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# POPULATION DYNAMICS AND POTENTIAL YIELD OF THREE SPECIES OF GIANT WINKLES IN THE WESTERN CAPE, SOUTH AFRICA

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Of the southern African intertidal and shallow subtidal trochid and turbinid gastropods, *Turbo sarmaticus*, *T. cidaris* and *Oxystele sinensis*, are the most abundant large species, and therefore obvious targets for a winkle fishery. *T. sarmaticus* is harvested by recreational snorkel divers, and an application has been made for a permit to experimentally harvest the other two species commercially. This study involves four major aspects, namely morphometrics and flesh yield, shore-based abundance estimates, subtidal abundance estimates, and an estimate of the potential yield for each of the three species off the South-Western Cape, South Africa. Abundance and biomass of the winkles increased from west to east, highest densities being recorded in the low intertidal regions to 2 m depth. Low biomasses of the three species were recorded west of Cape Hangklip and are unlikely to support a fishery there. East of Cape Hangklip, invasion of rock lobsters *Jasus lalandii* has had a considerable impact on *T. cidaris* and *O. sinensis* populations. Consequently, a boat-based fishery with an estimated annual total allowable catch of 75.5 tons for *T. cidaris*, with a bycatch of 9.9 tons for *O. sinensis*, can only be considered in the easternmost fisheries-management area between Kleinbaai and Quoin Point. Because previous studies on the harvesting potential of *T. sarmaticus* off the Western Cape concluded that it was not commercially sustainable, a total allowable catch for that species was not considered. Management options deserving considerations before the commencement of a giant winkle fishery are discussed.

Key words: commercial exploitation, *Oxystele sinensis,* stock assessment, *Turbo cidaris, Turbo sarmaticus,* yield

Trochids (topshells) and turbinids (turban shells) are conspicuous intertidal and subtidal herbivores in temperate and tropical waters. Most of the southern African winkle species are endemic to the region, and many have been harvested in large numbers, but at unknown rates, by indigenous coastal people since prehistoric times. Shell middens dating back at least 5 000 years include the shells and operculae of *Turbo* and *Oxystele* species (Voigt 1973, Lasiak 1992). Winkles are gathered for bait by fishers (Lombard 1977, McLachlan and Lombard 1981, Clark *et al.* 1996), and some are even considered a delicacy by local seafood lovers (Vicquery 1991).

One of the focal points of marine research in South Africa is the developing of new, small-scale commercial fisheries on previously unexploited species. The three most abundant large species of winkle, *Turbo sarmaticus* (alikreukel), *Turbo cidaris* (smooth turban shell) and *Oxystele sinensis* (pink-lipped topshell), are the most obvious targets for a winkle fishery. These edible marine gastropods have to date only been exploited by subsistence and recreational fishers, and no commercial harvesting has been attempted. However, a permit was issued in early 1996 to conduct an experimental commercial fishery for "giant winkles" (*T. cidaris* and *O. sinensis*) off the Western Cape. For the purposes of this paper, "subsistence fishing" refers to harvesting for personal consumption by indigenous people, "recreational fishing" describes leisure-time snorkeling and collection of the resource for personal consumption, whereas "commercial fishing" implies active targetting of the resource for financial gain.

The three species of giant winkle have wide distribution ranges along the rocky shores of southern Africa, extending from the South-Western to the Eastern Cape (McQuaid 1980, Griffiths 1981, Branch *et al.* 1994). In the Western Cape, they remain confined within the limits of kelp beds (*Ecklonia maxima* and *Laminaria pallida*). This habitat offers some degree of shelter from direct wave action and sand scouring, and high densities are not uncommon in rocky gullies and bays. In similar shallow habitats that are otherwise similar but experience high wave exposure, they are, however, scarce or absent, only re-appearing at depths at which a strong surge has less impact. *O. sinensis* primarily inhabit the mid and lower intertidal zones, although they occasionally penetrate into the

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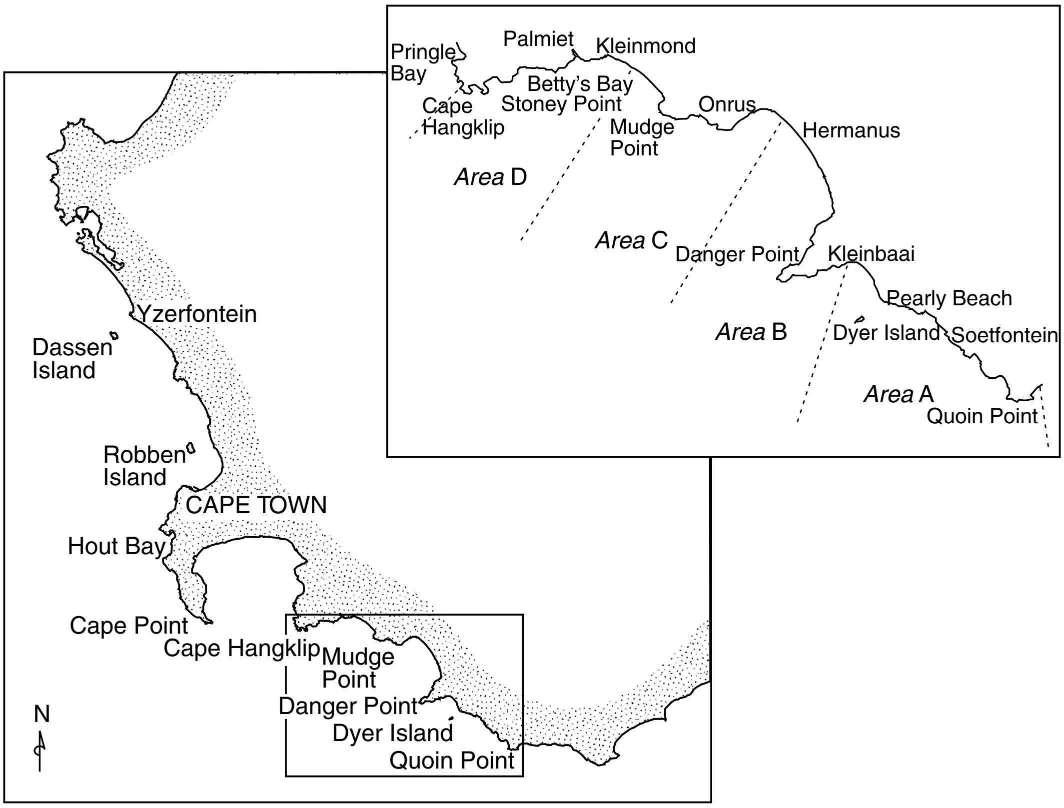

Fig. 1: Map of the Southern Cape showing the locality of some of the sampling areas. The study area between Cape Hangklip and Quoin Point depicts the suggested management areas for giant winkles. These are the same areas currently used for abalone in the region

subtidal (McQuaid 1980, Griffiths 1981, Branch *et al.* 1994). Adult *T. sarmaticus* are found scattered across the reef, but *T. cidaris* are usually clustered in crevices and under rocks. In calm conditions, *T. cidaris* become more dispersed and single animals may be observed climbing kelp stalks or actively feeding in understorey algae. Their accessibility and clumped distribution therefore make them easy and potentially high-yield targets for a recreational and/or commercial fishery.

Information on the biology and population dynamics of endemic local topshells and turban shells is limited primarily to studies on *T. sarmaticus* (de Villiers 1970, Eyre 1973, Lombard 1977, McLachlan and Lombard 1980, 1981, Pulfrich 1983, Yssel and Robinson 1988, Yssel 1989, Bruton *et al.* 1991, Clark *et al.* 1996, Foster 1997) and *T. coronatus* (Lasiak 1986), as well as the smaller intertidal species *Oxystele variegata*, *O. tabularis* and *Monodonta australis* (Joska and Branch 1983, Lasiak 1987, McQuaid 1982, 1983). In their investigation of the harvesting potential of *T. sarmaticus*, Bruton *et al.* (1991) suggested that the harvest levels of alikreukel at Cape St Francis are sustainable, and that the legislated width-at-capture (63.5 mm), prevented overexploitation of the spawning stocks off the Eastern Cape. In contrast, previous reports (de Villiers 1970, Lombard 1977, Yssel 1989) concluded that a commercial fishery for this species would not be sustainable because of its slow growth rates and irregular distribution.

The lack of research on the biology and distribution of *T. cidaris* and *O. sinensis* made it difficult to set a total allowable catch (*TAC*) for any proposed experimental fishery, or to decide on suitable fishing grounds. A project aimed at estimating the exploitable biomass and potential yield of these herbivorous gastropods off the South-Western Cape coast of South Africa was therefore initiated. Although not an intended target species, *T. sarmaticus* was also included in this investigation. The results of this study and the management suggestions based on these results are presented in this paper.

## MATERIAL AND METHODS

The study was undertaken between 1996 and 1999 on the South-Western Cape coast of South Africa, between Yzerfontein (33°30´S, 18°18´E) and Quoin Point (34°47´S, 19°39´E), with particular focus on the area proposed for the fishery between Cape Hangklip (34°20´S, 18°48´E) and Danger Point (34°38´S, 19°20´E; Fig. 1).

### Morphometrics and flesh yield

Samples of all three winkle species were collected from intertidal and subtidal regions throughout the study area. Whole wet weight was determined after blotting dry. Animals were immersed briefly in boiling water to kill them and to release the columella muscle. To obtain whole dry weight, shells were cracked to ensure complete dehydration to constant weight at 80°C. For shell-free weight, the animal was removed from the shell after being killed, the operculum separated from the foot, the flesh blotted dry and weighed before being dried and re-weighed to determine shell-free dry weight. A flesh-yield relationship for *T. cidaris* was ascertained by separating the foot from the visceral mass to establish wet and dry weights for the edible portion of the animal. The foot flesh yield for *T. cidaris* was estimated from the flesh yield power curve. All weights were measured to the nearest 0.01 g. Because of the availability of data from previous studies, shell-free and dry weight relationships for *T. sarmaticus* were not repeated. Because the most convenient shell size measure in the field is that of shell width, relationships of the morphometric parameters to shell width were established.

### Shore-based biomass estimates

Biannual surveys were conducted at nine locations between Cape Hangklip and Danger Point during 1996 and 1997 (Fig. 1). At each of the locations, the intertidal and immediate subtidal regions around the mean low water spring (MLWS) mark were divided into four broad ecological zones:

- Zone 1, Upper splash zone
- Zone 2, High intertidal zone dominated by *O. variegata*
- Zone 3, Around the MLWS tide mark
- Zone 4, Infratidal region down to 2 m depth.

Within each of these zones, 20 quadrats (0.5 m$^2$) were randomly placed and the numbers of *T. sarmaticus*, *T. cidaris* and *O. sinensis* were recorded. As all three species have a cryptic distribution, care was taken to include animals hidden in crevices and under boulders. Rocks and boulders that were overturned during sampling were carefully replaced. Width-frequency data were collected for each species for each zone. Having established the mean width of animals collected in each quadrat, the biomass per quadrat was subsequently calculated from:

$$\text{Biomass} = a\left(\frac{\sqrt[3]{\sum_{i=1}^{n}\left(L_i\right)^3}}{n}\right)^b \quad , \qquad (1)$$

where $a$ and $b$ are constants for the width/mass relationship, $L_i$ the width of the $i$th shell (mm) and $n$ is the number of shells in the sample.

The coefficient of variation ($CV$) for the estimates in each zone was calculated from:

$$CV_{zone} = \frac{\frac{\sigma_B}{\sqrt{n}}}{\mu_B} \quad , \qquad (2)$$

where $\sigma_B$ is the standard deviation of the estimates, $\mu_B$ the mean biomass/abundance and $n$ the number of quadrats or transects in the zone.

Because the estimates for each depth zone are assumed to be independent, the overall $CV$ for several zones is given by

$$CV_{total} = \frac{\sqrt{\sum_{i=1}^{n}\left(CV_i B_i\right)^2}}{\sum_{i=1}^{n} B_i} \quad , \qquad (3)$$

where $B_i$ is the biomass in the $i$th zones and $CV_i$ is the $CV$ of the biomass in the $i$th zone.

### Catch per unit effort

The abundance and biomass data for *T. cidaris* from

Zone 4 were compared to catch per unit effort (wet weight collected per 10-minute diving interval) recorded concurrently by two snorkel divers at each of the sites. The diving interval included searching time, so simulating the proposed commercial harvesting method.

### Subtidal biomass estimates

Underwater transects 10 m long (bottom distance) were swum on SCUBA in 2–5 m water depth, and the giant winkles in a 1-m wide strip were counted. Where possible, transects were spaced 0.5–2 km apart along the length of the rocky sections of coastline from Yzerfontein to Quoin Point, including Dassen, Robben and Dyer islands. In most of these regions, additional transects in depth gradients of 5–10 m and 10–15 m of water were also swum. Animals were collected to obtain width-frequency measures, and the biomass was calculated as described in Equation 1. In all, 1 512 transects were swum between 1996 and 1999. Data from broad geographical areas were pooled to obtain a mean density and biomass per square metre for that area.

### Potential yield

An attempt was made to calculate the potential yield of the three species of giant winkle between Cape Hangklip and Quoin Point. Although abundance and biomass estimates were available as far as Yzerfontein on the West Coast, appreciable densities of winkles were only recorded from Pringle Bay eastwards. As higher densities coincided with fishing zones A–D for abalone *Haliotis midae*, the same management areas were used for the giant winkles (Fig. 1). Area A included Dyer Island, Pearly Beach, Soetfontein and Quoin Point; Area B included Danger Point and Kleinbaai; Area C included Mudge Point, Onrus and Hermanus; and Area D included Cape Hangklip, Stoney Point, Betty's Bay, Palmiet and Kleinmond.

Biomass and density estimates for each management area were obtained by multiplying the density and biomass estimates obtained from individual depth zones in Equations 2 and 3 by the area of suitable habitat in each zone. For the intertidal region, "suitable habitat" was estimated by multiplying the coastline length by the average intertidal width in each zone; for subtidal data, it was presumed that the kelp area matched the distribution of winkles. Estimates of areas covered by kelp were obtained from Tarr (1993). In the absence of suitable field data, 40% of the kelp area from 0–5 m was assigned to the 0–2 m zone and 60% to the 2–5 m depth zone. It was assumed that the biomass estimates calculated in (2) and (3) above were for spawning biomass, and not total biomass. This assumption is supported by the fact that <1% (*T. sarmaticus*), 4% (*T. cidaris*) and 3% (*O. sinensis*) of the animals in the width-frequency distributions were smaller than the width at maturity.

### Reference points for harvesting

Three fisheries reference points were calculated: $F_{0.1}$; *MSY* and $0.5FB_0$. The $F_{0.1}$ reference point comes from a yield-per-recruit analysis and is widely used in fisheries management. The maximum sustainable yield (*MSY*) is theoretically the highest yield that can be indefinitely sustained without the fishery collapsing. It is normally used as an upper limit to the recommended fishing mortality level. The third reference point, $0.5FB_0$, is the level of fishing mortality that results in an equilibrium fishable biomass that is 50% of the pre-exploitation fishable biomass. Fishable biomass is the biomass above the width at first capture. A more usual reference point would be $0.5SB_0$, the fishing mortality that results in an equilibrium spawning biomass that is 0.5 times the pre-exploitation spawning biomass. However, because in all three winkle species the width at capture is much greater than the width at maturity, even an infinite fishing mortality would seldom result in a spawning stock biomass decreasing to this level.

### Model structure, equations and parameters

Assessments were performed using a preliminary version of the YIELD software (Branch *et al*. 2000). This is an age-structured model. Monthly time steps were used to calculate the reference points. Spawning and fishing were assumed to occur throughout the year.

Widths were converted to (and from) ages using the Von Bertalanffy growth equation (and its inverse):

$$L = L_\infty\,(1 - e^{-K(t-t_0)})$$

(to calculate the width at a given age) (4)

and

$$t = t_0 + \frac{\ell n\left(\dfrac{L_\infty}{L_\infty - L}\right)}{K}$$

(to calculate the age at a given width) , (5)

where $L$ is the width of the shell (mm), $L_\infty$ the asymptotic (maximum) width (mm), $K$ the growth rate (year$^{-1}$), $t$ the age (year) and $t_0$ is the theoretical age (year) at which the width is zero.

It was assumed that $t_0$ was 0 for all three species. Von Bertalanffy parameters for *T. sarmaticus* were taken from Yssel (1989): $L_\infty$ is 129 mm and $K$ is 0.205 year$^{-1}$.

Some data were available for *T. cidaris* from mark-recapture experiments. Animals were measured, marked and recaptured after 204 days. All 92 recaptured animals were between 44.5 and 59.1 mm, not a very wide range of widths. Nonetheless, two different methods were used to calculate the values of $K$ and $L_\infty$: Ford-Walford and Gulland-Holt, both described in Sparre and Venema (1998). The Ford-Walford method gave $K = 0.57$ year$^{-1}$; $L_\infty = 57.6$ mm; the Gulland-Holt method gave $K = 0.35$ year$^{-1}$; $L_\infty = 61.9$ mm. The estimates from the Gulland-Holt method provided a slightly better fit to the mark-recapture data, and are therefore preferred.

No data were available for *O. sinensis*. However, a very rough estimator for $L_\infty$ is given by Pauly (1984):

$$L_\infty = \frac{L_{max}}{0.95} \quad , \tag{6}$$

where $L_{\max}$ is the maximum sampled width in the population.

The maximum sampled width for *O. sinensis* was 53 mm, and hence $L_\infty = 56$ mm. Because *O. sinensis* is slightly smaller than *T. cidaris*, it seems likely that its growth rate would be slightly faster (McLachlan and Lombard 1981, McQuaid 1983, Jensen 1997). $K$ was therefore assumed to be 0.4 year$^{-1}$.

Shell widths were converted to mass (g) using the width-mass equation

$$W = \alpha L^{\beta} \quad , \tag{7}$$

where $W$ is the mass (g), $L$ the width (mm) and $\alpha$ and $\beta$ are constants.

Relative values for $\alpha$ and $\beta$ were 0.283 and 2.95 for *T. sarmaticus*, 0.322 and 3.04 for *T. cidaris* and 0.361 and 2.99 for *O. sinensis*.

The fishing selectivity function was assumed to be knife-edge in all three cases, and hence is defined by the value of the width at capture ($L_c$) alone. There is a legal minimum capture width of 74 mm for *T. sarmaticus*. Width at capture was assumed to be 40 mm for *T. cidaris* and *O. sinensis,* because below this size the flesh weight of the animal is trivial.

The maturity ogive was also assumed to be knife-edge, and is defined by the estimated width at maturity ($L_m$). Sexual maturity for *T. sarmaticus* was taken to be 50 mm, based on dissection results (Foster 1997), although this is smaller than previously reported values of 60 mm (Lombard 1977) and 64 mm (Bruton *et al.* 1991). Dissections gave estimates of $L_m$ of about 26 mm for *T. cidaris*. No data were available for *O. sinensis*, so the $L_m$ value for *T. cidaris* was decreased to an estimated value of 23 mm for the smaller *O. sinensis*.

Too few data were available to attempt to estimate stock-recruitment parameters. Nevertheless, Yssel (1989) describes a long-term time series for *T. sarmaticus* in the Tsitsikamma National Park on the east coast of South Africa, which suggests that recruitment might be independent of spawning stock size. Therefore, this relationship was assumed to be constant. However, because all three species are thought to be broadcast spawners (Lasiak 1986, 1987), there is a possibility that depensatory recruitment may occur (where the population may collapse at low spawning stock levels). From data presented in Yssel (1989), it was possible to estimate the recruitment $CV$ to be 0.84, although this value was not used in obtaining the results presented in this paper.

Natural mortality is notoriously difficult to estimate from population data. It was assumed that current fishing mortality is negligible for the three species (although this assumption is probably not correct for *T. sarmaticus*), and hence total mortality is assumed to be equal to natural mortality. Two methods were used to calculate total mortality ($Z$): the Beverton-Holt $Z$ equation, and the length-converted-catch-curve (LCCC) method (Ricker 1975). The latter provides a more direct measure of $Z$. For these methods, width-frequency distributions collected throughout the study area were grouped to increase the number of samples for each species.

The Beverton-Holt $Z$ equation is:

$$Z = \mathrm{K}\left[\frac{L_\infty - \bar{L}}{\bar{L} - L'}\right] \quad , \tag{8}$$

where $Z$ (year$^{-1}$) is total mortality (assumed equal to natural mortality), $\bar{L}$ the average width of all animals greater than $L'$ (mm) $L'$ and is the width just greater than the width of maximum frequency (mm).

The LCCC method proceeds as follows: plot the age of the animals on the horizontal axis and the log of the numbers divided by the change in age on the vertical axis. The gradient of this plot is $-Z$ for those ages greater than the age of maximum frequency.

Estimates of $M$ (for Beverton-Holt and LCCC respectively) were 0.40 and 0.36 for *T. sarmaticus*, 1.46 and 0.875 for *T. cidaris* and 2.35 and 1.70 for *O. sinensis*. The mean value for $M$ of the two methods was used for *T. sarmaticus* (0.38), and the more direct LCCC method preferred for the other two species. The mark-recapture experiment gave an estimate of $M$ of 3.03 for *T. cidaris*, but this must be treated as a maxi-

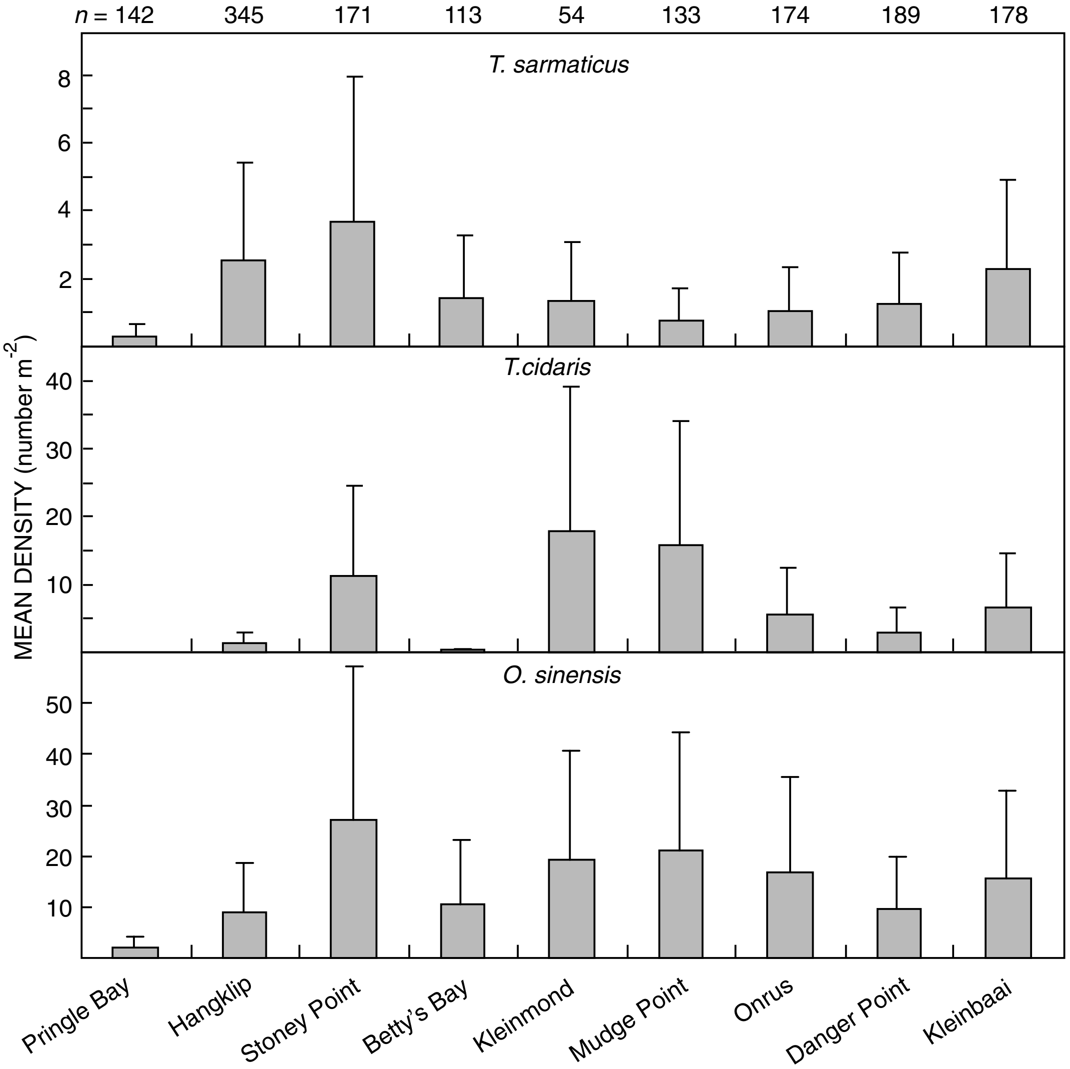

Fig. 2: Mean density of *T. sarmaticus, T. cidaris* and *O. sinensis* in the intertidal zones and at depths down to <2 m at nine sampling sites in the South-Western Cape. The standard error and number of quadrats (*n*) are also shown

mum value because tag loss, emigration and the failure to find marked animals would substantially inflate it.

**Incorporating uncertainty into the parameter estimates**

Estimating uncertainty is even more difficult than obtaining "best estimates". The distributions of uncertainty presented in this paper are equivalent to informative Bayesian priors, and are known to be difficult to obtain (Punt and Hilborn 1997). The shape of the distributions is lognormal where the parameters are expected to be skewed, and cannot be negative, normal for $\beta$ (which is not skewed), and uniform for $L_m$ and $t_0$. The *CV*s for biomass estimates were obtained directly from the survey results; for the other parameters, greater uncertainty is indicated by either higher *CV*s or wider

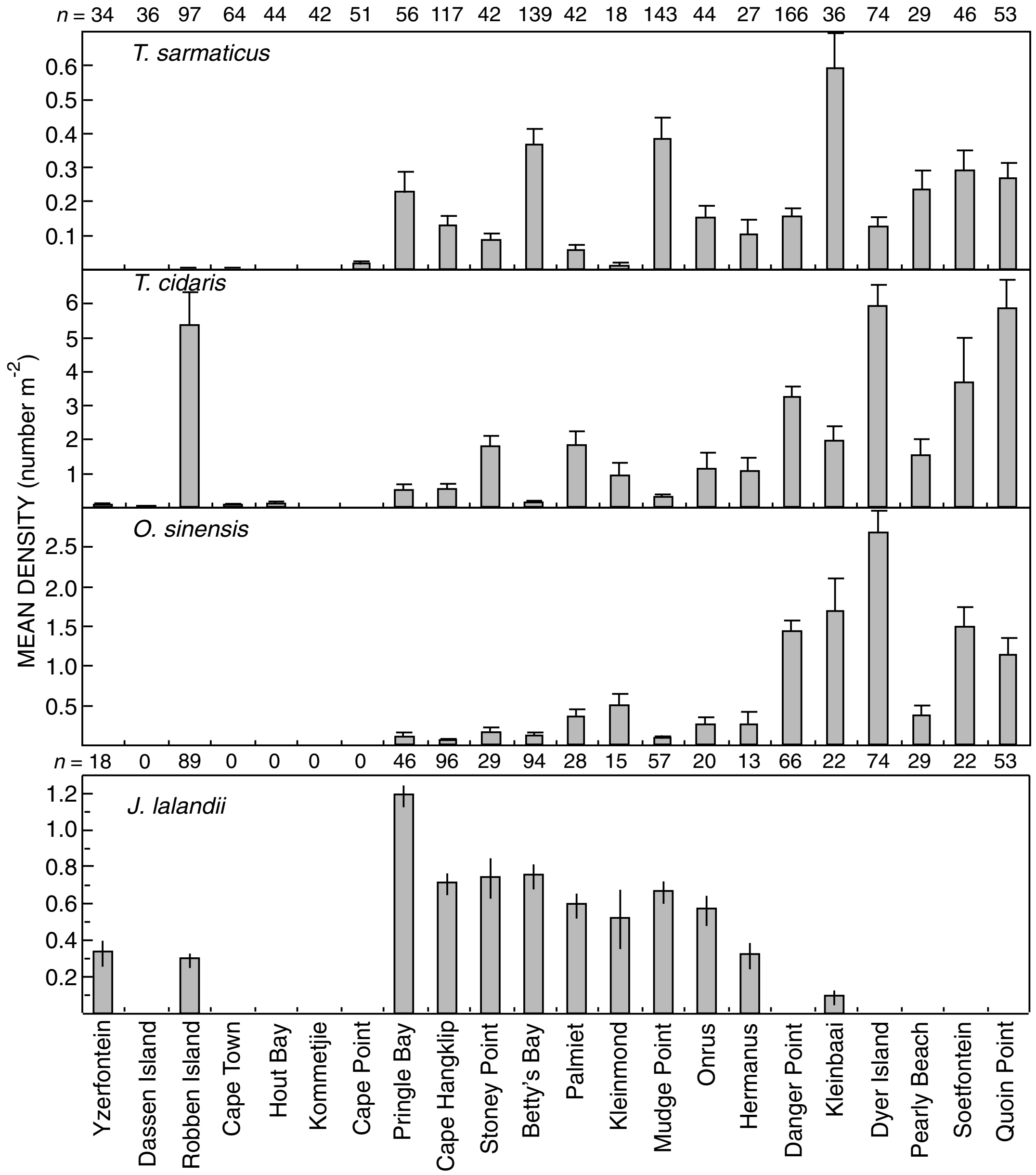

Fig. 3: Mean density of winkles *T. sarmaticus, T. cidaris* and *O. sinensis* and the rock lobster *J. lalandii* in 2–10 m depths in kelp-bed habitats between Yzerfontein and Quoin Point. The standard errors and number of 10 m transects for winkles and rock lobster (*n*) are also shown

ranges, depending on the type of distribution. In this study, as discussed above, some parameters ($L_\infty$, α, β, $L_m$ and $L_c$) are well known, and accordingly are assigned small *CV*s or ranges. Similarly, by definition, $t_0$ is expected to be close to 0. However, values for *K* and *M* are poorly known: essentially based on limited

Table I: Morphometric relationships to shell width ($w$, mm), $r^2$-values and the number of specimens in the sample ($n$) for *T. sarmaticus*, *T. cidaris* and *O. sinensis*

| Parameters | *T. sarmaticus* | *T. cidaris* | *O. sinensis* |
|---|---|---|---|
| Whole wet weight (g) | $0.000316w^{2.95}$ | $0.000294w^{3.04}$ | $0.000369w^{2.99}$ |
| $r^2$ | 0.99 | 0.98 | 0.95 |
| $n$ | 224 | 419 | 1 068 |
| Whole dry weight (g) | $0.0002w^{2.26}$ | $0.000382w^{2.86}$ | $0.0000752w^{3.35}$ |
| $r^2$ | 0.99 | 0.99 | 0.98 |
| $n$ | 151* | 243 | 144 |
| Shell-free wet weight (g) | | $0.000121w^{2.86}$ | $0.0000266w^{3.32}$ |
| $r^2$ | | 0.96 | 0.98 |
| $n$ | | 166 | 113 |
| Shell-free dry weight (g) | | $0.0000257w^{2.96}$ | $0.00000594w^{3.39}$ |
| $r^2$ | | 0.96 | 0.97 |
| $n$ | | 166 | 113 |
| Foot flesh wet yield (g) | $0.00005w^{2.95**}$ | $0.000195w^{2.48}$ | |
| $r^2$ | 0.99** | 0.90 | |
| $n$ | 151** | 119 | |
| Operculum diameter (mm) | $0.504w + 1.79$* | $0.351w + 1.15$ | |
| $r^2$ | 0.99* | 0.99 | |
| $n$ | 151* | 166 | |
| Shell length (mm) | $0.846w-1.221$ | $0.942w-4.187$ | $0.821w-0.895$ |
| $r^2$ | 0.98 | 0.94 | 0.86 |
| $n$ | 224 | 427 | 1 080 |

* from Lombard (1977)
** from Yssel (1989)

mark-recapture studies and the results of Yssel (1989). The value of $K$ for *T. sarmaticus* is obtained from Yssel (1989) and assumed to have greater confidence ($CV = 0.2$) than the estimates for *T. cidaris,* which were 0.57 and 0.35 from the two methods. When a $CV$ of 0.4 was assigned to $K$ for *T. cidaris*, there was some probability of $K$ being either of those two values. The $CV$ about $K$ for *O. sinensis* was based directly on that for *T. cidaris* and is therefore also assumed to be 0.4. $CV$s for $M$ were assumed to be the same for all three species and were the most difficult to estimate. However, estimates of this parameter were more uncertain than for the other parameters; mark-recapture experiments gave an upper limit on plausibility for *T. cidaris* at 3.03, and the probability distributions were required to give some probability that the Beverton-Holt and LCCC estimates could occur. A $CV$ of 0.5 for $M$ satisfied these three conditions.

## RESULTS

### Morphometrics and flesh yield

The results of the morphometric investigations are summarized in Table I. For animals wider than 30 mm, the mean foot flesh yield was 8.5% of whole wet weight and 48.9% of shell-free wet weight.

### Abundance and biomass estimates

The mean abundance and biomass of the three species of giant winkle recorded between Yzerfontein and Quoin Point differed markedly between ecological zones/depths as well as between sampling areas in both intertidal (Fig. 2) and subtidal (Fig. 3) habitats. None of the species in question was present in the high intertidal zone, but juveniles of all three species tended to frequent the low intertidal and shallow subtidal zones, as evidenced by an increase in mean size with depth (Fig. 4). Highest densities of *T. sarmaticus* were recorded intertidally, abundances subsequently decreasing with depth. With the exception of a few extremely large individuals recorded at Robben Island and in the Cape Point Nature Reserve (mean size >130 mm), *T. sarmaticus* were generally absent on the West Coast. However, in areas east of Cape Hangklip not readily accessible to shore-based recreational divers (e.g. Betty's Bay Reserve, Mudge Point and Kleinbaai), average densities of >2 m$^{-2}$ were regularly recorded. Furthermore, *T. sarmaticus* were almost absent from localities of extreme wave exposure, such

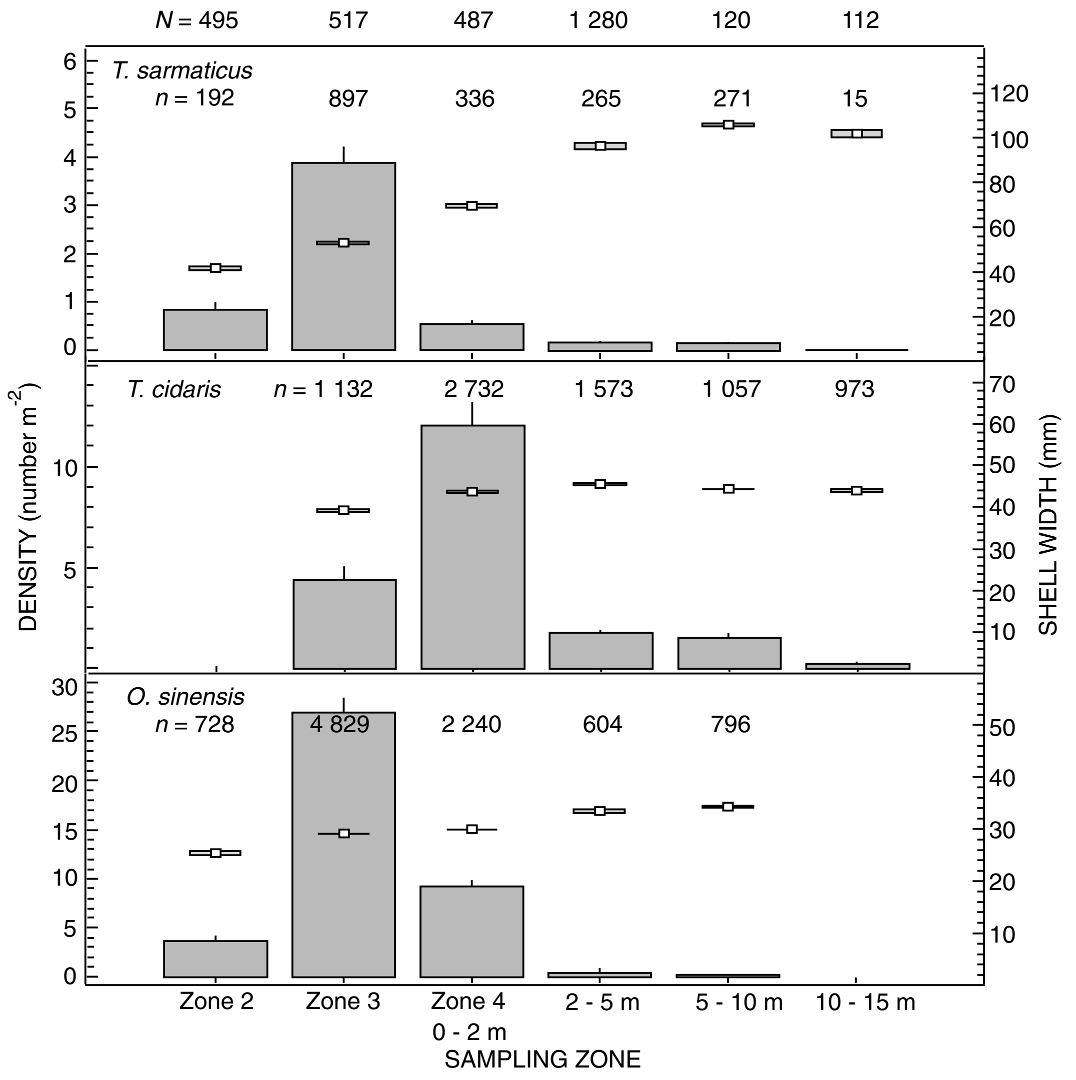

Fig. 4: Change in density (solid bars) and shell width (squares) with depth for *T. sarmaticus*, *T. cidaris* and *O. sinensis* showing the means and standard errors. *N* denotes the sample size for density data and *n* denotes the sample size for width data

as Kleinmond.

*T. cidaris* occurs only occasionally in the intertidal, where it is found in lower intertidal regions under boulders, in crevices and in tidal pools. Although observed at depths of 30 m (AP, pers. obs.), maximum densities were recorded at 0–2 m. *T. cidaris* is generally poorly represented on the West Coast, isolated populations being recorded at Bokpunt near Yzerfontein and at Robben Island. The mean abundance at this latter site is in fact one of the highest recorded in the entire study area (5.3 m$^{-2}$), with maximum densities of up to 72.5 m$^{-2}$ (170.4 g wet weight m$^{-2}$) on the sheltered side of the island. Only on the eastern limits of the study area, where extensive kelp beds offer a goos measure of shelter, did *T. cidaris* reach similar levels of abundance (5.9 and 5.8 m$^{-2}$ at Dyer Island and Quoin Point respectively).

Although *O. sinensis* was recorded to depths of 7 m,

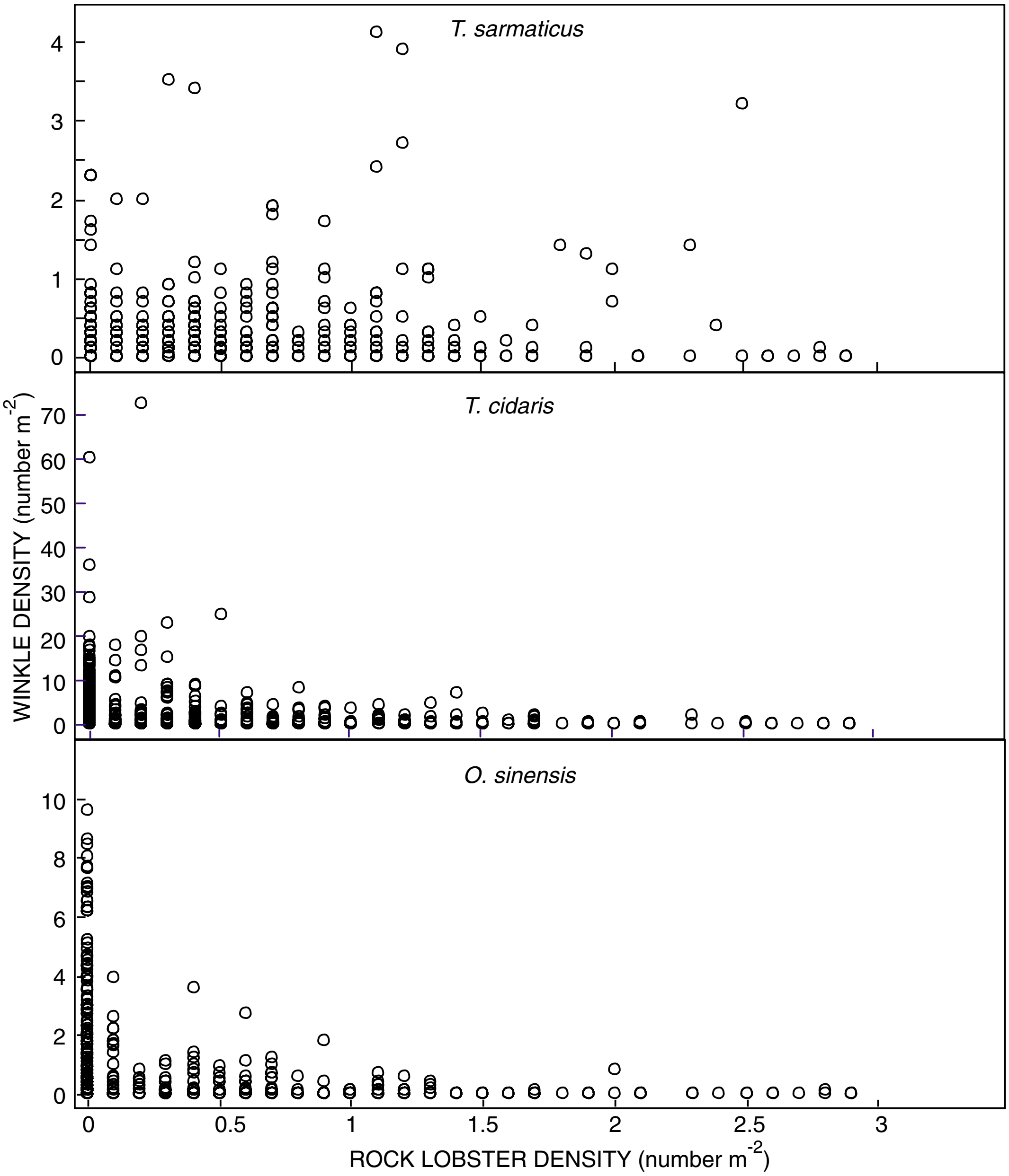

Fig. 5: Relationship between rock lobster *Jasus lalandii* density and the densities of *T. sarmaticus*, *T. cidaris* and *O. sinensis*

densities were highest in the lower intertidal. As with the other winkle species, only a few individuals were recorded off the West Coast, from Dassen and Robben islands, and numbers increased towards the eastern limits of the study area.

Of interest is the almost total absence of *T. cidaris* and *O. sinensis* from the subtidal of the Betty's Bay marine reserve. Large drifts of empty shells were ob-

Table II: Estimated mean density and mean biomass of *T. sarmaticus*, *T. cidaris* and *O. sinensis* in the Stoney Point, Betty's Bay Marine Reserve and Palmiet areas. The number of transects and significance values of ANOVA comparisons between sites are also given

| Species | Stoney Point | Betty's Bay | Palmiet | *p* |
|---|---|---|---|---|
| | | *Density ($m^{-2}$)* | | |
| *T. sarmaticus* | 0.073 | 0.325 | 0.047 | $3.356 \times 10^{-6}$ |
| *T. cidaris* | 1.567 | 0.132 | 1.587 | $6.667 \times 10^{-12}$ |
| *O. sinensis* | 0.139 | 0.096 | 0.299 | 0.005 |
| | | *Biomass (g $m^{-2}$)* | | |
| *T. sarmaticus* | 23.643 | 98.716 | 14.153 | $1.320 \times 10^{-5}$ |
| *T. cidaris* | 67.356 | 5.147 | 60.054 | $1.8989 \times 10^{-11}$ |
| *O. sinensis* | 4.496 | 2.853 | 7.161 | 0.050 |
| *n* | 49 | 158 | 50 | |

served, however, suggesting a recent catastrophic mortality. The density and biomass of *T. cidaris* and *O. sinensis* were significantly lower within the reserve than in neighbouring areas (ANOVA, Tukey HSD *post hoc* test for unequal *n*, $p < 0.05$). However, the density and biomass of *T. sarmaticus* was significantly higher (ANOVA, Tukey HSD *post hoc* test for unequal *n*, $p < 0.05$) than in neighbouring areas (Stoney Point and Palmiet , Table II).

Analysis of West Coast rock lobster *Jasus lalandii* abundances in these areas (AP, unpublished data) reveals that rock lobster densities have increased from 1998 to 1999, this increase being significant within the marine reserve (Student's *t*-test, $df = 92$, $p = 0.00007$) where the stocks are protected from recreational fishers. Furthermore, rock lobster densities are higher within the reserve than in adjacent areas, although not significantly so (ANOVA, Tukey HSD *post hoc* test for unequal *n*, $df = 148$, $p = 0.415$ – see also Mayfield and Branch 2000). The rock lobster data suggest a general decrease in their abundance in water <10 m deep from west to east throughout the study area, with a concomitant increase in abundance of *T. cidaris* (see Fig. 3). The relationships between rock lobster density and winkle densities are further illustrated in Figure 5. It appears that *T. cidaris* and *O. sinensis* are absent when there is a high density of rock lobsters, whereas the larger *T. sarmaticus* remains largely unaffected by increasing numbers of rock lobsters.

Pooling the width frequency distributions recorded from subtidal transects provides an indication of the mean size of the populations of the three species of winkle sampled on the Western Cape coast (Fig. 6). A decrease in mean size is apparent from west to east across the study area for all three species. This is paralleled by a decrease in maximum size of individuals recorded. For all three species of winkle, recruitment appears to be sporadic, young cohorts appearing at some localities yet being absent from other areas. Monthly sampling at three sites at Cape Hangklip indicated that recruitment was strongest during late summer and winter (AP, unpublished data), although age-class 0 cohorts of *T. cidaris* and *O. sinensis* were occasionally recorded as early as January/February.

## Catch per unit effort (*cpue*)

The width-frequency distributions of the diver-collected winkles differed significantly from those recorded in the quadrats (Wilcoxon's matched pairs test, $n = 496$, $p = 0.00003$), the median size of winkles

Table III: Habitat area in each of the four management areas. Kelp area in depths >10 m were excluded, because <0.1% of the biomass of any of the three species was recorded at such depths

| Depth zone | Fishery Management Areas ($m^2$) | | | |
|---|---|---|---|---|
| | A | B | C | D |
| High intertidal | 119 169 | 98 667 | 82 647 | 119 301 |
| MLWS | 158 892 | 131 556 | 110 196 | 159 068 |
| 0–2 m | 2 481 060 | 1 356 150 | 867 558 | 1 215 148 |
| 2–5 m | 3 721 590 | 2 034 224 | 1 301 338 | 1 822 723 |
| 5–10 m | 1 230 521 | 886 499 | 854 893 | 1 234 734 |

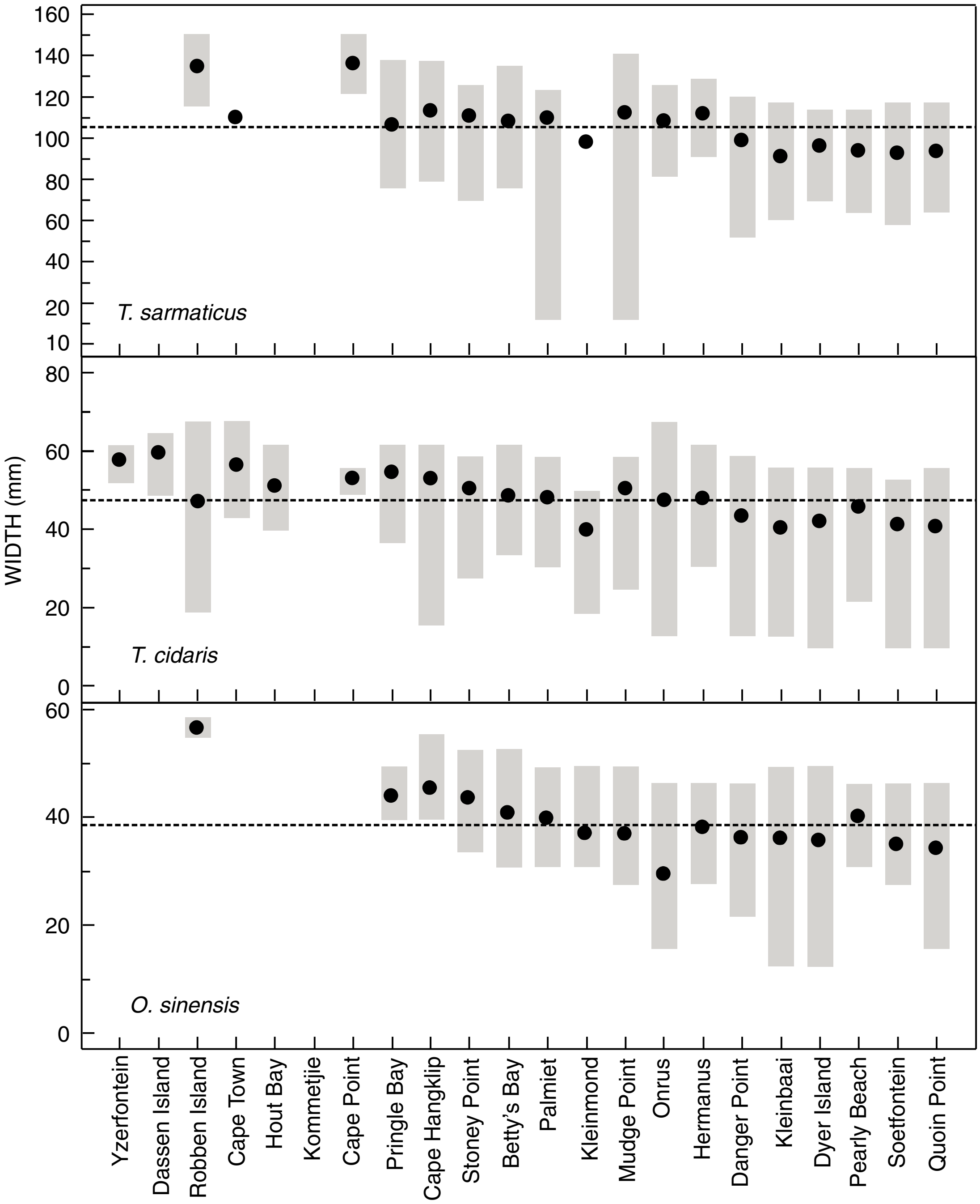

Fig. 6: Mean width (dots) and range (bars) of *T. sarmaticus*, *T. cidaris* and *O. sinensis* between Yzerfontein and Quoin Point. The overall mean width for each species is shown by a dotted line

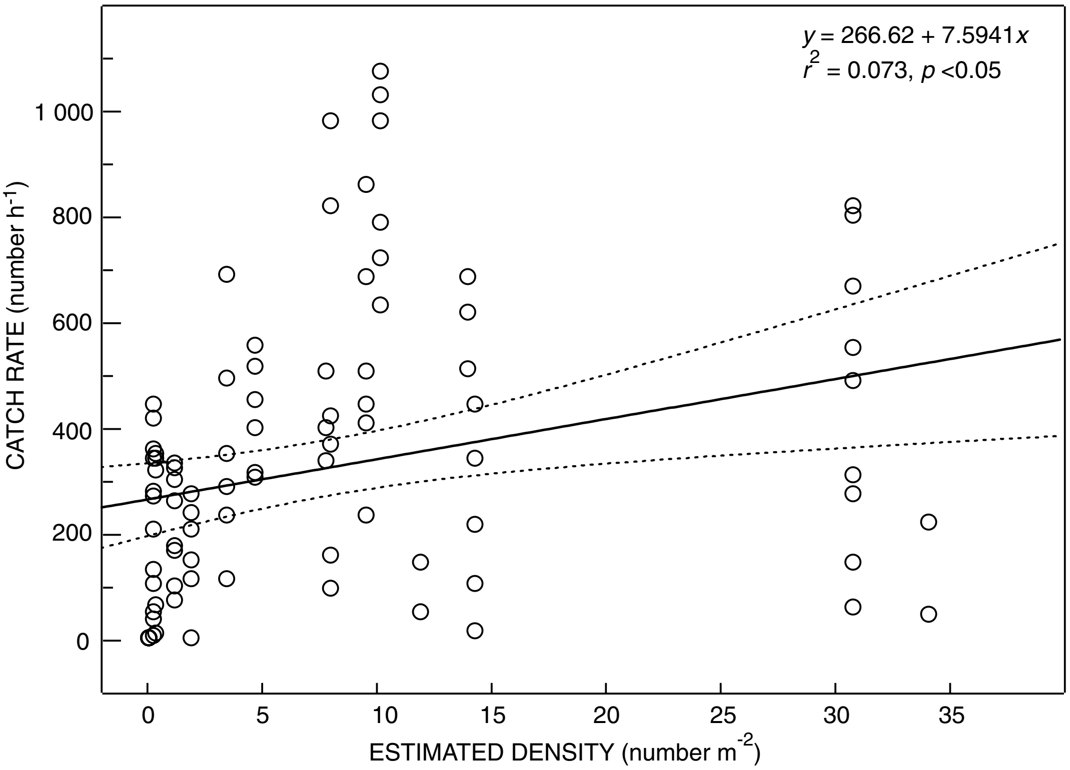

Fig. 7: Correlation between the catch rate of *T. cidaris* made by three divers and the estimated winkle density for the corresponding sampling site

collected by divers generally being larger than recorded from quadrats at the same sampling site. As the catch rates among the three divers used in the *cpue* experiment were not significantly different (ANOVA, $df = 93$, $p = 0.536$), the data were pooled. There was a significant, positive correlation between catch rates (number $h^{-1}$) and estimated mean density (Fig. 7, $r = 0.27$, $p < 0.05$). The mean catch rate was 320 $h^{-1}$, which corresponds to a weight of 13 kg $h^{-1}$.

## Potential yield

Of the total habitat area available to giant winkles, only 3–5% of was estimated to fall in the intertidal (Table III). The larger habitat area in the infratidal consequently resulted in greater estimated density and biomass below the MLWS level. Most of the biomass for *T. sarmaticus* was at 2–5 m, but *T. cidaris* and *O. sinensis* had greatest biomasses at 0–2 m (Tables IV, V). Greatest biomasses for all three species were in management area A; this finding was most pronounced for *O. sinensis*.

Parameters used in the yield assessments are summarized in Table VI. Results are separated into two groups: for animals at all depths, and for animals in depths >2 m only. These correspond to two scenarios: first, where the type of harvesting is unrestricted and animals may be caught in shallow water; second, where only a boat-based diving operation is allowed. The total yield from all four management areas (A–D) was calculated using the best point estimates of the parameters.

### BEST POINT ESTIMATES

If fishing is allowed at depths >2 m, the annual sustainable yield at $0.5FB_0$ is 77 tons for *T. sarmaticus*, 175 tons for *T. cidaris*, and 25 tons for *O. sinensis* (Table VII).

Table IV: Estimated density (whole wet weight in g $m^{-2}$) of each species in the four management areas. Estimates are split by depth zone. Densities estimates deeper than 2 m have been inflated by 15% to compensate for animals missed on transects at those depths

| Depth zone | Fishery Management Areas | | | | | | | | Average | |
|---|---|---|---|---|---|---|---|---|---|---|
| | A | | B | | C | | D | | | |
| | Density | *CV* | Density | *CV* | Density | *CV* | Density | *CV* | Density | *CV* |
| *T. sarmaticus* | | | | | | | | | | |
| High intertidal | 8.8 | 0.38 | 0.4 | 0.70 | 5.5 | 0.74 | 28.7 | 0.23 | 10.8 | 0.20 |
| Low intertidal | 33.5 | 0.21 | 78.3 | 0.21 | 134.4 | 0.22 | 226.5 | 0.12 | 118.2 | 0.09 |
| 0–2 m | 63.4 | 0.27 | 63.2 | 0.27 | 39.5 | 0.34 | 31.3 | 0.29 | 49.3 | 0.15 |
| 2–5 m | 56.4 | 0.11 | 59.9 | 0.14 | 147.4 | 0.20 | 80.0 | 0.11 | 85.9 | 0.09 |
| 5–10 m | 14.2 | 0.29 | 26.8 | 0.43 | 20.9 | 0.38 | 61.4 | 0.37 | 30.8 | 0.22 |
| *T. cidaris* | | | | | | | | | | |
| High intertidal | 0.0 | 0.00 | 0.0 | 0.00 | 0.0 | 0.00 | 0.0 | 0.00 | 0.0 | – |
| Low intertidal | 51.5 | 0.35 | 9.9 | 0.60 | 205.7 | 0.25 | 99.5 | 0.21 | 91.6 | 0.16 |
| 0–2 m | 153.8 | 0.24 | 328.5 | 0.23 | 731.2 | 0.16 | 332.9 | 0.15 | 386.6 | 0.10 |
| 2–5 m | 147.7 | 0.11 | 103.2 | 0.09 | 21.9 | 0.37 | 26.0 | 0.18 | 74.7 | 0.07 |
| 5–10 m | 66.2 | 0.25 | 35.9 | 0.40 | 56.8 | 0.31 | 21.2 | 0.42 | 45.0 | 0.16 |
| *O. sinensis* | | | | | | | | | | |
| High intertidal | 0.0 | 0.00 | 0.6 | 0.72 | 21.1 | 0.30 | 41.4 | 0.16 | 15.8 | 0.14 |
| Low intertidal | 68.6 | 0.19 | 249.8 | 0.14 | 287.8 | 0.10 | 396.3 | 0.07 | 250.6 | 0.05 |
| 0–2 m | 231.2 | 0.06 | 46.6 | 0.21 | 142.5 | 0.12 | 70.4 | 0.10 | 122.7 | 0.05 |
| 2–5 m | 38.0 | 0.08 | 51.2 | 0.20 | 5.2 | 0.20 | 4.6 | 0.16 | 24.8 | 0.11 |
| 5–10 m | 8.0 | 0.31 | 7.5 | 0.32 | 0.0 | 0.00 | 0.0 | 0.00 | 3.9 | 0.22 |

Note that the estimates for *MSY* involve an "infinite" fishing mortality for *T. cidaris* and *O. sinensis*. This is because the width at first capture is much higher than the width at maturity, so that the model predicts highest yields if animals are caught as soon as they reach the width at first capture. This in turn means that, although the spawning biomass is never reduced far below pre-exploitation levels, the fishable biomass is reduced to very low levels.

### INCORPORATING UNCERTAINTY

Providing best estimates alone would give a false impression of the reliability of these results, because they are based on many potentially inaccurate assumptions. However, by incorporating uncertainty into the parameter estimates, a better idea of the reliability of the results is obtained. Note that ranges quoted here are 95% probability intervals.

For *T. sarmaticus* (Fig. 8), there is greater confidence in the input parameters than for the other two species. Nonetheless, little more can be concluded other than that 0.5 $FB_0$ probably lies between 0.1 and 0.6. The corresponding annual sustainable catch (for zones >2 m deep) is 25–130 tons. Spawning biomass at these levels of fishing mortality is reduced to 15–96% of pre-exploitation spawning biomass. Uncertainty is much greater for *T. cidaris* (Fig. 9), where 0.5$FB_0$ has a greatest probability of lying between 0.2 and 1.6. Corresponding catches (>2 m deep) are 8–360 tons; spawning biomass is reduced to 20–99% of pre-exploitation spawning biomass. The uncertainties for *O. sinensis* (Fig. 10) overwhelm the yield estimates; 0.5 $FB_0$ is 0.5–3.8, with corresponding catches of 0.2–110 tons. Spawning biomass decreases to 42–100% of pre-exploitation levels.

## DISCUSSION

Clearly, *T. cidaris* usually makes up the bulk of the subtidal biomass of winkles, whereas *O. sinensis* contributes most to the estimated intertidal winkle biomass.

De Villiers (1970), Lombard (1977) and Clark *et al.* (1996) reported marked geographical differences in densities of *T. sarmaticus* associated with sampling areas of different topography and wave exposure along the east coast of South Africa. Worthington and Fairweather (1989) found that the density of an Australian *Turbo* varies greatly within an area, and ascribed this to differences in micro- as well as macrohabitat. This

Table V: Estimated biomass of each species in the four management areas. Estimates are split by depth zone. Biomass estimates are obtained by multiplying the estimated suitable habitat area (Table II) by the density estimates (Table III). Less than 0.1% of the biomass of any species occurred below 10 m

| Depth zone | Fishery Management Areas | | | | | | | | Average | |
|---|---|---|---|---|---|---|---|---|---|---|
| | A | | B | | C | | D | | | |
| | Biomass (tons) | *CV* | Biomass (tons) | *CV* | Biomass (tons) | *CV* | Biomass (tons) | *CV* | Biomass (tons) | *CV* |
| | | | | | *T. sarmaticus* | | | | | |
| High intertidal | 1.0 | 0.38 | 0.0 | 0.70 | 0.5 | 0.74 | 3.4 | 0.23 | 5.0 | 0.19 |
| Low intertidal | 5.3 | 0.21 | 10.3 | 0.21 | 14.8 | 0.22 | 36.0 | 0.12 | 66.5 | 0.09 |
| 0–2 m | 157.4 | 0.27 | 85.7 | 0.27 | 34.2 | 0.34 | 38.1 | 0.29 | 315.4 | 0.16 |
| 2–5 m | 209.9 | 0.11 | 121.9 | 0.14 | 191.8 | 0.20 | 145.8 | 0.11 | 669.3 | 0.08 |
| 5–10 m | 17.5 | 0.29 | 23.8 | 0.43 | 17.8 | 0.38 | 75.8 | 0.37 | 134.9 | 0.23 |
| 0–2 m | 227.3 | 0.11 | 145.7 | 0.14 | 209.6 | 0.18 | 221.5 | 0.15 | 804.2 | 0.07 |
| Total | 391.1 | 0.12 | 241.7 | 0.13 | 259.1 | 0.15 | 299.1 | 0.12 | 1 190.9 | 0.07 |
| | | | | | *T. cidaris* | | | | | |
| High intertidal | 0.0 | 0.00 | 0.0 | 0.00 | 0.0 | 0.00 | 0.0 | 0.00 | 0.0 | – |
| Low intertidal | 8.2 | 0.35 | 1.3 | 0.60 | 22.7 | 0.25 | 15.8 | 0.21 | 48.0 | 0.15 |
| 0–2 m | 381.5 | 0.24 | 445.4 | 0.23 | 634.3 | 0.16 | 404.5 | 0.15 | 1 865.8 | 0.10 |
| 2–5 m | 549.8 | 0.11 | 210.0 | 0.09 | 28.5 | 0.37 | 47.5 | 0.18 | 835.8 | 0.08 |
| 5–10 m | 81.5 | 0.25 | 31.8 | 0.40 | 48.6 | 0.31 | 26.2 | 0.42 | 188.1 | 0.16 |
| 2–10 m | 631.3 | 0.10 | 241.8 | 0.10 | 77.1 | 0.24 | 73.7 | 0.19 | 1 023.9 | 0.07 |
| Total | 1 021.0 | 0.11 | 688.5 | 0.15 | 734.1 | 0.14 | 494.0 | 0.13 | 2 937.6 | 0.07 |
| | | | | | *O. sinensis* | | | | | |
| High intertidal | 0.0 | 0.00 | 0.1 | 0.72 | 1.7 | 0.30 | 4.9 | 0.16 | 6.7 | 0.14 |
| Low intertidal | 10.9 | 0.19 | 32.9 | 0.14 | 31.7 | 0.10 | 63.0 | 0.07 | 138.5 | 0.05 |
| 0–2 m | 573.6 | 0.06 | 63.1 | 0.21 | 123.6 | 0.12 | 85.5 | 0.10 | 845.9 | 0.05 |
| 2–5 m | 141.3 | 0.08 | 104.7 | 0.20 | 6.8 | 0.20 | 8.4 | 0.16 | 261.2 | 0.09 |
| 5–10 m | 9.8 | 0.31 | 6.6 | 0.32 | 0.0 | 0.00 | 0.0 | 0.00 | 16.5 | 0.22 |
| 2–10 m | 151.1 | 0.07 | 111.3 | 0.19 | 6.8 | 0.20 | 8.4 | 0.16 | 277.7 | 0.08 |
| Total | 735.6 | 0.05 | 207.4 | 0.12 | 163.9 | 0.09 | 161.9 | 0.06 | 1 268.9 | 0.04 |

probably holds true for southern African turbinids and trochids, spatial differences in biomass and density recorded during this study being partly attributable to differences in the topography and exposure of the sampling sites.

The progressive eastward migration of the West Coast rock lobster resource over recent years (Tarr *et al.* 1996, Mayfield and Branch 2000, Mayfield *et al.* in press) is thought to be primarily responsible for the absence of *T. cidaris* and *O. sinensis* at Betty's Bay, as well as reduced densities of these species in the Mudge Point area. Rock lobsters are voracious predators that feed on a wide variety of benthic organisms, including subtidal gastropod grazers and sea urchins *Parechinus angulosus* (Mayfield *et al.* 2000). Van Zyl *et al.* (1998) established that rock lobsters readily prey on *T. cidaris* and *O. sinensis*, consuming the full size range of these winkles. Outside the Betty's Bay reserve, rock lobsters are caught by recreational fishermen, thus decreasing predation pressure on the winkles. Because that reserve is a sanctuary for rock lobster, they escape fishing pressure, and apparently reach densities capable of decimating the populations of smaller invertebrate grazers. Adult *T. sarmaticus*, however, enjoy refuge in size from predation by rock lobsters, as well as protection from exploitation by divers within the reserve. As a result, their numbers are significantly higher within the reserve than in adjacent unprotected areas. This contrasts with reports by Bruton *et al.* (1991), who found that densities of *T. sarmaticus* at Cape St. Francis did not differ significantly from those within a nearby coastal conservation area. Unlike *T. cidaris*, which is largely restricted to the subtidal, both *O. senensis* and *T. sarmaticus* have a broad distribution range across the intertidal and into the subtidal, and a proportion of their populations

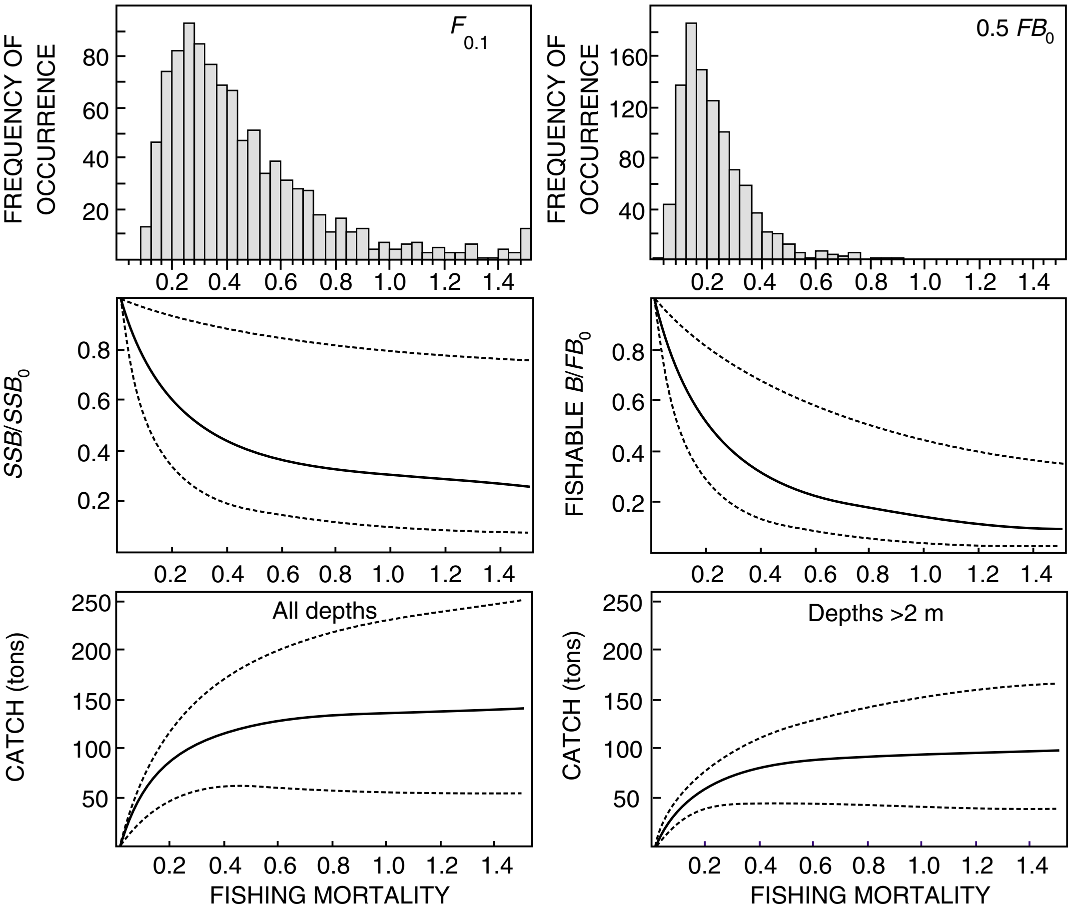

Fig. 8: Yield estimates for *T. sarmaticus* when uncertainty is included in the input parameters. The distribution of fishing mortality at two reference points ($F_{0.1}$ and $0.5FB_0$) are given. The spawning biomass and the fishable biomass is shown over the same range of fishing mortalities. The resulting catch is shown for two cases: when fishing is allowed at all depths and when fishing is restricted to deeper than 2 m. Medians and 95% confidence intervals are depicted in the lower four graphs

can therefore find spatial refuge from predation by lobsters. It was noted that the few *T. cidaris* recorded in the Betty's Bay area were mostly smaller individuals that could find refuge from rock lobsters in confined areas under boulders.

The affinity of rock lobsters for sea urchins as a prey item has an additional indirect effect on *T. cidaris*. Urchins offer shelter to juvenile *T. cidaris*, and their removal increases mortality through predation by other natural predators of winkles (crabs, fish and octopus), possibly leading to recruitment failure. Tarr *et al*. (1996) reported a decline in the number of juvenile abalone *Haliotis midae* at Betty's Bay and Mudge Point concurrent to a dramatic decline in abundance of sea urchins there. Day and Branch (2000, in press) subsequently demonstrated that removal of urchins results both in reduced abalone settlement, as a result of increased siltation of the settlement substratum, and subsequent recruitment failure of abalone, with important consequences for the sustainability of a stock experiencing severe harvesting pressure. It appears, therefore, that in the case of *T. cidaris*, the Betty's Bay marine sanctuary has a detrimental effect on the winkle population, because it acts as a haven for their major

Table VI: Uncertainty in parameters used in the assessments for the three species of winkles

| Parameter | | | *T. sarmaticus* | *T. cidaris* | *O. sinensis* |
|---|---|---|---|---|---|
| Von Bertalanffy | $L_\infty$ (mm) | Distribution | Lognormal | Lognormal | Lognormal |
| | | Mean | 129 | 62 | 56 |
| | | *CV* | 0.04 | 0.04 | 0.04 |
| | $K$ (year$^{-1}$) | Distribution | Lognormal | Lognormal | Lognormal |
| | | Mean | 0.205 | 0.35 | 0.4 |
| | | *CV* | 0.2 | 0.4 | 0.4 |
| | $t_0$ (year) | Distribution | Uniform | Uniform | Uniform |
| | | Mean | -0.001 | -0.001 | -0.001 |
| | | Range | 0.5 | 0.5 | 0.5 |
| Width-weight | Alpha (g mm$^{\text{beta}}$) | Distribution | Lognormal | Lognormal | Lognormal |
| | | Mean | 0.283 | 0.322 | 0.361 |
| | | *CV* | 0.02 | 0.02 | 0.02 |
| | Beta | Distribution | Normal | Normal | Normal |
| | | Mean | 2.95 | 3.04 | 2.99 |
| | | *CV* | 0.02 | 0.02 | 0.02 |
| Natural mortality | Fixed natural mortality (year$^{-1}$) | Distribution | Lognormal | Lognormal | Lognormal |
| | | Mean | 0.38 | 0.875 | 1.7 |
| | | *CV* | 0.5 | 0.5 | 0.5 |
| Maturity and capture | Width at maturity (mm) | Distribution | Uniform | Uniform | Uniform |
| | | Mean | 50 | 26 | 23 |
| | | Range | 1 | 0.5 | 0.5 |
| | Width at capture (mm) | Distribution | Fixed | Lognormal | Lognormal |
| | | Mean | 74 | 40 | 40 |
| | | *CV* | N/A | 0.05 | 0.05 |
| Seasons | Time steps | | Monthly | Monthly | Monthly |
| | Spawning start | | January | January | January |
| | Spawning end | | December | December | December |
| | Fishing start | | January | January | January |
| | Fishing end | | December | December | December |
| Stock-recruit relationship | Type | | Constant | Constant | Constant |
| | Recruitment *CV* | | 0.84 | 0.84 | 0.84 |
| | Spawning stock biomass | | Lognormal | Lognormal | Lognormal |
| | All depths | Mean | 1 190.9 | 2 937.6 | 1 268.9 |
| | | *CV* | 0.07 | 0.07 | 0.04 |
| | 2–10 m only | Mean | 804.2 | 1 023.9 | 277.7 |
| | | *CV* | 0.07 | 0.07 | 0.08 |

predator. Rather than offering a refuge from potential exploitation, the reserve effectively increases predation pressure on both juveniles and adults.

Winkles generally settle high on the shore, and progressively migrate downshore with increasing size. Such size-dependent zonation has been described in other trochids (Paine 1969, Vermeij 1972, Debrot 1990) and turbinids (De Villiers 1970, Lombard 1977, McLachlan and Lombard 1981, Yssel 1989), being ascribed to decreasing vulnerability to predation and increased tolerance to temperature and desiccation, with increasing size. The reverse pattern of zonation has been described by McQuaid (1982) for the mid/low-shore intertidal species *Oxystele variagata*, which co-occurs with *T. sarmaticus*, *T. cidaris* and *O. sinensis.* Variability in densities and biomass with microhabitat within the shore zonation are also evident. In the intertidal, the abundance of *T. sarmaticus* is generally higher in semi-sheltered boulder-field habitats, the animals sheltering in cracks and under rocks (Lom-

Table VII: "Best" estimates for three reference points: $F_{0.1}$, *MSY*, and $0.5FB_0$. The following data are given for each reference point: fishing mortality (*F*), spawning biomass (as a fraction of unexploited spawning biomass), fishable biomass (as a fraction of unexploited fishable biomass) and anual sustainable catch. The reference points are presented for total biomass and for biomass deeper than 2 m

| Species | Parameter | | | Catch (tons) | |
|---|---|---|---|---|---|
| | *F* | $SSB/SSB_0$ | $FB/FB_0$ | All depths | >2 m only |
| | | | $F_{0.1}$ | | |
| *T. sarmaticus* | 0.43 | 0.49 | 0.25 | 140.9 | 95.1 |
| *T. cidaris* | 1.22 | 0.64 | 0.15 | 648.3 | 226.0 |
| *O. sinensis* | 2.94 | 0.91 | 0.03 | 154.8 | 33.9 |
| | | | *MSY* | | |
| *T. sarmaticus* | 3.93 | 0.25 | 0.05 | 171.3 | 115.7 |
| *T. cidaris* | Infinite | 0.44 | 0.00 | 878.2 | 306.1 |
| *O. sinensis* | Infinite | 0.83 | 0.00 | 222.2 | 48.6 |
| | | | *Fishable biomass = 50% of unexploited* | | |
| *T. sarmaticus* | 0.24 | 0.61 | 0.50 | 113.5 | 76.7 |
| *T. cidaris* | 0.63 | 0.73 | 0.50 | 501.6 | 174.8 |
| *O. sinensis* | 1.41 | 0.94 | 0.50 | 115.4 | 25.3 |

bard 1977, Yssel 1989, Clark *et al.* 1996). Juvenile *O. sinensis* likewise remain cryptic and inactive at low water.

The spawning season in trochids and turbinids is extended, with two or more settlement peaks possible per year (Joll 1980, McLachlan and Lombard 1981, McQuaid 1983, Joska and Branch 1983, Lasiak 1986, Yssel 1989, Debrot 1990). The major reproductive period in southern African species appears to be between September and March, with recruits appearing in the intertidal during winter (Lombard 1977, McQuaid 1983, Yssel 1989). The monthly data collected at Cape Hangklip follow this pattern, although the appearance of recruits of *T. cidaris* and *O. sinensis* during summer suggests that spawning in late summer or winter cannot be excluded. Settlement of *T. sarmaticus* near the centre of its distribution range occurs irregularly on a small spatial scale, with recruitment failures and subsequent population fluctuations possible (Lombard 1977, Yssel 1989). This is supported by the absence of clear evidence of spawning in the Cape Hangklip data, suggesting that recruitment, and consequently biomass, of all three species fluctuates within a relatively small area, as well as regionally.

Joll (1980) concluded that sporadic recruitment occurs as a result of "reproductive difficulties" of a species at the edge of its distribution range, and questioned whether such populations are, in fact, reproductively self-maintaining. Being at the western limits of their distribution off the South-Western Cape, the turbinid species and *O. sinensis* may thus be experiencing reproductive difficulties. This is thought to be particularly applicable to the isolated West Coast winkle populations. The Robben Island *T. cidaris* population may be the result of a past sporadic migration of larvae around Cape Point and subsequent larval settlement and survival of recruits on the sheltered side of the island. However, whereas other scattered populations off the West Coast are represented by large and (judging by shell thickness and erosion) old individuals, the Robben Island population appears to maintain a limited degree of recruitment because the width frequency distributions indicate the presence of juvenile cohorts. The increasing proportion of small individuals, particularly of *T. sarmaticus* and *T. cidaris*, in width frequency distributions from west to east across the study area suggests that recruitment success improves in an easterly direction.

*Cpue* data have been applied with success to some gastropod fisheries (Sanders and Morgan 1976, Beinssen 1979a). Clear correlations between estimated abundance and numbers caught have been determined for the Australian abalone diver-fishery (Beinssen 1979b) and New England whelk trap-fishery (Davis and Sisson 1988). Although comparisons of the research divers used during this study could not distinguish a significant difference in hourly catch rates among divers, it is expected that differences between commercial snorkel divers fishing for *T. cidaris* in the shallow-water kelp habitat will be more marked, because their success would depend largely on their individual breath-hold abilities. Catch efficiency will also depend on diver swimming speeds, underwater orientation, minimizing repeated coverage of the same

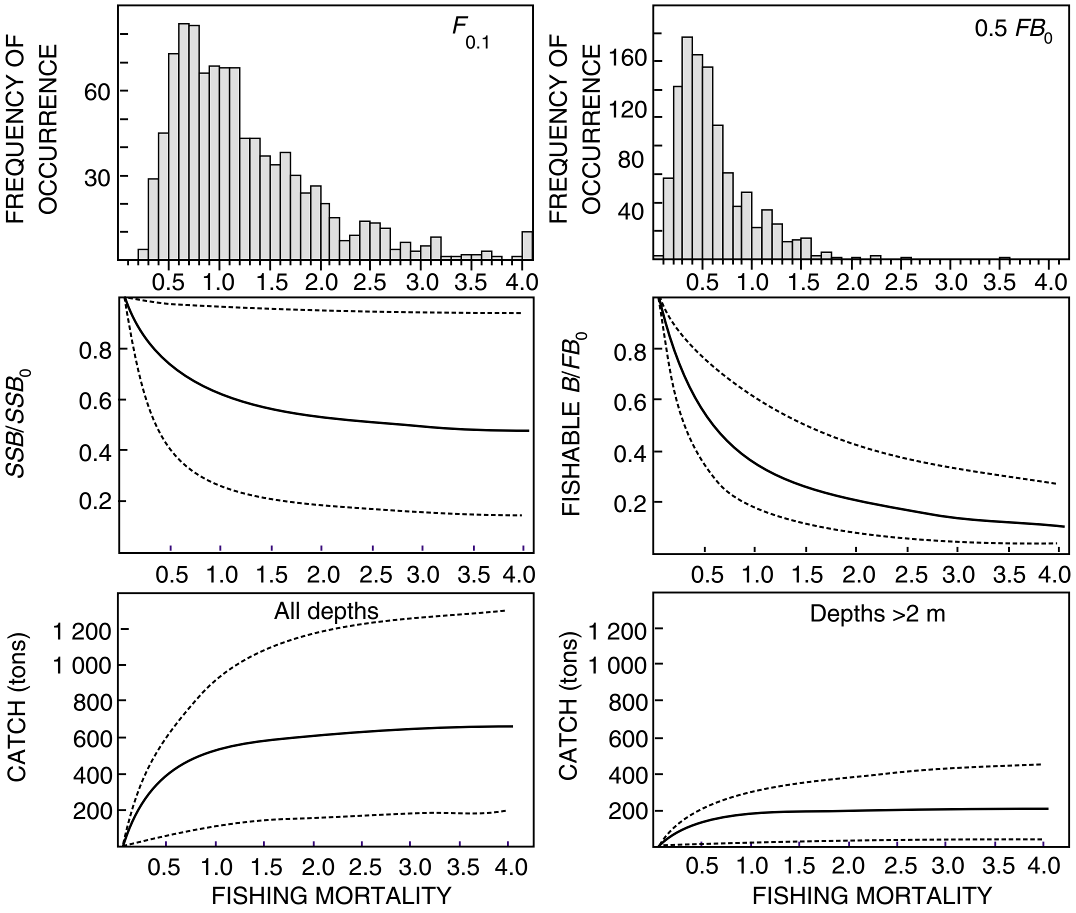

Fig. 9: Yield estimates for *T. cidaris* when uncertainty is included in the input parameters. The distribution of fishing mortality at two reference points ($F_{0.1}$ and $0.5FB_0$) are given. The spawning biomass and the fishable biomass is shown over the same range of fishing mortalities. The resulting catch is shown for two cases: when fishing is allowed at all depths and when fishing is restricted to deeper than 2 m. Medians and 95% confidence intervals are depicted in the lower four graphs

piece of reef, as well as fishing techniques that minimize handling time. The handling time as a percentage of total dive time will initially be high when fishing the pristine stock. However, this proportion would decrease as stocks are fished and more time must be spent searching. Beinssen (1979b) estimated that abalone divers fishing a virgin stock spent 75% in handling time, compared to 25% in a fished stock.

As *O. sinensis* recruits intertidally, and young *T. cidaris* have a dispersed and cryptic distribution, the juveniles of both target species would have a spatial refuge from the fishery. *MSY* is therefore not a reasonable reference point to use for giant periwinkles. For both species, *MSY* is only obtained at "infinite" fishing mortality, which would mean catching all animals as they reach the width at first capture. This would lead to highly variable harvests if there are indeed large fluctuations in recruitment levels or growth rates, a factor that has not been considered in the simulations. Given the low flesh yield and consequent reduced marketability of small winkles, reducing the width at first capture is not a viable option.

Although $F_{0.1}$ provides a reasonable choice for allowable yields from the three species, and spawning

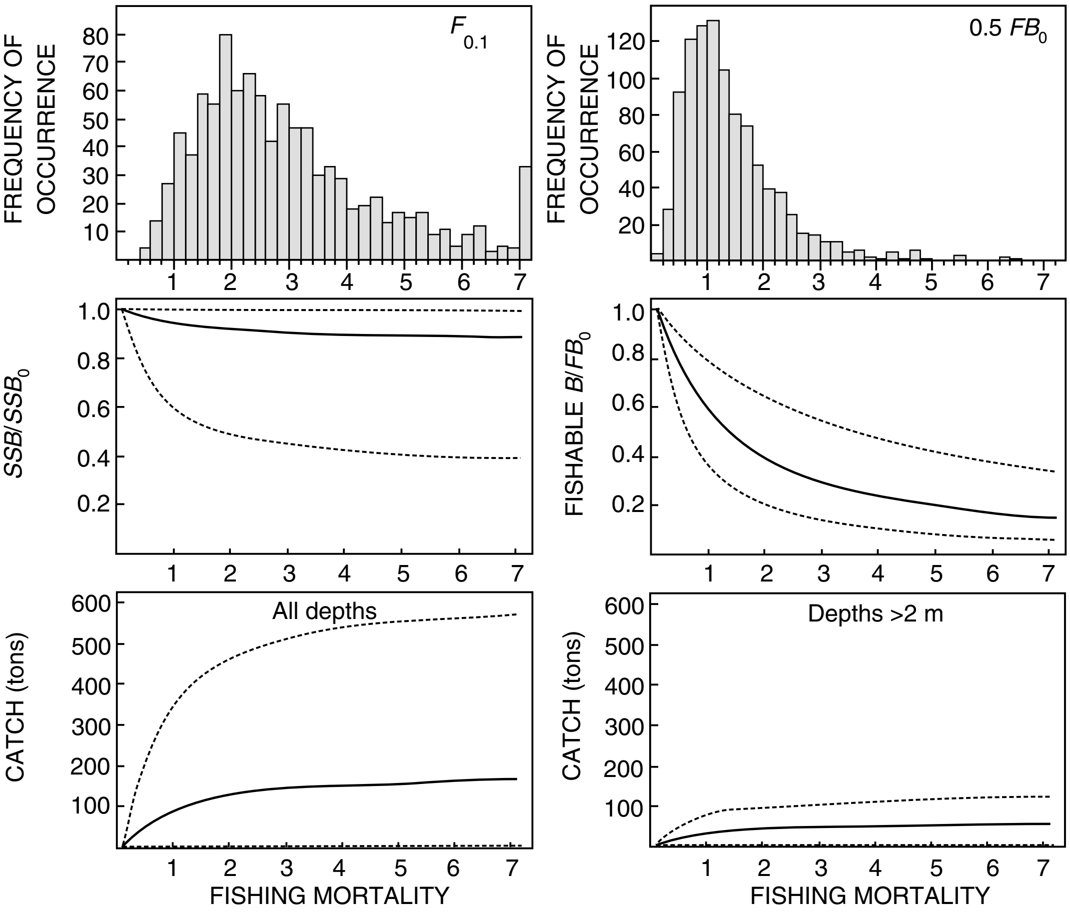

Fig. 10: Yield estimates for *O. sinensis* when uncertainty is included in the input parameters. The distribution of fishing mortality at two reference points ($F_{0.1}$ and $0.5FB_0$) are given. The spawning biomass and the fishable biomass is shown over the same range of fishing mortalities. The resulting catch is shown for two cases: when fishing is allowed at all depths and when fishing is restricted to deeper than 2 m. Medians and 95% confidence intervals are depicted in the lower four graphs

biomass would remain well protected, the fishable biomass would be reduced to a small fraction of pre-exploitation levels (25% for *T. sarmaticus*, 15% for *T. cidaris* and only 3% for *O. sinensis*). This would result in fishers expending considerable effort to find and harvest animals, particularly in the case of *T. cidaris,* which has a very clumped distribution. A strategy that would result in an equilibrium with the fishable biomass at 50% of the pre-exploitation fishable biomass ($0.5FB_0$), and where spawning biomass for all three species would remain well above 50% of pre-exploitation levels, therefore seems a more appropriate scenario. Estimated catches under this reference point would be 52–66% of *MSY*, and 75–81% of catches at $F_{0.1}$.

The uncertainties in the population parameters have an overwhelming effect on the precision of the final sustainable yield. If a viable commercial fishery were to be based on these species of winkles, emphasis should be placed on estimating the Von Bertalanffy growth parameters and natural mortality more accurately. As the uncertainty in the yield estimates is considerable, *TAC*s were based only on the lower 33%-ile of the $0.5FB_0$ estimates. The resulting catches

Table VIII: Possible *TAC*s in each of the four management areas under the 0.5$FB_0$ reference point. *TAC*s are given by the lower 33%-ile of the results when uncertainty is included

| Species | *TAC*s (tons) per Management Area | | | | |
|---|---|---|---|---|---|
| | A | B | C | D | Total |
| | | | *>2 m* | | |
| *T. sarmaticus* | 16.8 | 10.8 | 15.5 | 16.4 | 59.4 |
| *T. cidaris* | 73.3 | 28.1 | 8.9 | 8.6 | 118.8 |
| *O. sinensis* | 6.8 | 5.0 | <1 | <1 | 12.5 |
| Total | 96.9 | 43.8 | 24.7 | 25.3 | 190.8 |
| | | | *Unrestricted depths* | | |
| *T. sarmaticus* | 29.7 | 18.3 | 19.7 | 22.7 | 90.4 |
| *T. cidaris* | 111.9 | 75.5 | 80.5 | 54.2 | 322.1 |
| *O. sinensis* | 35.2 | 9.9 | 7.8 | 7.8 | 60.7 |
| Total | 176.8 | 103.8 | 108.0 | 84.6 | 473.2 |

were subsequently divided among the four management areas, according to the estimated biomass in each management area (Table VIII).

### Management

A number of management options deserve consideration before the initiating a fishery on giant winkles. It is as yet unclear whether any proposed winkle fishery would be a purely boat-based fishery or whether fishers would be allowed to operate at all depths (including intertidal catches). From a management viewpoint, a boat-based fishery would be easier to regulate and control, because the fishers would be restricted to operating from fewer access points. However, most of the biomass (and hence the potential yield) of *T. cidaris* and *O. sinensis* is shallower, and yields would therefore be much lower from a boat-based fishery than from a shore-based fishery; 68% for *T. sarmaticus*, 35% for *T. cidaris* and 22% for *O. sinensis*. A substantial portion of the biomass would, however, remain unexploited under this scenario, giving additional protection to the resource.

About 15 kg whole weight can be removed by a single diver per hour. If a boat-based fishery (>2 m) with a *TAC* suggested in Table VIII is considered, it would take 3 960 diving hours to land the total *T. sarmaticus* catch, 7 920 h for *T. cidaris* and 833 h for *O. sinensis*. This, however, does not take into consideration changes in handling time and searching time as stocks become progressively fished. Boat operators would need to weigh the income obtained from such catch levels against the expenses of the diver involved. The wide geographic area from which these catches would be made would further add to the expenses of such an operation. Although a shore-based fishery may prove to be more viable economically, it would be more difficult to ensure its long-term sustainability.

The listed *TAC*s are based on a minimum legal size of 40 mm. but there should be little incentive to harvest smaller individuals because of their low flesh yield. Therefore, a minimum legal size of 40 mm shell width seems appropriate for both *T. cidaris* and *O. sinensis*. This size is much greater than the width at maturity. Increase in the minimum size would therefore not afford much additional protection, but would decrease *TAC*s considerably. There is currently a legal minimum capture width of 63.5 mm shell width for *T. sarmaticus.*

In conclusion, it is unlikely that the biomasses of the three species are high enough to support a fishery west of Pringle Bay. As rock lobster invasions east of Cape Hangklip have had a considerable impact on the abundance of subtidal grazers, any future fishery would have to be restricted to Abalone Management Areas A (Dyer Island, Pearly Beach, Soetfontein and Quoin Point) and B (Danger Point and Kleinbaai), where winkle densities are naturally higher, and rock lobster abundances have not increased. Even then, fishing effort would have to be restricted to no more than 10 harvesting licenses operating from boats >2 m depth, so protecting the portion of the resource occurring in shallow water.

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