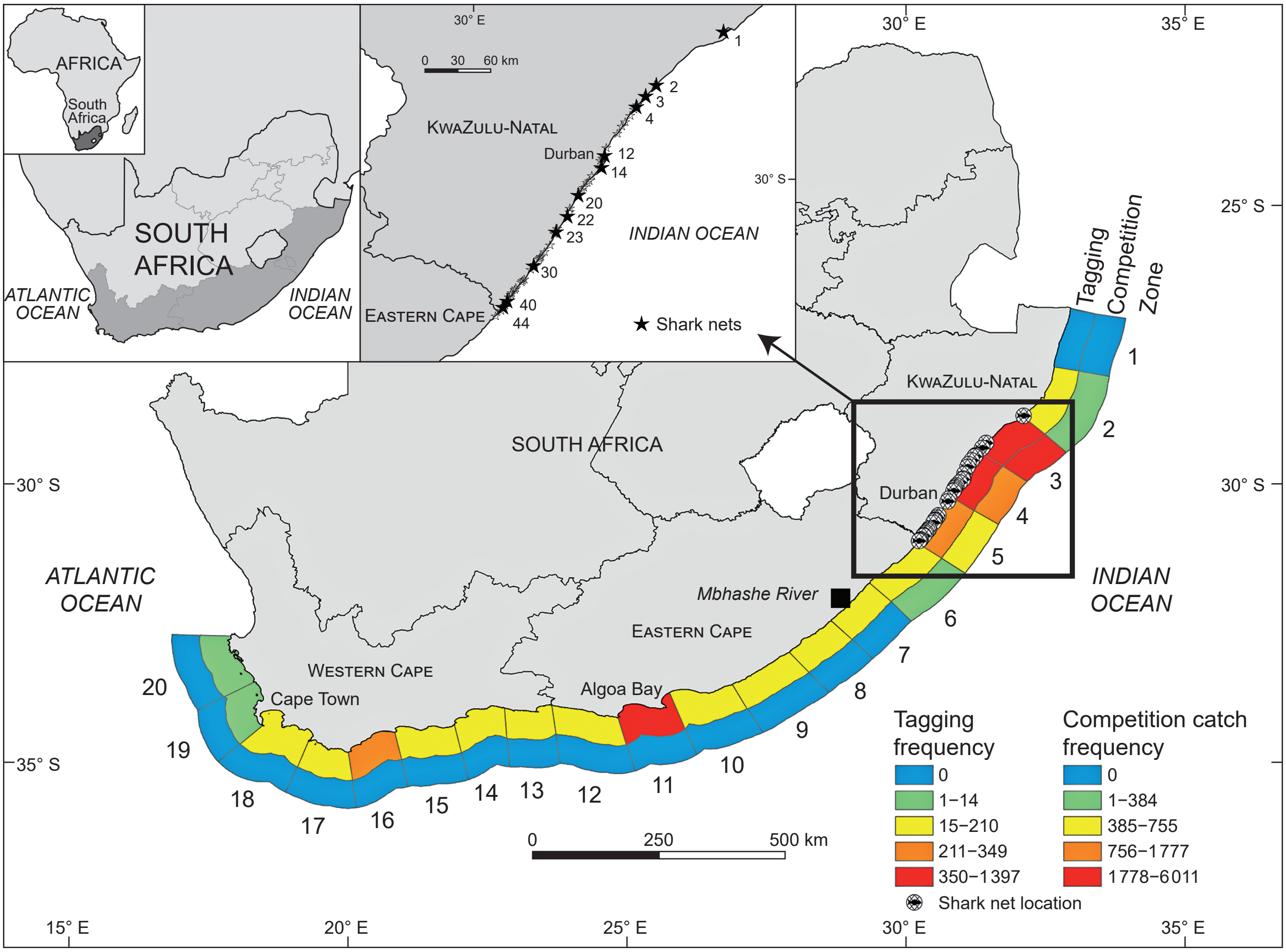

Figure 1: A map showing the pre-defined 100-km coastal zones (Zones 1 to 20) with the corresponding tagging and competition catch frequency of diamond rays *Gymnura natalensis* along the South African coast. Additionally, the location of shark nets in KwaZulu-Natal is shown (Zones 3 to 5), and the inset shows beach numbers 1 to 44 (of a total of 46) from north to south

where k is the kernel, h is the smoothing parameter called the bandwidth, $\bar{x}$ is the mean length (DW), x_i is the observed length (DW), and n is the number of observations. Kernel densities were fitted with the 'sm density' function in the R package 'sm' (Bowman and Azzalini 2010; Parker et al. 2017).

Standardisation of the probability of encounter

Generalised additive models (GAMs) were used to examine the relationships between the probability of encounter (0 = absent, 1 = present) of diamond rays and selected predictor variables, assuming a binomial error model. Catch data for diamond rays are zero-inflated and the probability-of-encounter (PE) method has been shown to be an appropriate index of abundance for such instances (Kerwath et al. 2019). Inferring trends in relative abundance from PE is dependent on the assumption that if the PE decreases below a certain threshold, determined to be 0.25, the information content in the non-zero observations is minimal. As such, the relationship between PE and abundance becomes approximately linear close to its origin.

Catch data from competitive shore angling and the shark nets were analysed separately. Covariates available for inclusion in the PE analyses of competitive shore angling data included Year, Month and Region. No attempt was made to account for targeting based on the assumption that there was no shift in species-specific targeting preference throughout the competition data time-series. The final model structure was:

$$\text{logit}(p) = \beta_0 + f_1(\text{Year}) + f_2(\text{Month}) + (\text{Region}) + \varepsilon \quad (3)$$

Covariates available for inclusion in the PE analyses of shark net data included Year, Month, Temperature (surface), Water Visibility, Wind Speed, Current Direction and Moon Phase. However, only Year and Month explained a significant proportion of variation in the data, and the final model structure was:

$$\text{logit}(p) = \beta_0 + f_1(\text{Year}) + f_2(\text{Month}) + \varepsilon \quad (4)$$

For both models, logit denotes the binomial link function, p is the probability of encountering at least one diamond ray individual per sampling unit (competition outing or shark net deployment), β_0 is the intercept, $f_{1\text{-}2}$ denote thin plate regression spline smoothers, and ε represents the model residuals (Wood 2006). The annual value of PE was standardised by fixing all covariates other than Year in the prediction dataset. Sequential *F*-tests were used to determine the covariates that contributed significantly ($p < 0.01$) to the deviance explained. All GAMs were fitted in R statistical software using the 'mgcv' and 'nlme' libraries described in Wood (2006).

Population risk assessment with JARA

The Bayesian state–space framework 'JARA' (Just Another Red-List Assessment) was designed as an IUCN Red List decision-support tool that utilises formal trends (i.e. catch per unit effort [CPUE] or probability of encounter [PE]) to calculate the Bayesian posterior probability of the percentage change (C%) in a population (Winker et al. 2020). Based on the distribution of the posterior probability, the estimated population trend is assigned a probability of satisfying each of the Criterion-A Categories adopted by the IUCN Red List procedure: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN) or Critically Endangered (CR). In this way, JARA allows for a quantitative approach to categorise the threat of extinction that accounts for both the process error and uncertainty which are inherent in estimated population trends (Sherley et al. 2020; Winker et al. 2020). Here, we applied the JARA approach to the diamond ray PE estimates, and their associated standard errors (SE), calculated from both the competitive shore-angling and shark net data. In the absence of reliable life-history information, a conservative generation period of 13 years was assumed for diamond rays. This is identical to that applied to *G. japonicus* (Rigby et al. 2021) and is within the 5–15-year range applied to other IUCN assessments of species from the genus *Gymnura* (Pollom et al. 2020; Dulvy et al. 2021).

Results

Tag-recapture results

A total of 3 739 diamond rays *Gymnura natalensis* were tagged in the ORI-CFTP between January 1984 and December 2018, most of which were adults (adults = 2 489, 67%; juveniles = 1 218, 33%). Only 30 (1%) were recaptured (Figure 2), of which 17 (57%) were adults, 3 (10%) were juveniles, and 10 (33%) were not measured. Most of the tag recaptures were recorded by recreational anglers (n = 28), with the remainder being recaptured by citizen scientists (n = 2) during scientific tagging trips.

Most tagging took place in KZN (n = 2 275, 61%) with most tag releases occurring in Zone 3 (n = 1 396) on the north coast (Figure 1). Most adults were tagged in KZN (76%) or the WC (61%), compared with in the EC where more juveniles were tagged (54%) (Figure 3). A seasonal catch trend was observed, with most of the diamond rays tagged (78%) and recaptured (83%) during the summer, which was apparent in both adults and juveniles (Figure 4).

Eighteen (60%) recaptured diamond rays had remained within 10 km of their original release site; five moved 11–50 km, one moved 51–100 km, two moved 101–500 km, two moved 501–1 000 km, and two moved >1 000 km (Figure 2). Regarding the direction moved (for those animals that moved more than 10 km), eight individuals moved in a northeasterly direction from their original tag-release location, with two moving between 501 and 1 000 km and two moving >1 000 km. Only four recaptured individuals moved in a southwesterly direction, with two of these moving between 101 and 500 km (Figure 2). The longest movement recorded (1 756 km) was from an individual originally tagged on 9 September 2016 at Vogelsteen, WC, measuring 190 cm DW, and then recaptured 334 days later at Port Durnford, KZN, measuring 188 cm DW (Figure 2). The second-longest movement (1 577 km) was from an individual originally tagged on 24 December 2004 at Muizenberg, WC, measuring 126 cm DW and recaptured 176 days later at Mtwalume, KZN, measuring 136 cm DW (Figure 2). Both individuals were adults tagged in the WC that made long migratory movements to KZN in less than a year at liberty. The time at liberty of all recaptured individuals ranged from 0 to 2 184 days (6.0 years) with a mean of 487 days (1.3 years). Most of the recapture events (n = 19, 63%) took place within one year of tagging.

Competition catch data

A total of 9 150 diamond rays were captured in KZNCAU shore angling competitions between 1977 and 2018 (Figure 5). The greatest number of diamond rays were captured in Zone 3 (n = 5 931) and Zone 4 (n = 1 771) on the north coast of KZN (Figure 1). The catch in Zones 2 and 3 was dominated by adult rays (94% and 98%, respectively) while the catch in the remaining Zones 4–6 in KZN had a slightly higher proportion of juveniles (Figure 3). The standardised PE of the competition catch was variable from 1977 to 2018 (Figure 6a), with peaks in encounter probability in 1994, 1999 and 2005 that were dominated by adult rays (Figure 7a). The greatest peak in PE was in 2015 and 2016, when the catch was again dominated by adults.

Shark net catch data

A total of 584 diamond rays were caught in the KZN shark nets between 1980 and 2018, of which 76% were found alive and released. The standardised PE of shark net catches of diamond rays showed a relatively stable trend throughout the 37-year study period, with slight peaks in 1989 and 2011 (Figure 6b); the variance around the PE in shark nets was much greater than around that in shore catches (Figure 6a). The shark net catches in general had a higher proportion of juveniles when compared with the competition catch data (Figure 7b). Analysis of the shark net catch data from KZN showed that the probability of catching diamond rays peaked in summer months (with a peak in November) and was lowest during winter (especially July) (Figure 8). Results of the GAM confirmed that Month was a significant predictor of PE, which accounted for 53.4% of the total deviation explained by the model.

Shark net catch composition was dominated by juvenile rays (76%) between 90 and 120 cm DW (Figure 9a). There was an even sex ratio (M:F, 1.04:1) and an overall ratio of 1:3.16 adult to juvenile rays. The lengths of diamond

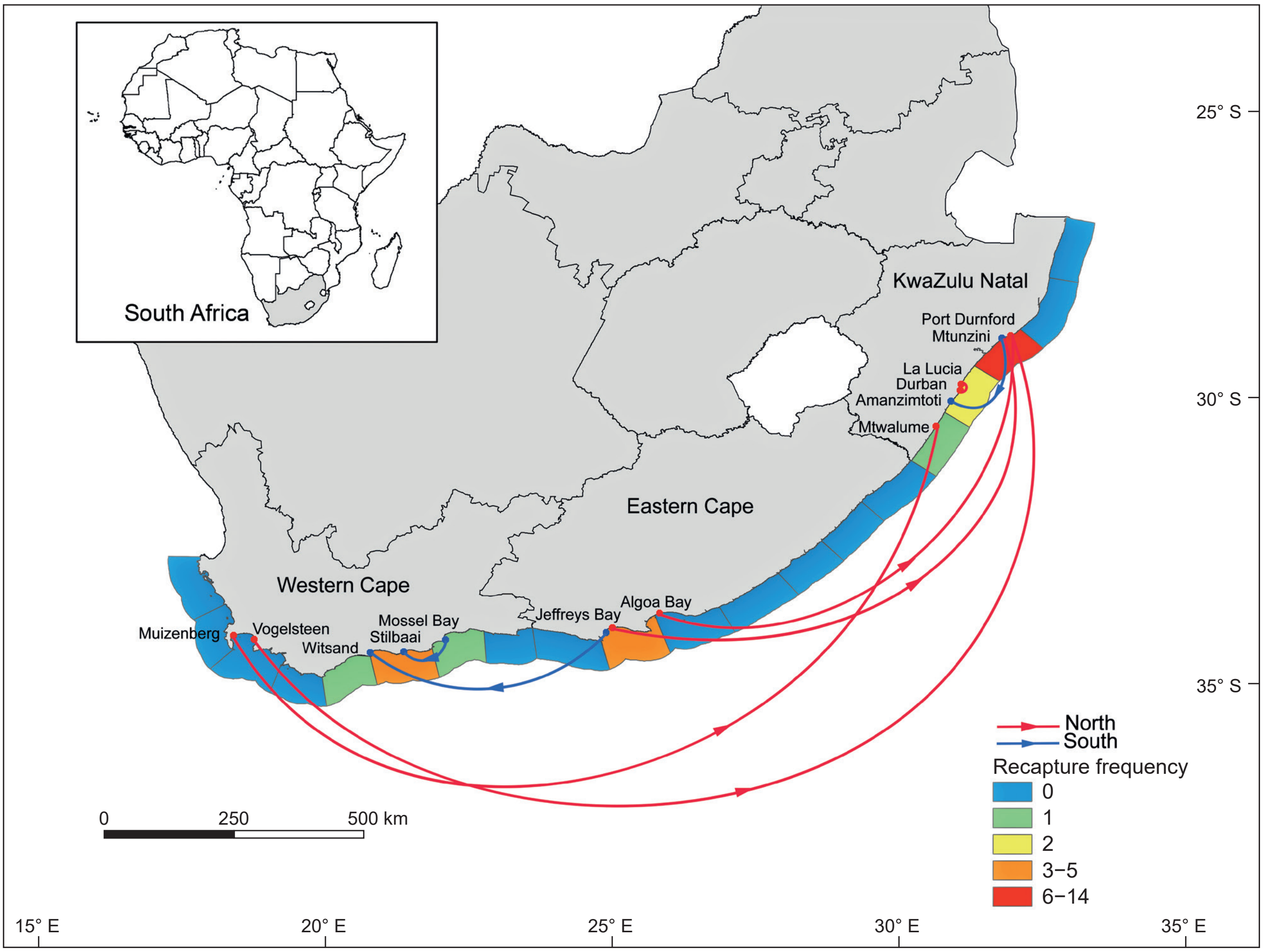

Figure 2: The frequency of all tagged diamond rays *Gymnura natalensis* recaptured along the coast of South Africa. The movement of rays that travelled more than 10 km is shown by lines with arrows and colours that indicate the direction of their movement northwards or southwards

rays caught by competitive shore anglers were generally larger than those caught in the shark nets (Figures 5 and 9). Durban (Beach 12) had the highest catch rate (representing 43% of the total catch) although this net installation only had about 20% of the total netting effort. The next highest catches were 40 km south of Durban at Karridene (Beach 19; Zone 5 in Figure 1), and 75 km north of Durban at Zinkwazi (Beach 2; Zone 3 in Figure 1) (Figure 9b). The shark nets selected for a smaller size class compared with the competition catches (Figure 10). There were no pregnant or reproductively active females among the total of 109 individuals that died in the nets during the study period and were sent to the laboratory for biological examination. There were three occasions when more than 10 individuals were captured in the same net installation on the same day. The largest such catch occurred in Durban in November 2018 and comprised 28 individuals (16 females: 79–115 cm DW; 12 males: 85–110 cm DW). This suggests the likelihood of diamond rays aggregating or moving in shoals/groups at certain times. All but two of the 62 rays caught in these mass capture events were released alive.

Risk assessment

Our risk assessment for diamond rays indicates a 104% increase in the population over a period of 39 years or three generation lengths (1979–2018) (Figure 11a). The rate of increase was relatively consistent over time, with the population increasing by 1.96% per year (Figure 11b). Based on these results, the sampled population of diamond rays should be classified as Least Concern in accordance with the IUCN Red List Categories and Criteria (IUCN 2012) (Figure 11c).

Discussion

There are few South African fish species that offer opportunities to include such diverse data sources as angling catches, tagging, and gillnet catches when undertaking population assessments, particularly where long-term datasets (of >30 years) are concerned, as is the case with the diamond ray.

Movement patterns

Of 3 739 diamond rays that were tagged between 1984 and 2018, only 1% were recaptured. The low recapture rate is

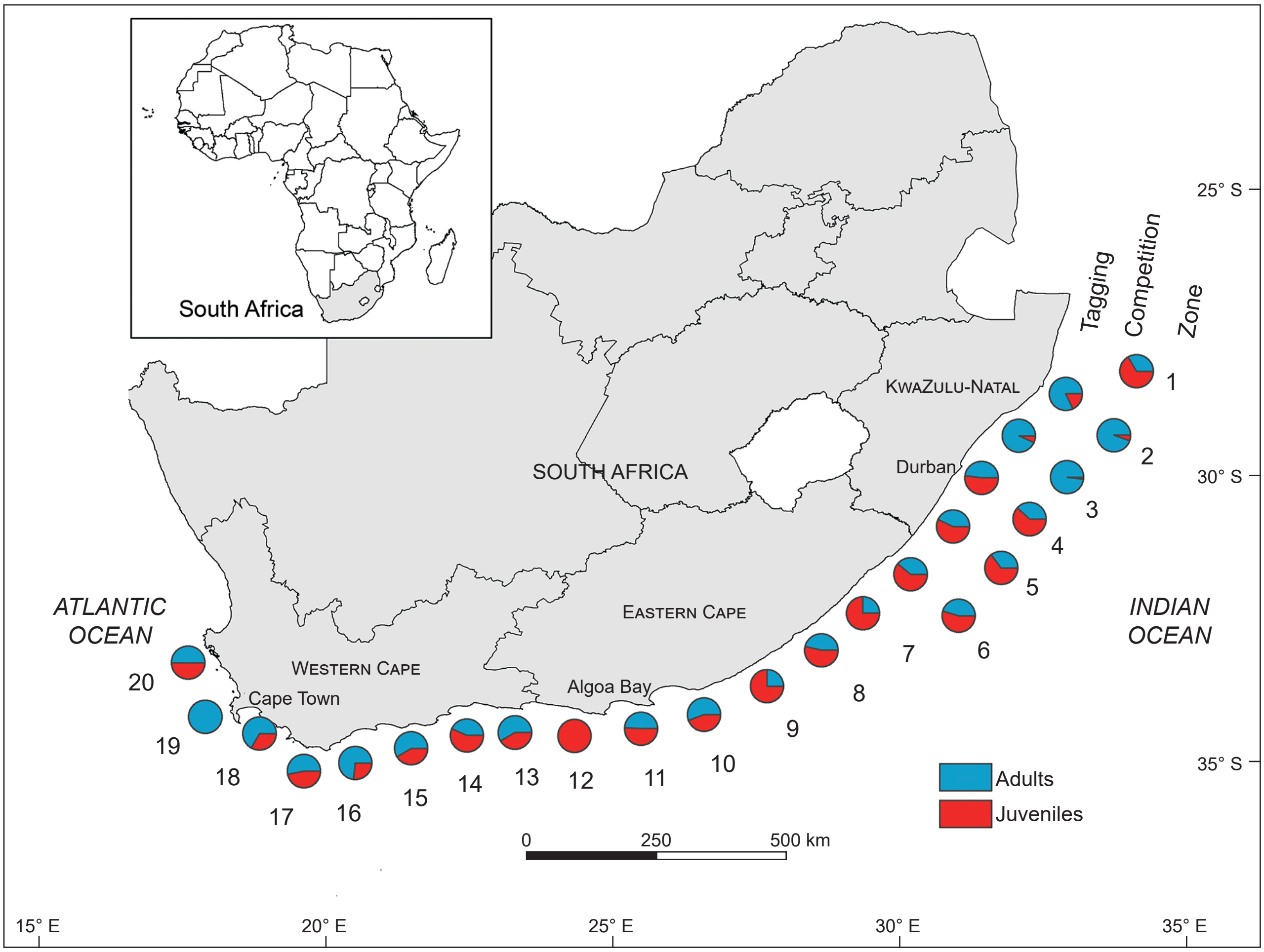

Figure 3: The proportion of adult and juvenile diamond rays *Gymnura natalensis* in each coastal zone tagged by members of the ORI-CFTP (tagging data) and those captured by members of the KZNCAU (competition data) in South Africa

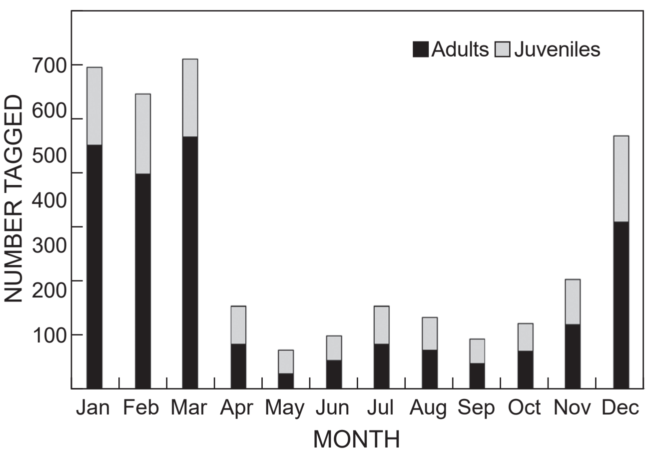

Figure 4: A monthly comparison of the number of *Gymnura natalensis* adults and juveniles tagged from January 1984 to December 2018

similar to many other ray species tagged in the ORI-CFTP, including *Dasyatis chrysonota* (0.5%), *Maculabatis gerrardi* (0.4%), *Himantura leoparda* (2.2%) and *Pteromylaeus bovinus* (1.2%) (Jordaan et al. 2021). The reasons for the poor recapture rate might include poor tag retention owing to the position where they were formerly tagged (i.e. on the posterior part of the pectoral fin in the case of roto tags [C-tags], which simply tore out) or because they were tagged incorrectly and not in the musculature at the base of the tail. Another reason for the low recapture rate could be post-release mortality from physiological stress or depredation (Laptikhovsky 2004; Heberer et al. 2010; Skomal and Mandelman 2012; Danylchuck et al. 2014; Gallagher et al. 2014; Mann et al. 2018; Mohan et al. 2020). Furthermore, if a tag is inserted into the side of the tail musculature, there is risk of the tagger puncturing the kidneys (which lie dorsally on either side of the spinal column), which could also cause post-release mortality. However, based on the high release rates of diamond rays from shark net catches (75%) and improved angler handling and release practices, it is unlikely that post-capture and tagging mortality is the primary reason for the low recapture rates.

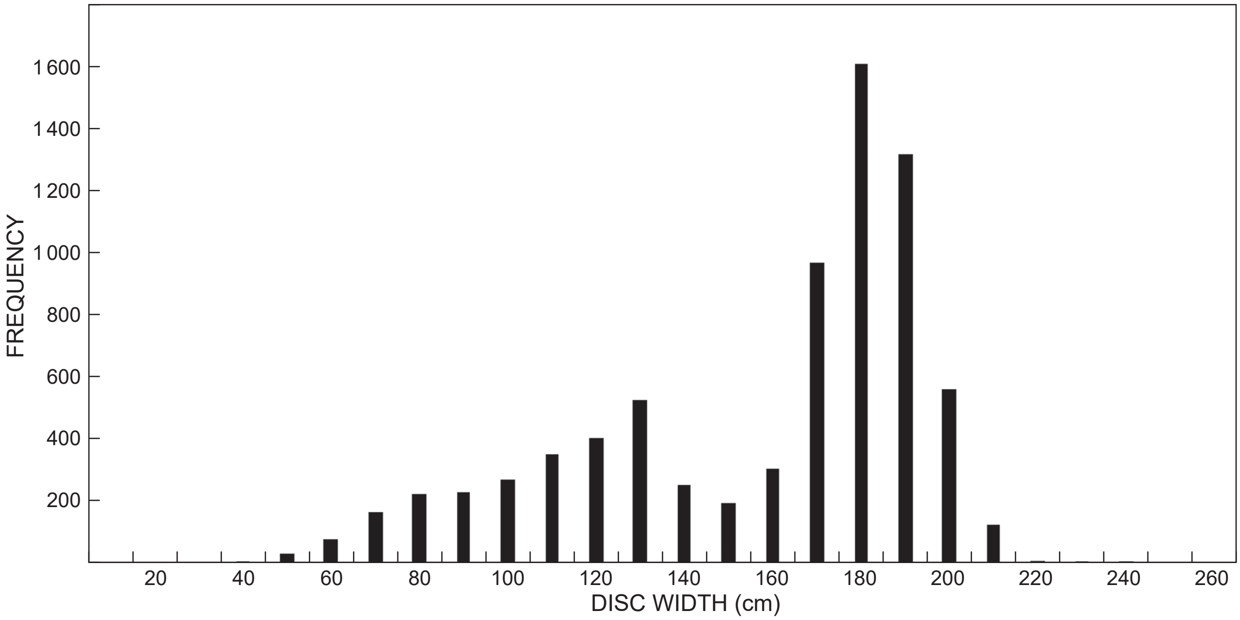

Figure 5: Length frequency distribution of *Gymnura natalensis* from the competitive angling catch in KwaZulu-Natal, South Africa, between 1977 and 2018

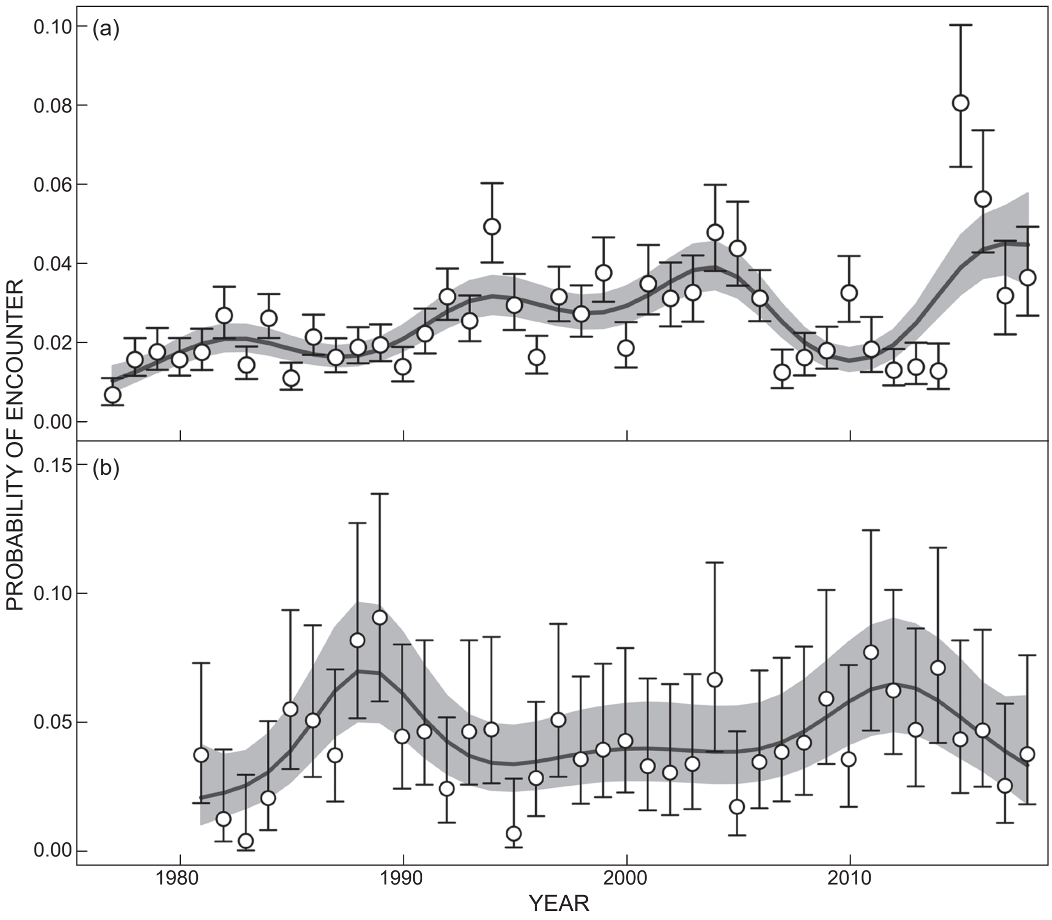

Figure 6: Standardised probability of encounter (PE) of *Gymnura natalensis* from (a) competitive shore angling and (b) shark nets. The generalised additive models were fitted using the variable Year as a factor (point estimates with 95% confidence intervals depicted with error bars) as well as with Year as a spline (solid line with 95% confidence interval depicted as grey shaded area)

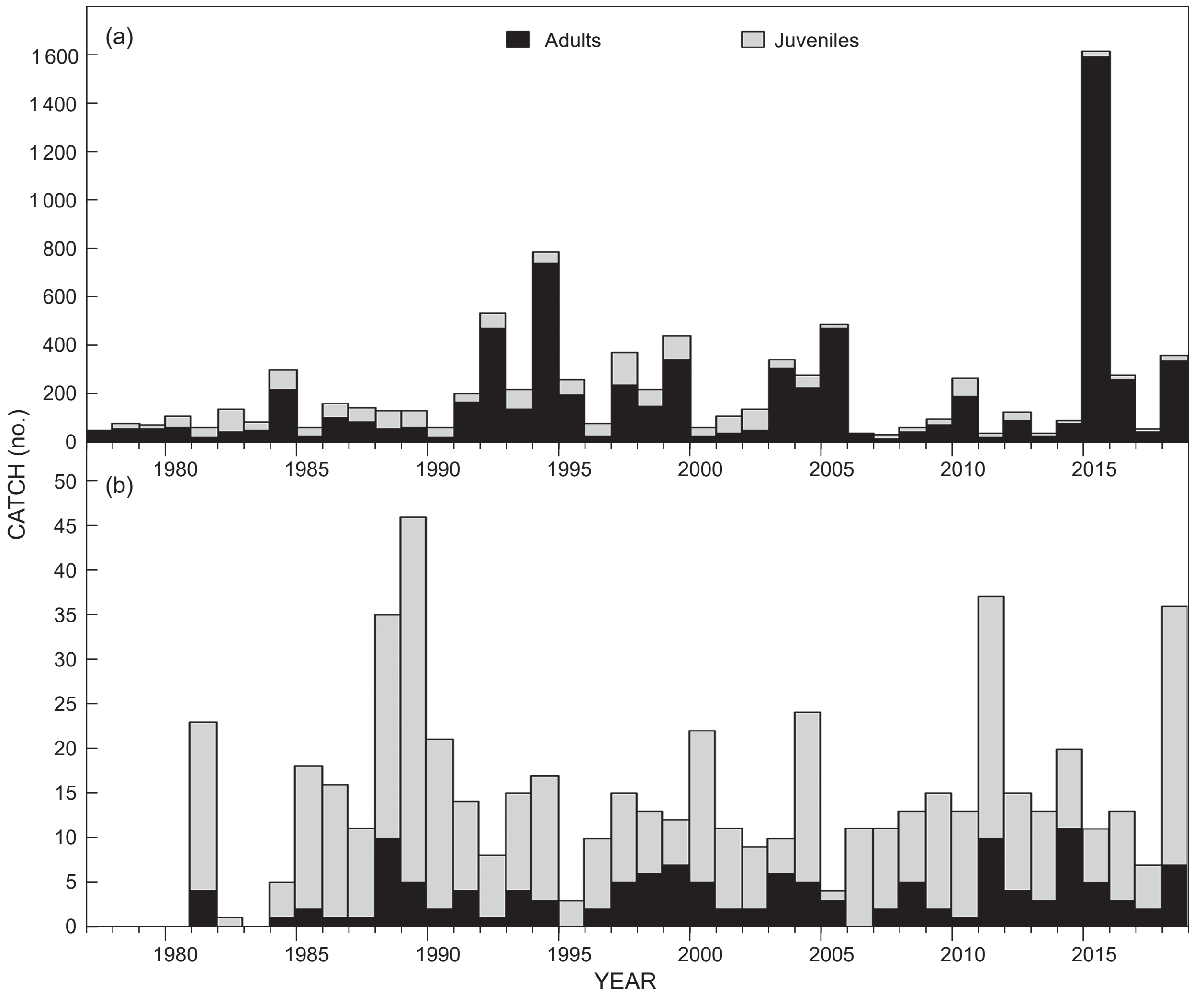

Figure 7: Catch and maturity status of *Gymnura natalensis* from (a) the competition catch and (b) shark net catch data from the east coast of South Africa

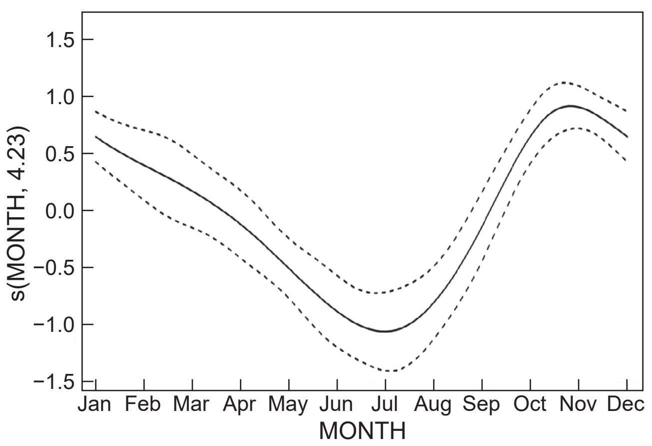

Figure 8: The modelled effect of the variable Month on the probability of encounter (PE) of *Gymnura natalensis* from shark net catches in KwaZulu-Natal from 1981 to 2018. Month accounted for 53.4% of the total deviation explained by the generalised additive model. Dashed lines represent 95% confidence intervals

Compared with other ray species recaptured in the ORI-CFTP, diamond rays exhibited the largest average distance moved ($\bar{x}$ = 395 [SD 604] km). In contrast with the movements of other ray species of similar size, such as *Aetobatus ocellatus* ($\bar{x}$ = 204 [SD 339] km), *Pteromylaeus bovinus* ($\bar{x}$ = 27 [SD 40] km), *Myliobatis aquila* ($\bar{x}$ = 16 [SD 22] km) and *Himantura leoparda* ($\bar{x}$ = 3 [SD 4] km) (Jordaan et al. 2021), diamond rays may be more mobile and undertake longer coastal migrations. Other batoid species such as *Raja clavata* and *Rhinoptera bonasus* may also undertake substantial repeat migrations, driven in part by reproduction (Hunter et al. 2005; Ogburn et al. 2018). Other co-occurring elasmobranch species, such as adults of *Carcharias taurus*, also show large seasonal migrations along the South African coastline (Dicken et al. 2007) and are thought to exhibit reproductive philopatry (Klein et al. 2019). Such long-distance migrations are mainly driven by reproduction, suggesting that the long-distance movements made by adult diamond rays could be for similar reasons. Possible evidence of this is indicated by the large number of juveniles caught in the EC as well as the large number of

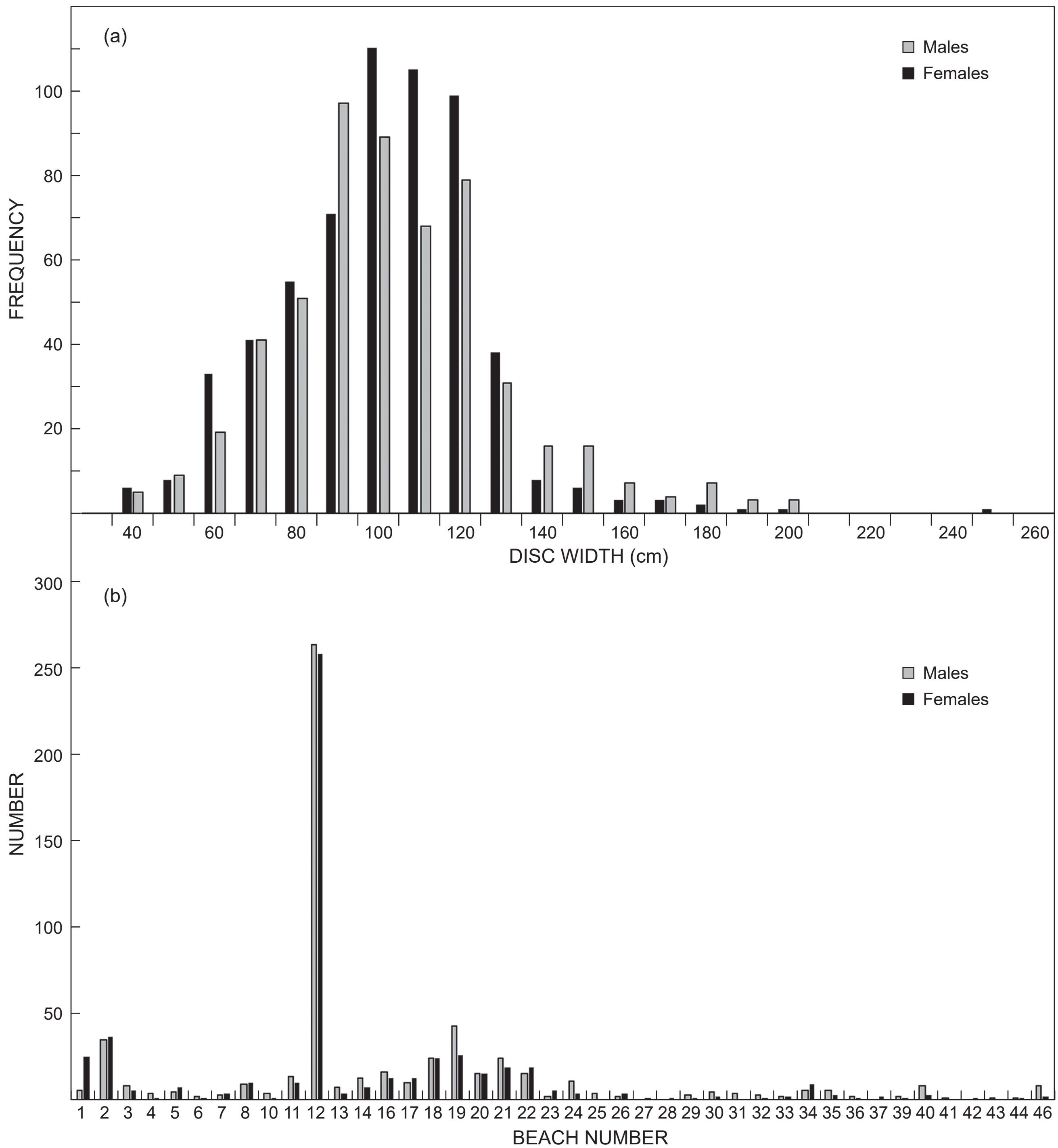

Figure 9: (a) Length frequency distribution of males (n = 591) and females (n = 545) of *Gymnura natalensis* caught in the KwaZulu-Natal shark nets in South Africa between 1981 and 2018, and (b) beach net installation numbers where the diamond rays were caught. Beach 12 represents the shark net installation at Durban (see Figure 1)

adults caught off KZN in this study. The seasonal abundance of larger individuals caught from the shore in KZN in the warmer summer to autumn months, coupled with long distance movements of tagged adults observed in this study, suggests the possibility of a seasonal migration from the cooler waters of the WC to KZN. Fennessy (1994) found that smaller individuals were more commonly caught in the uThukela Bank region (Zone 3) compared with medium and larger individuals, providing evidence that the region could be a pupping ground for diamond rays. Further investigation to determine what percentage of the population may be pupping in this region could help to determine whether the uThukela Bank constitutes a key biodiversity area for the species (IUCN 2016). However, the abundance of juvenile

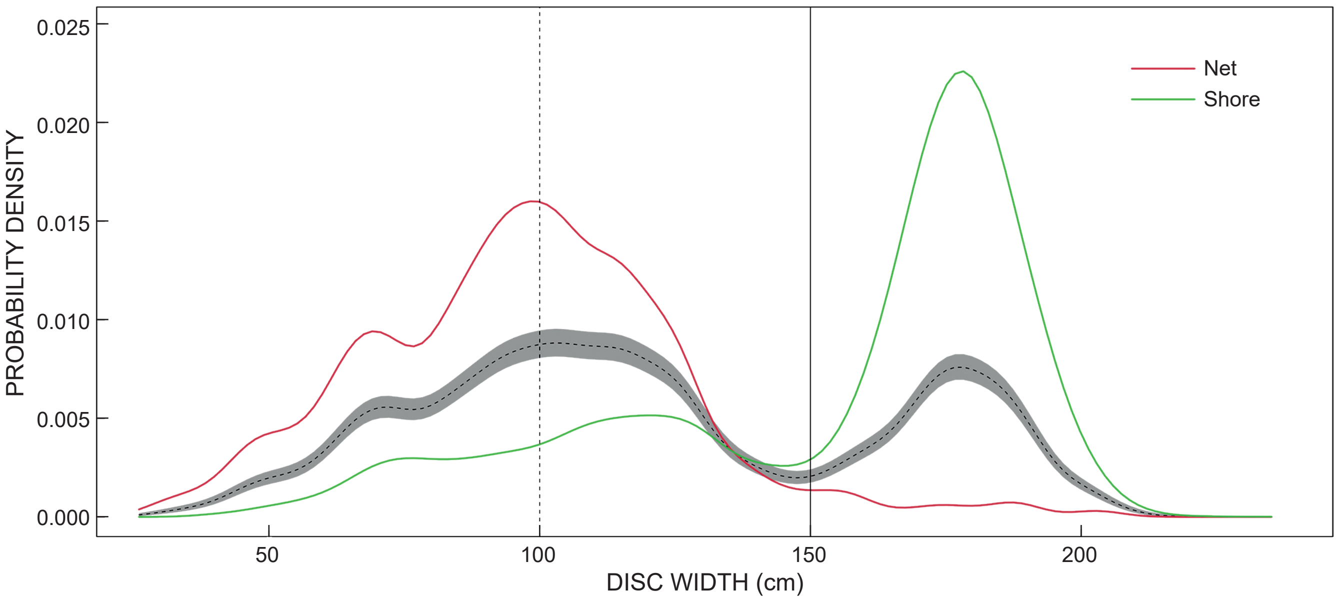

Figure 10: Kernel density estimates (KDEs) for the disc width (cm) of *Gymnura natalensis* caught in the competitive shore fishery and the shark nets combined. The null model helps identify differences in the size distribution selected by each capture method. Grey shading represents one standard error above and below the null model. Reported size at maturity for males and females shown as a vertical dashed line and solid line, respectively

diamond rays tagged in the EC (this study), their occurrence in shark net catches off Durban (this study) and their occurrence as bycatch in inshore trawl fisheries in the Cape (Buxton et al. 1984; Attwood et al. 2011), does not preclude the existence of other pupping areas or the possibility that juveniles undertake a southward migration from KZN.

In summary, this study identified that there are major gaps in our understanding of diamond ray movements, mainly due to the poor tag-recapture numbers. One way to overcome this would be to tag these animals with acoustic or pop-up archival satellite tags, to improve our understanding of their coastal movement or migration patterns and determine whether multi-year return migration patterns exist. Additionally, tagging individuals of varying size and sex could help to identify the primary drivers of their coastal migrations, such as reproduction. Acoustic or survivorship pop-up archival satellite tagging might also improve our understanding of post-release mortality rates (Curtis et al. 2015; Crossin et al. 2017; Musyl and Gilman 2018), as well as identify the physiological effects of capture stress, which have been poorly assessed in batoids (Skomal and Mandelman 2012).

Competition angling catch trends

Diamond rays are a popular target species for competitive shore anglers along much of the eastern seaboard of South Africa (Pradervand and Govender 2003; Pradervand 2004; Pradervand et al. 2007). While their seasonal occurrence off beaches along the northern coast of KZN has been known for many years, improvements in tackle (graphite rods, fixed-spool reels and lighter, stronger braided line) have enabled competitive anglers to target this species more effectively to some extent (i.e. casting farther with bigger baits). The improved gear might manifest in incremental increases in catch rates over the years despite no change in *G. natalensis* abundance (i.e. effort creep), the effect of which could potentially mask a real decline in abundance. Without means to accurately quantify (and therefore account for) the effort creep, we mitigated this potential bias by using probability of encounter (PE) as the index of relative abundance. This binary index (0 = absent, 1 = present) is probably more robust to effort creep than traditional CPUE estimations, as the latter is heavily influenced by instances of large catches. Furthermore, the shark net catches (representing a fixed gear type with no effort creep) over the same spatial and temporal scale showed a similar trend in PE, and there is circumstantial evidence from uThukela Bank trawl catches that relative abundance increased from the 1990s to the 2000s (ORI unpubl. data).

Over time, anglers have become more aware of the presence—sometimes in extremely large numbers—of diamond rays frequenting the surf-zone between the uThukela River mouth and Richards Bay (Zone 3) in late summer to autumn (January to April). This often follows a few days of strong northeasterly wind, and it is thought that movement of upwelled, cooler, low-oxygenated water onto the uThukela Bank following such conditions (Fennessy et al. 2016) forces diamond rays to move inshore into the warmer, highly oxygenated surf zone where they feed aggressively and become available to shore anglers. For example, in 2015 a total of 158 individuals (8 309 kg total weight) were caught by a team of eight competitive shore anglers within 8 hours on the same day within a 3-km stretch of coast north of the uThukela River mouth in Zone 3 (RK pers. obs.). All these rays were released alive. This phenomenon would also likely account for the observed peak in probability of encounter in 2015.

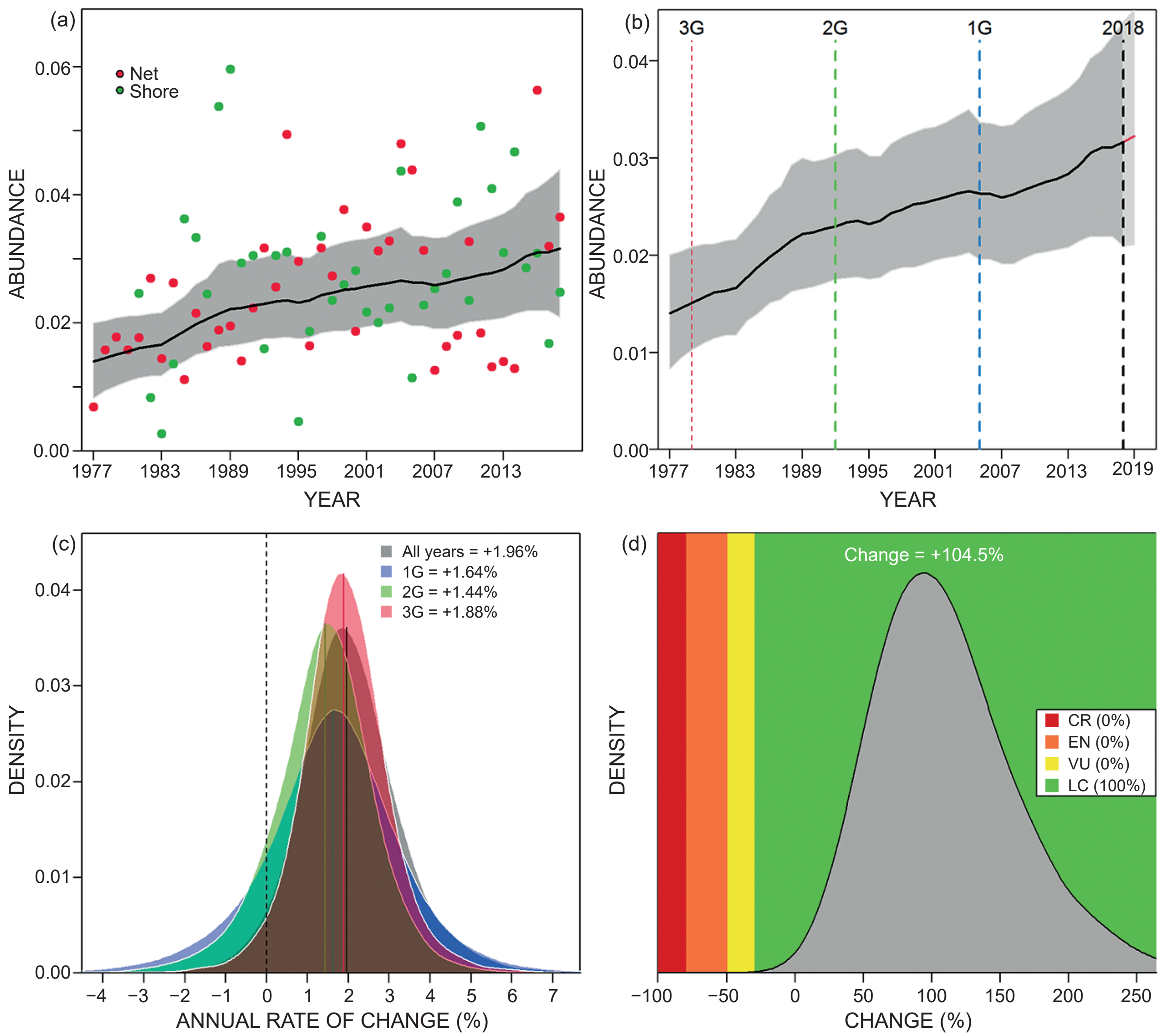

Figure 11: Results of the 'Just Another Red-List Assessment' (JARA) analysis. (a) The JARA fit (black line) and 95% credible intervals (grey polygon) when applied to the two probability-of-encounter (PE) time-series used for the JARA analysis: the competitive shore fishery data (red points) and the shark net data (green points); (b) the estimated population trajectories (black line, and 95% credible intervals) of *Gymnura natalensis* over three generations (1G, 2G and 3G, respectively, denoted by the span of the vertical dashed lines); (c) the posterior probability for the percentage annual population change calculated from the modelled PE trend, from the last one generation length (in blue), from the last two generation lengths (in green), and from the last three generation lengths (in red), with the medians (solid lines) shown relative to a stable population (0% change, black dashed line); (d) the median change in relative abundance of diamond rays over three generation lengths is 104%. The Bayesian posterior probability for that change is shown by the grey polygon, which is overlaid on the IUCN Red List category thresholds for the Red List Criterion A2. The values in the key show the percentage of the posterior probability distribution falling within each Red List Category (LC = Least Concern; VU = Vulnerable; EN = Endangered; CR = Critically Endangered)

Interestingly, the majority of the large diamond rays captured during summer by competitive shore anglers north of the uThukela River (Zone 3) were likely mature female rays, based on their size (RK pers. obs.). Stretches of beach near Port Durnford appeared to be important for these large female diamond rays during summer. This component of the population might not be sampled by nearby shark nets (e.g. at Richards Bay), as these rays appear to be too large to be caught by the mesh size used for the shark nets. Thus, it is possible that these large mature female rays occur in this region during summer as part of their reproductive cycle where they may be gestating in the warmer waters of northern KZN, in a similar way to ragged-tooth sharks *Carcharias taurus* (Dicken et al. 2007). Additionally, two of the few places on the South African coast where very small diamond rays (<50 cm DW) are caught by anglers (and in the shark nets) are Durban in KZN and St Francis Bay in the EC (Blayne Wareham, South African Shore Angling Association, pers. comm.), which may suggest that such sheltered bays are important nurseries for diamond rays.

Shark net catch trends

Diamond ray catches in the shark nets remained relatively stable throughout the study period in contrast with other elasmobranch species, such as the white-spotted wedgefish *Rhynchobatus djiddensis*, over the same period (Daly et al. 2021). Of the 578 individuals caught during the 34-year study period, the majority were juveniles (76%), likely reflecting the higher probability of the net mesh size to select and catch smaller rays (Figure 10). The greatest number of diamond rays was caught at Durban (43% of the total catch), immediately to the north of the entrance to the Port of Durban. In the three mass-capture events recorded in the shark nets, both males and females were recorded. The sizes of the males spanned both juveniles and adults whereas the females were all juveniles, which suggests that mating was probably not the reason for the aggregations. As also experienced in the competitive shore angler mass-catch events described above, a fresh northeasterly wind prevailed for four days prior to the largest of these events, in which 28 individuals were caught in 2018. This suggests that environmental factors such as sea temperature might be important drivers of localised movements, as with other ray species (Wallman and Bennett 2006).

Durban is significant in that it is the only known catch location of pregnant diamond rays. The 11 individuals examined by Wallace (1967) comprised one caught in the Durban shark nets, five caught from the northern breakwater of the Port of Durban, and five caught inside the port. The 69 embryos ranged from 9 to 38 cm DW (Wallace 1967). Size at birth is 35 cm DW (van der Elst 1981), which indicates that the sheltered waters of the port might function as a nursery area for this species. This is supported by the presence of potentially neonatal diamond rays in angler catches in the Durban area. It is possible that large sandy bays such as Durban could be important pupping or nursery habitats for diamond rays. However, further research is required to confirm where other nursery areas may be located (such as large sandy bays along the EC coast). The pregnant females were caught between January and August (Wallace 1967), but the absence of any additional details prevented the detection of any seasonal trend in embryo development.

Population risk assessment

This study employed long-term time-series catch data that provided evidence to support the recent IUCN Red List assessment of the diamond ray as Least Concern (Pollom et al. 2019). It is likely that the diamond ray in southern Africa exhibits a stable to increasing population trend, since it has few major sources of mortality within its southern African range. Indeed, a large proportion (78%) of the rays captured in the shark nets have historically been released alive (Dudley and Cliff 1993), and between 1999 and 2004 there was a substantial reduction in the length of nets in KZN, from a peak cumulative net length of 45 km in 1992 to 27 km in 2004 (Cliff and Dudley 2011). Additionally, since 1995 the recreational and competitive recreational angling community has greatly improved its fish-handling methods (i.e. a ban on gaffing) and generally practises catch and release with presumed lower post-release mortality rates (Pradervand et al. 2007; Daly et al. 2021). Earlier reductions in fishing mortality would also have been affected by the beach vehicle ban that was implemented in January 2002, resulting in greatly reduced shore fishing effort along the beaches of northern KZN (Mann et al. 2016; Mann and Mann-Lang 2020).

Historically, the diamond ray was the second-most-common elasmobranch caught in the nearshore (<50 m depth) KZN prawn trawl fishery operating on the uThukela Bank, with a mean annual catch of 1 314 individuals (range 994–1 876) and with an associated 46% mortality (Fennessy 1994). Subsequent onboard observer records in 2003–2005 suggested a doubling of relative abundance and a 5-fold increase in catch rate, although the increases were attributed to disparities in timing of monthly sampling in the two observer periods, rather than being directly attributable to reduced trawl effort (Fennessy et al. 2014). However, that fishery has been virtually dormant since 2002 owing to poor prawn recruitment and non-viable prawn catches, translating into much lower total catch numbers of diamond rays; furthermore, the uThukela area was recently declared a marine protected area in 2019 (RSA 2019) which thereby excludes trawling. Interestingly, there are no historical records of diamond rays from research trawls at depths of <100 m in the 1920s and 1930s in the uThukela area or elsewhere in KZN, albeit that this distinctive species was described from KZN by Gilchrist and Thompson (1911).

In the WC, the incidence of diamond rays has not been quantified in the inshore demersal trawl fishery which targets Cape hake *Merluccius capensis* and Agulhas sole *Austroglossus pectoralis* along the south and west coasts of South Africa. However, the annual catch of all stingrays for the period 2003–2006 was only 3.4 tons, while diamond rays comprised 0.1% of the discards during this period (Attwood et al. 2011), suggesting that catches in this fishery may be less than in the historical KZN uThukela prawn trawl fishery.

Although diamond rays remain vulnerable to nearshore fisheries because of their shallow coastal distribution, they are not a target of any commercial or subsistence fisheries. This contrasts with other co-occurring elasmobranchs, such as the white-spotted wedgefish which is commercially targeted for its valuable fins in neighbouring Mozambique, where it is presumed to have a high source of mortality resulting in severe population decline in South Africa (Daly et al. 2021). Although there are records of diamond rays caught in research trawl surveys in 2007, 2014 and 2018, between Xai-Xai and Zavora in southern Mozambique (ORI unpubl. data), they were not caught in large numbers. It is also apparent that diamond ray population recruitment is healthy judging from the number of juveniles caught in large sheltered sandy bays such as Durban Bay and those found in the EC as well as on offshore banks in KZN (i.e. uThukela Bank). However, more information is required on potential migrations associated with reproduction and key nursery habitats to ensure that these critical processes and habitats are sufficiently protected.

Summary
This study provided evidence to show that diamond rays are capable of substantial coastal movements from the cool-temperate waters of the WC to the warm subtropical waters of KZN on the east coast of South Africa. However, the potential environmental, reproductive or foraging-related drivers of such longshore movements still need to be identified. Thus, additional studies that employ acoustic and/or satellite telemetry should be used to investigate multi-seasonal movements, site fidelity and habitat preference of a range of size and sex classes of the South African population. This study also confirmed that the greatest numbers of large adult diamond rays are captured on the north coast of KZN, which could be an important area for mature and reproductively active rays. In contrast, sheltered sandy bays such as Durban and potentially others in the EC appeared to be important for juvenile rays, and further investigation is required to confirm the location of important nursery areas for this species on the South African coast. Ultimately, the risk assessment confirmed that the population of diamond rays found along the South African coast exhibits a stable to increasing trend, which supports the IUCN Red List classification of Least Concern for the species. The recently reduced trawl bycatch and improved post-release mortality from recreational and competitive angling, together with a lack of commercial and subsistence exploitation and mortality within the range of this regionally endemic ray species, probably contribute to the healthy population status of the species. However, the species remains vulnerable to capture from the shore as demonstrated by mass-capture events during summer on the north coast of KZN by competitive anglers. Additionally, the *K*-selected life-history traits and restricted range still make the species potentially vulnerable to population decline, which merits further research to identify critical habitats in South Africa, to ensure continued conservation of this important regionally endemic ray species.

Acknowledgements — Members of the ORI-CFTP, KZNCAU and staff of the KZNSB are thanked for providing the data that were used in this project. The South African Association for Marine Biological Research and Wild Oceans, through their Shark and Ray Conservation Project, are acknowledged for funding.

ORCID

Geremy Cliff: https://orcid.org/0000-0003-1790-6055
Ryan Daly: https://orcid.org/0000-0002-4409-6951
Gareth Jordaan: https://orcid.org/0000-0002-8296-9821
Bruce Mann: https://orcid.org/0000-0002-7130-6301
Denham Parker: https://orcid.org/0000-0001-7641-7804

References

Attwood CG, Petersen SL, Kerwath SE. 2011. Bycatch in South Africa's inshore trawl fishery as determined from observer records. *ICES Journal of Marine Science* 68: 2163–2174.

Beckley LE, Fennessy ST. 1996. The beach seine fishery off Durban, KwaZulu-Natal. *South African Journal of Zoology* 31: 186–192.

Bowman A, Azzalini A. 2010. R package "sm": nonparametric smoothing methods (version 2.2–5.4). Available at http://www.stats.gla.ac.uk/~adrian/sm [accessed 28 March 2020].

Buxton CD, Smale MJ, Wallace JH, Cockcroft VG. 1984. Inshore small-mesh trawling survey of the Cape south coast. Part 4. Contributions to the biology of some Teleostei and Chondrichthyes. *South African Journal of Zoology* 19: 180–188.

Cliff G, Dudley SFJ. 1992. Protection against shark attack in South Africa, 1952–90. *Marine and Freshwater Research* 43: 263–272.

Cliff G, Dudley SFJ. 2011. Reducing the environmental impact of shark control programs: a case study from KwaZulu-Natal, South Africa. *Marine and Freshwater Research* 62: 700–709.

Compagno LJV, Ebert DA, Smale MJ. 1989a. *Guide to the sharks and rays of southern Africa*. Cape Town, South Africa: Struik Publishers.

Crossin GT, Heupel MR, Holbrook CM, Hussey NE, Lowerre-Barbieri SK, Nguyen VM et al. 2017. Acoustic telemetry and fisheries management. *Ecological Applications* 27: 1031–1049.

Curtis JM, Johnson MW, Diamond SL, Stunz GW. 2015. Quantifying delayed mortality from barotrauma impairment in discarded red snapper using acoustic telemetry. *Marine and Coastal Fisheries* 7: 434–449.

Daly R, Parker D, Cliff G, Jordaan GL, Nomfundo N, Bennett RH, Mann BQ. 2021. Long-term catch trends and risk assessment of the Critically Endangered white-spotted wedgefish (*Rhynchobatus djiddensis*) from South Africa. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 777–788.

Danylchuk AJ, Suski CD, Mandelman JW, Murchie KJ, Haak CR, Brooks AM, Cooke SJ. 2014. Hooking injury, physiological status and short-term mortality of juvenile lemon sharks (*Negaprion bevirostris*) following catch-and-release recreational angling. *Conservation Physiology* 2: cot036.

Dicken ML, Booth AJ, Smale MJ, Cliff G. 2007. Spatial and seasonal distribution patterns of juvenile and adult raggedtooth sharks (*Carcharias taurus*) tagged off the east coast of South Africa. *Marine and Freshwater Research* 58: 127–134.

Dudley SFJ, Cliff G. 1993. Some effects of shark nets in the Natal nearshore environment. *Environmental Biology of Fishes* 36: 243–255.

Dulvy NK, Charvet P, Derrick D. 2021. *Gymnura micrura*. The IUCN Red List of Threatened Species 2021: e.T152784762A3088090.

Dunlop SW, Mann BQ. 2013. Diamond ray (*Gymnura natalensis*). In: Mann BQ (ed), *Southern African marine linefish species profiles*. *Special Publication* No. 9. Durban, South Africa: Oceanographic Research Institute. pp 55–56.

Dunlop SW, Mann BQ, van der Elst RP. 2013. A review of the Oceanographic Research Institute's Cooperative Fish Tagging Project: 27 years down the line. *African Journal of Marine Science* 35: 209–221.

Fennessy ST. 1994. Incidental capture of elasmobranchs by commercial prawn trawlers on the Tugela Bank, Natal, South Africa. *South African Journal of Marine Science* 14: 287–296.

Fennessy ST, Everett BI, Maggs JQ, Jordaan GL, Wintner SP. 2014. Changes in abundances of shallow-water elasmobranchs off the east coast of South Africa – attributable to trawling or not? Paper presented at Sharks International, Durban, South Africa, 2–6 June 2014.

Fennessy ST, Roberts MJ, Paterson AW. 2016. A brief overview of the ACEP project: ecosystem processes in the KwaZulu-Natal Bight. *African Journal of Marine Science* 38(Supplement): S1–S6.

Gallagher A, Serafy J, Cooke S, Hammerschlag N. 2014. Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. *Marine Ecology Progress Series* 496: 207–218.

Gilchrist JDF, Thompson WW. 1911. Descriptions of fishes from the coast of Natal (Part III.). *Annals of the South African Museum* 11: 29–58.

Heberer C, Aalbers SA, Bernal D, Kohin S, DiFiore B, Sepulveda CA. 2010. Insights into catch-and-release survivorship and stress-induced blood biochemistry of common thresher sharks (*Alopias vulpinus*) captured in the southern California recreational fishery. *Fisheries Research* 106: 495–500.

Hunter E, Buckley AA, Stewart C, Metcalfe JD. 2005. Migratory behaviour of the thornback ray, *Raja clavata*, in the southern North Sea. *Journal of the Marine Biological Association of the United Kingdom* 85: 1095–1105.

IUCN (International Union for Conservation of Nature). 2016. *A global standard for the identification of key biodiversity areas*, version 1.0. Gland, Switzerland: IUCN.

Jordaan G, Mann BQ, Martin D (eds). 2021. *Tagging News*. Durban, South Africa: Oceanographic Research Institute.

Kerwath SE, Parker D, Winker H, Potts WM, Mann BQ, Wilke CG, Attwood CG. 2019. Tracking the decline of the world's largest seabream against policy adjustments. *Marine Ecology Progress Series* 610: 163–173.

Klein JD, Bester-van der Merwe AE, Dicken ML, Mmonwa KL, Teske PR. 2019. Reproductive philopatry in a coastal shark drives age-related population structure. *Marine Biology* 166: article 26.

Lamberth SJ, Bennett BA, Clark BM. 1994. Catch composition of the commercial beach-seine fishery in False Bay, South Africa. *South African Journal of Marine Science* 14: 69–78.

Laptikhovsky V. 2004. Survival rates of rays discarded by the bottom trawl squid fishery off the Falkland Islands. *Fishery Bulletin* 102: 757–759.

Mann BQ, Winker H, Maggs JQ, Porter SN. 2016. Monitoring the recovery of a previously exploited surf-zone fish community in the St Lucia Marine Reserve, South Africa, using a no-take sanctuary area as a benchmark. *African Journal of Marine Science* 38: 423–441.

Mann BQ, Cowley PD, Dunlop SW, Potts WM. 2018. Is catch-and-release shore angling compatible with the conservation goals of marine protected areas? A case study from the iSimangaliso Wetland Park in South Africa. *Fisheries Research* 208: 179–188.

Mann BQ, Mann-Lang JB. 2020. Trends in shore-based angling effort determined from aerial surveys: a case study from KwaZulu-Natal, South Africa. *Linefish resilience in the Anthropocene*. *African Journal of Marine Science* 42: 269–281.

Mohan J, Jones E, Hendon J, Falterman B, Boswell K, Hoffmayer E, Wells R. 2020. Capture stress and post-release mortality of blacktip sharks in recreational charter fisheries of the Gulf of Mexico. *Conservation Physiology* 8: coaa041.

Musyl MK, Gilman EL. 2018. Post-release fishing mortality of blue (*Prionace glauca*) and silky shark (*Carcharhinus falciformes*) from a Palauan-based commercial longline fishery. *Reviews in Fish Biology and Fisheries* 28: 567–586.

Ogburn MB, Bangley CW, Aguilar R, Fisher RA, Curran MC, Webb SF, Hines AH. 2018. Migratory connectivity and philopatry of cownose rays *Rhinoptera bonasus* along the Atlantic coast, USA. *Marine Ecology Progress Series* 602: 197–211.

Parker D, Kerwath SE, Næsje TF, Arendse CJ, Keulder-Stenevik FJ, Hutchings K et al. 2017. When plenty is not enough: an assessment of the white stumpnose (*Rhabdosargus globiceps*) fishery of Saldanha Bay, South Africa. *African Journal of Marine Science* 39: 153–166.

Pollom R, da Silva C, Fennessy S, Fernando S, Gledhill K, McCord ME et al. 2019. *Gymnura natalensis*. The IUCN Red List of Threatened Species 2019: e.T60116A124440092.

Pollom R, Bizzarro JJ, Burgos-Vázquez MI, Avalos C, Herman K, Pérez Jiménez JC, Sosa-Nishizaki O. 2020. *Gymnura marmorata*. The IUCN Red List of Threatened Species 2020: e.T14134429A124548901.

Pradervand P. 2004. Long-term trends in the shore fishery of the Transkei coast, South Africa. *African Zoology* 39: 247–261.

Pradervand P, Govender RD. 2003. Assessment of catches in shore angling competitions from the border region of the Eastern Cape, South Africa. *African Zoology* 38: 1–14.

Pradervand P, Mann BQ, Bellis MF. 2007. Long-term trends in the competitive shore fishery along the KwaZulu-Natal coast, South Africa. *African Zoology* 42: 216–236.

Rigby CL, Walls RHL, Derrick D, Dyldin YV, Herman K, Ishihara H et al. 2021. *Gymnura japonica*. The IUCN Red List of Threatened Species 2021: e.T161630A124518082.

RSA (Republic of South Africa). 2019. Department of Environmental Affairs, Government Notices 757–776 declaring 20 marine protected areas in terms of Section 22A of the National Environmental Management: Protected Areas Act (Act No. 57 of 2003). *Government Gazette, South Africa* 647 (42478).

Sherley RB, Winker H, Rigby CL, Kyne PM, Pollom R, Pacoureau N et al. 2020. Estimating IUCN Red List population reduction: JARA—a decision-support tool applied to pelagic sharks. *Conservation Letters* 13: e12688.

Skomal GB, Mandelman JW. 2012. The physiological response to anthropogenic stressors in marine elasmobranch fishes: a review with a focus on the secondary response. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 162: 146–155.

Smale M, Sauer W, Roberts M. 2001. Behavioural interactions of predators and spawning chokka squid off South Africa: towards quantification. *Marine Biology* 139: 1095–1105.

Smith MM, Heemstra PC (eds). 1991. *Smiths' sea fishes*. Johannesburg, South Africa: Southern Book Publishers.

van der Elst RP. 1993. *A guide to the common sea fishes of southern Africa* (3rd edn). Cape Town, South Africa: Struik Publishers.

Wallace MH. 1967. The batoid fishes of the east coast of southern Africa. II: manta, eagle, duckbill, cow nose, butterfly and stingrays. *Investigational Report* No. 16. Durban, South Africa: Oceanographic Research Institute.

Wallman HL, Bennett WA. 2006. Effects of parturition and feeding on thermal preference of Atlantic stingray, *Dasyatis sabina* (Lesueur). *Environmental Biology of Fishes 75:* 259–267.

Winker H, Pacoureau N, Sherley RB. 2020. JARA: 'Just Another Red-List Assessment'. *bioRxiv*. Available at https://doi.org/10.1101/672899.

Wood SN. 2006. *Generalized additive models: an introduction with R*. New York: Chapman and Hall.

Young N. 2001. An analysis of the trends in bycatch of turtle species, angelsharks and batoid species in the protective gillnets off KwaZulu-Natal, South Africa. MSc thesis, University of Reading, UK.

Manuscript received October 2021 / revised November 2021 / accepted December 2021