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Movement patterns and growth rate of cavebass *Dinoperca petersi* (Pisces: Dinopercidae) in the iSimangaliso Marine Protected Area, South Africa

Bruce Q. Mann[1]*, Gareth L. Jordaan[1], Ryan Daly[1,2]

[1] Oceanographic Research Institute, South African Association for Marine Biological Research, PO Box 10712, Marine Parade, 4056, Durban, South Africa

[2] South African Institute for Aquatic Biodiversity, Makhanda, South Africa

* Corresponding author: bruce@ori.org.za

Abstract

Dinoperca petersi is a relatively common fish species caught in the line-fishery in KwaZulu-Natal (KZN), South Africa. Yet, little is known about the biology and ecology of this species. Movement patterns and growth rate of this species were studied based on data obtained from a long-term tag-recapture study conducted in the iSimangaliso Marine Protected Area in northern KZN between 2001-2019. Results showed that *D. petersi* is a highly resident species with a linear home-range size of 290-405 m. While most fish showed high site fidelity, 8.8 % of the tagged fish showed wider ranging movements of 2.4-90 km. However, only 5 fish showed movements out of no-take zones into adjacent exploited areas, suggesting limited adult spillover. Growth rate of tagged fish was found to be reasonably slow compared to other sympatric predatory reef fish with an average growth rate of 61.76 mm y^{-1} for smaller fish (g_α = 300) and 9.58 mm y^{-1} for larger fish (g_β = 550). Based on these life history characteristics, options for the future conservation and management of this species are discussed.

Keywords: tag-recapture, station-keeping, ranging, no-take area

Introduction

Dinoperca petersi, known locally as cavebass or lampfish, has a patchy, coastal distribution throughout the Western Indian Ocean including Pakistan, southern Oman, Kenya, Mozambique and the eastern seaboard of South Africa, extending south to Mossel Bay (Heemstra and Heemstra, 2004, Froese and Pauly, 2019). They inhabit high profile rocky and coral reefs to depths of 75 m. While often found in caves and under ledges during the day, they are generally more active nocturnally. They feed on a variety of reef invertebrates such as shrimps, crabs, octopus, as well as small fish (van der Elst, 1993). *D. petersi* can reach a maximum size of 75 cm total length (TL) and a weight of 5.8 kg (van der Elst, 1993). Although fairly common in KwaZulu-Natal (KZN), they form a relatively minor component of catches in the line-fishery contributing 0.07 % to the shore fishery (Dunlop and Mann, 2012), 1.5 % to the recreational ski-boat fishery, and 0.33 % to catches of the commercial line-fishery, by number

(Dunlop and Mann, 2013). They are also occasionally taken by spearfishers (Lloyd *et al.*, 2012, Fennessy and Mann, 2013). Despite an extensive literature review, there is very little published information on catches of this species elsewhere within its distribution range.

Considering their local abundance in KZN waters, surprisingly little is known about the biology and ecology of this species (van der Elst, 1993, Heemstra and Heemstra, 2004). *D. petersi* comprise an important component of the catch in the surf-zone within the iSimangaliso Marine Protected Area (MPA) in northern KZN (Mann *et al.*, 2015), providing an ideal opportunity to learn more about this species. A surf-zone fish monitoring and tagging project has been undertaken in the iSimangaliso MPA by the Oceanographic Research Institute (ORI) since 2001 (Mann *et al.*, 2015, 2016a, 2016b, 2016c, 2018) and a substantial amount of data have been collected on *D. petersi* over the past 19 years. More specifically, the tagging project has enabled the collection

of data on both movement patterns (Mann *et al.*, 2015) and growth rates (Mann *et al.*, 2016c) of focal species. The primary aim of this study was therefore to use the available tag-recapture data that have been collected on *D. petersi* to describe their movement patterns and estimate their growth rate. This study also provided the opportunity to comment on the effectiveness of the iSimangaliso MPA in providing protection for this species.

Materials and Methods

Research line-fishing, using standardised shore fishing gear, has been undertaken by teams of trained anglers on a quarterly basis within the iSimangaliso MPA since 2001 (see detailed description of the methods used in Mann *et al.*, 2015, 2016a, 2018). Research catch-and-release fishing was conducted in zoned no-take and exploited areas in four accessible parts of the MPA. These included (from north to south): Bhanga Nek, Sodwana, Cape Vidal and Maphelane (Fig. 1). Research fishing normally took place during approaching spring tides so that low tide was in the early morning and evening. This enabled fishing teams to reach the designated sampling areas by driving a 4x4 vehicle on the hard sand at low tide. Most fishing days were therefore at least 12 hours in duration (depending on prevailing weather conditions). Use of barbless hooks was strictly enforced (the barb on the hook being crimped using long-nose pliers) as this inflicted less damage on the fish and made their release considerably quicker and easier (Casselman, 2005). If a fish was 'gut-hooked' (i.e. with the hook lodged in the oesophagus) no attempt was made to remove the hook and the snood was simply cut off near to the eye of the hook (Schaeffer and Hoffman, 2002; Butcher *et al.* 2010). Use of circle hooks was encouraged (Cooke and Suski, 2004) but not enforced due to the higher price of these hooks and the gear preferences of some anglers.

All fish caught were immediately placed into a bucket of fresh seawater before being carried to the tagging station. Once removed from the bucket, they were covered with a wet cloth and quickly measured (total length [TL] in mm) on a wet plastic stretcher with a ruler down the centre, before being returned to the water. Emphasis was placed on keeping the fish out of the water for as short a time as possible and all surfaces were kept moist to reduce injury and stress (Cooke and Wilde, 2007). All fish >300 mm TL were tagged using plastic dart tags (Hallprint©) supplied by ORI's Cooperative Fish Tagging Project (ORI-CFTP) (Dunlop *et al.*, 2013). Only D-tags (85 mm in length and 1.6 mm in diameter) were used to tag *D. petersi*.

Each time a fish was tagged or recaptured, the tag number, species, length (mm TL), date, time and GPS locality was recorded. The GPS position was linked to markers placed every 100 m for the length of all four sampling areas so that fish movement could be determined with an accuracy of 50 m. A note was made if there was a tagging scar present on the fish, indicating that it had been previously tagged but the tag had been shed. Aside from fish recaptured by the research team, members of the angling public also reported recaptures from adjacent exploited areas north and south of the study area. Fish recaptured by members of the angling public were reported through the ORI-CFTP, which uses locality codes that corresponded to a coastal location such as a town, estuary, and/or popular fishing site along the coast with a resolution of approximately one kilometre (Dunlop *et al.*, 2013).

Data analysis
Movement patterns
Movement was categorised as station-keeping (generally refers to movements within a home range and is usually linked to foraging) or ranging (an exploratory movement that takes an individual permanently beyond its home range to settle eventually into a new one) as defined by Dingle (1996) and Dingle and Drake (2007). In this study, because of the relatively small size of the original sampling areas (see Mann *et al.*, 2015), a fish was considered to be station-keeping if it was recaptured within 2 km of its release site. If a fish moved >2 km and did not return to its original tagging location, it was considered to be displaying ranging behaviour. Station-keeping is a good indicator of the potential for fish to remain within a protected area and was used to quantify the degree of residency. Ranging behaviour on the other hand indicates the potential for export of fish to adjacent fisheries out of a no-take area.

Station-keeping
In the current study, station-keeping behaviour was quantified for each species by taking the 95th percentile of intra-study site movement distances only (Maggs *et al.*, 2013) and excluded all long-distance (>2 km) movements (Attwood and Cowley 2005). The resulting value is referred to as 'single linear distance' (SLD) in the current study. Assuming that a fish is randomly drawn from within the boundaries of its home range at first capture (tag-release) and then redrawn from that same home range at a later stage (recapture), the Euclidean distance between the two points (SLD) can be considered to represent

some unknown proportion of the length of the home range. Repeating this several times, with different individuals of the same species, provides a good reflection of the degree of residency for that spe-

individual fish. In this case, an alternative method for quantifying station-keeping behaviour was applied by taking the 'greatest linear distance' (GLD) between all the recapture locations from the origi-
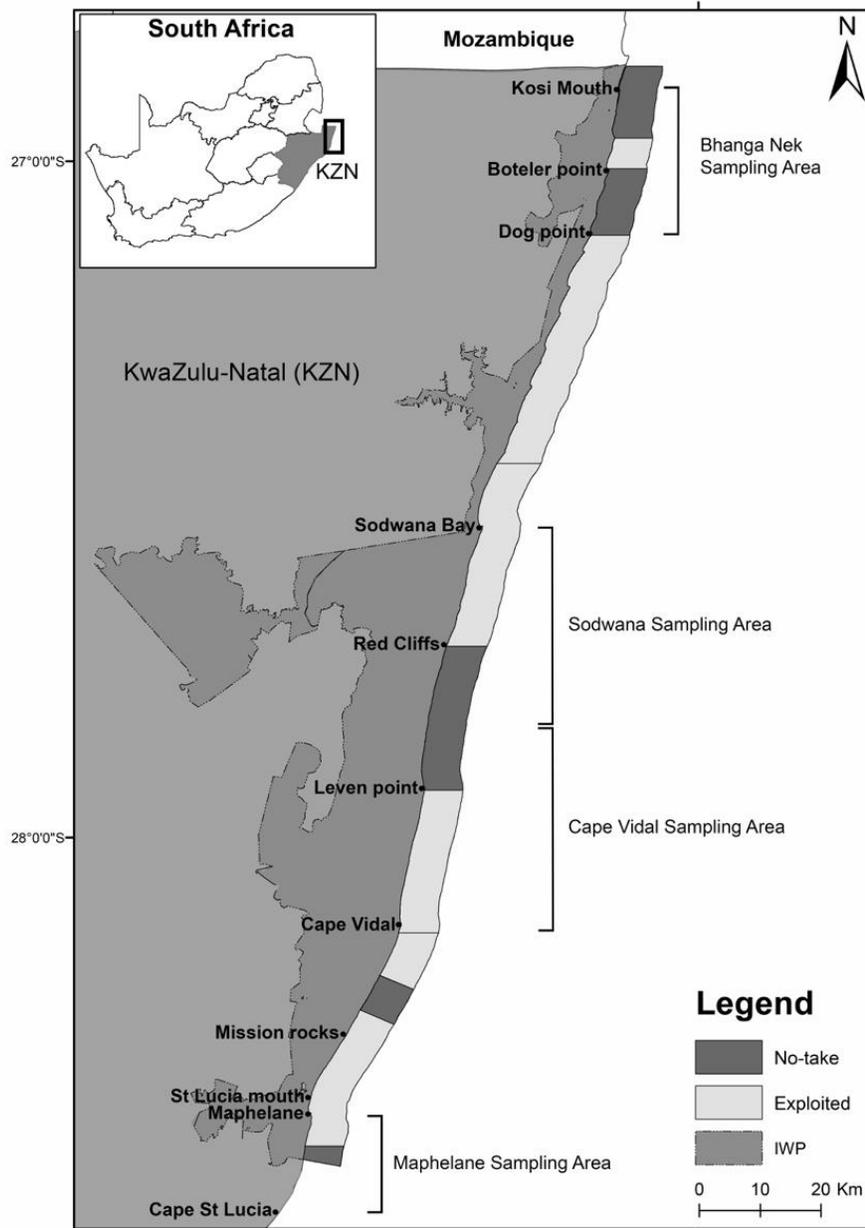
Figure 1. Map of the iSimangaliso Wetland Park (IWP) showing the zonation and areas sampled in this study. Note that this map does not show the new inshore and offshore zonation plan or the southern extension of the MPA that was implemented in August 2019 (see https://www.saambr.org.za/new-mpas-for-anglers/ for further information).

cies. To prevent pseudo-replication, the calculation of SLD used only the distance between the original tagging site and the first recapture location.

Multiple recaptures (three or more capture points) provide stronger evidence of area utilisation by an

nal tagging location (provided that all recaptures were within 2 km of the original tagging location). The resulting estimate was used to validate the SLD calculated above. Note that the GLD could be less than the SLD as only multiple recaptures were used to calculate the GLD.

Ranging

The potential of the no-take zones to export fish was evaluated using records of long-distance movements (i.e. tagged fish leaving the no-take zones). Most of the recaptures of ranging fish were recorded by the research team, but some recaptures were also reported by members of the angling public through the ORI-CFTP. Although relatively few long-distance movements were reported by members of the public, there was potential for non-reporting (Dunlop *et al.*, 2013), particularly if fish were recaptured by local subsistence fishermen who did not possess means of communication (i.e. a cell phone) to report the recapture.

Capture time was plotted as a rose diagram using the statistical software Oriana (Version 4, Kovach Computing Services). A Chi-square test was used to determine if the number of fish moving north or south was significantly different. A two-sample *t* test assuming unequal variances was used to determine if the distance moved north or south was significantly different. Time at liberty was compared to distance moved using a linear regression. Similarly, fish length was compared with distance moved.

Growth rate

Tag-recapture length data were initially filtered to remove all recaptures where length was not reported or where there were obvious measurement discrepancies. The tag-recapture data were represented by T_1, T_2, L_1 and L_2 where T denotes time (date) and L length (mm, TL). The subscripts 1 and 2 refer to the dates of tagging and recapture, respectively. Increments in length and time are given as ΔL and ΔT, respectively. Growth rates were modelled from the tag-recapture data using the maximum-likelihood approach described by Francis (1988a, 1988b) in the statistical package "R" (R Core Development Team, 2020), running the function (grotag) from the R-Package 'fishmethods' (Nelson, 2019). The usual form of the von Bertalanffy growth function, as used with tag-recapture data, may be written as:

$$\Delta L = (L_\infty - L_1)(1 - e^{-K(t_2 - t_1)}) \tag{1}$$

Francis (1988a) described a re-parameterisation and extension of the Faben's (1965) growth model for tag-recapture data that incorporates seasonal growth:

$$\Delta L = \left[\frac{\beta g_a - \alpha g_\beta}{g_a - g_\beta} - L_1 \right] \left[1 - \left(1 - \frac{g_a - g_\beta}{a - \beta} \right)^{\Delta T + (\varphi_2 - \varphi_1)} \right] \tag{2}$$

where

$$\varphi_i = u \frac{\sin\left[2\pi(T_i - w) \right]}{2\pi} \text{ for } i = 1, 2 \tag{3}$$

The parameters g_α and g_β are the estimated mean annual growth (mm y^{-1}) of fish of initial lengths α mm and β mm, respectively, where α<β. The reference lengths α (300 mm) and β (550 mm) were chosen such that the majority of values of L_1, the length at tagging, fell between them. Seasonal growth is parameterised as w (reflecting the portion of the year in relation to 1 January when growth is at its maximum) and u (with $u = 0$ indicating no seasonal growth through to $u = 1$ indicating maximum seasonal growth effect).

The measured growth increment of the *i*th fish, ΔL_i, has a corresponding expected mean growth increment u_i, where u_i is normally distributed with standard deviation σ_i. In this study, σ_i was assumed to be a function of the expected growth increment u_i:

$$\sigma_i = \nu \mu_i \tag{4}$$

where v is estimated as a scaling factor of individual growth variability.

The model was fitted by minimizing the negative log-likelihood function λ for each dataset, made up of i=1 to n growth increments:

$$\lambda = \sum_i \ln\left[(1-p)\lambda_i + \frac{p}{R} \right] \tag{5}$$

where

$$\lambda_i = e^{\dfrac{-\frac{1}{2}(\Delta L_i - u_i - m)^2 / \left(\sigma_i^2 + s^2 \right)}{\left[2\pi \left(\sigma_i^2 + s^2 \right) \right]^{\frac{1}{2}}}} \tag{6}$$

When the model is fully parameterised, the likelihood function estimates the population measurement error in ΔL as being normally distributed, with a mean m and standard deviation s. The proportion of outliers was identified by the parameter p, the probability that the growth increment for any individual could exist erroneously in the dataset as any value, within the observed range of growth increments R.

The optimal model parameterisation was determined by following a stepwise fitting procedure. Initially, a simple 3-parameter model was fitted and then parameters were added in the order determined by selecting
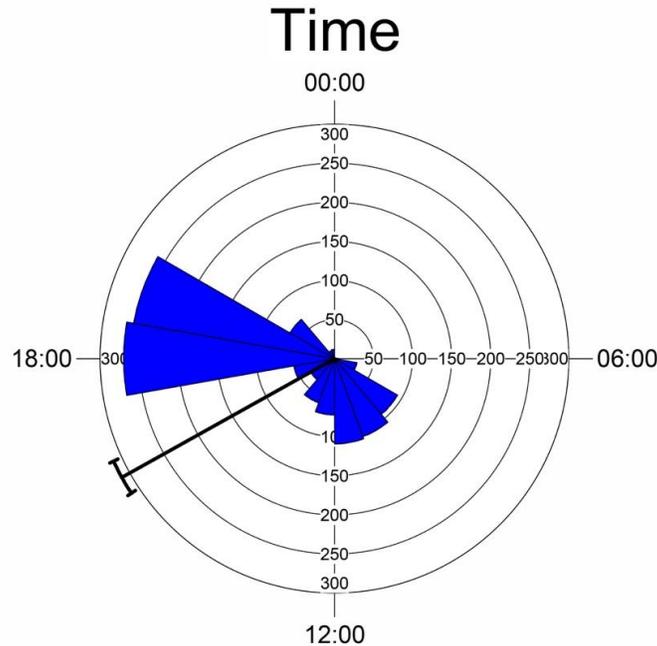
Figure 2. A rose diagram showing the time of capture of 1173 *Dinoperca petersi* caught during research fishing in the iSimangaliso MPA between 2001 and 2019. Note that on most days, fishing seldom took place beyond 21:00, except on a few occasions when fishing occurred later due to logistical reasons. The dark line represents mean capture time and capped line represents 95 % confidence interval.

the parameter that gave the greatest reduction in the Akaike Information Criterion (AIC) value, with unfitted parameters held at zero. When the introduction of an additional parameter did not result in a significantly better model fit, these results were excluded from the analyses. The final model was bootstrapped 1 000 times and 95% confidence intervals were calculated for parameter estimates.

Results

From November 2001 to November 2019 a total of 83 field trips was conducted, during which 1 173 *D. petersi* were caught. Time of capture for each fish is shown in Fig. 2 highlighting the number of fish caught at dusk and during the first few hours of darkness. Of the *D. petersi* caught, 775 were tagged and released and 111 were recaptured at least once (the remainder being
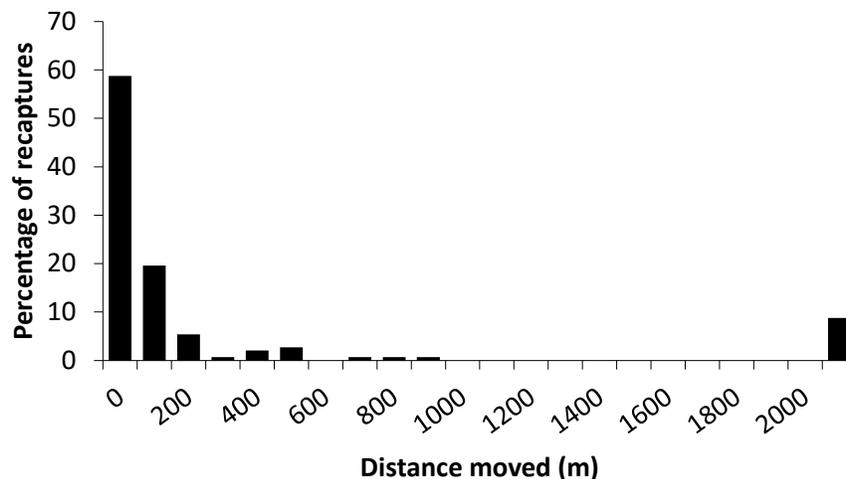
Figure 3. Movement displayed by 148 *Dinoperca petersi* recaptured in the iSimangaliso Marine Protected Area between 2001 and 2019. Note that the last column of the graph cluster all the individuals that moved > 2 000 m.
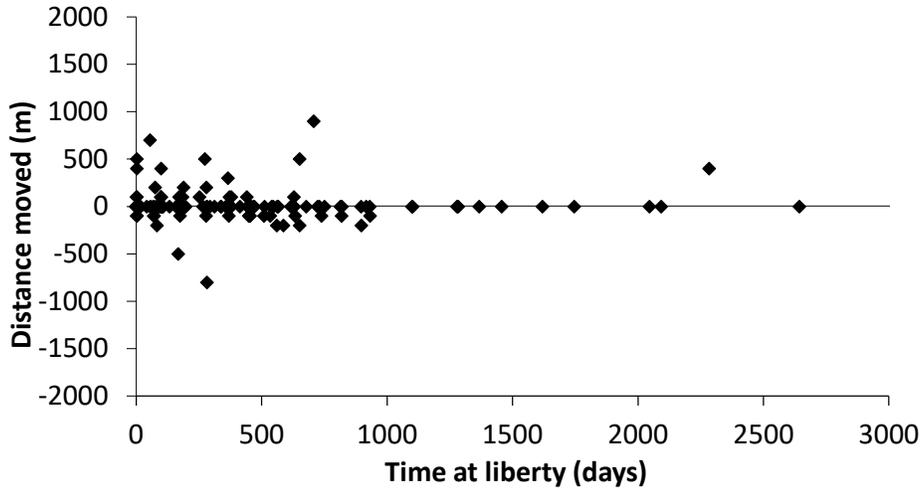
Figure 4. Distance and direction of movement and time at liberty displayed by 148 *Dinoperca petersi* recaptured in the iSimangaliso Marine Protected Area between 2001 and 2019. Positive values indicate northward movement while negative values indicate southward movement. Note that 13 fish which moved >2 km are not displayed.
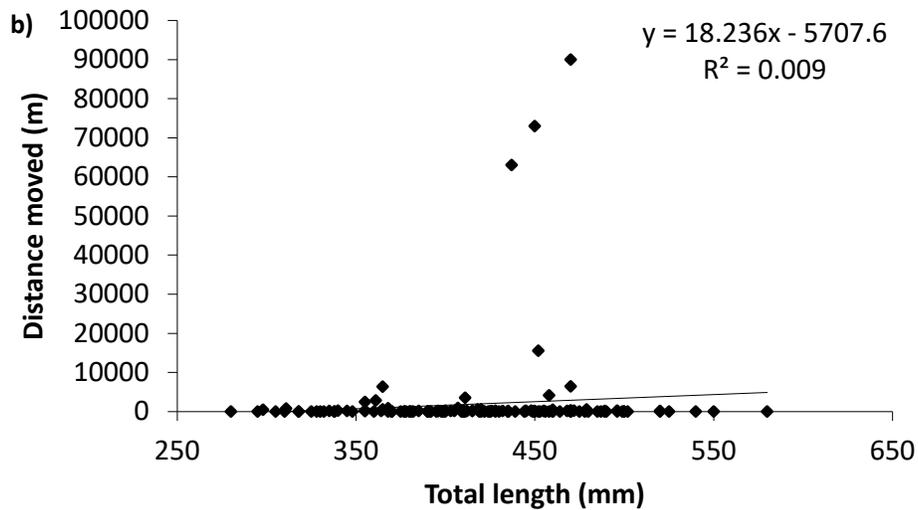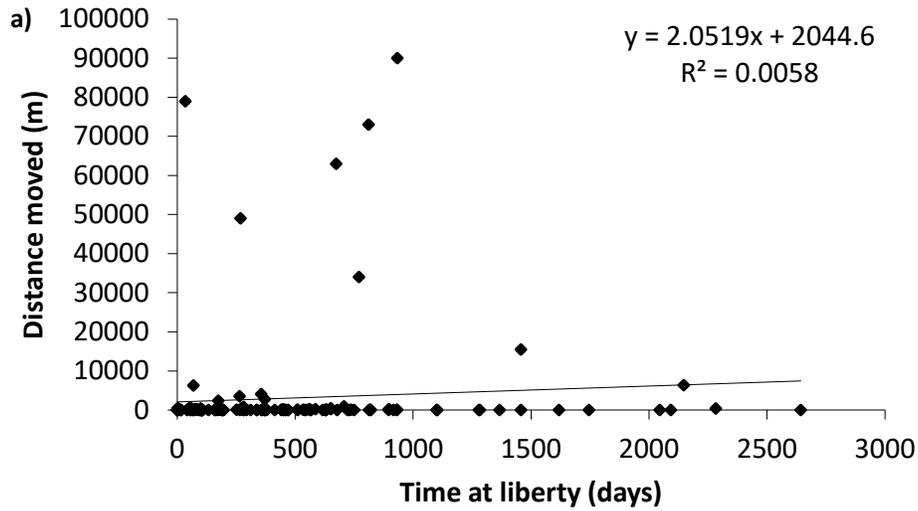
Figure 5. a) A correlation between time at liberty and distance moved (n=148); and b) a correlation between total length and distance moved (n=145) by *Dinoperca petersi* recaptured in the iSimangaliso MPA (note that 3 fish recaptured by members of the public were not measured).

<300 mm TL and thus too small to tag). A further 37 multiple recaptures (fish having three or more capture points) and six fish with tag scars (i.e. tag had been shed) were also recorded. Of the 37 multiple recaptures, 24 fish were recaptured twice, 6 were recaptured thrice, 4 were recaptured 4 times, 2 were recaptured 5 times and 1 fish was recaptured 6 times.

Movement patterns

Of all the recaptures (including multiple recaptures) 83.1 % were recaptured within 200 m of their original tagging locality, thereby predominantly displaying station-keeping behaviour. Only 13 recaptures (8.8 %) were from fish recorded moving distances greater than 2 km, thereby displaying ranging movement behaviour (Fig. 3).

In terms of direction moved, there was no significant difference (χ^2 = 0.41, p > 0.05) between the number of fish that moved in a northerly or southerly direction (Fig. 4). However, the distance that fish travelled in a northerly direction was significantly greater (*t* = -2.32, df = 33, p < 0.05) than those that travelled in a southerly direction. The greatest movement recorded was by a fish that moved 90 km in a northerly direction. Time at liberty ranged from 0 – 2643 days (7.2 years) (Fig. 4). There was no significant correlation (p > 0.05, R^2 = 0.006) between time at liberty and distance moved (Fig. 5a) or between fish length and distance moved (p > 0.05, R^2 = 0.009) (Fig. 5b).

The home range size (linear distance) of *D. petersi* was calculated to be 405 m based on the SLD (95th percentile) of 100 recaptures that moved less than 2 km. Using movements of 35 multiple recaptures that moved less than 2 km, the GLD (95th percentile) was calculated to be 290 m.

In terms of movement between zoned areas within the iSimangaliso MPA (Table 1), 5 tagged *D. petersi* moved out of a zoned no-take area, 3 moved directly through a no-take area, 1 moved into a no-take area and the remaining 102 fish stayed in the same zone that they were originally tagged in (n=111). No fish were recaptured outside of the MPA and no fish were recorded moving out of their home range and then moving back later.

Growth

Of the 148 recaptures obtained during the 19-year study period, 109 had suitable length data that could be used in the growth study following filtering out of unrealistic data. The length frequency of fish lengths at tagging and at recapture are shown in Fig. 6 and ranged between 300-600 mm TL.

To understand the importance of interpretation of the different parameters, a stepwise fitting procedure was followed, starting with the simplest 3-parameter model. Successive parameters were included for all the combinations that improved the fitted model best (Table 2).

Table 1. A summary of the movements of 111 *Dinoperca petersi* tagged and recaptured in the iSimangaliso MPA between 2001 and 2019.

	Number	%	Mean distance moved (km + SD)
No. tagged	775		-
No. recaptured	148	19.1	2.97 ± 13.37
No. of single recaptures	111	14.3	3.46 ± 14.71
No. of multiple recaptures	37	4.8	1.49 ± 8.06
No. of fish caught with tag scars	6	0.8	-
No. tagged and recaptured in an exploited zone	55	49.5	0.34 ± 1.22
No. tagged and recaptured in a no-take zone	47	42.3	0.1 ± 0.21
No. that moved out of a no-take zone	5	4.5	41.2 ± 35.32
No. that moved into a no-take zone	1	0.9	2.80
No. that moved right through a no-take zone	3	2.7	67.0 ± 15.87
No. recaptured outside the MPA	0	0	0
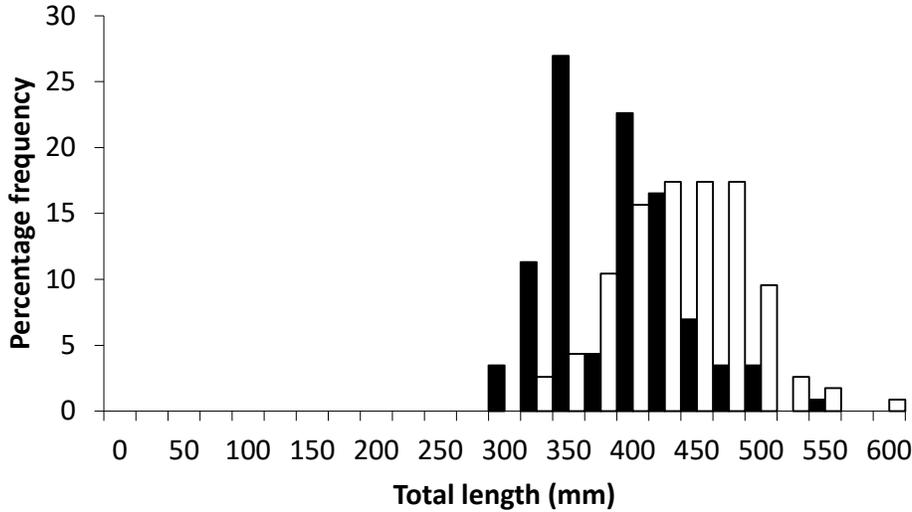
Figure 6. Length of *Dinoperca petersi* at tagging (solid bars) and recapture (clear bars) in the iSimangaliso MPA between 2001 and 2019 (n=109).

The remaining combinations that did not improve the model were excluded. The best fit model (Model 5, Table 2) consisted of the following parameters:

- g_α – the mean annual growth rate of fish at length α (300 mm TL was selected as this reflected the smaller size range of the sample).
- g_β – the mean annual growth rate of fish at length β (550 mm TL was selected as this reflected the larger size range of sampled fish).
- s – the root mean square error, which comprises possible measurement error during sampling, individual growth variability and lack of fit of the model.
- v – the growth variability parameter. The addition of this resulted in the slight increase of both the L_∞ and k values.

- m – the combined mean measurement error (mm) at tagging and recapture.
- p – the probability that the growth increment for any individual could exist erroneously in the dataset as any value within the observed range of growth increments R.
- u (year) - based on 0 reflecting no seasonal variability and 1 indicating strong seasonal variability. The resultant value (0.23) indicated that there is weak seasonal variation in growth for *D. petersi*.
- w (year) – a value reflecting time (data) as a fraction of the year when growth rate is at its maximum. The value 0.52 indicated that the growth peaked in June/July.
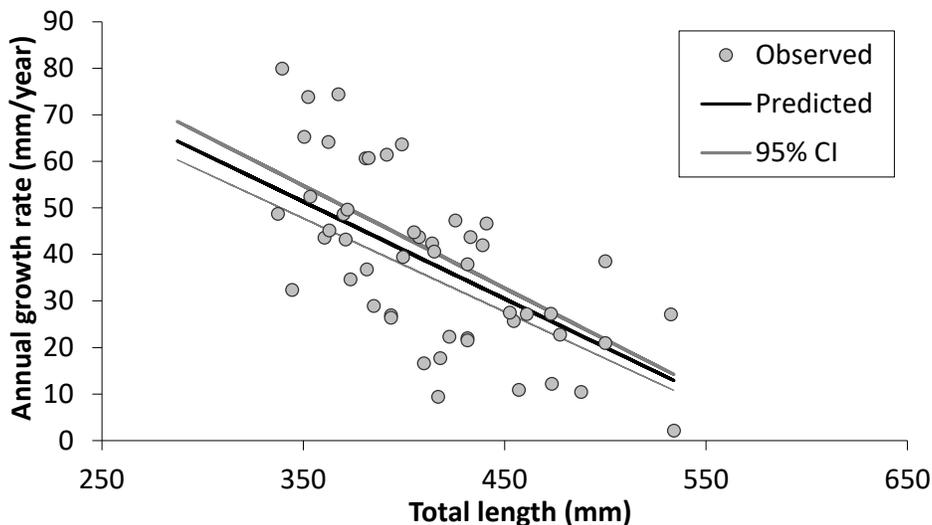
Figure 7. Observed and predicted growth rate for *Dinoperca petersi* tagged and recaptured in the iSimangaliso MPA between 2001 and 2019 (n=109). (Note: observed data points for recaptures <1 year-at-liberty (n = 59) were excluded from the figure for clarity).

Table 2. Parameters estimated for the growth rate of *Dinoperca petersi* in the iSimangaliso MPA between 2001 and 2019 using five different tag-recapture growth models (following Francis 1988a, b). The final and best estimates are shown in bold. See the methods section for an explanation of the parameters.

Parameter	Symbol (unit)	Model 1 Estimate	Model 1 Error	Model 2 Estimate	Model 2 Error	Model 3 Estimate	Model 3 Error	Model 4 Estimate	Model 4 Error	Model 5 Estimate	Model 5 Error
Mean growth rates	$g300$ (mm/y)	54.840	3.630	57.330	3.850	56.620	3.320	64.420	3.880	**61.760**	**3.860**
Mean growth rates	$g550$ (mm/y)	9.580	3.320	9.580	4.900	9.580	4.190	9.580	4.040	**9.580**	**4.030**
Seasonal variation	u (year)	*0	0.000	*0	0.000	*0	0.000	*0	0.000	**0.231**	**0.142**
	w (year)	*0	0.000	*0	0.000	*0	0.000	*0	0.000	**0.523**	**0.134**
Growth variability	v	*0	0.000	0.393	0.050	0.284	0.041	0.270	0.038	**0.271**	**0.037**
Measurement error	s (mm)	20.233	1.683	6.484	1.065	6.805	0.922	6.308	0.907	**6.079**	**0.892**
	m (mm)	*0	0.000	*0	0.000	*0	0.000	-2.808	1.220	**-2.947**	**1.186**
Outliers	p	*0	0.000	*0	0.000	0.031	0.022	0.031	0.022	**0.031**	**0.022**
Negative log likelihood		482.50		449.20		442.10		439.60		**438.200**	
AIC		970.90		906.30		894.10		891.10		**892.400**	
Parameters											
Maximum theoretical length	L_∞	-602.32		-600.15		-600.91		-596.20		**-595.893**	
Growth rate parameter	k	0.200		0.212		0.208		0.232		**0.234124**	

*0 parameter held fixed (see explanation in text)

As with most reef fish species, growth rate declined with increase in length, although there was a high degree of variability in individual growth rates (Fig. 7). Relatively fast growth (61.76 mm.y^{-1} ± 3.86) was recorded in smaller fish compared to larger fish (9.58 mm.y^{-1} ± 4.03) (Table 2). There was a weak seasonal influence (0.23 ± 0.14) with fastest growth rate recorded in June/July. The mean measurement error in ΔL was low and estimated at -2.95 mm ($\pm$ 1.19). The probability of outliers detected in the model fit was also relatively low (0.031 $\pm$ 0.022), although 59 recaptures were caught after being at liberty for less than one year which increased the number of outliers.

Discussion
Movement patterns
Station-keeping
The results of this study showed that *D. petersi* is a highly resident reef fish with a home range size of between 290-405 m. Most of the movements undertaken by recaptured fish were relatively small (mean = 83 $\pm$ 100 m, n=100) inferring station-keeping behaviour. With its large eyes and nocturnal habits, it is likely that *D. petersi* remains in caves or under ledges during the day and moves out to forage at night. This nocturnal foraging behaviour was confirmed by examining the time when most of the fish were caught. As shown in Fig. 2, although some fish were caught during the day, especially on the pushing tide between 09:00 and 12:00, most fish were caught at dusk and into the evening between 18:00 and 20:00. Another interesting observation to support this theory was that the tags of most recaptured *D. petersi* were remarkably clean and not covered with biofouling as observed with many other fish species tagged in this project. This suggests that the fish are remaining out of direct sunlight during the day thereby limiting growth of photosynthetic algae on the tags.

As *D. petersi* is found on both inshore and offshore reefs down to depths of 75 m (van der Elst, 1993), there is scope for ontogenetic movement offshore, which would not have been observed in this study as sampling was confined to the surf-zone. However, the fact that fish were caught throughout their adult size range in the surf-zone (estimated size at maturity is ~30 cm TL), suggests that they are not only using surf-zone reefs as juvenile nursery areas as found with some other sympatric species in this habitat (e.g. *Epinephelus tukula* and *E. marginatus*) (Mann *et al.*, 2015). High levels of site fidelity (i.e. station-keeping) as observed in *D. petersi* can lead to localised depletion in

exploited areas but can be of benefit in no-take areas. All the inshore no-take zones sampled in the iSimangaliso MPA during this study were longer than 2 km in coastline length (range = 2.5-25 km, Fig. 1). This suggests that retention of fishes within the no-take zones is likely to be high. This is supported by the observed movements of *D. petersi* where only 5 recaptured fish (9.6 %) were recorded moving out of a no-take zone, whereas the remaining 47 (90.4 %) recaptures remained resident in the no-take zone that they were originally tagged in (Table 1). No-take areas of suitable size and habitat therefore undoubtedly provide some insurance against fishing pressure in adjacent fished areas by acting as a refuge for *D. petersi*. Based on the methodology used by Mann *et al.* (2016b), it is estimated that the minimum size of a no-take area with suitable surf-zone reef habitat required to protect a resident population of *D. petersi* should be at least 1.5 km in length. There is also the potential for these resident fish to spawn within a no-take zone and provide a source of eggs and larvae that could be dispersed to adjacent fished areas (Brouwer *et al.*, 2003; Harrison *et al.*, 2012), however this aspect was beyond the scope of this study.

Ranging
Only 13 fish were observed undertaking longer distance, ranging-type movements of between 2.4 and 90 km (mean = 33 $\pm$ 13 km, n=13). These fish clearly abandoned their home range and moved elsewhere to find better habitat, which fits well with Dingle's (1996) definition for ranging, described as 'exploratory movements over wide areas in search of resources'. None of the tagged fish were recorded displaying homing behaviour (i.e. moving out of their home range and then coming back to it later). There are several possible reasons why a normally resident reef fish would undertake long-distance movements of this nature. These include inter- or intra-species competition for food, displacement because of territorial aggression, deterioration in habitat quality and/or movement to a spawning site, amongst others. Within the surf-zone of the iSimangaliso MPA, frequent sanding events were observed where reef patches would occasionally get covered with sand while others would be scoured out. With a sanding event taking place, it is likely that resident fish would move away to find better reef habitat. While these phenomena could explain movements of a few hundred metres to a few kilometres in extent, it does not explain why some fish would move distances of up to 90 km away from their original home range. However, this type of extensive movement behaviour

is not unique to *D. petersi* and has been observed to take place in a large variety of different reef fish species including species such as *Dichistius capensis* (Attwood and Cowley, 2005), *Epinephelus marginatus* (Maggs *et al.*, 2013), *Lutjanus rivulatus* (Mann *et al.*, 2015) and many others (see review by Maggs *et al.*, 2019).

Attwood and Cowley (2005) suggested two models to explain similar movement behaviour (i.e. station-keeping and ranging) of *Dichistius capensis*, a warm-temperate surf-zone fish in South Africa. Firstly, these authors proposed polymorphism to explain that within a species, some individuals remain resident whereas others are nomadic and may move continuously (Attwood and Bennett, 1994). Reasons for the differentiation may be either genetic or dependent on social or environmental cues (Swingland, 1984; Dingle, 1996) and the variation could be used as a hedge against inbreeding in geographically isolated reef fish populations. Their other alternative, the "tourist" model (Craig and Hulley, 1994), predicts that individuals of a given species will spend part of their time exhibiting resident behaviour, but will temporarily abandon their home range to feed elsewhere before returning later. Despite the relatively large number of multiple recaptures, this latter behaviour was not observed in *D. petersi*. Based on these observations, it was predicted that polymorphism is the more likely model to explain the movement behaviour in *D. petersi*, but on-going monitoring and/or an acoustic telemetry study would be necessary to test this. The movement behaviour observed would also discount the possibility of seasonal movements for reproductive purposes unless this took place offshore.

The relevance of these two models to no-take MPAs is that in the case of polymorphism, only certain individuals may become available to an adjacent fishery, whereas in the tourist model all individuals may at some time become available to the fishery (Attwood and Cowley, 2005; Maggs *et al.*, 2013). The possibility of both behaviours being present in a population should also not be discounted; some individuals could be highly resident, with some ranging, whereas others might maintain temporary home ranges. Should the differentiation be due to polymorphism, the effect of differential selection on different movement behaviours could pose an ecological problem for the population (Attwood, 2002, Parsons *et al.*, 2010). In addition to removing resident fishes, fishing in an exploited area would also opportunistically remove nomadic (or ranging) individuals that leave a no-take area. This

would select for residency in the no-take area, which, although potentially important from a conservation perspective, may have unforeseen ecological consequences for the population. With the tourist model, in which all individuals move, the population should not suffer from differential selection in the same way (Maggs *et al.*, 2013; Mann *et al.*, 2015).

In this study, movements of ranging fish were undoubtedly under-sampled because very little shore angling takes place in remote areas far from beach access points in the MPA (Mann *et al.*, 2016a; Mann and Mann-Lang, 2020). In addition, Dunlop *et al.* (2013) estimated a non-reporting rate of 42 % by members of the angling public, which would further hamper data collection on ranging fishes that had been recaptured. Despite these biases, it can be concluded that exploited areas adjacent to no-take areas were supplied with a limited number of adult fishes, which had been under temporary protection within no-take areas.

Many studies have failed to discriminate between spillover and variability in individual movement patterns (Zeller *et al.*, 2003). Spillover, which is the net export of adult fish from a no-take area (Abesamis and Russ, 2005), implies that fishes will move from a no-take area where there is a high concentration of individuals, to areas where fishing has reduced the number and size of fish (Kramer and Chapman, 1999; Kerwath *et al.*, 2013). While there may be some true density-dependent spillover of *D. petersi* from the no-take zones into the adjacent exploited zones within the iSimangaliso MPA, the remoteness of many of the areas and the low fishing effort adjacent to the no-take zones, especially since the implementation of the beach vehicle ban in 2002 (Mann *et al.*, 2016a; Mann and Mann-Lang, 2020), has likely reduced the gradient in fish density between the zones (Mann *et al.*, 2016a), with the result that much of the dispersal observed in this study is more likely to have been as a consequence of variability in individual movement patterns. This observation is supported by the fact that ranging movements were undertaken by 4 fish tagged in an exploited zone, 1 of which moved into a no-take zone and the other 3 swam right through a no-take zone and were recaptured in an exploited zone on the other side (Table 1). A further contributing factor is because there is no offshore (i.e. boat-based) exploitation of reef fish allowed throughout the iSimangaliso MPA, meaning that the *D. petersi* population beyond the surf-zone remains largely unexploited.

Table 3. Published growth parameters of 5 sympatric reef fish species based on the median record of phi-prime (Ø) obtained from FishBase (Froese and Pauly, 2019).

Species	L_∞	K	Ø	Region	References
Dinoperca petersi	59.6 cm TL	0.23	2.92	South Africa	This study
Epinephelus marginatus	135.9 cm TL	0.1	3.17	France	Bouchereau *et al.* (1999)
E. tukula	115 cm TL	0.1	3.24	Seychelles	Grandcourt (2005)
Lutjanus argentimaculatus	105 cm TL	0.19	3.32	Malaysia	Ambak *et al.* (1986)
L. rivulatus	91.8 cm FL	0.06	2.69	South Africa	Mann *et al.* (2016c)

Growth

The high recapture rate of *D. petersi* (19.1 % including multiple recaptures) can be ascribed to a combination of factors including good fish handling and tagging, suitability of the species for tagging, and the high level of residency and site fidelity displayed by this species (Mann *et al.*, 2015). The low number of fish observed with tag scars (n=6) also suggests that this species takes and retains the tag well. Although some tagged fish had swallowed the hook, which may affect growth rate (Aalbers *et al.*, 2003), there were too few to enable a comparison of growth to be made. Despite the effects on growth rate of the tagging procedure, the physiological burden of carrying the tag (Attwood and Swart, 2000) and/or swallowing the hook could not be assessed, *D. petersi* appeared to be a suitable species for calculation of growth rate using tag-recapture methods.

The L_∞ parameter derived from tag-recapture data has a fundamentally different meaning to the L_∞ parameter obtained from length-at-age data (Francis, 1988b). Consequently, due to the correlation between L_∞ and K, the K parameter also has a different meaning/interpretation (Mann *et al.*, 2016c). The L_∞ value obtained in this study (L_∞ = 596 mm TL) was smaller than the maximum size recorded for this species i.e. 750 mm TL (van der Elst, 1993) but this can be explained by the fact that the largest fish captured only measured 580 mm TL. This may also suggest that fish living in the surf-zone with its higher energetic requirements do not reach as large a size as those living on deeper offshore reefs. Tag-recapture growth modelling primarily solves two parameters, namely g_α and g_β (i.e. annual growth rate at length α and β). These parameters are also easily obtained from growth models derived from length-at-age data (including the von Bertalanffy Growth Function) and have been shown to be mathematically comparable (Francis, 1995). Therefore, the results of growth studies utilising these different types of data are comparable, highlighting the value of growth information that can be extracted from tag-recapture datasets.

Acknowledging the above limitations, the present results suggest that *D. petersi* is a relatively slow-growing species with an average growth rate of 61.76 mm.y^{-1} for smaller fish (g_α = 300) and 9.58 mm.y^{-1} for larger fish (g_β = 550). Growth rate at 300 mm TL was significantly faster compared to that of larger fish at 550 mm TL. In order to compare this growth rate to other sympatric reef fish species, the index phi-prime (Ø), developed for this purpose by Pauly and Munro (1984), was used. This suggests that the growth rate of *D. petersi* is comparatively slower than that estimated for several other sympatric reef fish species, except for *Lutjanus rivulatus* (Table 3).

The growth model suggested relatively low seasonal differences (0.23) in the growth rate of *D. petersi* with fastest growth in June/July (0.52). This period is associated with cooler seawater temperatures in the iSimangaliso MPA, averaging around 22 °C (BQM unpublished data). Considering that Connell (2012) reported the highest frequency of *D. petersi* eggs during summer (December to April) on the KZN south coast, it may be that somatic growth is faster during the winter months when adult fish are not investing energy into reproduction.

Conclusion

Life-history parameters such as slow growth and high residency result in fish species being more vulnerable to overexploitation (Smale and Punt, 1991; Buxton, 1993). *D. petersi* displays both these characteristics and a conservative approach is thus required for its management. Although this study has shown that *D. petersi* receives protection from fishing within no-take zones in the iSimangaliso MPA, it is not currently listed in

the suite of fish species regulated by species-specific minimum size and bag limits in South African fisheries legislation (RSA, 2005). As such, and based on the results of this study, a minimum size limit of 300 mm TL based on the estimated size-at-maturity (van der Elst, 1993) and a daily bag limit of 5 fish per person per day is recommended as a precautionary approach for the future management of this species in South African waters. This would then make the bag limit the same as the current limit for other related "rockcod" species (Family Serranidae).

Acknowledgements

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