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Alternate explanations of the dispersal pattern of galjoen *Dichistius capensis*

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The movement behaviour of galjoen *Dichistius capensis* (>250mm total length) was studied by using a tag and recapture technique. A total of 25 191 galjoen was tagged at four sites in South Africa. Three of the sites were in fully protected reserves (two in the De Hoop Marine Protected Area, one in the Tsitsikamma National Park), whereas the fourth site was at the Cape Peninsula where fishing is permitted. In all, 2 174 fish were recaptured, some of them several times. The vast majority of fish were caught at the site of release. After correcting for differences in recovery effort between the release sites and other areas, it was estimated that 95% of tagged fish remained at the release site. The remaining 5% moved throughout the South African range of galjoen, which was separated from the Namibian range. There

was no evidence to suggest that movement is linked to season, age or sex. Although not territorial, galjoen do hold home ranges, which were estimated to be no larger than 1.38km in extent, but probably much smaller. Two likely models, the polymorphic and the tourist, are advanced to explain the movement behaviour. The polymorphic model is a combination of two movement patterns, one resident and another nomadic. The balance between the two may represent a mixed evolutionary stable strategy. The tourist model does not differentiate between fish. Each fish spends its time at a small number of widely separated sites, moving between them as conditions dictate. The tag and recovery data do not favour one model above the other unequivocally.

Keywords: *Dichistius capensis*, dispersal, home range, mark and recapture, marine protected area

Introduction

Galjoen *Dichistius capensis* and banded galjoen *Dichistius multifasciatus* are the sole members of the family Dichistiidae, and both are endemic to the southern African shallow coastal zone. *D. capensis* is among the most frequently caught fish by the recreational shore-fishery in South Africa and Namibia. Its distribution is bimodal, stretching from Durban to the Kunene River mouth, but remarkably few are caught in the area between Lambert's Bay and Lüderitz where upwelling and the occurrence of cold, low-oxygen water is a frequent event. Galjoen eggs do not hatch below 14°C (van der Lingen 1994). Nonetheless, galjoen migrate across this area (Anon. 1984), thereby maintaining a link between the stocks. *D. multifasciatus* has a subtropical distribution, stretching from Cape Agulhas to northern Moçambique, which overlaps partly with that of *D. capensis*. It is a species of lesser importance to the fishery.

Galjoen have been well studied when compared with other species targeted by recreational shore-anglers. It is a medium-sized fish, which attains a maximum mass of 6kg. They are usually found along turbulent, wave-exposed shores where they feed on epilithic invertebrates, and are less frequently found beyond the surf zone on shallow reefs

and wrecks, and then often in large shoals (Bennett and Griffiths 1986, Rust and Rust 2000).

Galjoen eggs float and hatch within a day into larvae, with limited endogenous food supplies (van der Lingen 1994). The fish must feed within the first week, an act that necessitates at least a weak swimming capacity. During that time, there is tremendous scope for dispersal. Van der Lingen (1994) calculated that typical inshore currents could transport the young galjoen 240km before feeding, but queried whether such a linear extrapolation is valid. The coast consists of a series of bays and capes, which would cause current retention. It is not uncommon for the larvae of reef fish to show strong positioning capabilities, and it is likely that larval dispersal of galjoen is restricted. Reef fish larvae are often concentrated over reefs and not randomly distributed (Marliave 1986, Tilney *et al.* 1996, Warner *et al.* 2000), and there is circumstantial evidence that physical and behavioural mechanisms facilitate larval retention near source populations (Leis 1994, Swearer *et al.* 1999, Warner *et al.* 2000). Despite the abundance of galjoen, their larvae have yet to be found, despite extensive inshore larval surveys.

Although Attwood and Bennett (1994) attempted to explain

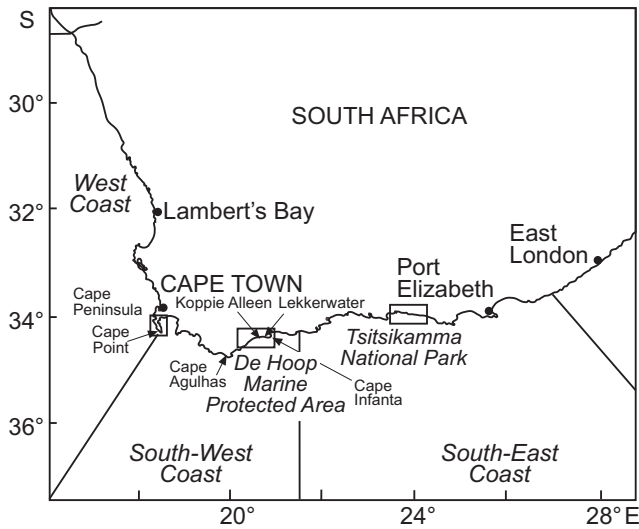


Figure 1: Locations of research sites and places mentioned in the text

the movement pattern of adult galjoen, there appears to be no clear support for accepting any of the conventional fish-movement models. Galjoen swim in small groups and large shoals (Rust and Rust 2000), display resident behaviour and undertake large, unpredictable migrations (Attwood and Bennett 1994).

The study of movement behaviour of fish has a strong applied value, because such behaviour will influence the effectiveness of marine protected areas as a mechanism of fish conservation, and it may affect the design of fishery monitoring programmes. This study is a detailed examination of galjoen tag-recapture information collected at four sites, three of which were protected from fishing (Figure 1). The fishery-independent research that was undertaken at these protected sites benefited from the complete control that could be exerted on the tagging experiment in the absence of a conventional fishery. The aim of the study was to develop a model of galjoen movement patterns.

Material and Methods

Study areas

Fish were tagged from the shore at four sites, Koppie Alleen, Lekkerwater (both within the De Hoop Marine Protected Area [MPA]), Tsitsikamma National Park and the Cape Peninsula (Figure 1). The shoreline at the De Hoop sites consists of high-energy, broken sandy-shores, interspersed with wave-cut sandstone platforms. Highly exposed, steep rocky headlands dominate the entire length of Tsitsikamma National Park, but with occasional tiny pocket beaches, boulder beaches and sandy gulleys. The inshore area of the Cape Peninsula is also a high-energy environment, but wave action is partly damped by extensive kelp forests, which also reduces the available fishing area. Full descriptions of these sites are given in Attwood (2003). Only the Cape Peninsula site was exploited by recreational anglers, the others fell within 'no-take' marine protected areas.

Table 1: Fishing effort per year. The number of fishing trips (usually five days each) per year at the three protected sites are shown, whereas at the Cape Peninsula, only the number of days fished is shown

Year	Number of trips per year			Number of days fished
	Koppie Alleen	Lekkerwater	Tsitsikamma	Cape Peninsula
1987	4			29
1988	6	5		18
1989	6	5		62
1990	6	5		39
1991	6	5		75
1992	6	5		59
1993	6	5		63
1994	3	3		71
1995	2	3	11	60
1996	3	3	12	62
1997	3	3	6	44
1998	3	3	6	38
1999	3	3	6	5
2000	1		1	
Total	58	48	42	625

Fishing and tagging

De Hoop

A controlled shore-angling programme was initiated at Koppie Alleen to study galjoen in 1984, one year before the De Hoop MPA was proclaimed. Thereafter, the programme was allowed to continue as a fishery-independent survey, but all other fishing was stopped. Initially, the programme involved fishing by a small group of anglers during monthly trips at Koppie Alleen, which lasted for four or five days each. Prior to 1987, 959 galjoen were killed for a biological study (Bennett 1988). From 1987 onwards, all fish were tagged and returned to the sea, and the trips alternated between Koppie Alleen and Lekkerwater. From 1995 onwards, the trips were reduced to six per year (three at each site), each lasting five days (Table 1).

Volunteer anglers assisted the senior author (CGA) and two other fishery scientists in the capture and tagging of fish. The composition of the volunteer angling team was kept as constant as possible. Although, in total, use was made of 86 anglers during 126 trips, most effort was accounted for by only eight anglers.

All fish caught were measured to the nearest mm in total length (TL). Galjoen were tagged if they were >250mm, using plastic dart tags 89mm long and 1.4mm diameter (manufactured by Hallprint, Australia). Inscribed on each tag was a unique alpha-numerical code and the postal address of the Oceanographic Research Institute in Durban. The fish handling procedure was gradually improved during the course of the programme. Initially, fish were measured with tape measures. These were replaced by rigid measuring boards. Later, a special sling with a central rigid baton and tape measure was used to land, tag, carry and measure fish with the minimum of human contact (Attwood 1998). Measurement error amounted to 3.2mm standard deviation of total length (Attwood and Swart 2000). Timed tagging

trials show that the average capture and tagging procedure kept the fish out of water for 1 minute and 20 seconds.

Tagged fish caught by the public were reported to the Oceanographic Research Institute, where the position of the recapture was recorded as the coastline distance from the northern Mozambique border, measured in km (called the ORI locality code). The greatest drawback of this study was that the public was relied upon to return tags from fish recaptured outside the protected study sites. Although this did happen frequently, it was clear that a substantial fraction of tags was never reported. Lamberth (1997) estimated that only 58% of recaptured fish were successfully reported. Obviously, those recaptured at the protected research sites were all recorded.

From 1998 onwards, both sites were marked at 100-m intervals along the beach by boards with a number ranging from 1 to 35; anglers operated within the 3.4-km stretch. The position at which each fish was released or recaptured was recorded by the angler as the marker closest to the point where the fish was hooked. All recaptured fish were again returned to the water once the tag was cleaned of encrusting growth. In rare cases, the fish was sacrificed if the tag could not be read without being removed. In total, the number of galjeon that was sacrificed (either to read the tag, or because of a 'gill-hook') never exceeded 1% of the fish caught.

Tsitsikamma

A research programme was initiated at the Tsitsikamma National Park in 1995, based on a similar design to the De Hoop programme (Table 1). A small number of volunteer anglers assisted the junior author (PDC) on scheduled monthly (pre-1997) or bimonthly (1997 onwards) fishing trips. All fishing trips took place along a small, designated area near the western boundary of the Park (Cowley *et al.* 2002). Fish were caught and tagged in the same way as at De Hoop, except that fish were measured along their fork length and later converted to total length using the conversion supplied by Bennett and Griffiths (1986). Being in a MPA, the only fishing undertaken at the research site was by the research team, although there was concern that a small amount of poaching occurred. The stable, rocky nature of the shoreline meant that the use of distance markers was unnecessary. Instead, all fishing spots were named and identified on a 1:10 000 orthophoto map so that distances could be calculated accurately.

Cape Peninsula

The Cape Peninsula data did not result from a structured experiment. One of the anglers who participated in the tagging studies at De Hoop also fished regularly at Cape Peninsula. The fish were tagged and recorded in the same way as described for De Hoop. The anglers' fishing days were randomly distributed throughout the 7.5-month recreational season (1 March–15 October). Each fishing spot was named, and the distance between fishing spots was measured with a GPS unit. Records were maintained from 1987 to the present (Table 1).

Statistical methods

There were two biases that masked the true recapture distri-

bution, and they acted in opposite directions. On the one hand, there was a greater recapture effort applied outside the protected research sites by recreational anglers than applied at the research site by the research team. On the other hand, not all of the recaptures outside of the protected sites were reported. Crude correction factors were calculated as the ratio of effort applied inside the protected release site to that applied in each of three broad recapture regions, divided by the rate of reporting (Table 2). The observed frequency of recaptures in each region was multiplied by the correction factors appropriate for the release site, to estimate a recapture frequency that was comparable to that observed inside the protected sites, where recapture effort and recaptures were all recorded. Estimates of recreational effort per recapture region were taken from Brouwer *et al.* (1997), and a constant reporting ratio (58%) was applied to all areas (Lamberth 1997).

The data on the movement of fish within the release sites were used to estimate home-range size and the use of space within the home-range. The displacement of each recapture taken at the release site was calculated as the distance between the release and recapture position, in increments of 100m. Each dataset was summarised as a set of frequencies of occurrence of each displacement increment. For example, if seven fish were re-caught within 50m of the release site, then $\Delta x = 0$ and $f_{(\Delta x = 0)} = 7$. If three fish moved 200m (irrespective of direction), then $f_{(\Delta x = 0.2)} = 3$. The frequencies of all Δx values, from $\Delta x = 0$ to $\Delta x = 2.5$, hold information about home-range size and the use of space within that range.

Probability distributions were used to model the use of space by fish within the home-range. Each distribution gave the probability that a fish occupied position x (each position covering 0.1km of coastline length) at a random capture time. To compare the models to the displacement frequency data described above, theoretical displacement distributions were generated by repeatedly drawing two positions from a probability distribution — representing release and recapture positions — and then calculating the absolute difference between them. These differences were rounded off to the nearest 0.1km, so that the theoretical displacement distributions could be presented with same resolution as the data.

Three types of theoretical probability distributions were developed: (i) the flat (uniform) distribution (i.e. fish spend an equal amount of time at all areas within the home-range), (ii) the normal distribution (i.e. fish spend most time in the

Table 2: Correction factors applied to the observed number of recaptures outside of the research sites in each of three broad recapture regions (Figure 1). The factors differed between the four release sites

Recapture regions	Correction factors			
	Koppie Alleen	Lekkerwater	Tsitsikamma	Cape Peninsula
West Coast	0.34	0.39	0.73	1.00
South-West Coast	0.11	0.12	0.23	0.31
South-East Coast	0.35	0.40	0.75	1.03

centre of the home-range) and (iii) the gamma distribution (i.e. as above, but the distribution of frequency of occupancy of sites within the home-range is either leptokurtic or platykurtic):

$$\text{Uniform: } p(x) = 1/v \quad (1)$$

$$\text{Normal: } p(x) = \frac{1}{\sigma\sqrt{2\pi}} e^{-(x^2/2\sigma^2)} \quad (2)$$

$$\text{Gamma: } p(x) = \frac{x^{\alpha-1}}{\beta^\alpha \Gamma(\alpha)} e^{(-x/\beta)^\alpha} \quad (3)$$

The corresponding theoretical displacement distributions are referred to as the difference of flat deviates (DFD), the difference of normal deviates (DND) and the difference of gamma deviates (DGD).

Whereas the first two distributions require little explanation, the gamma distribution is not used frequently in behavioural studies. The generalised gamma distribution is an extremely adaptable distribution, which, it has been claimed (Taylor 1980), can fit dispersal patterns of any organism including humans. The probability density function, using two parameters, was used. The factor $\Gamma(\alpha)$ is the gamma function (Press *et al.* 1992).

The parameters of the models were total home-range size (v) for DFD, the standard deviation (σ) for DND, and α and β for DGD. The resulting probability distributions of differences were calculated analytically for DFD and numerically for DND and DGD. Numerical solutions used 10 000 iterations to get a smooth curve. These probabilities, which represent multinomial coefficients, were referenced as $p(\Delta x)$. Multinomial coefficients were used to compute the log-likelihood (LLH) of the set of displacement frequencies, given any of the three models (Lebreton *et al.* 1992):

$$\text{LLH}(v \text{ or } \sigma \text{ or } \alpha, \beta) = \sum_{\Delta x} f(\Delta x) \ln p(\Delta x) \quad (4)$$

The log-likelihood was maximised by adjusting the relevant parameters (v , σ or α and β).

The DFD model gave a direct estimate of v . The DND model used the relation $v \approx 4s$ (i.e. two standard deviations either side of the mean), based on the convention that the home-range includes 95% of the animal's activity (Anderson 1992). No simple relation could be found in terms of α and β in this context. Instead, for the DGD model, the gamma distribution was used to calculate the length that corresponded to the 0.95 cumulative probability.

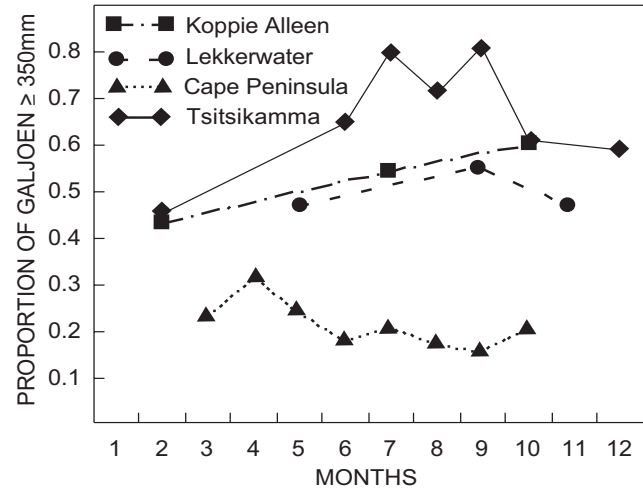


Figure 2: Proportion of mature galjoen in monthly samples taken at four research sites

Results

Sample size

The study is based on information derived from the capture of 27 606 galjoen from four research sites from 1987 to 2000 (Table 3). Most effort was expended at the two De Hoop sites, Koppie Alleen and Lekkerwater, and the majority of the sample came from there. The third largest contribution came from the Cape Peninsula, where the data spanned a similar period. Sampling at Tsitsikamma covered a shorter period from 1995 to 2000.

Tagged fish were recaptured at the experimental sites and elsewhere. Recapture rates varied between 0.12 (Koppie Alleen releases) and 0.043 (Tsitsikamma releases). Included in these rates are those fish that were recaptured more than once and those that were caught outside of the study site. Recapture records were complete at De Hoop and Tsitsikamma, but there were unknown losses as a result of non-reporting outside of these areas, including the Cape Peninsula site.

Size distributions

Captured galjoen ranged in size from 110mm to 604mm. Average sizes differed significantly among sites (one-way ANOVA, $F = 665.1$, $df = 27\ 387$, $p < 0.05$; Table 4). The average size of fish at the Cape Peninsula was smaller

Table 3: Number of galjoen that were captured, tagged and recaptured n-times, and the recapture rate (all recapture events divided by first releases)

Recapture regions	Koppie Alleen	Lekkerwater	Tsitsikamma	Cape Peninsula
Captured	9 322	14 823	2 590	871
Tagged	8 310	13 686	2 360	835
Recaptured once only	763	964	218	32
Recaptured twice only	76	70	9	2
Recaptured more than twice	28	11	1	0
Recapture rate	0.12	0.083	0.10	0.043

Table 4: Comparison of the total length distributions of captured galjoen from the four research sites

Site	n	Total length (mm)					
		Min.	Max.	5%ile	95%ile	Mean	SD
Koppie Alleen	10 200	122	604	265	475	362.1	72.9
Lekkerwater	13 907	110	595	275	475	359.7	63.4
Cape Peninsula*	2 447	177	514	277	373	327.6	31.0
Tsitsikamma	834	187	588	283	502	380.6	64.0

n = sample size; Min. = smallest fish; Max. = largest fish; 5%ile = length of the 5th percentile; 95%ile = length of the 95th percentile

* Unprotected site

than at the other sites, which may be attributed to the fact that the fish were exploited there. There was very little difference between the size distributions at the two De Hoop sites, but proportionately there were more large fish at Tsitsikamma, as suggested by the 95th percentile (Table 4). All sites had similar values for the 5th percentile, indicating similar proportions of small fish.

Adult fish may behave differently from immature fish with respect to feeding behaviour and migration. Such differences may be linked to the breeding cycle. If this was the case, then the ratio of mature to immature fish in the samples might differ between months at each site. Accordingly, the following null hypothesis was tested for each of the four sites, using a Chi-square contingency table: there is no difference in the relative numbers of mature and immature galjoen between months. A mature fish was classed as any galjoen >349mm TL.

The null hypothesis was rejected for the two De Hoop samples and for the Tsitsikamma sample (Table 5). In these cases, the percentage of mature fish (≥ 350 mm TL) peaked between July and November (Figure 2). The fact that the period in which the relative number of mature fish is at its lowest corresponds with the period of lowest catch per unit effort (cpue; i.e. winter/spring) suggests that it is the availability of mature fish, and not immature fish, that varies seasonally (Attwood 2003). The monthly differences in the Cape Peninsula sample were not significant ($p > 0.05$). A trend at the Cape Peninsula may have been masked by the effects of fishing, as suggested by the low overall percentage of mature fish. There is no evidence to suggest that adults migrate to a spawning site that occupies only a small part of the range. The timing of peaks in abundance of adults did not differ between sites.

Tag-recapture data

A substantial portion of tagged galjoen moved great distances, but most were recaptured at the release site

(Figure 3, Table 6). The movements covered the entire range of galjoen in South African waters. Several of the De Hoop releases were recaptured north of Cape Point and east of East London, with the maximum displacement being over 1 000km. The farthest distance moved by a Cape Peninsula fish was 1 300km, covering almost the entire range. Only two fish from Tsitsikamma were recaptured outside of that study site, one of which covered 750km westwards. The other was discovered in a fresh state in the stomach of a large kob *Argyrosomus japonicus* in the Gamtoos Estuary to the east of Tsitsikamma, and it was assumed that the fish was eaten in that vicinity. At the De Hoop and Cape Peninsula sites, both lying slightly on the western side of the range, most of the 'movers' went eastwards.

The frequency of recaptures decreased with the absolute displacement distance (Figure 4). This distribution has a long tail. The most notable feature of these data is that the majority of recaptures (approximately 80%) were made at the release site. After correcting for the effort and reporting biases, the fraction that was recaptured at the release site was even greater (Table 6). These corrected frequencies are a more reliable indication of the true movement patterns, despite the crude calculation of 'correction' factors. It is a reasonable assumption that the ratio of effort applied inside vs outside the study sites was less than the reporting rate outside of the study sites, and therefore the observed recapture frequencies outside of the research sites should be adjusted downwards.

After correction, the proportion of recaptures taken at the release site was similar for the two De Hoop sites and Tsitsikamma (approximately 95%), but smaller for the Cape Peninsula (83%).

A number of hypotheses can be tested in the search for a unifying theory for these distributions. The first is that the movement can be described by a diffusion process, whereby small, random movements of individuals cause the population to spread out, according to Fick's equation (Okubo 1980). According to that equation, the variance in displacement

Table 5: Proportions of samples that were >349mm (% mature), and the results of a Chi-square test on the differences in frequency of mature (≥ 350 mm) and immature (<350mm) fish in monthly samples

Site	n	% Mature	Chi-square	df	p
Koppie Alleen	10 200	54.6	86.1	2	<0.05
Lekkerwater	13 907	50.6	64.8	2	<0.05
Cape Peninsula	2 477	19.3	15.02	8	<0.10
Tsitsikamma	834	66.8	46.1	11	<0.05

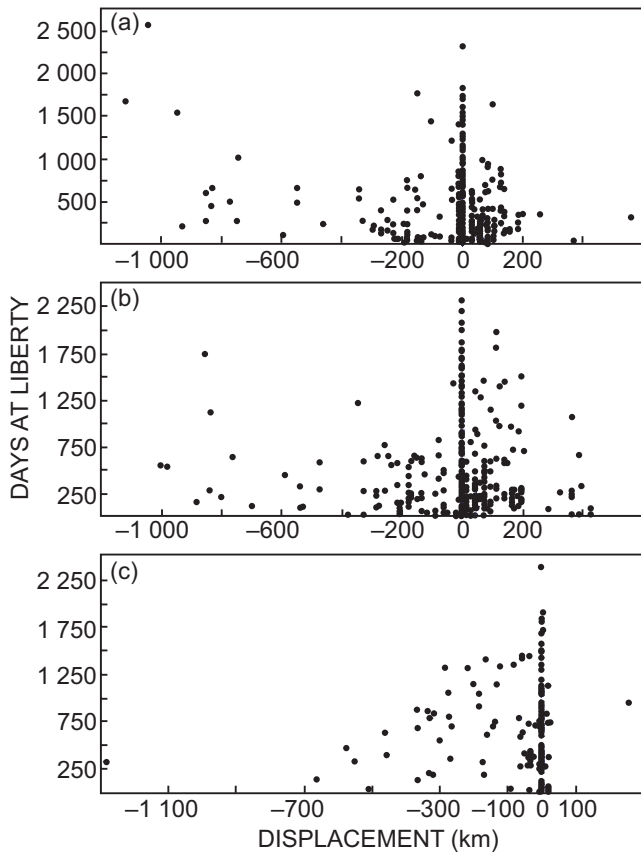


Figure 3: A scattergram of days at liberty against distance moved by galjoen for (a) Koppie Alleen, (b) Lekkerwater and (c) Cape Peninsula. The x-axes indicate relative distance (west is positive)

(distance moved) increases linearly over time, by the rate D (the diffusion parameter), and the spatial distribution would be normal for tagged fish that have been free for any given time at liberty. Direct tests of these predictions are not possible, because the biases introduced by non-reporting and unequal effort distributions will mask any prediction cast in terms of absolute frequencies. Furthermore, it would be

Table 6: The actual frequency and corrected relative frequency (based on correction factors applied to recapture regions listed in Table 2) of tagged fish that were re-captured to the west of the release site, at the release site, and to the east of the release site. Because the Cape Peninsula site was very large, only fish that moved <2km were considered to have been recaptured at the 'same site'

Parameter	Koppie Alleen	Lekkerwater	Cape Peninsula	Tsitsikamma
<i>Actual frequencies</i>				
West	103	91	12	1
Same site	811	901	153	32
East	96	145	64	1
<i>Corrected relative frequencies</i>				
West	0.013	0.016	0.065	0.021
Same site	0.96	0.95	0.828	0.957
East	0.027	0.038	0.107	0.022

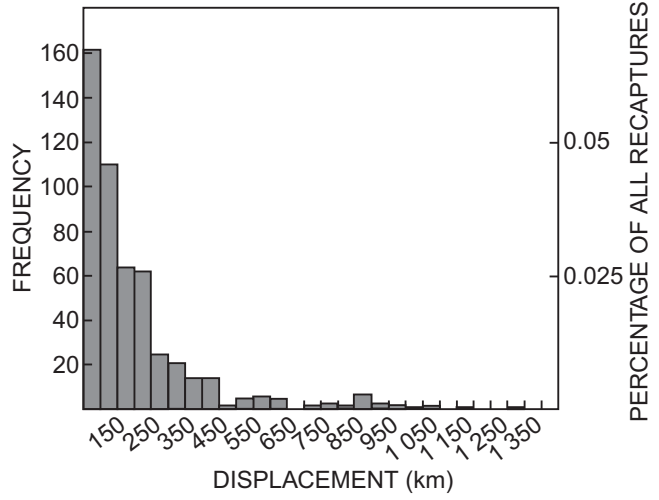


Figure 4: Frequency histogram of distance moved by galjoen tagged at all sites. The 0–50km bin is excluded, because its frequency ($n = 1\ 907$) vastly exceeds those in all other bins combined

incorrect to dismiss diffusion simply because the variance does not increase linearly over time. The range of galjoen is limited, and it is clear that a maximum variance will be reached as fish reach the ends of the distribution. Judging from the recapture distribution (Figure 3), this could happen quite quickly.

The most basic prediction of diffusion is that particles spread out over time, as the net movement of individuals at any point opposes the concentration gradient. Diffusion would predict that the proportion of fish remaining within close proximity of the point of origin will decrease over time. In this case, the proportion of recaptures made at the release site should decrease with increasing time at liberty. This can be tested with the available data, because it is a prediction of temporal change that is unaffected by spatial biases in the recapture frequencies.

The following null hypothesis was tested with a Chi-square test: the proportion of recaptures taken at the release site is independent of time at liberty. For data from each site (except for Tsitsikamma, which had too few data for this test), a contingency table was constructed with the absolute frequency of zero and non-zero displacements against time-at-liberty categories. There were sufficient data for seven time-at-liberty categories for the De Hoop sites, but only five for the Cape Peninsula site. The proportion of zero displacements show no discernible trend over time at liberty, with perhaps the exception of the Cape Peninsula recaptures (Figure 5). The null hypothesis was accepted at the 5% level in the case of Koppie Alleen and the Cape Peninsula (Table 7).

Even the significant difference in proportions between time at liberty categories at Lekkerwater does not support the diffusion hypothesis, because the result was driven by low proportions in only one category (201–300 days). This was confirmed by a one-tailed Spearman's rank correlation test on the percentages vs the time at liberty categories shown in Figure 5 ($r = -0.46$, $p > 0.1$). Diffusion alone does not appear to explain the recapture pattern. If diffusion does play

a role, it is well masked by other processes, which may involve seasonal or sex-related behaviours.

The microscale, within-site, movements shed more light on the movement behaviour. Those recaptures taken at the protected research sites, for which exact locations were recorded for release and recapture events, can be used to estimate home-range size, provided that the home range is substantially smaller than the study sites. The displacement data (Figure 6) confirm that the three protected sites (smallest = 3.4km) were large enough to contain home ranges. The rationale for omitting those fish that left the study site in the calculation of home-range size is that they must have abandoned the home range. For galjoen ($l_{\infty} \approx 670\text{mm}$) the maximum predicted home-range size is 700m, based on the allometric relationships reported by Kramer and Chapman (1999) for tropical reef fish.

At De Hoop and Tsitsikamma, it is clear that galjoen show a high degree of site fidelity, with 60% of the within-site recaptures having been taken within 200m of the release position (Figure 6). At the Cape Peninsula, the site fidelity is more extreme. Of the 31 recaptures at the Cape Peninsula for which positions were accurately recorded, 24 were displaced by <100m. However, these data were not used to estimate home-range size, because they were biased by the fact that the fishing effort was not concentrated in a small area, but rather at nodes distributed over a large area. These nodes were isolated from others by distances that varied up to 2km, which reduced the frequency of recaptures with displacements in this interval. As a result, home-range size would have been under-estimated at the Cape Peninsula.

The Cape Peninsula data were useful in that they showed a continuum in the spatial recapture distribution from 2km to 1 300km. In other words, those fish that abandoned their home range moved to sites anywhere within this range of distances from the original home range. This fact could not be established at the protected sites because the reserves prevented recaptures from large areas either side of the study sites. For example, the study sites at De Hoop each measured 3.4km, but the MPA is much larger, at 51km.

The DFD, DND and DGD models represent different types of space-use within the home range. The model that provides the best fit is the one that should be used to estimate the home-range size. For each of the three study sites, the DFD and DND models did not fit the data satisfactorily (Figure 6). The discrepancy in each case was the same — the observed frequencies for small Δx values were too high, indicating a high degree of central tendency.

The DFD model estimated v to lie between 200m (at Tsitsikamma) and 1 400m (at Lekkerwater). The σ parameter of the DND model could not be estimated using the likelihood method, because the best fit (when gauged by eye) produced zero $p(\Delta x)$ values at the high end of the Δx range. Zero $p(\Delta x)$ values required the calculation of the logarithm of zero, a mathematical impossibility. Very low likelihood values could have been assigned to such cases, but that would have biased the fit to an unknown extent. No attempt was made to use another method of fitting (e.g. sum-of-squares), because the model was inappropriate. The DND curves illustrated in Figure 6 were based on σ values of one-quarter of the estimate of v provided by the DFD model.

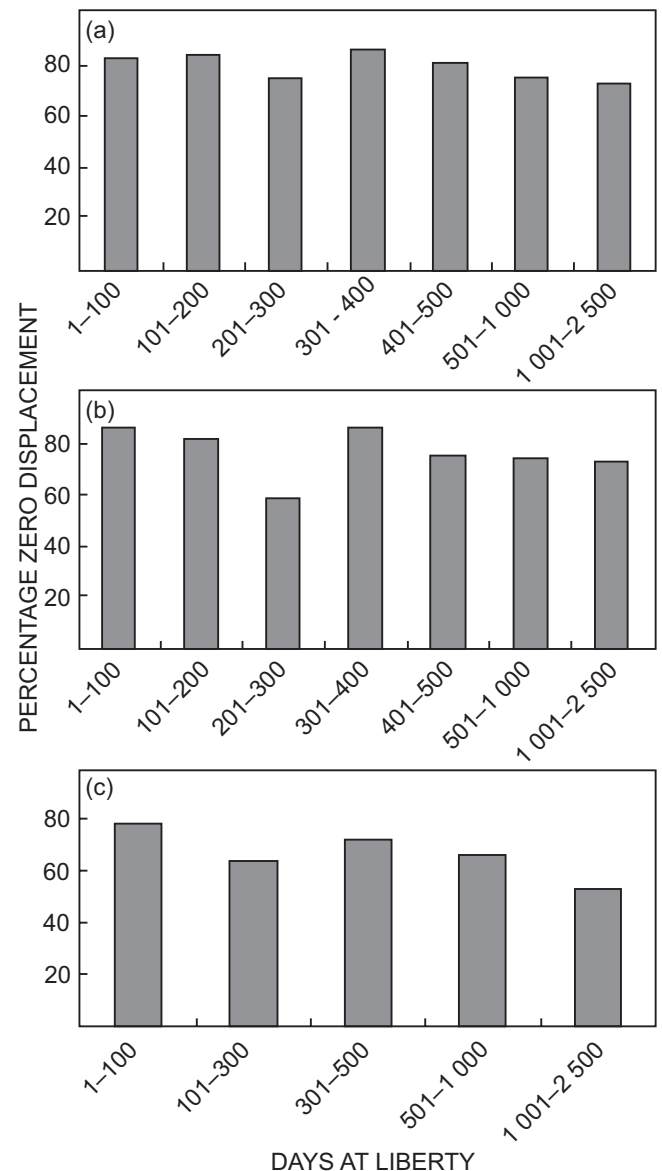


Figure 5: Percentage of recaptures that were taken at the release site in a range of categories of days at liberty for (a) Koppie Alleen, (b) Lekkerwater and (c) Cape Peninsula

Table 7: Results of Chi-square tests on the frequency of zero and non-zero displacements from recaptures that were grouped by days at liberty

Location	df	Chi-square	p
Koppie Alleen	6	10.87	0.092
Lekkerwater	6	45.51	< 0.001
Cape Peninsula	4	6.15	0.187

It is not surprising that the DGD model fitted the data best. With two free parameters it is considerably more flexible than either of the others. Based on these fits, home ranges were estimated to lie between 340m (Tsitsikamma) and 1 380m (Lekkerwater, Table 8).

The calculation of these home-range estimates is based on a sample that consisted of a range of fish sizes from 250mm to 588mm. Home-range size varies allometrically, in accordance with the animals' resource requirements. Over this size range, home ranges of tropical reef fish were predicted to lie between 76m and 572m (Kramer and Chapman 1999). If the same pattern were true for galjoen, it would skew the distribution of displacement probabilities, and in so doing mask the true pattern of space-use. On the other hand, small fish may struggle to maintain a home range, and may be forced to shift it over the course of a few months, thereby creating the impression of a larger home range. When the data were split by size (<350mm and ≥ 350 mm), there was no evidence to support any of these size-based differences. Small and large fish showed the same distribution of space-use within the home range (Figure 7).

If it is accepted that at least some galjoen hold home ranges for at least some of the time, then what causes some fish to abandon the home range and undertake long-distance movements? Such movements could be related to seasonal changes or spawning. It has already been established that there are differences in the availability of mature fish within sites between months. The peaks in availability occur during winter/spring at all sites, which rules out a seasonal, longshore mass migration. However, galjoen could still be more prone to leave the home range at certain times of the year (e.g. non-breeding season), without participating in a mass migration or going in a predictable direction. Home-range behaviour could be seasonal. To investigate this possibility, it was necessary to look at those recaptures with a short time at liberty and investigate if the proportion of recaptures that were taken at the release site varied with release month.

A time-at-liberty period of three months was considered sufficiently small to detect seasonal effects, yet not so small as to exclude too much data. All recaptures that were at liberty for longer than three months were excluded from this analysis. Those that were recaptured beyond the home range were classed as 'movers' (i.e. displacement exceeded 2km). At De Hoop, the percentage of short time-at-liberty recaptures that were taken at the release site did not show a consistent monthly trend (Figure 8). This finding argues against any seasonal effect in home-range behaviour. There were insufficient data to test this hypothesis at the other sites.

Are fish equally likely to be found away from the release site, irrespective of size? It would be better to ask this question in terms of age, but the practical problem of assigning ages to unsexed galjoen prevents this approach (male and female galjoen grow at different rates, Bennett and Griffiths 1986). At the two De Hoop sites, the size of fish differed between those that were recaptured at the release

site, those that were recaptured to the east and those that were recaptured to the west (Table 9). The equivalent size differences at the Cape Peninsula site were not significant. At each site, the fish that moved were larger, but the

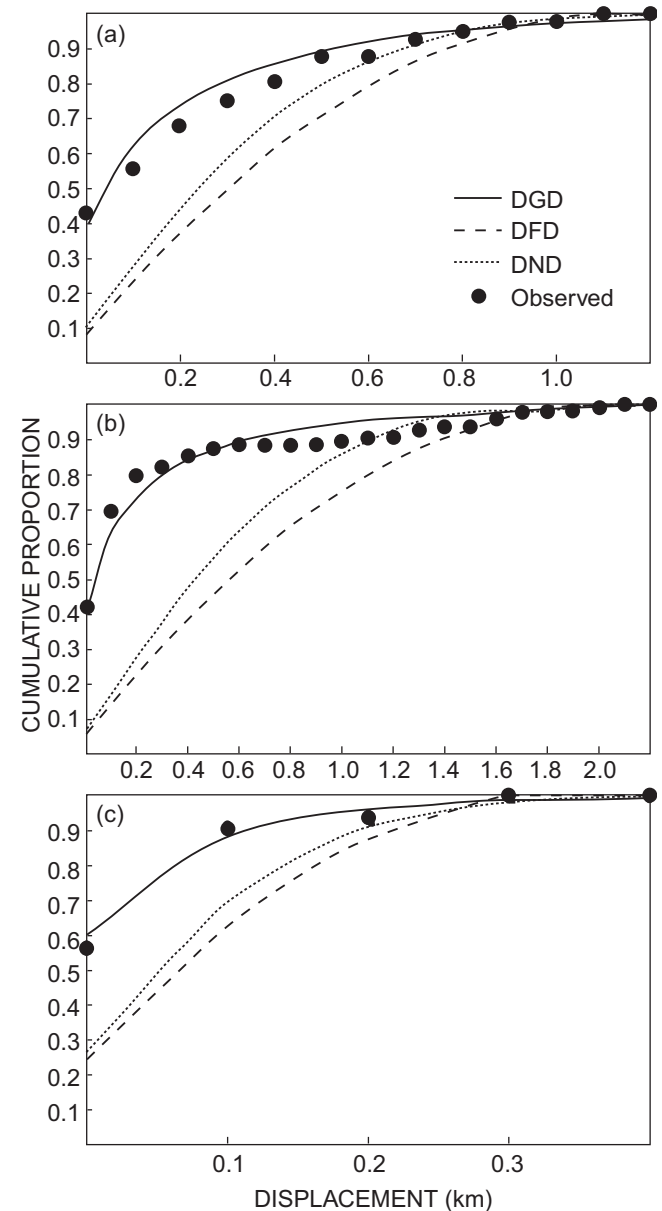


Figure 6: The cumulative proportion of recaptures taken at the release site at increasing distances from the point of release. Three model predictions are shown for comparison for (a) Koppie Alleen, (b) Lekkerwater and (c) Tsitsikamma (see text for model details)

Table 8: Home-range size estimates based on the difference of flat deviates (DFD) and the difference of gamma deviates (DGD) models. The DGD model gave the best fit in every case, and its parameters are listed. The Kramer and Chapman (1999) predictions for the home-range based on fish size are listed for comparison

Location	n	DFD (m)	DGD (m)	α	β	K&C prediction (m)
Koppie Alleen	41	800	1 180	0.27	4.8	76–572
Lekkerwater	82	1 400	1 380	0.17	7.5	76–400
Tsitsikamma	32	200	340	0.42	0.95	76–373

differences were not clear-cut as the overlap in ranges between samples indicates. Many large fish were recaptured at the release site, whereas many small fish moved.

Another possibility that needs to be examined is that fish that leave a home range may ultimately return to it. Such a process would explain why the proportion of recaptures taken at the release site did not decrease over time. To test whether such a 'round trip' does occur, it is necessary to

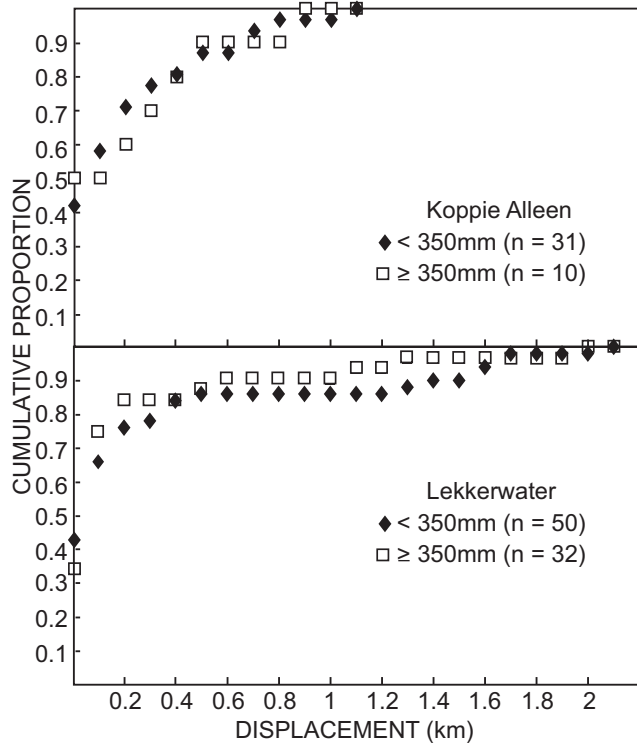


Figure 7: The cumulative proportion of recaptures taken at the Koppie Alleen and Lekkerwater release sites at increasing distances from the point of release for two size-classes

know the positions occupied by a single fish at three or more times in its life. Telemetry is most suitable for such an investigation, but, by chance, the tag study occasionally yielded fish that were recaptured more than once. The probability of a fish being recaptured n times should equal the recapture rate raised to the power of n . The second-recapture frequencies match this prediction (Table 3). Multiple recaptures were more frequent at the research sites, but elsewhere the recaptured fish were seldom returned alive, and if they were returned alive they were not reported as very few anglers carry pen and paper at the water's edge for the purpose of writing down tag codes.

The multiple recaptures provide perhaps the best evidence for site-fidelity and home-range behaviour. Most multiple recaptures were at the release site (Table 10). Many fish were encountered several times at the same site, with two

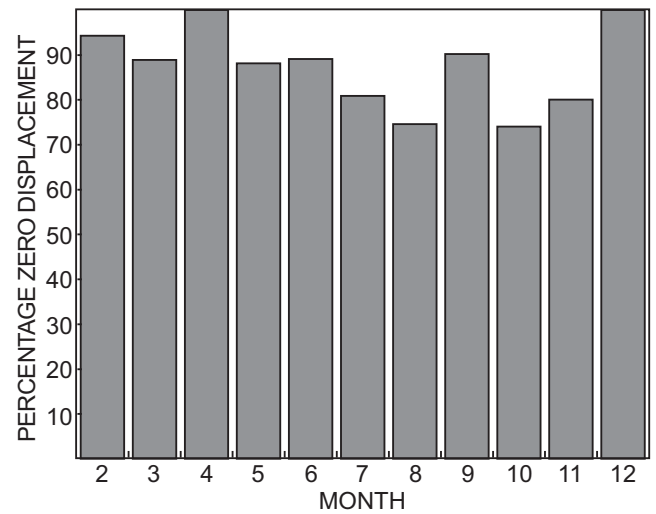


Figure 8: Percentage of recaptures that were taken at the release site by month. Only fish that were at liberty for <3 months were included in the analysis

Table 9: Parameters of total length distributions for recaptures that were taken at the release site, to the east and to the west, for three study sites. Displacements >2km were considered as non-zero. The results of one-way ANOVA are listed for each site. The Tsitsikamma data were omitted due to small sample size

Site	n	Range (mm)	Mean (mm)	SE (mm)	F	p
<i>Koppie Alleen</i>						
East	96	249–455	356.6	5.2	50.2	<0.01
Zero	811	239–588	329.7	2.2		
West	103	260–510	391.1	5.6		
<i>Lekkerwater</i>						
East	91	252–485	361.2	5.0	20.8	<0.01
Zero	899	240–556	343.5	1.8		
West	145	250–545	372.1	14.7		
<i>Cape Peninsula</i>						
East	64	277–513	331.0	4.1	2.3	>0.05
Zero	152	258–409	321.3	2.4		
West	12	288–365	324.3	6.6		

being caught seven times. The next most common patterns were those that included two identical sites, and a third distant site, once again suggesting a degree of site fidelity.

Clarification is required on the meaning of 'same site'. At the De Hoop sites, the 'same site' means anywhere within the 3.4km-long research site. The data shown in Figure 6, based on recaptures taken from 1998 onwards, suggest that most recaptures would have remained in a much smaller area. At Tsitsikamma and the Cape Peninsula, the 'same site' means within 200m. The A-B-B (Table 10) pattern indicates that the fish was caught once at the research site, and then twice at another site. In this case, the fish were reported as having been caught twice in the same area (i.e. with a common ORI locality code). This reporting system is in practice not accurate to within 1km – in some cases it may be out by as much as 5km. Whereas it is assumed, on the strength of the data from the research sites, that two recaptures of the same fish, both recorded against a common ORI locality code, were caught within a distance corresponding to a typical home range, this may not have been the case.

At both De Hoop sites, there was one record of a fish that moved and then returned to the site of original capture, and one fish that moved between three separate sites. These last two patterns were obviously biased against, because of the small probability that a fish caught outside of the release sites was both reported and returned to the sea alive. The best a researcher can hope for is to have a recapture reported, in which case the angler would normally have taken the fish home to report the tag.

Discussion

Tag-recapture data do not provide much information on fish movement behaviour. Each record gives two positions (rarely more than two) that a fish occupied at specific times in its life. The main problem with tag-recapture data is not knowing what the fish did between captures. Therefore, numerous records are needed to elucidate persistent patterns. Telemetry is a superior means of studying home-range behaviour, but not extensive movements. To follow a galjoen that does migrate would be very difficult, given the extent and pace of some movements. The most rapid displacement recorded was 83km in three days, and the actual movement could have been faster still! Acoustic reception in the high-energy surf zone may prove to be a further difficulty with telemetry in the case of galjoen. For these reasons, the movements of galjoen are most practically studied with the use of visible coded tags, each bearing a postal address.

Galjoen appear to be robust fish. They live in a turbulent environment and do not shed scales except during severe abrasion. They also remain calm when out of water, which facilitates tagging, but they return to the water with much vigour. This behaviour may be attributed to their habit of feeding in shallow water, which occasionally leaves them stranded between successive waves. Galjoen are probably adapted behaviourally and anatomically to short periods of exposure and tolerate handling better than most fish. These characteristics give the impression that post-tagging survival is high for galjoen. By contrast, other species are difficult to restrain when out of water, some shed scales easily and a few require a period of 'resuscitation' before they swim away. Nonetheless, tagging does affect the growth rate of galjoen, as it does for many other species (Attwood and Swart 2000). Other possible effects cannot be discounted.

The tag-recapture data from widely separated sites were remarkably consistent. In each case, the vast majority of galjoen were recaptured in the immediate vicinity of the release site. Those fish that were recaptured away from the release site provided evidence of extensive movements throughout the range. Given that some fish have been reported to move from Namibia to South Africa (Anon. 1984, but no evidence of the reverse movement), it is likely that the entire species is represented by one stock.

Galjoen probably spawn throughout their range. Bennett and Griffiths (1986) found ripe females between Cape Infanta and Lambert's Bay (Figure 1). The paucity of fish in the area between Lambert's Bay and Lüderitz, Namibia, is most likely attributable to the failure of eggs to hatch in these cold waters.

The most appealing means of explaining the recapture distribution is that galjoen follow a random-walk, and that their movements can be described by a modified diffusion model. This type of model has been widely applied to animal movement behaviours (Okubo 1980, Kareiva 1983), but it fails to explain an intriguing feature that recurs in all the galjoen datasets. The probability of a tagged fish being found at the release-site is less than one, but that probability does not decrease with time at liberty (Figure 5). This is a unique feature for which no analogue could be found in the literature on fish, or any other species. It suggests that galjoen may abandon their home ranges, but without a gradual 'leakage' of tagged galjoen from the release site.

A logical step was to search for some factor that differentiated those fish that had moved from those that were recaptured at the release site, but none could be found. There is no apparent differentiation on the basis of size, sex or season, notwithstanding the slight trend of larger fish to move more frequently (Table 9). All fish >470mm were

Table 10: The frequency of different patterns of multiple recapture records. Each letter refers to a capture event, e.g. A-A-A indicates that the fish was caught three times. Identical letters imply that the captures were made at the same site, and different letters at different sites

Site	A-A-A	A-A-B	A-B-B	A-B-A	A-B-C	A-A-A-A-.. up to 7
Koppie Alleen	65	4	5	1	1	29
Lekkerwater	46	13	4	1	1	11
Cape Peninsula	7	2	0	0	0	1
Tsitsikamma	2	0	0	0	0	0
Total	120	19	9	1	2	41

female (Bennett and Griffiths 1986) and fish of this size were recaptured both at the release sites, as well as away from them. Consequently, it is assumed that sex is not the differentiating factor. The ratios between those that were recaptured at the release sites and those that were not were very skewed, which also argues against a sexual distinction in movement behaviour.

Why was a minority of tagged fish caught outside the study sites? It is possible that the distinction between those that moved and those that were recaptured at the release site may be spurious, because some of those that were recaptured at the release site may have moved and returned during their time at liberty. Arguably, the most significant insight into their behaviour is the fact that galjoen hold home ranges, and any movement beyond home ranges should be regarded as infrequent deviations from this behaviour.

Home-range behaviour

There is clear evidence of site-fidelity and home-range behaviour among galjoen. The evidence is not direct, but rather statistical. When so many fish are each found to be in the same location at two randomly chosen times, then it can be inferred that they spend a lot of time at that location (Figures 4, 6). The multiple recapture patterns provide additional confirmation of home-range behaviour (Table 10). Even among those fish that did leave the release site, the most common pattern still included two captures at the same site. Some fish that appeared to have kept a home range (two captures in the same place) later abandoned it (a third captured elsewhere), or fish that moved from a site established a home-range elsewhere (two recaptures at a common, distant site).

Regarding home-range size, the four datasets were not in agreement. Recapture records from the two De Hoop sites pointed to larger home ranges than those from the other sites, irrespective of the estimation method used (Table 8). The De Hoop estimates also exceeded the predictions based on the allometric relationship presented by Kramer and Chapman (1999), whereas the Tsitsikamma estimates were consistent with these predictions. The Cape Peninsula estimates were smaller, but those data were disqualified, *a priori*, on account of the uneven recapture effort distribution, which served to underestimate home-range size.

Those studies that have focused intensively on short-term fish movements have shown that shallow-water species typically follow the same paths in their daily routine and spend disproportionate amounts of time in certain areas (Helfman *et al.* 1982, Ogden and Quinn 1984, Holland *et al.* 1993, 1996). Even within the home range, the use of resources is spatially structured. The same may be true of galjoen, because there was a high degree of central tendency in the displacement data, as confirmed by the fitted DGD model (which was leptokurtic), and the failures of the DFD and DND models (Figure 6). This leptokurtic distribution could not be explained on the basis of fish size (Figure 7), despite the fact that home range is in part a function of fish size (Kramer and Chapman 1999).

Galjoen generally do not show signs of being territorial, because many fish of all sizes are simultaneously encoun-

tered in very confined areas, and they are known to swim in shoals (Rust and Rust 2000). This interpretation is confirmed by the data, which showed that large fish move more frequently than small fish — the opposite of the pattern is found among territorial animals. Captive, ripe females display aggression towards other fish (CD van der Lingen, Marine and Coastal Management, pers. comm.), but this behaviour is linked to either spawning or captivity.

The larger De Hoop estimates of home-range size could be explained by the unstable habitat at those sites. The shifting sand dunes at De Hoop may cause fish to move their ranges either east or west over long periods of time. The Kramer and Chapman (1999) prediction was based on short-term observations in tropical waters, whereby the movements of fish were mapped by divers or by telemetry. In contrast, the tag-recapture study used displacements over long periods, often exceeding a year, to estimate home ranges. During such long periods home ranges may shift location slightly, thereby giving the impression of large home ranges, whereas fish use smaller areas in the short-term. If this is the case, then the home-range sizes for De Hoop presented in Table 8 are overestimated and the true home-range size here would be closer to the predictions in tropical waters.

Another aspect to consider is that the fish were caught with baited hooks, implying that they were encountered in the feeding part of range, and therefore the study may have failed to reveal any parts of the home range not associated with feeding behaviour.

Polymorphic model

The hypothesis developed by Attwood and Bennett (1994) that the galjoen population may be differentiated on the basis of movement behaviour, with a large part of the population being resident, while the remainder is nomadic, is still valid as a possible explanation of the recapture distribution. This is termed the *polymorphic* model and the results presented here do not contradict its predictions. Fish that display nomadic behaviour move continuously, such that, if one of them is tagged, it will depart the release site shortly. The polymorphic model therefore explains why the fraction of tagged fish found away from the release site is independent of time at liberty.

There are many examples throughout the animal kingdom of similar differentiations with respect to movement behaviour. These differences may be genetic or conditional on some environmental factor (Swingland 1984, Dingle 1996).

Tourist model

Another model could also explain the existence of 'migrants and non-migrants', but without invoking any differentiation within the stock. According to the *tourist* model, a term taken from Craig and Hulley (1994) who used it to describe sunbird movements, galjoen may simply be moving between two or a small number of sites, where they may establish home ranges. If tagged fish abandon home ranges regularly to visit other sites, from which they later return, then the relative frequency of 'zero displacements' will remain approximately constant over time at liberty, as was observed. The ratio of

'zero' to 'non-zero' displacements will be a reflection of the relative amount of time spent in the home range at the release site, as opposed to other sites, but will also be influenced by recovery effort. The tourist model predicts that fish will temporarily abandon the home range to feed elsewhere. The data dispel any suggestions that such movements may be linked to spawning (Figure 8, Table 9).

There are no clear analogues of the tourist model among fish, although it is appealing on the grounds of parsimony. Why invoke a split in the stock if another model can explain the data simply on the basis of time partitioning?

Comparison of the two models

The polymorphic and the tourist models are fundamentally different in terms of their ethological mechanisms, but they are very difficult to distinguish on the basis of the data presented here. Following Dingle's (1996) classification scheme, the behaviour of the movers should differ in terms of the two models. According to the polymorphic model, those fish that moved would be following a nomadic existence, continuously in search of new resources. According to the tourist model, the movers are migrants, abandoning their home range temporarily for an alternative site. As migrants, the tourist fish will move rapidly and directly to the new site, probably without feeding along the way. Records of very rapid movements, together with occasional records of galjoen taken in deep water by trawlers, suggest that migration is outside the surf zone, where they do not feed. (Of the 3 600 survey trawls undertaken by the research vessel *RV Africana* on the Agulhas Bank between 1982 and 1999, only two trawls captured galjoen, one off Danger Point and one off Mossel Bay.)

Telemetry data on galjoen are needed to effectively discriminate between these hypotheses, but their small size and turbulent environment preclude the use of archival tags and acoustic tracking methods. The tagging method used provides only two positions occupied by a fish at specific times in its life. Only occasionally are tagged fish re-caught more than once.

Of the multiple recaptures, only two fish were recaptured at three separate sites (A-B-C), whereas two moved and then returned to the original site (A-B-A, Table 10). Had there been a distinct bias in the relative frequencies of these patterns, it would have pointed to one model in favour of the other. Nonetheless, some of the multiple recaptures were difficult to reconcile with the polymorphic model (according to which fish are either resident or nomadic), which should result in a prevalence of the A-A-A and A-B-C patterns. Those fish that were captured three times with only two captures at the same site (i.e. A-A-B, A-B-B and A-B-A) indicated that a single fish could display both types of behaviour, i.e. resident behaviour followed by a migration or *vice versa*. Such an interpretation is not necessarily correct, because a truly nomadic fish could visit the same site twice, resulting in patterns that could be mistaken for site fidelity. However, the proportion of three-time captures that followed these patterns was reasonably high. There were 152 three-time captures in total, and the A-A-B, A-B-B and A-B-A patterns together accounted for 19% of these (Table 10). Of these three patterns, the recaptures taken outside of the

study sites (i.e. the Bs) accounted for 12.8% of the recapture events of the three-time captures. (There were 304 recaptures [152×2], the A-A-B pattern had 19 at B, the A-B-B had 18 at B and the A-B-A had two at B; therefore, $[19+18+2]/304 = 0.128$.) Based on the two-time-captured fish, which were far more numerous than the three-time captures, the percentage of recaptures taken outside the study site was 21% (Table 6). It follows therefore that the majority of fish that moved from the release sites displayed the A-A-B, A-B-B and A-B-A patterns (12.8% of 21%). The discrepancy between these percentages is likely because fish that were recaptured at B did not survive that capture, and hence could not be re-caught, thereby under-representing both the A-B-A and A-B-C patterns. The proportions of the different patterns indicate that even the majority of fish that move display resident behaviour at some stage, which is at odds with the polymorphic model.

The long distance movements of fish are almost certainly an adaptive strategy, because fish of all sizes abandoned the home range. If such movements were maladaptive, there would have been a prevalence of small fish moving most frequently, either because they could not maintain a home range (e.g. Pellett *et al.* 1998) or because they were sub-dominants (e.g. Nakano 1995). The trend of larger galjoen moving more frequently is perhaps a reflection of the reduced cost of movement with increasing size. It may also indicate that fish with greater knowledge of their environment (age = experience) are likely to move more regularly because they have more options.

The distinction between the models is not merely of academic interest — it will have important implications for fisheries management. Mixed evolutionary stable strategies explain the persistence of two (or more) genetically based behavioural patterns within a population, if the selective advantage of each is frequency-dependent (Swingland 1984). If the polymorphic model has a genetic basis, then the resident morph will be selected against outside of refugia, whereas the nomadic morph will be selected against inside refugia. Is the higher proportion of migrants from the Cape Peninsula, the only exploited site under study, an indication of such an effect? Approximately 5% of the fish tagged at the protected sites moved, whereas the fraction in the Cape Peninsula sample was 17%. This discrepancy is more easily explained by the polymorphic model than the tourist model.

In terms of the polymorphic model, a conditional response, for example, to deteriorating feeding conditions, is unlikely. If fish abandon a home range because of a conditional response that may occur at any time, then the relative frequency of 'zero displacements' should gradually decrease with time at liberty. Such a decrease was not observed. It could be argued that some factor could condition fish early in life (i.e. before the age at which they were tagged) to either a nomadic or a resident existence, but it is not clear what such a factor might be.

For supporters of the use of refugia for fisheries management, the tourist model is more promising. Tourists will be protected in a refuge, but will occasionally leave and become available for capture elsewhere. The large ratio of 'zero to non-zero' displacements suggests that such exchange will not 'drain' the protected stock, whereas it may provide modest replenishments of adult fish to exploited

areas, in addition to any additional supply of recruitment.

Dispersal, relative to within-patch movements, is an understudied process (Travis and French 2000). The factors that cause animals to move, which determine the distance they move, and the site that they eventually choose remain elusive. Among trout, which is generally considered to be resident species, it has been found that they occasionally and unpredictably undertake large migrations (Gowan and Faush 1996). Such movement may be an attempt by the fish to escape unfavourable conditions or reconnoitre their environment for the purpose of selecting new sites (Railsback *et al.* 1999).

Travis and French (2000) argue that most spatial models that incorporate animal movement are 'generally misleading', because they treat animal dispersal simplistically. Dispersal is usually modelled as either a move to a neighbouring patch, or a 'global' move that could take it to any patch (e.g. Fryxell and Lundberg 1993). In reality, animal dispersal lies between these extremes, tempered by such factors as density, cost of movement, and familiarity with the environment. For galjoen, the distribution of distance moved, although very wide and occupying almost the entire range, is strongly leptokurtic. It is clear that 'spill-over' (Russ and Alcalá 1996, Jennings 2001) takes place among galjoen, but it is not a local phenomenon, detectable at reserve boundaries by a linefishery, because migrants do not feed *en route* (Dingle 1996). (In contrast, a gill-net fishery would catch migrants at the reserve boundary.) Those that abandon the home range move widely, so that if a fishery enhancement occurs immediately adjacent to a marine protected area, the mechanism is more likely to be larval dispersal than adult movement.

This interpretation is not at odds with the situation described by Alcalá and Russ (1990) at Sumilon Island. They found that fish yields on the coral atoll were enhanced by the proximity of a small reserve, which they ascribe to adult fish moving ('migrating', by their terminology) from the protected area to the fished area. Because of the small areas involved (the size of the reserve was 0.5km²), these fish movements were most likely not migrations or ranging movements, but rather movements within a home range that straddled the reserve boundaries.

Divers report a variety of behavioural types with regard to shoaling and aggregation of galjoen (Rust and Rust 2000). Large shoals of similar-sized fish are usually encountered outside of the surf zone on shallow reefs and particularly on wrecks. These fish do not appear to be feeding. In the surf zone, galjoen of all sizes may aggregate in large feeding shoals, or they may be encountered in small groups of <10 individuals. Galjoen travel in schools, and may suddenly 'appear' in an area in large numbers. Shoaling behaviour could be explained by the polymorphic or the tourist model.

Home-range behaviour is very common among reef fish, and indeed among fish from all habitats. Gerkin (1959) listed 34 examples of fish that display resident behaviour. Studies of departures from the home range, despite being a common behaviour, have been very few, largely because of the difficulty of studying fish movement intensively (to establish the home-range pattern) and extensively (to follow large-scale movements). The swallowtail dart *Trachinotus botla* shows an over-dispersed spatial recapture distribution

(McPhee *et al.* 1999). Like galjoen, there is a trend of large fish moving more frequently; but unlike galjoen, the mean displacement distance was positively correlated with time at liberty. Movements of swallowtail dart are more reminiscent of ranging behaviour, whereby each fish has the potential to move widely. However, there was no evidence to suggest that swallowtail dart return to home ranges, or that they hold home ranges at all. The sablefish *Anoplopoma fimbria* shows the same pattern, but on a much larger scale, with some movements exceeding 2 000km (Beamish and McFarlane 1988). There is also no indication that sablefish hold home ranges.

Off New Zealand, the hapuku *Polyprion oxygeneios* displays a mix of station-keeping, ranging and spawning migrations (Beentjes and Francis 1999). Some fish moved widely, and others were caught in exactly the same place over a period of five years. Other examples of populations that include an apparent mix of strategies were described by Morrisey and Gruber (1993), Sheaves (1993), Holland *et al.* (1996) and Pellett *et al.* (1998). The galjoen recapture pattern therefore is not unusual. Many fish species display a curious mix of station-keeping and migration or ranging, but for most there has not been much interest in the pattern, or any explanation why fish should abandon a home range. It may be necessary to concede a substantial degree of plasticity in movement behaviour of fish.

Theoretical considerations

Are there any theoretical considerations that might point to one model instead of the other? Cury's (1994) discussion of obstinate behaviour argues strongly for site fidelity, particularly when it comes to spawning. The most successful strategy in the face of environmental uncertainty is simply to use the same area as your parents, who must have bred successfully. Cury (1994) does point to the occasional strays that 'are essential for long-term dynamics by exploring and fixing new environmental solutions that later become possible for the species'. By this the author implies that straying is adaptive. These arguments, and others along those lines, might be interpreted to favour the polymorphic model.

Another hypothesis is the ideal-free distribution, which states that animals will be distributed in such a manner that each individual experiences the same food availability. The model predicts that the distribution of animals will match the distribution of food. The process of distribution can include active movement, or selective mortality and reproduction rates that ultimately lead to different densities in different areas. MacCall (1990) developed a fish movement model on the assumptions of the ideal-free distribution. That model predicted a gradual diffusion away from highly productive areas, due to larval drift, and a subsequent return towards productive areas by adults. Whether or not such a process occurs among galjoen cannot be established, largely because of the difficulty of determining where the productive areas are, other than by measuring adult density. Galjoen may frequently abandon home ranges to sample areas elsewhere, and in that way routinely establish if their home ranges offer the best feeding environment. Such a pattern is consistent with the tourist model. Travis and French (2000) term this 'intelligent-dispersal'. Some form of reconnaissance

and information sharing between fish will make such migrations less risky.

Chitty's model (Krebs *et al.* 1973), which was based on voles, predicts that cycles of population abundance are caused by density-dependent changes in the selection of behaviour. High densities favour aggression and migration, whereas low densities favour high reproductive potential and resident behaviour. Chitty's hypothesis has a direct bearing on a common debate on the effect of marine protected areas in fisheries. If fish reach carrying capacity in a refuge, will there be a greater tendency for emigration? In other words, is the frequency of movement density-dependent? Fish may leave the home range more frequently if density or intra-specific competition for resources is high. Not all observations of density-dependent migration support such a model (Travis and French 2000). Galjoen appeared to have the greatest frequency of residency in protected areas, where density was greatest (Attwood 2003), whereas those at the exploited site showed the greatest frequency of movement. There is no evidence that increased galjoen density promoted dispersal of the adult stages. Doherty and Williams (1988) found little evidence for resource saturation among natural populations of coral reef-fish. The concept of local adult 'spill-over' from populations near carrying capacity in protected areas has little supporting evidence.

The choice of model is not made easier by the fact that they are not mutually exclusive. Many fish may remain resident their entire lives, whereas others display tourist-type behaviour. At this stage, both models are regarded as possibilities, but the investigation will be pursued by way of an individual-based model that can simulate the frequencies of recapture patterns for comparison.

Conclusions

Galjoen are principally resident fish with no set migration routes. They breed throughout their range, but the low survivorship of eggs below 15°C is likely to be the cause of the paucity of galjoen in the strong upwelling area between South Africa and Namibia. Egg dispersal is unlikely to be widespread in view of the fact that neither galjoen eggs nor larvae have ever been sampled, despite extensive surveys that have detected eggs and larvae of hundreds of other species within the range occupied by galjoen (Buxton and Smale 1984, Beckley 1986, 1993, Tilney *et al.* 1996). There is sufficient evidence of long-range adult movement to suggest that the Namibian and South African stocks are part of the same population.

The size of the home range is possibly larger than the allometric prediction of Kramer and Chapman (1999) based on an analysis of tropical reef fish. The difference may be attributable to home-range shifts forced by local physical conditions at De Hoop, or because of differences in the way that the home range was estimated.

Whether all fish follow the same strategy, which entails visiting a small number of sites, or whether a small fraction of the stock display a distinct nomadic type behaviour, while the remainder hold home ranges, is unclear. An examination of the relative frequencies of multiple recapture patterns suggested that individual fish may display resident and migratory behaviour, but the evidence is far from conclusive.

A careful consideration of fitness-enhancing, fish-movement rules, such as that undertaken by Railsback *et al.* (1999) for stream fish, may be necessary to resolve this issue.

Fish movement behaviour will have consequences for fisheries management. The stock is obviously not well mixed on the short time-scales that are relevant to fisheries management, which implies that the galjoen stock should be assessed at lightly and heavily exploited areas. Galjoen found in unexploited areas will be predominantly resident, whereas those found in heavily exploited areas will be either nomadic or recent arrivals. The fact that large fish move more frequently suggests that catch-at-size distributions derived from fishery data in areas where there has been a recruitment failure will be positively skewed because of the scarcity of young fish, compared with old fish that are replenished from elsewhere. Such a bias in catch-at-age analyses could have serious consequences for stock assessment.

The results obtained by this study indicate that any model of galjoen movement that is based on diffusion or constant transfer rates, as has been commonly applied to other species (see generic model of Hilborn 1990), will provide erroneous results. This conclusion is shared by Travis and French (2000). Galjoen movements are clearly structured, and any model that successfully reproduces observed patterns will have to account for individual variability and behavioural plasticity.

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