

DYNAMICS OF THE FISHERY FOR GALJOEN *DICHISTIUS CAPENSIS*, WITH AN ASSESSMENT OF MONITORING METHODS

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The dynamics of the fishery for galjoen *Dichistius capensis* were investigated at four sites in South Africa from 1987 to 2000. At three sites, which were protected from fishing, Koppie Alleen, Lekkerwater (both in the De Hoop Marine Protected Area) and Tsitsikamma National Park, fishery-independent surveys were conducted. Data for the Cape Peninsula (the fourth site) were obtained from records kept by a recreational angler. Catch per unit effort (*cpue*) was highest at De Hoop and lowest at Tsitsikamma. At De Hoop, *cpue* varied significantly among anglers, months, years and gear type. The mortality rate was greater at the exploited site than at protected sites, where mortality rates were taken as estimates of natural mortality. Tag and recovery data were used to estimate density and catchability. Fishing mortality rates were very high, whether inferred from size distributions or from the product of effort counts and the catchability coefficient. Such high rates can be sustained only through refuges. Variation in fishery parameters among habitats and the high variance in *cpue* data suggest that an effective monitoring programme will need to be intensive. To provide adequate stock assessments, fishery-dependent surveys should be augmented by studies in marine protected areas.

Key words: *cpue*, *Dichistius capensis*, fishery dynamics, monitoring methods, mortality rate, South Africa

Like so many of South Africa's linefish species, the galjoen *Dichistius capensis* has been heavily exploited. Prior to World War II it was reported that its numbers were in decline in certain areas (Smith 1935). By 1973, galjoen were considered to be in serious trouble and a size limit was introduced. In 1984, the restrictions were revised again, to further curb fishing mortality by adding a closed season and a bag limit. The first study of galjoen was undertaken by Bennett and Griffiths (1986) who worded their assessment of the stock carefully: "Hard evidence to substantiate the contention that the numbers of galjoen are decreasing is difficult to find, ..."

Hard evidence is unnecessary for experienced fishers – they know that the resource is severely depleted. A recent compilation of articles and quotes about galjoen (Rust and Rust 2000) leaves no doubt that what was once an abundant species is now comparatively scarce. Bennett and Griffiths (1986) were referring to the frustration of not having accurate catch statistics to measure the decline in abundance. The only means of assessment was a per-recruit analysis, which Bennett (1988) based on the female stock. Only 16% of the original spawner-biomass-per-recruit remained. That classifies galjoen as a collapsed fishery (Griffiths 1997).

Management of the galjoen fishery, and that of most other South African linefish, is far from satisfactory. Since the 1973 regulations were promulgated, there has been no attempt to ascertain whether they have been

successful in recovering the stock. The need to monitor the stock on a regular basis is now being addressed in a nationwide programme to improve linefish management (Griffiths 1997). However, the design of an effective monitoring strategy will depend on a better understanding of galjoen fishery dynamics than available at present. In particular, it is crucial to how much monitoring is required to estimate the chosen indicators with sufficient accuracy to be useful for assessment. The error in the indicator sets the limit for detection of change.

Most assessments of South African linefish stocks have been based on per-recruit models, but these give no indication in absolute numbers of population size or density, or the level of depletion attributable to fishing. Another difficulty with per-recruit calculations is the estimation of the natural mortality rate. In South Africa, catch-at-age data are used to estimate the total mortality rate, from which the rate of natural mortality is subtracted, leaving a remainder that is attributed to fishing. In Bennett's (1988) galjoen assessment, natural mortality was derived from a statistical analysis of natural mortality rates and water temperature combinations across many species. Although these two variables are positively related, there is considerable scatter about the regression, which clearly calls for an alternative assessment of the natural mortality rate.

In theory, because galjoen are largely resident, mortality rates and catch per unit effort rates (*cpue*) should vary between protected and exploited areas. This study

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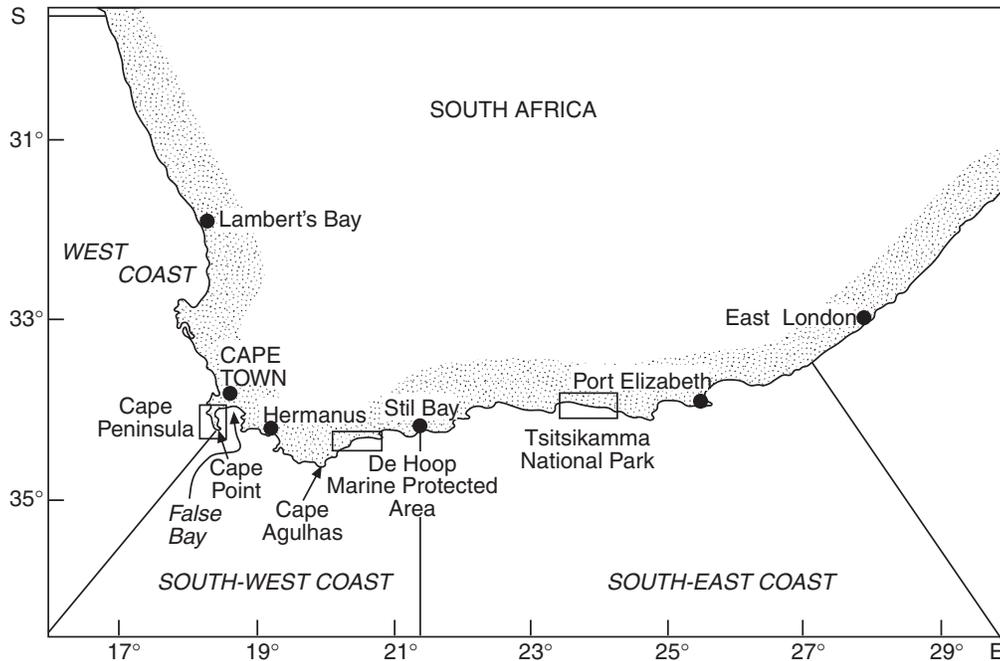


Fig. 1: Map of South Africa showing the location of the sampling sites and places mentioned in the text

compares data from fishery-independent surveys undertaken in three protected areas and one exploited area to provide a fresh analysis of the impact of fishing on the stock. The surveys made use of tag-and-recovery data, which presented the opportunity to estimate population density and catchability. The assessments are then used as a basis to plan a monitoring programme.

MATERIAL AND METHODS

Study areas

DE HOOP MARINE PROTECTED AREA

De Hoop is centrally situated along the warm temperate South Coast (Fig. 1). The 51-km marine protected area (MPA) was proclaimed in 1984 and took effect from 1985, excluding all forms of fishing within a distance of three nautical miles from the shore. Fish were sampled in the MPA at two 3.4 km-long sites, Koppie Alleen (34°28.65'S, 20°30.70'E) and Lekkerwater (34°26.92'S, 20°39.15'E), which are 11 km apart.

At De Hoop, sea temperatures range between 12 and 20°C.

At both sites, the shore is a mixture of exposed sandy beach and aeolianite rock platforms, or fossil dunes. These platforms have been eroded, leaving a mosaic of reef in the surf zone. The reefs are exclusively at depths <6 m and are all within the surf zone, which extends out 200 m from the shore. Strong winds and high wave exposure cause the sand to be extremely mobile, covering and uncovering reefs on spatial scales of metres to hundreds of metres, and on temporal scales from hours to years. The beach at Koppie Alleen is a shifting dune system, in which sand is clearly transported back and forth between the land and the sea over great distances. The dunes there are sparsely vegetated. At Lekkerwater, the dunes have more vegetation, but they are nonetheless unstable. The most notable qualitative difference between the sites is that the western two-thirds of the Koppie Alleen site has few reefs and constitutes a high-energy sandy beach that extends a further 15 km westwards beyond the site.

The two sites have different exploitation histories. Prior to 1984, Koppie Alleen was heavily exploited

by recreational anglers. Lekkerwater, where the shore was once privately owned, was lightly exploited. It was estimated that, prior to 1984, the Koppie Alleen site was fished for some 31 000 angler-hours per year, whereas the effort at Lekkerwater was only 3% of this estimate (Bennett and Attwood 1991). By 1991, the Koppie Alleen population recovered to a density that was indistinguishable on the basis of fishery-independent *cpue* from that at Lekkerwater (Bennett and Attwood 1991).

TSITSIKAMMA NATIONAL PARK

Tsitsikamma is the easternmost of the three research sites (Fig. 1). The shore there is made of steep sandstone headlands that are exposed to strong seas. Pocket beaches are rare, but sand does fill the bottom of many subtidal gulleys. Water temperatures are warmer than at the other sites, but less stable (range 10–24°C). Upwelling frequently causes sea surface temperature to drop sharply over a few hours. These events mask a small seasonal trend in temperature (Tilney *et al.* 1996).

Tsitsikamma was declared a National Park in 1964, when it became one of the largest “no-take” marine protected areas in the world. The 58-km coastline was protected from shore-angling, with the exception of a 3-km stretch of coast in the centre, which was kept open for visitors who stay at the only lodge in the entire Park. (This concession was abolished in 2001). Apart from being restricted by law, access to the remaining areas is physically demanding, involving an approximate 180 m cliff descent. Despite these challenges, poaching has been a problem at times. Nonetheless, fishing effort must be very low, when considering the inaccessible nature of the coast and that regular law enforcement patrols seldom encounter poachers (J. Allen, Tsitsikamma National Park, pers. comm.).

The research site lies on the western side of Tsitsikamma and is split into four areas, namely Lotterings River Mouth, Bloukrans River Mouth, Clintons Bank and Klip River Mouth. The last three areas form a continuous stretch of coast, whereas Lottering is separated from them by a 3-km stretch of inaccessible coast. In total, the areas cover about 4 km of coastline.

CAPE PENINSULA

The Cape Peninsula (34°20'S, 18°24'E) marks the border between the warm-temperate and cool-temperate zones (Fig. 1). The western shore of the peninsula is exposed, whereas the eastern shore ranges from low to moderate exposure. Sea surface temperature

varies greatly across the Peninsula, being influenced by cool upwelling on the western side (temperature range 9–16°C) and sun-warmed water on the False Bay side (temperature range 12–20°C). The shores on both sides are formed by quartzitic sandstone rocks and platforms, interspersed with small pocket beaches and boulder beaches. The inshore reefs support kelp forests that form extensive canopies from the low-tide mark to 15-m depth contour. Heavy kelp wracks fuel a rich decomposer community in the intertidal zone. The physical habitat is fairly stable there by comparison with De Hoop, with only small changes caused by sand movements.

Parts of the western and eastern shore of the peninsula are marine protected areas, but all fishing was undertaken in areas that are exploited by recreational shore-anglers, and to a lesser extent by spearfishers. Access to the southernmost part of the peninsula is controlled by permit. Permit sales indicate that there were, on average, 2 800 visits by galjoen anglers to this area annually (Q. Vaughan, Cape Peninsula National Park, pers. comm.). This amounts to approximately 12 anglers day⁻¹ over the 7.5 month season. There is approximately 10 km of fishable coastline in this area, which gives a rough effort estimate of 1.2 anglers km⁻¹ day⁻¹.

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 4 or 5 days each. Prior to 1987, 959 galjoen were killed for a biological study (Bennett 1988). From 1987, all fish were tagged and returned to the sea, and trips alternated between Koppie Alleen and Lekkerwater. From 1995, trips were reduced to six per year (three at each site), each lasting five days (Table I).

A small number of volunteer anglers assisted the author 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 (Table I), most effort was accounted for by only eight anglers.

On each day of each trip anglers fished continuously, starting usually an hour after sunrise and finishing at

Table I: Details of fishing trips for the four study sites. Note that only one angler fished at the Cape Peninsula

Year	Number of trips			Days fished
	Koppie Alleen	Lekker-water	Tsitsi-kamma	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	

sunset. The number of hours fished per angler was recorded. Apart from a reduction of the number of trips in 1994, sampling trips were undertaken in the same months of each year.

Prior to 1995, the anglers kept to a single standard technique. They used 3–4 m fishing rods, with multiplier reels loaded with 10–15 kg breaking strain nylon fishing line. Lead sinkers weighing between 100 and 150 g were used to cast bait on or near reefs in broken surf. The bait was limited to white mussels *Donax serra*, red-bait *Pyura stolonifera* and wonderworm *Marphysa* sp. Mustad 92570 hooks were used, ranging in size from #1 to #2/0. This technique, which targeted small epilithic feeders, was called the small-fish technique or SFT.

From 1995, a second fishing technique was introduced to target larger piscivorous fish, for which additional information was needed. Heavier tackle was used: sinkers weighed between 150 and 200 g, hook size varied from #3/0 to #10/0 and bait included bloodworm *Arenicola loveni*, sardine *Sardinops sagax* and chokka squid *Loligo vulgaris reynaudii*. These baits were cast out into deep, unbroken surf, where the larger species were encountered more frequently. This technique was referred to as the big-fish technique or BFT. Anglers were instructed to use one or the other technique, which was recorded against that angler's catch. Both techniques caught galjoen, although galjoen were not a target of the BFT.

A third technique that was introduced to target elasmobranch species never caught galjoen and therefore does not contribute to this study. The combination of the three techniques covers the complete spectrum

of methods used by shore-anglers in the Western and Eastern Cape. Spear-fishing is the only other technique that is used to catch galjoen legally, although there are reliable reports of localized illegal gill-net fishing for galjoen (Hutchings 2000).

All fish caught were measured to the nearest millimetre total length. Galjoen were tagged if they were >250 mm, using plastic dart tags 89 mm long and 1.4 mm diameter (manufactured by Hallprint, Australia). Inscribed on each tag was a unique alphanumeric code and the return 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, but these were replaced by rigid measuring-boards. In later years, 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 was 3.2 mm 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.

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 Moçambique 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 tag findings was never reported. Lamberth (1997) estimated that 58% of recaptured fish were reported. Obviously, those recaptured at the protected research sites were all recorded.

From 1998 onwards, both De Hoop 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 percentage of galjoen 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 in 1995, based on

Table II: Definitions and their units of mathematical symbols used in text

Symbol	Definition	Unit
C_i	i^{th} record of the number of fish caught by one angler in one day	Fish
E_i	i^{th} record of the number of hours fished by one angler in one day	Hour
$C_{a,k}$	Number of fish caught at site a , during trip k	Fish
$T_{a,k}$	Number of fish tagged at site a , during trip k	Fish
$R_{a,k}$	Number of fish recaptured at site a , during trip k	Fish
$S_{a,k}$	Number of tagged fish still at large at site a , during trip k	Fish
$N_{a,k}$	Number of fish at site a , during trip k	Fish
H_k	Total effort applied during trip k	Hour
n_{ik}	Number of times fish i was recaptured during trip k	Captures
t_k	Date in the middle of trip k	Julian day
L_i	Total length of fish i	mm
F	Instantaneous per capita fishing mortality rate	year ⁻¹
M	Instantaneous per capita natural mortality rate	year ⁻¹
Z	Instantaneous per capita total mortality rate	year ⁻¹
β	Instantaneous per capita tag-mortality rate	year ⁻¹
θ	Migrating fraction	Ratio
q	Catchability	km h ⁻¹
r	Recatchability	Captures h ⁻¹
ω	Proportion of male fish at recruitment	Ratio

a similar design to the De Hoop programme (Table I). Fishing trips were scheduled monthly or bimonthly. A small number of volunteer anglers assisted a scientist from the Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown. Fish were caught and tagged in the same way as at De Hoop. 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. All fishing spots were named and identified on a 1:10 000 orthophoto chart so that distances could be calculated accurately.

Fish were caught, tagged and released using the SFT as described for De Hoop. In all important respects the data capture system was the same as that used at De Hoop.

CAPE PENINSULA

The Cape Peninsula data did not result from a designed experiment. One of the anglers who participated in the tagging studies at De Hoop also fished regularly in this region. The fish were caught, tagged and recorded in the same way as described for De Hoop. Fishing days were randomly distributed throughout the 7.5 month recreational season. 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 I).

Fish were caught, tagged and released using the SFT as described for De Hoop. In all important respects the data capture system was same as that used at De Hoop.

Statistical methods

Symbols routinely used in text are explained with a listing of their units in Table II.

GENERALIZED LINEAR MODELLING OF CPUE AT DE HOOP

Cpue rates are frequently used as a relative measure of fish density, but they are likely to be influenced by a number of factors other than fish density. Ideally, the influences need to be factored out before *cpue* is used as an indicator of density between years and months. To examine the extent of the influences, a log-linear model was used to model the effect of angler, month and year, and the interactions between them, on the *cpue* rates. This exercise was performed on the De Hoop surveys only, for the following reasons: (i) *cpue* was very low and insufficient effort was applied at Tsitsikamma to get meaningful results; (ii) at the Cape Peninsula, only one angler and one fishing technique was used, and the *cpue* was strongly affected by the fishery at that site.

Catch rate was expressed as a discrete count, C_i (number of fish caught by an angler during one day), for which the errors were assumed to be Poisson-distributed (McCullagh and Nelder 1989). The model with a log-link expected value was

$$\begin{aligned} \log(C_i) + \text{error}_i &= \log(\lambda_{amys}) \\ &= \mu + \mu_a + \mu_m + \mu_y + \mu_s \\ &\quad + \mu_{(m*y)} + \mu_{(a*s)} + \log(E_i), \quad (1) \end{aligned}$$

where λ_{amys} is the predicted catch rate, μ the overall mean, and $\mu_{\#}$ are the factors for which the subscripts $\# = a, m, y$ and s refer to angler, month, year and technique (SFT or BFT) respectively.

Cpue records from the two De Hoop sites were modelled separately, for the years 1993–1999 (consistent use of anglers was made during this period). Although it was possible to lump the two datasets and then add *area* as another explanatory variable, the *month* and *area* factors would have been confused because different months were sampled in different areas according to a schedule that did not change between years. Two interaction terms were deemed meaningful as explanatory variables, namely [*month* × *year*], which accounts for variability at the trip level, and [*angler* × *technique*], which accounts for variability associated with the individual angler's use of different gear types. Catch was assumed to be proportional to effort, measured in hours.

The GLM model was fitted using the SAS (Version 6.12) macro GENMOD (SAS Institute Inc. 1993), to minimize the deviance, which is twice the difference between the maximum attainable log-likelihood and the log-likelihood of the model under consideration.

The variance equation was adjusted by a factor related to the deviance (GENMOD DSCALE option) to allow for an error distribution that was over-dispersed with respect to the Poisson distribution. Over-dispersion could indicate an inappropriate choice of model. In this case, over-dispersion was expected, given a large daily variation in catch rates that was more likely to reflect changes in feeding conditions of the fish than changes in local fish abundance or angler performance. The over-dispersion factor does not affect the parameter estimates, only the associated errors and significance tests.

The GENMOD TYPE 1 ANALYSIS was used to test the significance of each of the terms in Equation 1. It starts by fitting the most basic version of Equation 1, i.e. $\log(C_i) + error_i = \mu$, for which it calculates the deviance. It then progressively adds the remaining terms, each time calculating the deviance and testing whether the additional term provided a significant improvement in the explanation of the variance about C_i . To do so it uses the *F*-statistic, calculated from the difference in the deviance caused by the additional term. A large *F*-statistic translates into a small probability that the reduction of the deviance was due to chance. If that probability was <5%, then the term was regarded as significant.

MORTALITY RATE

Mortality rates of exploited fish can be calculated from

the declining frequency of catch-at-age (Butterworth *et al.* 1989), but it requires converting catch-at-size to catch-at-age data. This procedure is difficult to apply to galjoen, because the males and females grow at different rates (Bennett and Griffiths 1986). Fish sex was not determined at any of the sites during the tagging experiment because galjoen sex cannot be identified without killing the fish. Using blood samples, Van der Lingen (1990) was able to identify the sex of most mature females for a few months prior to and during the breeding season, but the sex of immature fish and fish outside the breeding season could not be determined in this manner.

In theory, given that males and females grow at different rates, a large enough random sample of fish lengths should hold information about the total mortality rate and the relative proportion of each sex. A likelihood function was developed to estimate both these parameters from catch-at-length data. The method assumes that recruitment is constant.

If the numbers-at-age are exponentially distributed, then the probability (p) of selecting a fish of age t is

$$p(t) = Ze^{-Zt} \quad (2)$$

and the probability of selecting a fish of length L is

$$p(L) = Ze^{-Zt(L)} \partial t / \partial L \quad , \quad (3)$$

where $t(L)$ is the age of a length L fish and $\partial t / \partial L$ is the rate of change of age with length. A galjoen of length L could be either age $t_m(L)$ or $t_f(L)$, depending on its sex. These deterministic age-length functions are given by Bennett and Griffiths (1986). The probability of drawing a galjoen of length L that is either male ω or female $(1-\omega)$ from a population that experiences a constant mortality rate Z can be formulated as follows:

$$p(L_i) = \omega Ze^{-Zt_m(L_i)} \partial t_m / \partial L + (1-\omega) Ze^{-Zt_f(L_i)} \partial t_f / \partial L \quad . \quad (4)$$

In Equation 4, ω is the proportion of newborn fish that are male.

However, the full size range of fish is never available from any one sampling technique. In the case of angling, the sample is truncated, eliminating all $L < 325$ mm, which is approximately the size at full selectivity, i.e. the length category with the highest frequency in the catch. To account for truncation, Equation 4 was modified as follows:

$$p(L_i) = \omega Ze^{-Z(t_m(L_i) - t_m(325))} \partial t_m / \partial L + (1-\omega) Ze^{-Z(t_f(L_i) - t_f(325))} \partial t_f / \partial L \quad . \quad (5)$$

In Equation 5, ω is the proportion of males at recruit-

ment ($L = 325$ mm). If a fish exceeded the maximum length for a male galjoen, then the first term in Equation 5 was dropped. Given the vector of catch-at-lengths L , the maximum likelihood estimates of Z and ω were obtained by minimizing the negative log-likelihood:

$$LLH(L | Z, \omega) = -\sum_i \ln p(L_i) \quad (6)$$

The asymptotic variance-covariance matrix was computed from the inverse of the Hessian (a matrix of second partial derivatives of the likelihood along the Z and ω axes evaluated at the maximum likelihood estimate), which provided estimates of the variance and covariance of the parameter estimates (Lebreton *et al.* 1992). The first and second derivatives were calculated using a fourth-order, finite-difference method. The square-roots of the second derivatives yielded the standard errors.

The confidence intervals on these estimates were also calculated using the likelihood profiling method, which is regarded as more accurate for parameters that occur near a natural boundary (e.g. zero; Lebreton *et al.* 1992).

To test the estimation procedure, a random number generator was used to produce synthetic datasets of catch-at-length, using different combinations of Z and ω values. The sex of each artificial fish was determined randomly (with mean ω), and its lifespan was drawn randomly from a negative exponential distribution (with slope $-Z$). Bennett and Griffith's (1986) age-length functions were used to convert age to length. Datasets of two sizes were generated for a variety of sex

ratios and mortality rates, and the estimator (Equation 6) was tested once on each dataset. The estimates were compared with the Z and ω used to generate the datasets.

For sample sizes of 10^3 and 10^4 , the 95% confidence intervals (calculated by the likelihood profile method) included the true values for each simulation (Table III). However, length data hold little information on sex ratio, particularly for high mortality rates. High mortality rates reduce the number of old fish, whose lengths carry most of the sex information. (The size difference between sexes increases with age.) As a result, the confidence intervals on ω estimates were considerably narrower for small values of Z . Because there was covariance between the two parameters, the same was true of the confidence intervals about the Z estimates. The second partial derivative of the likelihood surface ($\partial^2 LLH^2 / \partial Z \partial \omega$) was always strongly negative, which indicates that estimates of Z and ω are negatively correlated, i.e. an underestimate of ω would be accompanied by an overestimate of Z .

A similar procedure was used to investigate the dependence of standard errors on sample size. Datasets of various size were generated for two parameter sets, namely $\{\omega = 0.5; Z = 0.4 \text{ year}^{-1}\}$ and $\{\omega = 0.5; Z = 2.0 \text{ year}^{-1}\}$. Standard errors decrease abruptly with an increase in sample size initially, but gradually flatten out at a sample size of about 8 000 (Fig. 2).

TAG MORTALITY RATE

The rate at which tagged fish are lost is the sum of the rates of natural mortality, fishing mortality, tag-induced mortality and tag shedding. From tag-recapture data

Table III: Results of trials of the mortality rate estimation procedure with simulated datasets of two sizes. True values of the male proportion (ω) and mortality rate (Z) are given. The lower (L) and upper (U) 95% confidence limits are listed for each trial

True value		Trials with $n = 1\ 000$				Trials with $n = 10\ 000$			
ω	Z	ω		Z		ω		Z	
		L	U	L	U	L	U	L	U
0.25	0.2	0.08	0.29	0.19	0.26	0.21	0.31	0.18	0.21
0.25	0.4	0.15	0.48	0.32	0.43	0.00	0.45	0.34	0.46
0.25	0.6	0.0	0.31	0.56	0.70	0.00	0.38	0.55	0.66
0.25	0.8	0.0	0.57	0.73	0.98	0.00	0.65	0.66	0.91
0.50	0.2	0.47	0.65	0.18	0.23	0.46	0.55	0.19	0.22
0.50	0.4	0.28	0.60	0.37	0.47	0.39	0.60	0.37	0.43
0.50	0.6	0.39	0.76	0.49	0.63	0.28	0.65	0.55	0.68
0.50	0.8	0.0	0.85	0.63	1.04	0.14	0.64	0.74	0.91
0.75	0.2	0.72	0.82	0.17	0.20	0.72	0.80	0.18	0.21
0.75	0.4	0.61	0.82	0.37	0.44	0.69	0.80	0.38	0.43
0.75	0.6	0.37	0.82	0.55	0.72	0.69	0.82	0.56	0.62
0.75	0.8	0.39	0.92	0.70	0.94	0.46	0.88	0.75	0.92

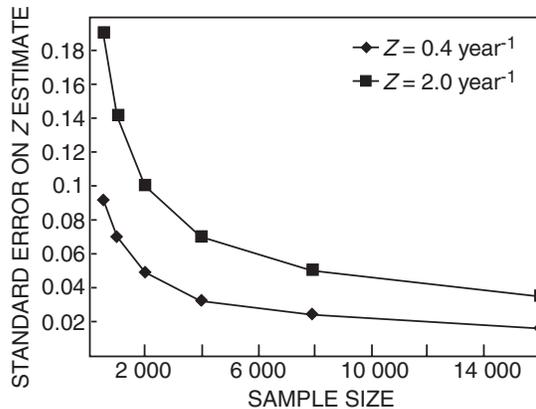


Fig. 2: Relationship between the standard error of the estimate of mortality (Z) for galjoen based on catch-at-age data and sample size

alone it is not possible to estimate the relative contributions of these processes, unless a double tagging procedure is used to quantify the tag-shedding component.

The tag mortality rate can be estimated from the distribution of time-at-liberty measurements for all recaptured fish. The number of recaptures should follow an exponential distribution with respect to time at liberty. The tag mortality rate equals the inverse of the average time at liberty for all recaptured fish. The proof for this equality is given by Butterworth *et al.* (1989).

Such a simple procedure could not be used in this study because fish were tagged over a long period of time, and the time available for recapture was greater for those fish tagged in the early stages of the experiment and less for those tagged towards the end. Furthermore, recapture effort was not evenly distributed over time. At the protected sites, all fishing was restricted to three short fishing trips distributed unevenly during the year. At Cape Peninsula, the amount of recapture fishing effort was unknown, and it was limited to only 7.5 months of the year. Asymmetry in the recapture distribution could bias the simple estimation procedure based on average time at liberty.

Another procedure was devised that evaluated the likelihood of the observed temporal distribution of recapture frequencies. If fish i was released during trip j and recaptured three times, twice during trip $k = j+2$ and once during trip $k = j+4$, then its recapture record over the next 10 trips would be $[0,2,0,1,0,0,0,0,0,0]$. Each element in this vector is notated n_{ik} . The proba-

bility of recapturing a specific tagged fish during trip k depends on the amount of effort applied during the k^{th} trip, and the probability of the fish being alive at the release site with its tag during trip k . Therefore, each trip has a unique expected frequency of recapture for each tagged fish, and the likelihood of the observed counts can be related to these expected frequencies using the Poisson distribution. This distribution is appropriate because of the random element associated with capturing a tagged fish and the very low observed recapture frequencies for individual fish. The likelihood of a single recapture record is the product of these probabilities over all trips subsequent to release, and the likelihood of the entire dataset is the product of the likelihood of each recapture record of every released fish.

Two parameters are required to compute the expected mean recapture frequency, tag mortality rate and recatchability. In reality, there are more than two processes involved, but some of these become confounded, as discussed above, and cannot be identified separately. For example, the probability of a fish being present with its tag during trip k is the combined probability of it not having emigrated, died or lost its tag. The last two of these at least are confounded, and tag mortality rate (β) is assumed to be the rate at which tagged fish disappear, covering the different processes mentioned above.

The recatchability parameter (r) is the average number of times a specific fish will be caught with one unit of effort. Recatchability (units = captures per hour) includes catchability (q), but the two should not be confused. Using standard fisheries notation, where C is catch, E effort and N population size, $C = qEN$. If $N = 1$ (the one tagged fish), then qN is the hyperparameter referred to here as recatchability. Unfortunately, because of confounding, the effects of emigration are mixed in the estimate of r . Because the net movement of tagged galjoen from the release area was rapid, and not a gradual leakage (Attwood 2002), emigration was more likely to be confounded with recatchability than tag mortality. For this reason, it was preferable to keep recatchability separate from catchability, which is to be estimated in another way.

The mean Poisson frequency (ϕ_{ik}) of recapture during trip k of fish i , which was tagged during trip j is

$$\phi_{ik} = rH_k e^{-\beta(t_k - t_j)} \quad (7)$$

The probability (p_{ik}) of recapturing fish i a total of n_{ik} times during trip k is

$$p_{ik} = \frac{e^{-\beta_{ik}} \beta_{ik}^{n_{ik}}}{n_{ik}!} \quad (8)$$

The negative log-likelihood of the entire dataset is therefore

$$LLH = -\sum_i \sum_k \log(p_{ik}) \quad (9)$$

The best estimates of r and β were obtained by minimizing LLH . The confidence intervals were calculated using the likelihood profiling method, as described above for the mortality rate procedure.

This model is of the general form described by Lebreton *et al.* (1992) to estimate survival rate, but in contrast to their examples, it has only two estimated parameters. Lebreton *et al.* (1992) showed that time-dependent survival rates can be calculated for each period between release-recapture events. In general, one can estimate $(k-1)^2$ time-dependent survival rates and capture probabilities, given k sampling events. In this case, there were certainly enough data to attempt such a multi-parameter model. However, in the interest of accuracy and because the relevance of time-dependent changes in tag mortality rate to this study is questionable, a single mortality rate was estimated. This model extends the basic Lebreton *et al.* (1992) model by specifically incorporating time and capture effort, so reducing the need to estimate each capture probability separately. It also uses the log-link, instead of the logit-link, because there is no need to constrain the predicted mean value between zero and one.

GALJOEN DENSITY AT DE HOOP

The results of the controlled tagging experiment at the two De Hoop sites were used to estimate the average number of fish at those sites during all trips. A multiple mark-recapture method, which accounted for tag mortality and emigration, was developed. The rationale is that the ratio of the number of recaptures to the total number of fish caught during a trip is equal to the ratio of the total number of tagged fish alive at that site to the total number of fish at that site. The total number of fish tagged and recaptured at the release sites was known exactly (but not at Cape Point, where density could not be assessed). Estimates were available of the tag mortality rate and the emigration rate.

An important condition for this method to yield an unbiased estimate is that each fish has an equal chance of capture. The tagging study showed that galjoen were not well mixed, but that they held home ranges (Attwood 2002). This was not a problem, provided that fish were caught throughout the site and not just at one or a few points. If, for example, there were gaps in the effort distribution exceeding the home-range size, then clearly some fish would never have been available for capture, thus negatively biasing the esti-

mate.

Anglers at De Hoop were free to move throughout the study sites and did not follow any predetermined pattern. This strategy allowed effort to track abundance and presumably resulted in the highest catch rates. Although galjoen were caught at every 100 m interval at the release sites, the effort distribution was not perfectly flat. However, the distribution of captures within the release sites showed irregularities that had a smaller length scale than the home-range size (<400 m). From this it was assumed that the entire population at each site was accessible to shore-anglers and that no fish were "hidden". The Tsitsikamma data were disqualified for this reason – there was a 3-km stretch within the site that was not sampled.

Another bias could result if some fish were more "catchable" than others (the "trap-happy" effect). If this was the case, then the percentage of released fish that were recaptured should be exceeded by the percentage of re-released fish that were recaptured a second time. Intensive tag-and-release experiments showed that these rates were not different (Attwood 2002), and that all galjoen were therefore equally catchable.

The number of tagged fish available for capture at site a , at time t , is a function of the sum of all the fish tagged at that site over all prior trips. Tag mortality is an exponential loss, whereas migration is a once-off loss that takes place shortly after tagging, with very small net losses thereafter. The number of tagged fish available at site a , during trip k , was estimated sequentially:

$$S_{ak} = [S_{ak-1} + (T_{ak-1} - \theta)]e^{-\beta(t_k - t_{k-1})} \quad (10)$$

The number of recaptures made at site a during trip k could then be predicted by

$$\hat{R}_{ak} = \frac{G_{ak} S_{ak}}{N_{ak}} \quad (11)$$

A single estimate N_a was used to represent a mean of all N_{ak} values. The value of N_a which minimized the sum of squares,

$$SS = \sum_k (R_{ak} - \hat{R}_{ak})^2 \quad (12)$$

was chosen as the best estimate of the average population size at site a during all trips. Sum of squares was used as a measure of discrepancy instead of a likelihood procedure based on the Poisson distribution, because the numbers of recaptures per trip were never small. The Poisson distribution becomes symmetrical for large mean values (McCullagh and Nelder 1989),

Table IV: Number of galjoen captured, tagged and recaptured ("n" times), and the recapture rate (all recapture events divided by first releases) for the four study sites

Parameter	Koppie Alleen	Lekkerwater	Cape Peninsula	Tsitsikamma
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

so the more convenient, symmetrical measure of discrepancy could be used.

The error on the density estimate was calculated using the bootstrap method (Press *et al.* 1992). Trip records were sampled randomly with replacement, i.e. Equation 11 was evaluated repeatedly on a random selection of trip records, including duplications.

Each site at De Hoop covered 3.4 km of shoreline. Therefore, the average density of galjoen at each site was calculated by dividing the estimates of N_d by this length, to express density per metre of shoreline, as is the convention with sandy beach ecology (Brown and McLachlan 1990). This linear approach assumes that galjoen are limited to the surf zone. This is a reasonable assumption for De Hoop where there is an absence of reefs beyond the surf zone at both sites. Baits could be positioned up to 150 m from the high-water mark, so covering all potential galjoen habitat.

RESULTS

Sample size

This study is based on information derived from the capture of 27 606 galjoen from four research sites from 1987 to 2000 (Table IV). Most effort was expended at the two De Hoop sites, Koppie Alleen and

Lekkerwater, and most fish came from there. The third largest contribution came from the Cape Peninsula, where sampling spanned a similar period. Sampling at Tsitsikamma covered a shorter period, from 1995 to 2000.

Tagged fish were recaptured at the sampling sites and elsewhere. Recapture rates varied between 0.12 at Koppie Alleen and 0.043 at Tsitsikamma. Included in these rates are those fish that were recaptured more than once and those that were recaptured outside the study site. All recaptures at De Hoop and Tsitsikamma were recorded, but there was a loss of data attributable to non-reporting outside these areas, including the Cape Peninsula site.

Catch rate

Values of catch rate (*cpue*) were greatest at the De Hoop sites, followed by the Cape Peninsula and Tsitsikamma (Table V), and the differences were statistically significant (one-way ANOVA, $F = 356.4$, $p < 0.01$). If the SFT component of the De Hoop data is examined separately to make it more comparable with the other sites where only the SFT was employed, then the *cpue* was even greater at De Hoop, averaging double the Cape Peninsula rate and >10 times the Tsitsikamma rate (Table V). The SFT *cpue* was at least five times greater than that of the BFT at De Hoop. Smaller mean values were associated with relatively greater variation.

The four factors, fishing technique, month, year, angler, and the two interaction terms (year \times month and angler \times technique), all significantly affected *cpue* ($p < 0.05$) at both sites (Table VI). The "technique" parameter had the greatest explanatory power, showing that anglers in the multispecies fishery are able to target galjoen successfully. Year and month also accounted for substantial variance.

There were 5.5 and 2.6-fold variations in *cpue* that could be attributed to interannual difference at Koppie Alleen and Lekkerwater respectively (Table VII). There was not much agreement in the ranking of years at

Table V: Average *cpue* and associated standard deviation (SD) for the four study sites

Parameter	<i>Cpue</i> (fish angler ⁻¹ h ⁻¹)			
	Koppie Alleen	Lekkerwater	Cape Peninsula	Tsitsikamma
<i>Cpue</i> total	0.92	1.23	0.64	0.10
<i>SD</i>	0.91	1.04	0.67	0.31
<i>Cpue</i> SFT	1.19	1.49	0.64	0.10
<i>SD</i>	0.90	1.01	0.67	0.31
<i>Cpue</i> BFT	0.16	0.33		
<i>SD</i>	0.32	0.47		

Table VI: Results of the GLM applied to *cpue* data for the De Hoop sites, and the deviance and likelihood ratio statistics calculated by the progressive inclusion of additional parameters in the model in the order listed; $p > F$ is the probability that the F value could be exceeded by chance

Parameter	Deviance	df	F	$p > F$
<i>Koppie Alleen</i>				
Intercept	3 895	0		
Year	3 276	6	44	0.0001
Month	3 036	2	51	0.0001
Angler	2 833	10	9	0.0001
Technique	1 038	1	767	0.0001
Month \times Year	971	8	4	0.0004
Angler \times Technique	874	10	4	0.0001
<i>Lekkerwater</i>				
Intercept	4 725	0		
Year	4 607	6	6	0.0001
Month	4 537	2	11	0.0001
Angler	3 925	11	18	0.0001
Technique	1 800	1	700	0.0001
Month \times Year	1 563	11	7	0.0001
Angler \times Technique	1 488	11	2	0.0109

the two sites according to *cpue*. At both sites, 1998 and 1999 emerged as the weakest years, but for other years there was no agreement.

The seasonal trend was consistent between sites. In both cases, the *cpue* appeared to peak between July and September, with a minimum in midsummer (Table VIII). The total extent of the seasonal effect on *cpue* cannot be calculated because only the same three months per year were sampled at each site, and those months differed between sites. The first of the interaction terms (Table VI) accounts for variability associated with short-term changes by assigning a separate factor to each trip (five consecutive days). There was a considerable variation at the daily level, which this model would not have been able to take into

Table VII: *Cpue* factors associated with each year for the two De Hoop sites. The years are ranked in descending order. The factors, which are log-transformed, are not comparable between sites

Koppie Alleen		Lekkerwater	
Year	Factor	Year	Factor
1993	1.18	1994	1.00
1995	1.15	1995	0.72
1997	1.12	1996	0.41
1996	1.08	1993	0.40
1994	0.94	1997	0.34
1998	0.31	1998	0.19
1999	0.00	1999	0.00

Table VIII: *Cpue* factors associated with each month for the two De Hoop sites. The months are ranked in descending order. The factors, which are log-transformed, are not comparable between sites

Koppie Alleen		Lekkerwater	
Month	Factor	Month	Factor
July	0.27	September	0.12
October	0.00	May	0.03
February	-0.37	November	0.00

account. As a result, the fit was over-dispersed. To overcome this problem, it would have been necessary to include a three-way interaction term (day \times month \times year), but such an inclusion was deemed impractical in view of the large number of days fished, and it would not provide useful information.

Angler performance is a “nuisance” parameter when designing *cpue* monitoring programmes. Can random ensembles of *cpue* records be analysed without attention to the performance of individual anglers? The angler factor was significant at both sites, suggesting that angler skill will affect the interpretation of *cpue* data if the number of anglers in the sample is small. The total amount of variation explained by angler differences was consistent between sites; 3.3- and 3.4-fold variation between the smallest and largest factors for Koppie Alleen and Lekkerwater respectively.

The influence of angler skill is diminished because the ranking of anglers by performance was not consistent between sites. The correlation of angler factors between sites was tested statistically. Spearman’s rank correlation coefficient for these data is 0.42 ($n = 11$), which corresponds to a p -value of 0.1 for a one-way test (Zar 1984). In other words, there is some doubt whether the performance of individual anglers across sites was correlated. Some anglers who performed consistently well (relative to others) at one site, performed consistently poorly at another, which suggests an interaction between site and angler performance. The second interaction term, between angler and technique, shows that an angler’s performance is dependent not only on the site, but also on the technique used. These results suggest that *cpue* should be calculated from a large ensemble of anglers covering a variety of areas to ensure that the “law of averages” reduces the influence of individual variation and the influences of targeting on the *cpue* statistic.

Size distributions

The size distributions of fish taken at each site were

Table IX: Total mortality rate estimated from galjoen size distributions (total length ≥ 325 mm) for the four study sites

Site	n	Z	CI	ω	CI	$-LLH$
Koppie Alleen	2 269	0.42	0.32–0.48	0.58	0.38–0.73	11 826
Lekkerwater	3 504	0.61	0.51–0.77	0.17	0.00–0.52	17 796
Cape Peninsula*	1 297	2.01	1.88–2.34	0.69	0.21–0.85	5 227
Tsitsikamma	686	0.43	0.36–0.54	0.32	0.00–0.53	3 603

n = Sample size

Z = Instantaneous total mortality rate (year⁻¹)

CI = 95% confidence interval

ω = Male fraction at recruitment

$-LLH$ = Negative log-likelihood

* Unprotected site

used here to calculate mortality rates, which were ascribed to natural mortality in the protected sites, but which included fishing mortality at the Cape Peninsula.

To estimate the natural mortality rate at De Hoop, only fish caught from 1995 were analysed. It was necessary to omit the earlier samples, because the marine protected area came into effect at the beginning of 1985. Galjoen live to a maximum age of at least 13 years, and the age at first capture is 4 years (Bennett and Griffiths 1986). Assuming that recruitment was constant, 10 years had to pass before the age structure of the protected fish lost the effect of the earlier fishing (i.e. the 3-year-old cohort in 1985 would be the 13-year-old cohort in 1995). Such an omission of data was not necessary at Tsitsikamma, where protection took effect from 1964.

The size distributions of galjoen caught translate into instantaneous mortality rates (Z) between 0.32 and 2.34 year⁻¹, depending on the site (Table IX). The best estimates in the protected sites ranged from 0.42 to 0.61 year⁻¹, whereas the best estimate for the unprotected site was 2.01 year⁻¹. The Lekkerwater site had the highest Z estimate of the three protected sites, but this was associated with a low estimate of the male fraction. It is difficult to explain why the sex ratio estimated at Lekkerwater is skewed, although the confidence interval included 0.5. Because the male fraction and Z estimates are negatively correlated by the assessment procedure (see explanation in Material and Methods), a more even sex ratio should be associated

with a lower Z estimate, which would be closer to estimates at the other protected sites. The confidence intervals of the Z estimates did not overlap between the two De Hoop sites, indicating a difference in size distributions. The Koppie Alleen and Tsitsikamma estimates were not significantly different.

Tag mortality rate

The estimated tag mortality rates were similar at the two De Hoop sites, but much lower at Tsitsikamma (Table X). The very small recapture rate at Tsitsikamma and the small sample size (Table IV) produced a very wide confidence interval on the tag-mortality estimate and these should be treated as less reliable than the other estimates. Indeed, the tag-mortality estimate is lower than the mortality estimate, which, in theory, should not be possible. The very low recatchability could have masked the decline of recapture frequency over time at this site. If the average time-at-liberty method is used (Butterworth *et al.* 1989), then the tag mortality for Tsitsikamma is estimated at 1.16 year⁻¹ (with a confidence interval of 0.5–1.8 year⁻¹), which is in agreement with the De Hoop estimates. The tag mortality rates at De Hoop translate into a tag survivorship of approximately 32% per annum.

Tag-mortality rate was estimated in conjunction with a recatchability rate. The recatchability, which accounts for catchability and for losses to emigration,

Table X: Estimated instantaneous tag mortality rate, the associated 95% confidence interval (CI) and estimated recatchability

Site	n	Tag mortality rate (year ⁻¹)	CI	Recatchability (captures per hour)
Koppie Alleen	8 311	1.15	1.05–1.23	1.84×10^{-4}
Lekkerwater	13 687	0.99	0.91–1.07	0.83×10^{-4}
Tsitsikamma	34	0.17	0.0–0.35	0.12×10^{-4}

n = sample size

Table XI: Estimated average density of galjoen (in numbers per km) and standard errors. The model fit is indicated by sum-of-squares

Site	<i>n</i>	Mean density	<i>SE</i>	Sum of squares
Koppie Alleen	57	1 829	102	1 740
Lekkerwater	49	4 924	386	1 671

was smallest at Tsitsikamma and greatest at Koppie Alleen. Given that the rates of emigration from these sites were similar (Attwood 2002), these estimates should reflect differences in catchability.

Density at De Hoop sites

The average number of galjoen >250 mm *TL* present during all sampling trips was significantly greater at Lekkerwater than at Koppie Alleen (Table XI). The coefficient of variation on these estimates was of the order of 7%. Based on a sex-ratio of 1:1 and mortality rates reported in Table IX, the average-sized galjoen (>250 mm) at Koppie Alleen and Lekkerwater weighed 818 g and 583 g respectively, which translates into biomass values of 1.49 and 2.87 kg m⁻¹ respectively.

Catchability

Catchability (*q*) is the impact that a unit of effort has on the stock. In the present case, it is calculated on a beach-length basis, in km h⁻¹. The equation of catchability of galjoen is $q = F/E$, where *E* is effort measured in h km⁻¹ year⁻¹, and *F* is the ratio of the instantaneous catch rate per year to the population size. Furthermore, $F = C/N$, where *C* is the instantaneous catch-rate measured in fish km⁻¹ year⁻¹, and *N* is the fish density measured in fish km⁻¹. Estimates of fish density, together with the catch records from the De Hoop data, provide the opportunity to calculate *F*, the fishing mortality rate potentially caused by the research sampling, and hence *q*. (The qualifier “potentially” is used because the fish were returned and not killed, but this does not affect the calculation.) From the recorded annual catch (fish km⁻¹ year⁻¹), and population density

(fish km⁻¹), *F* at the two De Hoop sites is calculated to be in the order of 0.1 year⁻¹. Despite the higher *cpue* at Lekkerwater, the catchability of galjoen there is lower than at Koppie Alleen (Table XII).

The catchability and recatchability estimates (Table X) were calculated differently and they have different units, but they should still be numerically comparable. At both sites, catchability exceeded recatchability by a factor of 3.8. This difference can partly be ascribed to the inclusion of the effects of emigration as well as catchability in the recatchability estimate. More important, the ratios of these parameters between sites are remarkably consistent. The ratio between the *q* estimates at Koppie Alleen and Lekkerwater is 2.19, whereas the ratio of *r* estimates (Table X) between these sites is 2.21. This information allows *q* to be estimated for Tsitsikamma. The ratio of the *r* estimates between Koppie Alleen and Tsitsikamma is 15.3, which means that the *q* estimate at Tsitsikamma should be 4.6×10^{-5} km h⁻¹.

DISCUSSION

Natural mortality rate

The total mortality rate of galjoen at the protected sampling sites should equal the natural mortality rate (*M*). Galjoen were protected at those sites for periods that allowed at least one cohort to reach its maximum age without losses to fishing. The estimate of 0.43 year⁻¹ is the median of the three estimates, and also the one that came from the oldest marine protected area, Tsitsikamma National Park. The age distribution is probably most stable at that site, because the population could be growing at the De Hoop sites after the reserve was brought into effect in 1985. A growing population would skew the age distribution in favour of young fish, and mortality would be overestimated as a result.

By comparison, the models used by Bennett (1988) to estimate *M*, i.e. those of Pauly (1980) and Rikhter and Efanov (1977), yielded estimates that were approximately 0.1 year⁻¹ lower (0.38 year⁻¹ for males and 0.32 year⁻¹ for females). It is preferable to adopt the measured rate reported here, instead of extrapolating a value from models based on studies of other

Table XII: Estimates of “potential” *F* and catchability of galjoen for De Hoop

Site	Catch (fish km ⁻¹ year ⁻¹)	<i>F</i> (year ⁻¹)	<i>E</i> (h km ⁻¹ year ⁻¹)	<i>q</i> (km h ⁻¹)
Koppie Alleen	182	0.100	150	6.7×10^{-4}
Lekkerwater	345	0.073	240	3.2×10^{-4}

Table XIII: Instantaneous per capita mortality rates estimated from catch-at-age and catch-at-length data. The 95% confidence intervals are given. Only point estimates were available from Bennett's (1988) study

Area	Period	Sex	Data	Z	Source
Lambert's Bay to Cape Infanta	1938–1986	Male	Catch-at-age	0.91	Bennett (1988)
Lambert's Bay to Cape Infanta	1938–1986	Female	Catch-at-age	1.40	Bennett (1988)
Cape Hangklip to Walker Bay	1995–1996	Both	Catch-at-length	0.56–1.06	Attwood & Farquhar (1999)
Cape Point to Arniston	1995–1996	Both	Catch-at-length	0.66–1.2	Brouwer <i>et al.</i> (1997)
Still Bay	August 1995, 1996	Both	Catch-at-length	0.23–0.68	Records of Galjoen Derby
Cape Peninsula	1987–2000	Both	Catch-at-length	1.88–2.34	This study

species. However, the galjoen population structure at protected sites could have been impacted by fishing in other areas, because of a small amount of exchange of adult fish.

Galjoen at De Hoop were estimated to exchange with those from exploited areas at a rate of approximately 5% (Attwood 2002). It is difficult to put a time dimension to this estimate, because of the difficulty of deciding on the appropriate movement model. Either 5% of the fish exchange freely with those from outside areas or fish spend 5% of their time in other areas. In either case, the number of adult galjoen entering the protected area would be fewer than the number leaving by a factor of at least e^{-F} . Assuming F in adjacent exploited areas to be 1.0 year^{-1} , the net loss from the protected sites caused by fishing in other areas is $0.05(1-e^{-F})$, or $\approx 0.03 \text{ year}^{-1}$. (The MPA loses 0.05 of its density through emigration, but gains only $0.05e^{-F}$ by immigration from exploited areas.) The total mortality rate estimated for protected sites should therefore be decreased by this value to represent the true natural mortality rate, i.e. $M = 0.43 - 0.03 = 0.4$. This adjustment is conservative because it does not account for possible recruitment failures in exploited areas, which could have reduced density by more than e^{-F} in such cases.

Impact of fishing

The tag-and-recapture information led to an estimate of galjoen density at two protected sites. With records of total catch and effort, it was then possible to estimate the impact of a unit of effort. The F estimates in Table XII are not dependent on estimates of M , which is a weakness of assessments based solely on catch-at-age data. The estimates of F and q were based on 13-year time-series, and therefore averaged out much of the interannual variation. The experimental fishing at De Hoop could potentially have reduced the local galjoen density at an instantaneous rate of F of approximately 0.1 year^{-1} , if the fish had been removed. Available estimates of Z from the

fishing grounds range between 0.23 and 2.34 year^{-1} (Table XIII), all based on catch-at-length data sampled at various locations and dates.

Corresponding estimates of effort are patchy and in some cases unreliable, particularly when instantaneous counts were extrapolated to estimate the total effort expended in a day. In addition, not all anglers target galjoen and it is difficult to allocate the amount of effort that was directed at galjoen. Brouwer *et al.* (1997) estimated from a questionnaire study that only 30% of anglers targeted galjoen, a proportion likely to vary spatially and seasonally. The GLM model of *cpue* shows that such targeting strongly affects the *cpue* statistic. Consequently, there is considerable variation among the estimates of effort that are available (Table XIV). The estimates from Cape Peninsula and Koppie Alleen (prior to the reserve) are regarded here as reliable, because the vast majority of anglers there were fishing for galjoen, using the small-fish technique described here. Typical effort counts are in the region of $2\,500 \text{ h km}^{-1} \text{ year}^{-1}$. The estimate of $7\,449 \text{ h km}^{-1} \text{ year}^{-1}$ by Brouwer *et al.* (1997) should be reduced to 30% (i.e. the percentage of that sample that targeted galjoen), yielding $2\,234 \text{ h km}^{-1} \text{ year}^{-1}$. If $2\,500 \text{ h km}^{-1} \text{ year}^{-1}$ is multiplied by the q estimates in Table XII, the predicted F values lie between 0.8 and 1.75 year^{-1} . These estimates are within the range of those calculated from catch-at-length data (Table XIII), after correcting for natural mortality. Without a size limit, such high rates of fishing mortality translate into reductions of potential female spawner-biomass-per-recruit of 98.4 and 99.4% respectively. Such reductions guarantee extinction.

Galjoen will not be able to sustain the present harvest rate, as predicted by dynamic models with stock recruit relationships (Attwood and Bennett 1990, 1995). However, the galjoen catch makes a substantial contribution to the shore-fishery in the South-Western Cape (Brouwer *et al.* 1997), and the stock is clearly not close to extinction, even in areas that are heavily exploited. How can this discrepancy be explained?

The values of F and q estimated for De Hoop depend linearly on the density estimate. There is no reason

Table XIV: Estimates of shore-angling effort

Area	Period	Method	Effort (h km ⁻¹ year ⁻¹)	Source
Port Elizabeth	August 1985–August 1986	RC	1 604	Clarke & Buxton (1989)
South-Western Cape	Not specified	RC	2 299	Bennett (1993)
Koppie Alleen	1984–1985	AP	2 227	Bennett & Attwood (1991)
Cape Peninsula to Arniston	1995–1996	RC	7 449	Brouwer <i>et al.</i> (1997)
Cape Peninsula	June 1999–May 2000	AP	2 689	Gate records

AP = Access point count

RC = Roving creel count

to suspect a bias in the density calculations. Good estimates of tag mortality and emigration were obtained, and the fish were sampled throughout the study sites, so overcoming the mixing problem. As a check, the estimates can be compared with the results of studies of biomass of sandy-beach and rocky-shore ecosystems. Total macro faunal biomass on a South African warm-temperate, high-energy, sandy beach is in the vicinity of 500 gC m⁻¹, of which 130 gC m⁻¹ is attributable to fish (McLachlan and Bate 1984). Using their conversion from wet mass to carbon, the De Hoop galjoen densities amount to 192 and 370 gC m⁻¹ for Koppie Alleen and Lekkerwater respectively. This comparison serves to show that galjoen biomass exceeds the average biomass for all fish combined on a sandy beach. The biomass of about another 40 species at De Hoop has still to be added! If the De Hoop density estimates are in error, they cannot be much higher. As a result, the *q* estimates (and hence *F* estimates) in Table XII are not likely to be overestimates.

Two other ways of explaining the discrepancy are possible. The first is that the stock is on its way to extinction; current catch rates may not be sustainable. A counter-argument is that the *cpue* over the decade prior to 1992 did not show a sustained decrease (Bennett *et al.* 1994). On the other hand, constant improvements in fishing technology (particularly the introduction of carbon-fibre rods, aerodynamic grab sinkers, chemically sharpened hooks, and dyneema fishing lines) and the sharing of information (cellular phones and fishing magazines) could be increasing catchability, so masking the effect of a declining stock on *cpue*.

The second possibility is that the fishing mortality is applied unevenly, leaving many areas unexploited as natural refuges, while the remaining areas take the majority of the fishing effort. In this case, the natural refuges could be acting as a source of recruitment to other areas where exploitation is very heavy (i.e. greater than the average). Small natural refuges, provided that their size exceeds the home-range of the fish, could provide a vital source of protection. A high

value of *F*, which would otherwise cause extinction, can be sustained provided that it is not applied throughout the stock. This has been shown in theory (Polachek 1990, DeMartini 1993, Quinn *et al.* 1993, Attwood and Bennett 1995), and it serves as a strong argument for supporting marine protected areas as a strategy for the conservation of fish.

Habitat effects

A weakness in the above extrapolation of natural mortality rates and catchability is that the estimates are not necessarily transferable from one area to another. Indeed, the estimates differed among the De Hoop and Tsitsikamma sites, which were all protected from fishing. Spatial differences in population parameters are likely, owing to habitat type differences (Table XV).

The exploited site did not have the lowest *cpue*, but mortality there was highest. The Cape Peninsula has long been known as a productive area for galjoen (Biden 1930). The carrying capacity of galjoen must be high there to sustain a moderate *cpue* after many years of intense exploitation, as suggested by the high effort (Table XIV) and mortality estimates (Table IX).

The low *cpue* at the protected Tsitsikamma site suggests either that there are few fish there or that they are very difficult to catch. The poor catchability estimated suggests difficulty in catching, but the carrying capacity there could be lower than at De Hoop. Tsitsikamma is at the eastern side of the range, where galjoen have never been a dominant part of the catch. Galjoen contribute only 2% to shore anglers' catches in the Eastern Cape (Clark and Buxton 1989). Rocky headlands are also not regarded as prime habitat for galjoen.

The differences in density, *cpue* and catchability between the two De Hoop sites (Table XV) could be explained by the relative proportion of mixed rock and sand versus pure sandy beach. Mixed rock and sandy shores are where most galjoen are usually encountered. Approximately two-thirds of the Koppie Alleen site is a pure sandy beach, where fewer galjoen

Table XV: Qualitative estimates of population and fishery parameters for the four study sites. Z is the total mortality rate estimated from size distributions. F is measured as the difference between Z and M at the Cape Peninsula

Parameter	Koppie Alleen	Lekkerwater	Cape Peninsula	Tsitsikamma
Habitat type	Broken sandstone and sandy beach	Broken sandstone	Rocky shore and kelp forest	Exposed headland
Fish density	Low	High		
Catchability	High	Intermediate		Low
Recatchability	High	Intermediate		Low
Z	Low	Intermediate	High	Low
F	Zero	Zero	High	
$Cpue$	High	Very high	Intermediate	Low

are caught than on mixed rock and sandy shores. Accordingly, density is higher at Lekkerwater (Table X), whereas catchability is higher at Koppie Alleen (Table XII). Again, this could be explained by the difficulty of catching galjoen among rocks, of which there are fewer at Koppie Alleen. Therefore, the ratio of *cpue* between the two sites is not as skewed as would be predicted from the ratio of densities.

The above comparisons serve to illustrate that any assessment of the stock of galjoen should take habitat and location into account. Extensive use was made of protected areas for this study. Without them, the study as a whole would not have been possible. More specifically, this study constitutes the first attempt at quantifying the density of any South African linefish and measuring M directly, which was only possible because of the availability of an undisturbed research site. It follows that such sites have tremendous value for fishery assessment and that they should be distributed across all biogeographic regions and habitats for optimal effect for conservation and fishery assessment.

The great degree of patchiness also serves as a warning to those who study the effects of fishing by comparing exploited and unexploited sites. No two sites are identical, stressing the need for adequate replication of both protected area and such studies.

Information content of catch data

Galjoen confound most standard attempts at quantifying fish. They live in a high-energy environment where diving is physically impossible and visibility is poor. Even under good conditions, diver counts of fish are notoriously variable and often biased (Lincoln-Smith 1989). Underwater video techniques overcome many of these problems (Willis *et al.* 2000), but the habitat of galjoen will not allow this technique either. Catch data are all that can be used to assess stocks in inaccessible or turbulent environments, but permit

only indirect or relative assessments.

Three types of data are available to researchers, tag-and-recapture data, catch rate and catch-at-length frequencies. The last two could be derived from fishery-independent or fishery-dependent surveys. This study has made use of all three types in a fishery-independent survey, and some insights have been gained on the usefulness and costs of collection of each with respect to the galjoen fishery.

- (i) *Tag-and-recapture data* — This type of information is a luxury for fishery researchers. The data provide information on movement and density that is not available from any other method. In the present case, the data led to the calculation of catchability. However, the data provide no real-time estimates. A 10-year dataset provides estimates of parameters that are averages over that period. Large sample sizes are also required. In this study, data from >27 000 tagged fish yielded density estimates with a 95% confidence interval of $\pm 15\%$.

Another drawback is the fact that tag-and-recapture data can only be put to optimal use in a marine protected area, where the experiment will not be disturbed. Such data could provide a useful monitoring function, especially as *cpue* data will be generated as a by-product, but will not provide any information on the state of the fishery *per se*. Additional surveys, as described for other types of data, will be required.

Tag-and-recapture data are expensive in terms of labour and equipment, and their collection is time-consuming. To illustrate these costs, the De Hoop tagging study required an average of 170 fisher-days per year (or R40 000), and the equipment and data-handling costs amounted to approximately R80 000 per year at current rates (US\$1 = R9 in 2002). This investment has to be maintained for at least five years. The entire exercise should be conducted at a few sites across the range of the species and habitat types. Taking three sites as a minimum,

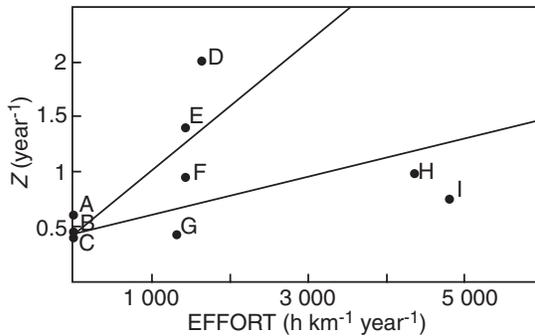


Fig. 3: Scatterplot of total mortality rate estimates (Table XIII) and effort counts (Table XIV) for galjoen. A = Lekkerwater, B = Tsitsikamma, C = Koppie Alleen, D = Cape Peninsula, E = South-Western Cape females, F = South-Western Cape males, G = Still Bay, H = Hermanus, I = Southern Cape. The effort for samples H and I are overestimates because they include targeting on many other species besides galjoen. The straight lines represent the upper and lower estimates of catchability, with a natural mortality rate of 0.4 year^{-1} .

this amounts to R360 000 per annum. Mitigating some of these costs is the possibility of attracting volunteer assistance, as was done in this case, as part of a fishery extension project. Of concern is the effect of tags on the fish. Apart from mortality, it is strongly suspected that tags affect galjoen growth (Attwood and Swart 2000).

- (ii) *Catch rate* — The catch by anglers can be monitored to provide two useful indices, average *cpue* and total catch. The same measurements are taken in both cases (i.e. the number of fish caught by an angler), but the statistical treatment differs between the two.

Cpue provides a reliable, but relative, measure of reef fish density (Willis *et al.* 2000), and it has been used to infer spatial and temporal differences in density (e.g. Bennett and Attwood 1991, Rakitin and Kramer 1996, Millar and Willis 1999). *Cpue* is a real-time measure, in contrast to catch-at-length or tag-and-recapture data, both of which reflect processes over several years. The major difficulty with *cpue* as an index of abundance is the dependence on gear type and angler. Not only is *cpue* affected by the type of gear used (or targeting), but it is also increased by technological improvements. The effect of changes in gear type is difficult to quantify, but records of such changes should be kept. The influence of the variability between anglers should disappear with large sample

sizes that include many anglers.

- (iii) *Catch-at-length* — At present, catch-at-length (-age) is the most commonly used variable for linefish assessment. A random sample of fish lengths caught by a particular gear type is converted to catch-at-age data, which are then used to estimate mortality rate, which itself feeds into per-recruit models. Spawner-biomass-per-recruit can be used to assess the status of a stock, and to make adjustments to fishing regulations (Clark 1991, Punt 1993, Mace *et al.* 1994). The common practice in South Africa has been to use one global estimate of mortality rate to estimate the remaining percentage of unfished spawner-biomass-per-recruit (e.g. Bennett 1988, 1993, Buxton 1992, Van der Walt and Govender 1996). The reliability of this technique depends on several unrealistic assumptions, some of which have come to light from this study.

First, per-recruit models assume that recruitment is constant. In fisheries that are expanding or shrinking (because of restrictions), this assumption is incorrect. In the galjoen example both scenarios could apply. Anglers are accessing remote areas more frequently, so reducing recruitment there. Additional restrictions in the form of closed areas could have the opposite effect. Measures of fishing effort and mortality estimates based on catch-at-length of galjoen do not correlate (Fig. 3). At Lekkerwater, where fish have been protected for 16 years, the mortality rate is apparently higher than at Still Bay, a holiday resort that has expanded greatly over the past decade. A likely explanation of this discrepancy is that recruitment has increased at Lekkerwater since protection took effect, so giving an overestimate of mortality, whereas recruitment at Still Bay is collapsing, thereby giving an underestimate of mortality.

Second, catch-at-length sampled from the fishery biases the estimates of fishing mortality rate towards the rates at exploited areas. Natural refuges, or protected areas, where fish are not caught or are caught less frequently, are under-represented in samples, thereby providing a pessimistic overall estimate of mortality. Although a fishery-independent survey could be designed to derive estimates uniformly across all areas, some natural refuges are simply impossible to sample.

Third, per-recruit models depend on the availability of reliable estimates of the natural mortality rate. Estimating the rate of natural mortality in an established fishery will always be a problem. The estimate provided here for galjoen depended

Table XVI: Number of *cpue* observations and fish measurements that must be made to estimate *cpue* and *Z* respectively, to within the given accuracies in exploited and unexploited areas. Calculations were based on data from Koppie Alleen (as a protected area) and Cape Peninsula (as an exploited area)

Area	<i>Cpue</i> (within 5%)	<i>Z</i> (within 0.1 year ⁻¹)	<i>Cpue</i> (within 10%)	<i>Z</i> (within 0.2 year ⁻¹)
Exploited area	1 754	8 000	438	2 000
Protected area	915	2 000	229	400

on the existence of a marine protected area and a fishery-independent survey. Natural mortality is likely to vary across the animal's range, implying that several such protected research sites are needed.

Fourth, a problem not mentioned thus far is that catch-at-length data can only be translated into mortality with reliable length-age relationships. It is, for example, worrying that estimates of growth rate for galjoen and white steenbras *Lithognathus lithognathus* based on tagging and otolith readings do not concur (Attwood and Swart 2000). Age-length relationships are also known to change over time, perhaps partly as a result of exploitation (Law 2000), requiring frequent re-assessment.

Finally, per-recruit models that use estimates of mortality derived from catch-at-length data do not allow for proactive management. The effect of excessive harvest can only be detected a few years after the effect has been etched on the age structure. At that point it is difficult to reverse the trend. For this reason alone, *cpue* monitoring is preferable to catch-at-length methods.

Monitoring requirements

The relationship between the standard deviation (*SD*) of a sample and the standard error (*SE*) of the mean of that sample, $SD^2 = n(SE^2)$, can be used to roughly scale the monitoring requirements in the galjoen fishery. The observed variability in catch rates and mortality rates based on catch-at-length indicates that exploited areas will have greater sampling requirements than lightly exploited areas if the same relative precision is desired everywhere (Table XVI). In the case of catch-at-length data, more fish measurements are required from the areas where fewer fish are available, so presenting an even greater burden on the assessment of stocks in heavily exploited areas.

Because of the variability observed between habitats and between geographical locations, it will be necessary to estimate these parameters separately along discrete lengths of coastline, separated on the basis of habitat type. An area such as False Bay will

require at least three estimates, one for the western rocky shore (34 km), one for the northern sandy shore (60 km), and another for the eastern rocky shore (33 km).

Further, using a realistic target of achieving a confidence of 10%, and taking the average assessment area to be 50 km of exploited coast, approximately 17 500 *cpue* measurements and 16 000 fish measurements will be needed for the entire 2 000 km range of the species. Again, using a typical effort count of 2 500 h km⁻¹ year⁻¹ or 500 angler-days km⁻¹ year⁻¹ and catch rate of 0.1 fish h⁻¹, these demands will require a roving creel census covering approximately 13 000 km-days per year for *cpue* and 117 000 km-days per year for size measurement. Of these two, the catch rate requirements are lower (and realistic). Fortunately, catch rate is the better parameter to measure.

At a cost of R100 000 per observer per annum (including running expenses), and with a modest target of 1 200 km days per observer per year (5 km per day for 238 working days), the annual cost of an effective catch-rate monitoring programme is just over R1 million. Such a programme could cover all shore-based fisheries with a moderate expansion. That cost could be recovered by charging anglers R1 per fishing trip, which is negligible in relation to their total costs (McGrath *et al.* 1997). The current annual fee is R40 per angler.

CONCLUSIONS

- The natural mortality rate of galjoen is slightly higher than the estimate used by Bennett (1988) for his per-recruit analysis. The estimate presented here may still be biased by errors in the length-age relationship of galjoen, and by the possibility that the protected stocks that were analysed were either shrinking or expanding.
- Galjoen density and population structure has been heavily impacted by fishing, where fishing effort has been high. However, the impact remains localized, and protected sites differ from exploited sites with respect to *cpue* and age structure.
- Fishing mortality rates as estimated from fishery-dependent data are higher than can be sustained.

- Two possible explanations of the persistence of the fishery are that (a) technological improvements are masking the effect on *cpue* of a continued downward trend in density, or (b) the high fishing mortality is not applied evenly, leaving many pockets of fish that are sufficiently protected to act as a source of recruitment to exploited areas. The continuation of the fishery may depend on the existence of natural refuges or the provision of marine protected areas where those natural refuges have broken down.
- Patchiness in habitat suitability results in spatial variations in carrying capacity. A heavily exploited but productive site, such as the Cape Peninsula, could hold more fish than a protected but unproductive site, such as Tsitsikamma. In these two examples, the observed population size structures confirm that galjoen at the less productive site have a greater life expectancy. The scale of spatial patchiness can be very small, as shown by the large differences in density between the two nearby De Hoop sites. The implication for monitoring is to maintain spatial consistency in sampling for the detection of interannual changes. The implication for stock assessment is to develop a comprehensive sampling strategy covering all habitat types throughout the range.
 - Further considerations for the design of a fishery-dependent survey are the need to cover the season systematically, because of strong seasonal effects in *cpue* and catch-at-length, and the need to record ancillary information such as gear type and targeting. The strong effect of angler on catch data can be overcome by sampling large numbers of anglers.
 - The rough scaling exercise undertaken on the basis of measured variability in *cpue* suggests that a comprehensive monitoring programme for stock assessment of galjoen is economically viable. As galjoen form part of a multispecies fishery, the requirements for monitoring the catch of other species should be assessed in a similar way, because one monitoring programme will have to cater for the entire fishery. It is clear, however, that fishery-independent studies using marine protected areas are required to provide information that cannot be obtained from fishery-dependent surveys.

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