Effects of rotational harvesting on rock oyster *Striostrea margaritacea* size composition in eastern South Africa

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Abstract

A commercial fishery for Cape rock oysters *Striostrea margaritacea* along the KwaZulu-Natal North Coast follows a 4-year rotational cycle, with each harvest year followed by three fallow years across four harvest zones. We analysed reported harvesting effort and catch information, and fishery-independent oyster size composition data collected over 18 years to investigate the sustainability of rotational harvesting. Total harvesting effort and catches declined over the study period, but on average, the number of oysters collected per outing increased. Fewer outings in recent years were attributed to incomplete reporting and a progressive loss of access to harvest sites. Generalized linear mixed models (GLMMs) were used to estimate trends in oyster mean size in relation to fishing method (divers and intertidal collectors), harvest zone, 4-year rotational cycles, and months spent in a zone. Oyster mean size increased from north to south along the coast. Oysters caught by divers on newly exploited deeper reefs were initially larger than those caught by intertidal collectors. Mean oyster size decreased monthly during 1-year harvest periods but recovered to pre-harvest size over three fallow years. Results confirmed that the current rotational harvest strategy is well-suited to oyster biology and sustainable at the present level of effort. Improved reporting on harvesting effort and catch are required to verify longer-term spatio-temporal trends in the fishery. More effective stakeholder communication is needed to resolve potential user conflict.

Keywords: Cape rock oyster, intertidal, small-scale fishery, western Indian Ocean, effort and catch reports, gender-segregated fishery

Introduction

The Cape rock oyster *Striostrea margaritacea* is endemic to southeast Africa, from False Bay to southern Mozambique, where it occurs on inter- and subtidal rocky reefs to about 5-m depth (Branch et al. 2010). Oysters are popular seafood and have a long history of exploitation in South Africa (Thompson 1913; Haupt et al. 2010). Wild oysters are harvested by a limited recreational fishery, a largely uncontrolled and undocumented subsistence fishery, and commercial fisheries along the Southern Cape and KwaZulu-Natal (KZN) coasts (de Bruyn et al. 2008; Haupt et al. 2010). The commercial sector has been managed as a single national fishery since 2003, in four oyster-harvesting areas (i.e., Southern Cape Coast, Port Elizabeth, KZN South Coast and KZN North Coast) (Haupt et al. 2010; DEFF 2020). Harvesting patterns and regulations differ between the four areas. We focussed on the commercial oyster fishery along the KZN North Coast, from where ~80% of the reported catch in KZN province originate (de Bruyn 2006).

Oyster harvesting along the KZN North Coast takes place during spring low tides. Traditionally, participants in the fishery were women; they locate oysters by sight or touch when the tide recedes, and then lever them off reefs with a pointed steel crowbar (oyster pick). Men joined the fishery after 2001; they wear a mask, snorkel, and weight-belt and harvest oysters to a depth of about 1.5 m. The use of fins and artificial breathing apparatus is not allowed as a management measure to restrict harvesting to the intertidal and shallow subtidal fringe (DEFF 2020). The unexploited deeper subtidal oyster beds are considered to replenish the fished populations on intertidal reefs (de Bruyn 2006).

The total commercial catch of oysters in KZN has declined progressively from more than 600 000 oysters per year in 1987 to 54 000 in 2018 (Haupt et al. 2010; DEFF 2020). It remains unclear whether the decline is a result of reduced harvesting effort (non-activation of permits), poor catch reporting, and/or a decline in resource availability (DEFF 2020). The most recent assessment was undertaken in 2006 (de Bruyn 2006; de Bruyn et al. 2008), when the resource was found to be fully exploited, albeit at a lower level than before. More recently, sharp declines in reported harvesting numbers coincided with a period when fishing rights were redistributed from established concession-holders employing several harvesters each to individual harvesters (DAFF 2013). The process led to a change in the self-reporting system which may have compromised the quality of recent catch and effort data (DFFE 2020).

Rotational harvest strategies in which demarcated zones are harvested and then left fallow (unharvested) to recover before fishing resumes are not uncommon in oyster fisheries (Kjelland et al. 2015; Kennon et al. 2023); and their success depends on target species biology, length of closure, fishing pressure and compliance/law enforcement capacities (Hart 2003; Cohen and Foale 2013; Plagányi et al. 2015; Purcell et al. 2016). Rotational harvesting of oyster fisheries in South Africa most likely began in the 1950s (de Bruyn et al. 2008) and is detailed by Haupt et al. (2010). Along the KZN North Coast, rotational harvesting of oysters takes place in four zones. Each zone is harvested for a 12-month period and then left fallow for three years (de Bruyn 2006; de Bruyn et al. 2008). The 3-year fallow period after rotation is consistent with the time (~33 months) needed for oyster recruits to grow to a marketable size in KZN (Schleyer and Kruger 1992). Based on a Total Allowable Effort (TAE) management system, a maximum of 25 commercial harvesters are permitted to fish for oysters along the KZN North Coast each year, but not all of them are active.

Catch size frequency data are useful indicators of the effects of fishing on invertebrate populations (Pauly and Morgan 1987). Declines in average body size are common in heavily exploited populations, particularly when fisheries expand to target previously unexploited populations (e.g., Groeneveld et al. 2012). To determine the effects of the rotational harvest strategy on oyster size structure in the KZN North Coast fishery, we analysed 18 years (2003-2020) of reported harvest effort and catch information, and oyster size data collected independently from the harvest reports.

Methods

Study area

The KZN North Coast oyster fishery is confined to the area between the Thukela and uMngeni River mouths (Figure 1). From north to south, the four rotational zones are Zinkwazi (Zi; between Zinkwazi town and Tinley Manor), Ballito (Bo), La Mercy to Westbrook (LW) and uMhlanga to eMdloti (UU). The northern-most Zi zone requires longer travelling time for harvesters, and they sometimes need permission from private landowners to access oyster beds. The Bo and UU zones are in densely populated residential and resort areas; oyster beds are easy to reach, but conflict over shared coastal resources with locals and tourists affect access (pers. obs. ES). The LW zone comprises of lower density residential and resort areas with easy access to oyster beds and a lower risk of resource-user conflict.

Reporting of harvesting effort and catches

Self-reporting of daily catch and effort data to the Department of Forestry, Fisheries and the Environment (DFFE) is required from commercial permit holders, although not strictly enforced. Two reporting formats were used over the study period, for concession holders employing groups of harvesters (2003-2005) and for individual harvesters (2006-2020). The required data per sampling date prior to 2006 were location, number of oysters collected / discarded, and number of harvesters deployed. Number of harvesters was replaced by harvesting method (intertidal collection or diving) and duration of outing (hours) after 2006, to be completed by individual harvesters.

The consistency and quality of catch reports varied. A total of 6 151 reports were available for analysis, unevenly spread across years. No reports were available for 2006 and 2016, and only one report was submitted for 2019. With these exceptions, more than 250 concession holder group reports per year where available for 2003-2005, more than 600 individual harvester reports per year for 2007-2010 and less than 500 per year for 2011-2020. Catch reports were available for 11-12 months per year between 2003 and 2005, when concession holders reported on a total of 13-24 harvesters in the fishery. The changeover to individual reporting in 2006 led to a decline in reporting rate, from 18 harvesters in 2007 (10 divers and eight collectors) to eight in 2020 (four divers and four collectors). On average, divers submitted catch reports for 5.2 ± 2.8 [SD] months per year (ranging from 1-11 months per year) and collectors for 3.9 ± 2.4 months per year (1-9 months per year).

Variation in rotation dates between zones affected the duration of harvest and fallow periods during each cycle of four years. Rotation dates were nominally set at 1st January (50%) or 1st November (33%) of each year but varied in some years because of administrative issues and misunderstandings (2011-2012), conflict with private landowners that prevented access to harvesting sites (2019) and early closure of the fishery in 2020 because of Covid-19 regulations. Harvest duration was 12 months in 72% of cases between 2003 and 2020, 14-22 months in 17% and less than 9 months in 11% of cases. Associated fallow periods of at least 36 months were achieved in 78% of cases, with only four shorter fallow periods recorded (22 – 34 months).

Trends in the total number of outings per harvester, mean number of outings per harvester per month, numbers of marketable oysters caught, and catch per unit effort (CPUE; oysters per outing) were derived from the catch reports for the 2003-2020 period.

Analysis of size composition data

Oyster size data were obtained from 170 monthly field sampling events over 18 years (Feb 2003 – Feb 2020) stratified across harvest zones, cycles and fishing method (Table 1). The right valve lengths (RVL ± 1 mm) of 100 randomly selected oysters collected by harvesters during each sampling trip was measured. To ensure that small oyster recruits that had settled onto larger oysters were also included in samples, measurements were made prior to cleaning of oysters by harvesters.

Diver catches were sampled in all zones and cycles (n = 170 samples) with an average of nine months sampled per zone in each cycle. Intertidal collector catches were sampled on 68 events with an average of nine months sampled per zone during cycle 1 (2003-2006); less than three months per zone during cycle 2 (2007-2010) and cycle 3 (2011-2014), and four months per zone during cycle 4 (2015-2018). No intertidal collector catches were sampled during cycle 5 (2019-2020).

Trends in RVL were analysed with generalized linear mixed models (GLMMs), using R 4.2.1 (R Core Team 2022) and the statistical software package ‘glmmTMB’ (Brooks et al. 2017). The ‘dplyr’ (Wickham et al. 2022) and ‘performance’ (Lüdecke et al. 2021) packages were used for data manipulation and evaluating model fit. Two models were used, for divers and for divers vs collectors. All diver size samples were used in the diver model, but only diver and collector size data sampled on the same day were used in the diver vs collector model. Models were fit to the data by maximum likelihood estimation using the Template Model Builder (Kristensen et al. 2016). Independent variables tested in the models were harvest zone, cycle, method, number of months in zone and season (Table 1). Months in zone was used to explore the short-term effects of harvesting pressure on oyster size over successive months in a 1-year harvest period. Harvest cycle was used to estimate the recovery in oyster size during 3-year fallow periods. Sample day was used as a random effect as sea and tidal conditions may impact harvesting success. Model intercepts were set to Zi, February 2003 and collector catches.

A stepwise approach of modelling combinations of error structure, link functions and explanatory variables; followed by model comparisons with likelihood ratio tests were used to select the final models. Models with the lowest Akaike’s information criterion (AIC) and randomly distributed residuals on plots were selected as the best-fitting final models. GLMMs with a gaussian error structure and identity link function were selected for both the diver and diver vs collector models.

Results

Effort, catch and CPUE

Reported harvesting effort declined from more than 1 900 outings per year before 2005 to 43 outings in 2020 (Figure 2a). Effort generally peaked during periods when harvesting took place in the southern zones (LW, UU; 2009-2010, 2013-2014, 2017-2018). Overall, divers undertook 63% of all outings in 2007-2020. Diver and collector effort followed broadly similar trends between 2007 and 2020, except for 2009, when collectors reported few outings (Figure 2a). The average number of outings reported per individual harvester ranged between 6-14 outings per month, with greater variability in 2007-2015 than at the onset of the timeseries, and declined to 6-7 outings per month in 2018-2020 (Figure 2b). By month, most outings took place between January and June, thereafter declining gradually to the fewest outings in December (Figure 3).

Reported catches declined from more than 156 000 oysters per year before 2005 to ~7 000 oysters in 2020 (Figure 4a). As with effort, catches peaked when the southern zones (LW, UU) were harvested, but even these peaks declined over time. Diver and collector catches followed broadly similar trends, except in 2009, when catch and effort of collectors appear to be under-reported. Overall, divers caught 71% of all oysters reported in 2007-2020. By month, most oysters were harvested in January to June, declining to smaller numbers in November and December (Figure 3).

The CPUE increased from 85 ± 52 [SD] oysters per outing in 2003 to 158 ± 36 in 2020, with anomalously lower values in 2007 and 2012 (Figure 4b). Diver and collector CPUE trends were similar, but over the whole 2003-2020 period, diver CPUE (123 ± 51 oysters per outing) exceeded collector CPUE (92 ± 52 oysters). Collector CPUE peaked at more than 130 oysters per outing in 2014-2015 and 2018, when it exceeded diver CPUE.

Size composition analysis

A total of 22 964 oysters ranging between 3 – 152 mm RVL were measured, with an average RVL of 66 ± 18 mm. Size histograms were unimodal, with 4% of oysters measuring smaller than 30 mm, 29% between 30 and 60 mm, 59% between 60 and 90 mm and 9% larger than 90 mm. These RVL categories represent oyster age-classes of younger than one year; 1-2 years; 3-5 years and older than five years (de Bruyn 2006). The size composition of oysters harvested by divers (mean RVL: 67 ± 19 mm, n = 16 788) differed markedly from those harvested by collectors (64 ± 16 mm, n = 6176) (Figure 5a). Divers collected higher proportions of larger oysters (>80 mm RVL, 24% of sample) and very small oysters (<40 mm, 9%) than collectors (16% and 7%). The mean RVL of oysters caught by divers increased towards the south, from 63 ± 17 mm at Zi to 71 ± 20 mm at UU (Figure 5b). Seasonal differences were less pronounced than between zones, ranging from an average of 69 mm in summer to 65 – 66 mm in autumn, winter and spring (Figure 5c).

Diver model

Harvest zone, cycle, months in zone and random day were retained in the best-fitting diver model (Table 2). The model showed a progressive increase in oyster RVL from north to south, with the mean size at LW (+4.1 mm) and UU (+9.4 mm) larger and significantly different than at Zi (model intercept at 63 mm RVL in February 2003; Figure 6a). The mean RVL decreased by 0.4 mm per month harvested in a zone, summing to a total decrease of 4.1 mm over a 12-month harvesting period (Figure 6b). However, the mean RVL at the start of each harvesting cycle was 5 mm larger than at the beginning of the 36-month fallow period, indicating an increase in RVL of 0.9 mm per harvest cycle, maintained over 18 years between 2003 and 2020.

Diver vs Collector model

Harvest zone, cycle, method and random day were retained in the best-fitting diver vs collector model (Table 2), with the interaction of harvest method and cycle also significant ($p < 0.05$). Months in zone was not retained in the final model. Like the diver model, oyster RVL increased from north to south, with mean size in LW (+4.0 mm) and UU (+8.2 mm) larger and significantly different than at Zi (59 mm RVL during 2003 for collector catches; Figure 7a). In contrast with the diver model, the mean RVL of diver samples decreased significantly by -0.9 mm per cycle, while the mean RVL of collector samples increased, albeit nonsignificant by 0.9 mm per cycle (Figure 7b). Thus, during the first harvest cycle the mean RVL of diver catches was 2.0 mm larger than the collector RVL, but by the fourth cycle, oysters harvested by divers were, on average, 0.8 mm smaller than those harvested by collectors (Figure 7b).

Discussion

Catch reports and independent size composition data collected over 18 years were analysed to investigate the effects of rotational harvesting on oysters caught in the KZN North Coast fishery. Reported harvesting effort and total catches declined substantially, but CPUE and mean oyster size increased or remained stable. Declines in harvesting effort and catches prior to 2010 were attributed to poor reporting, following changes to the self-reporting system in 2005, when fishing rights were redistributed (Haupt et al. 2010; DAFF 2013). More recent evidence that reporting remains poor is that no official catch reports were submitted for 37 months of the study period, during which harvesting is known to have occurred (pers. obs. ES). In combination with the unrealistically low harvesting effort (43 outings) and catch (~7 000 oysters) reported for 2020, the available information confirms that reporting compliance has not improved since 2005.

Actual harvesting effort also appears to have declined, with several harvesters being inactive at present (pers. obs. ES). The decline in activity can be explained by a combination of the rising costs of travel to harvest sites, obstructed access across private land and harassment by locals while harvesting, and administrative hurdles (e.g., loss of permits because of non-compliance with application processes or permit conditions). Oyster harvesting was severely restricted during the

Covid-19 pandemic in 2020. Catch reports submitted by the remaining harvesters showed a decline in the average number of outings reported per individual harvester, from 6-14 outings per month in 2007-2015 to 6-7 outings per month in 2018-2020 (see Figure 2b). A decline in fishing effort has similarly been shown for a recreational mussel fishery in the UU zone, following the establishment of a no-take conservancy on exploited reefs in 1998 (Steyn et al. 2022). In that case, the reduction in reported effort was abrupt and directly related to the loss of access to exploited reefs (Steyn et al. 2022). In comparison, harvesting effort in the oyster fishery has declined more gradually over a longer period, and may not be as severe as it appears from submitted catch reports, because of incomplete reporting after 2005.

Uncertain harvesting effort and catch data for the past 18 years precludes any firm conclusion on the status of the oyster stock and fishery. This is the unfortunate result of the fishery receiving little research effort (apart from de Bruyn 2006; de Bruyn et al. 2008) and management attention, because of its low value compared to other commercial fisheries (Haupt et al. 2010; DAFF 2020). A recent report (DAFF 2020) states that initiatives are underway to improve the quality of oyster catch and effort data, towards undertaking resource assessments. For this purpose, the collection of accurate harvesting effort and catch data needs to be prioritized, through outreach and training of individual fishers in self-reporting, a firmer link between reporting compliance and granting of fishing permits, and patrols to enforce fishing regulations.

Oyster size data were obtained independently from the catch report information and were therefore unaffected by reporting compliance. A GLMM framework allowed for quantification of the spatio-temporal effects of harvesting on oyster size structure, with post hoc inferences of stock status. A longer timeseries was available for divers, justifying the use of separate GLMMs for divers and for divers vs collectors. The diver model captured the longer-term cyclical effects of the rotational harvest strategy well, whereas the diver vs collector model better accommodated harvest method, as a proxy for two effects that could not be partitioned with the available data; harvesting on intertidal vs shallow sub-tidal reefs, and a gender dichotomy with women as intertidal collectors and men as divers. Gender-segregation in nearshore fisheries is common in the western Indian Ocean region (Murunga 2021) where women typically glean or use mosquito nets in the intertidal to catch invertebrates or small fish (Samoilys et al. 2019; Stiepani et al. 2023). The distinct fishing practices of women can provide important ecological information on the human role in marine ecosystems (Kleiber et al. 2015) but was not pursued in our study.

Harvest zone was a significant determinant of oyster size in both models. We considered two hypotheses to explain an increasing oyster size between Zi (north) and UU (south); environmental influences or uneven harvest pressure across zones. All four zones are located along a coastal stretch of less than 100 km within the sheltered KZN Bight. The bight falls wholly within the Subtropical Natal Bioregion, where shallow subtidal reefs are dominated by filter-feeders (Porter et al. 2013). All four zones are influenced by seasonal enrichment from riverine discharge and similar temperature and salinity regimes (Porter et al. 2014; Scharler et al. 2016). Even so, oyster growth and mortality rates are highly sensitive to environmental factors, and subtle differences in food availability, temperature and salinity may explain the size gradient along the coast (Brown 1988; La Peyre et al. 2016; Lowe et al. 2017). Also plausible, is that harvesting on comparatively smaller and fewer reefs in the north (Zi), for similar durations, results in greater relative harvest pressure (pers. obs. ES). We suggest that a smaller mean oyster size reflect more rapid depletion of smaller populations at Zi per harvest period, compared to UU, where larger oyster beds are more resilient and yield larger oysters in greater quantities. The latter hypothesis can partly explain the greater popularity of UU among harvesters, observed as more outings when the UU zone is harvested (see Figure 2a).

The variables months in zone and harvest cycle were both significant in the diver model, revealing the cyclical effects of rotational harvesting on oyster size. Months in zone showed a gradual decline in mean RVL during each 12-month harvest period, whereas harvest cycle highlighted the recovery in RVL after the subsequent 36-month fallow period. Mean RVL values consistently recovered to pre-harvest levels at the beginning of each cycle, implying that the 36-month fallow period facilitates sustainability of the fishery.

Few oysters older than five years (RVL>90 mm) were observed in samples, indicating that the fishery relies mainly on oysters recruited during the foregoing fallow period. A fast growth rate in *S. margaritacea*, which reaches maturity within a year (de Bruyn 2006) and marketable size (RVL>60 mm) in 33 months (Schleyer and Kruger 1992) further support use of a 36-month fallow period. Few oysters younger than one year (RVL<30 mm) were observed, and size histograms were consistently unimodal without secondary recruitment peaks. This result aligns well with the reproductive biology of oysters in KZN, whereby breeding and settlement takes place throughout the year with a slight increase during summer and autumn (Schleyer 1988; Schleyer and Kruger 1991). The rotational harvest strategy for oysters is therefore well-founded from a resource perspective, with the duration of the fallow period consistent with the biology of the target species and level of fishing pressure (Hart 2003; Cohen and Foale 2013; Plagányi et al. 2015; Purcell et al. 2016). However, the short and long-term benefits of the strategy for harvesters remain unclear, as demonstrated by long-term declines in harvesting effort and catches, especially when the less popular Zi zone is harvested.

Both harvest method and the interaction between harvest cycle and method were significant in the diver vs collector model. The mean RVL of oysters harvested by divers was larger than those taken by collectors during the first harvest cycle (2003-2006), when divers first entered the fishery. Divers could access deeper reefs with unexploited oyster beds, and a larger proportion of their harvest would have consisted of oysters older than five years (RVL>90 mm), compared to the traditional collector fishery (see above). The mean RVL of diver catches declined over successive harvest cycles, presumably because the accumulated biomass of older oysters was gradually fished out. By the fourth cycle (2015-2018) the mean RVLs of diver and collector harvests were similar, indicating a similar size structure in exploited inter- and shallow subtidal populations. In a contrasting result, the RVL of oysters harvested by divers increased significantly over successive cycles in the diver model.

The trends estimated by the two models were, however, not directly comparable, because the diver model was based on a longer time series than the diver vs collector model. Neither model suggested significant long-term declines in RVL indicative of overharvesting, irrespective of the harvest method used in inter- and shallow subtidal areas.

In conclusion, two independent datasets spanning an 18-year period were analysed to evaluate the suitability of a rotational harvest system in a commercial oyster fishery. An empirical analysis of size composition data showed cyclical trends, in which a 3-year fallow period after each year of harvesting allowed for the recovery of mean oyster size to initial pre-harvest levels, irrespective of fishing method used (diver or intertidal collector) or harvest zone. The analysis confirmed that the rotational harvest strategy was consistent with the biology of the species, and sustainable at the level of effort observed. Declines in harvesting effort and catches occurred over the study period, but on average, the number of oysters collected per outing increased. Fewer outings in recent years were attributed to incomplete reporting and a progressive loss of access to harvest sites. Improved reporting is required to verify longer-term spatio-temporal trends in the fishery.

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Tables

Table 1: Independent variables tested in GLMMs of oyster RVL (right valve length, mm) in the commercial fishery along the KZN North Coast between 2003 and 2020. One harvest period (~12 months) plus a fallow period (~36 months) makes up a 4-year cycle.

Independent variables	**Type**	**Description**
Zone (Harvest zone)	Categorical	-Four zones along the KZN North Coast -Zinkwazi (Zi), Ballito (Bo), La Mercy-Westbrook (LW), eMdloti-uMhlanga (UU)
Cycle (Harvest cycle)	Continuous	-One cycle = 4-year period during which each zone is harvested for 12 months and remains unharvested (fallow) for 36 months. Some variability in duration of harvest and fallow periods was caused by administrative inconsistencies. -The dataset included 5 harvest cycles for Zi and Bo zones and 4 cycles for LW and UU.
Months in zone	Continuous	-Number of months spent harvesting in a harvest zone during a cycle Mostly 12 months but ranging from 5-22 months because of variable rotation dates.
Method (Harvest method)	Categorical	-Two levels: Intertidal collectors (Col) comprising mostly women and divers (Div) comprising mainly men.
Season	Categorical	-Four levels: Summer (Dec-Feb), Autumn (Mar-May), Winter (Jun-Aug), Spring (Sep-Nov). Variable tested but not included in final models.
Day (Sample day)	Categorical	170 sample dates for Diver model; 68 samples dates for Diver vs Collector model

Table 2: GLMMs used to describe trends in oyster RVL (right valve length, mm), based on sampling of the commercial oyster fishery along the KZN North Coast. Two models are shown, for Divers and for Divers vs Collectors. The factors retained, analysis performed, error structure, link functions used, Akaike's information criterion (AIC) and the numbers of observations (n) are shown. Parameter estimates (±SE) marked with * were significantly different from the intercept ($p < 0.05$). Miz = Months in zone; Bo = Ballito; LW = La Mercy to Westbrook; UU = eMdloti to uMhlanga

	Diver Catches	**Diver vs Collector Catches**
Factors	Zone + Cycle + Miz +Random(Day)	Method x Cycle +Zone + Random(Day)
Analysis	GLMM	GLMM
Error	Gaussian	Gaussian
Link	Identity	Identity
AIC	144 267	109086
n	16 788	12 844
Data	Diver catch composition, RVL	Diver and Collector catch composition, RVL Only sample days with both used in analysis
	Estimate (SE)	Estimate (SE)
(Intercept)	62.77 (1.60)*	58.71 (1.57)*
Zone: Bo	+1.65 (1.37)	+2.62 (1.73)
Zone: LW	+4.05 (1.41)*	+3.97 (1.56)*
Zone: UU	+9.42 (1.39)*	+8.23 (1.64)*
Cycle	+0.85 (0.36)*	+0.90 (0.49)
Miz	-0.37 (0.12)*	
Method: Diver		+2.91 (0.57)*
Cycle x Method: Diver		-0.94 (0.24)*
Random(Day)	-0.00004 (0.15)	+0.00003 (0.21)

Figures

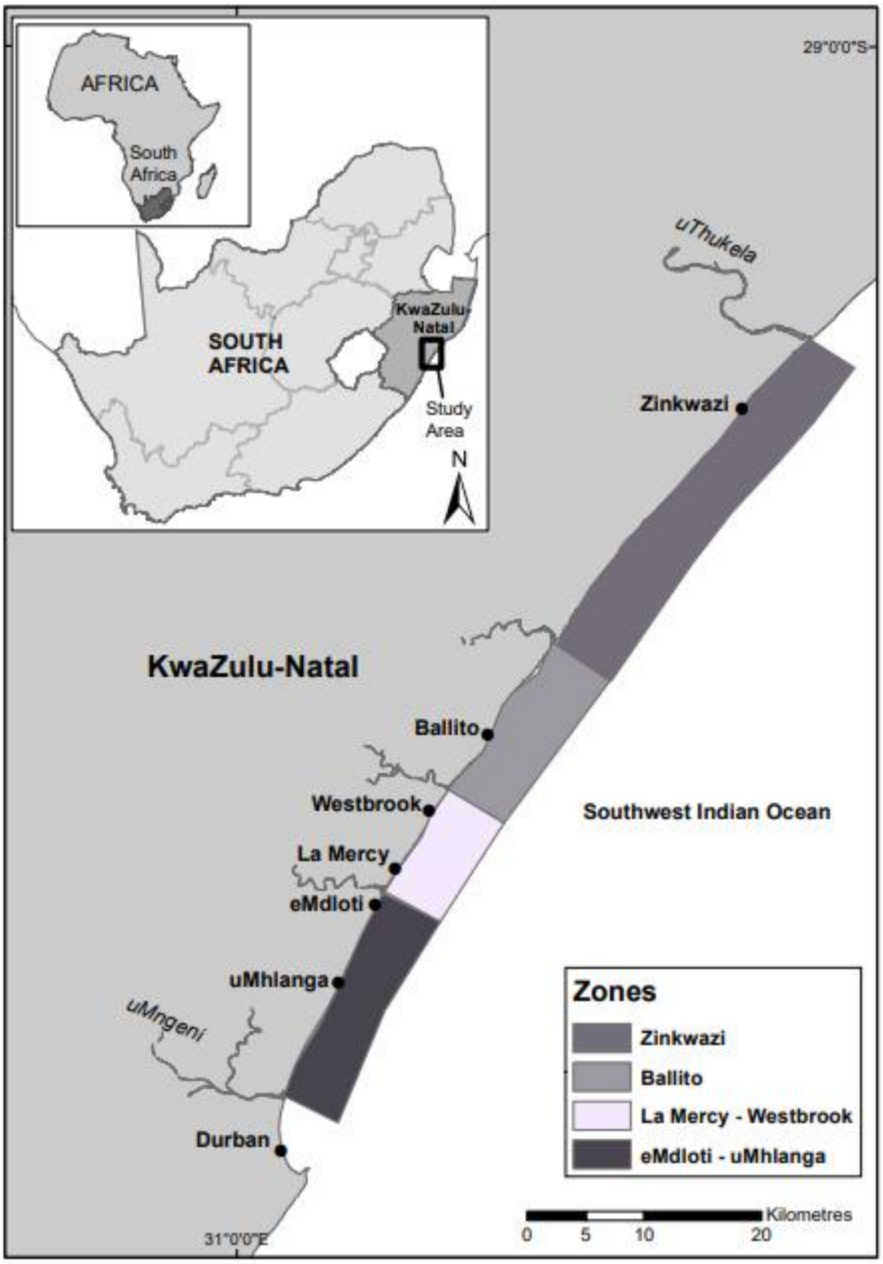

Figure 1: Oyster harvesting zones along the KZN North Coast in eastern South Africa.

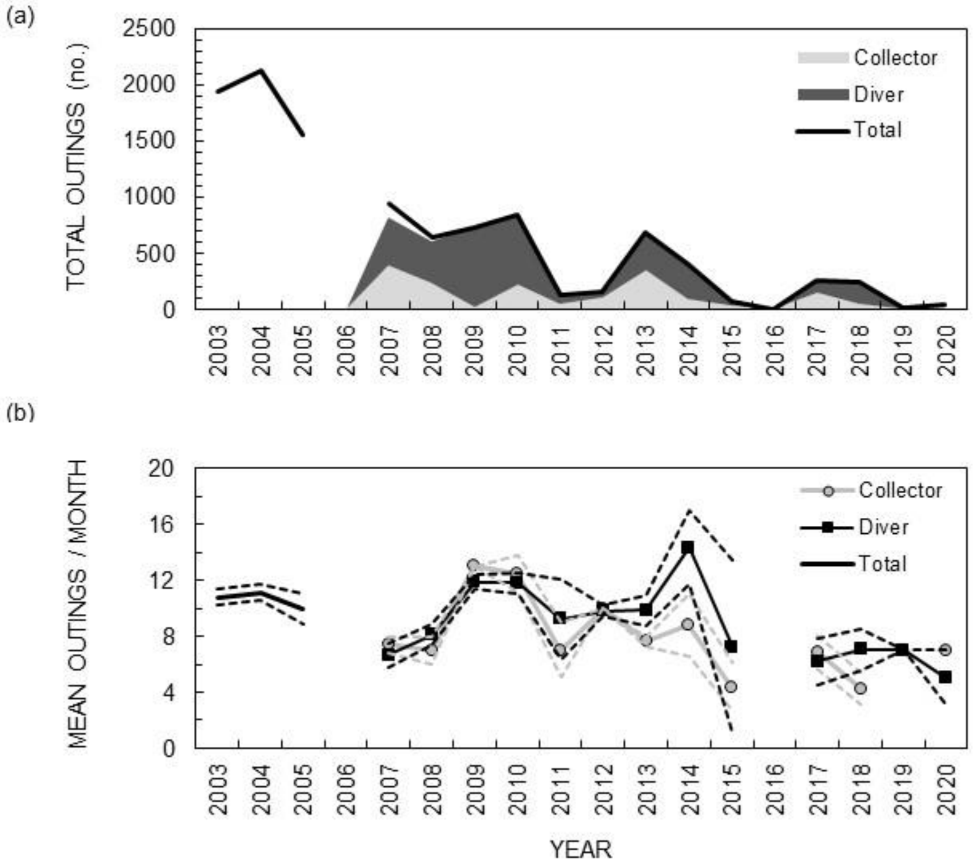

Figure 2: (a) Total reported outings per year and (b) mean number of outings per harvester per month for intertidal collectors, divers, and both combined (only 2003-2005 data) in the KZN North Coast oyster fishery for the 2003-2020 period. The 95% confidence intervals are shown for Figure 2b.

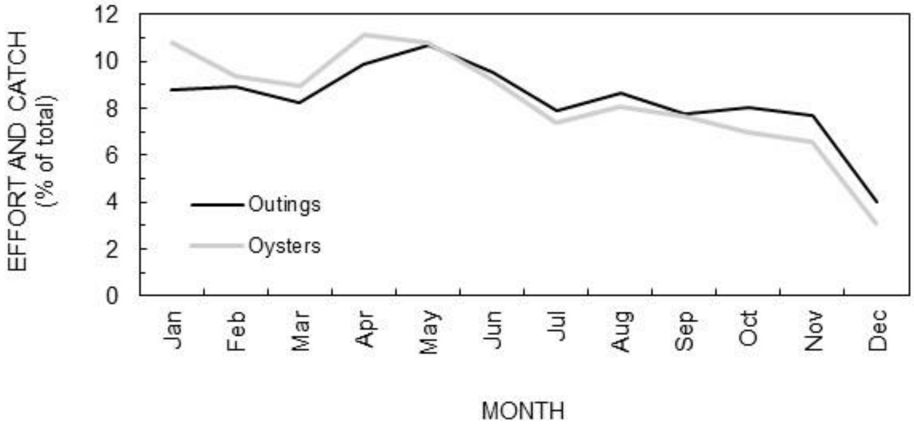

Figure 3: Average number of outings as a proportion of the total, by month, and associated oyster catch (number of marketable oysters) in the KZN North Coast commercial oyster fishery. Partial data (2001-2010) were used because harvesting started in January during this period and the number of individual reports per year were more than 600.

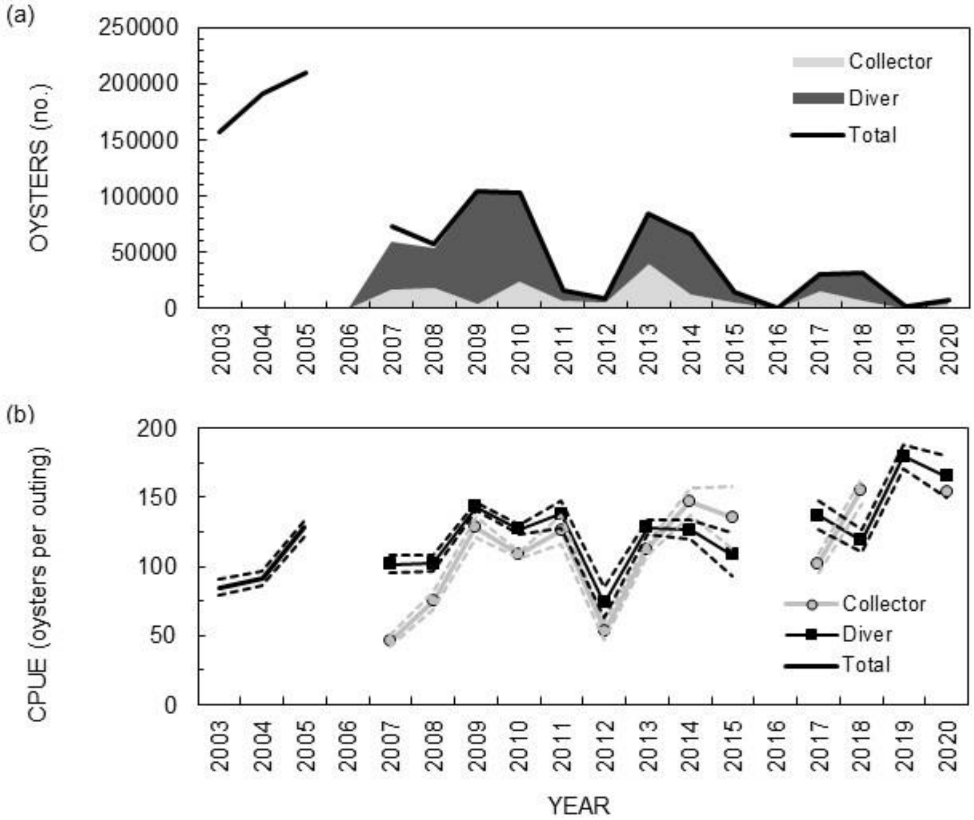

Figure 4: (a) Annual oyster catch (number of marketable oysters) and (b) CPUE (oysters per harvester per outing) of KZN North Coast divers, intertidal collectors and combined derived from catch reports submitted between 2003 and 2020. The 95% confidence intervals are shown for Figure 4b.

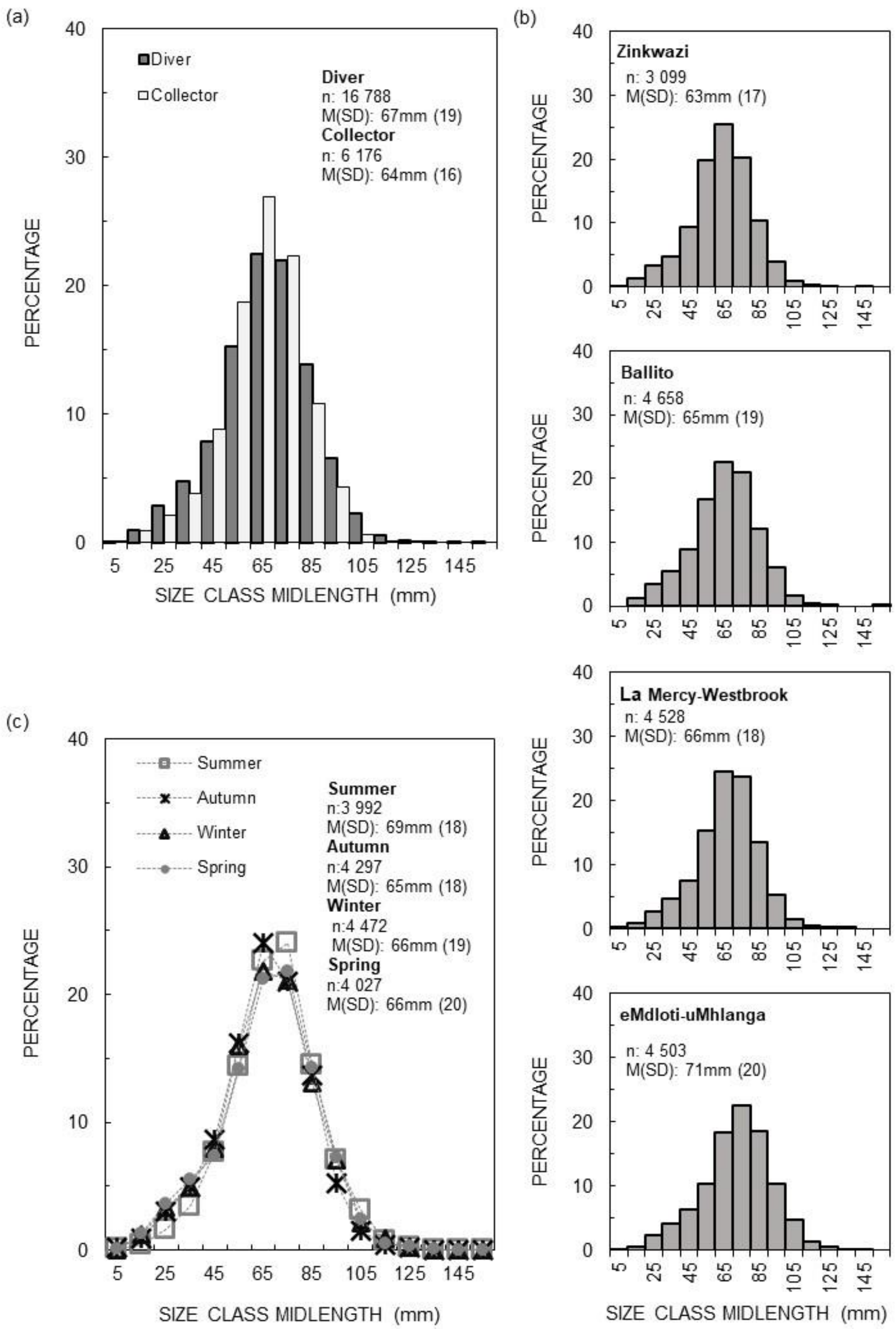

Figure 5: (a) Size frequencies (right valve length; RVL in mm) of all samples of diver and intertidal collector catches for the 2003-2020 period; (b) by harvest zone; and (c) by season. Mean oyster size (M), standard deviation (SD) and sample size (n) are shown.

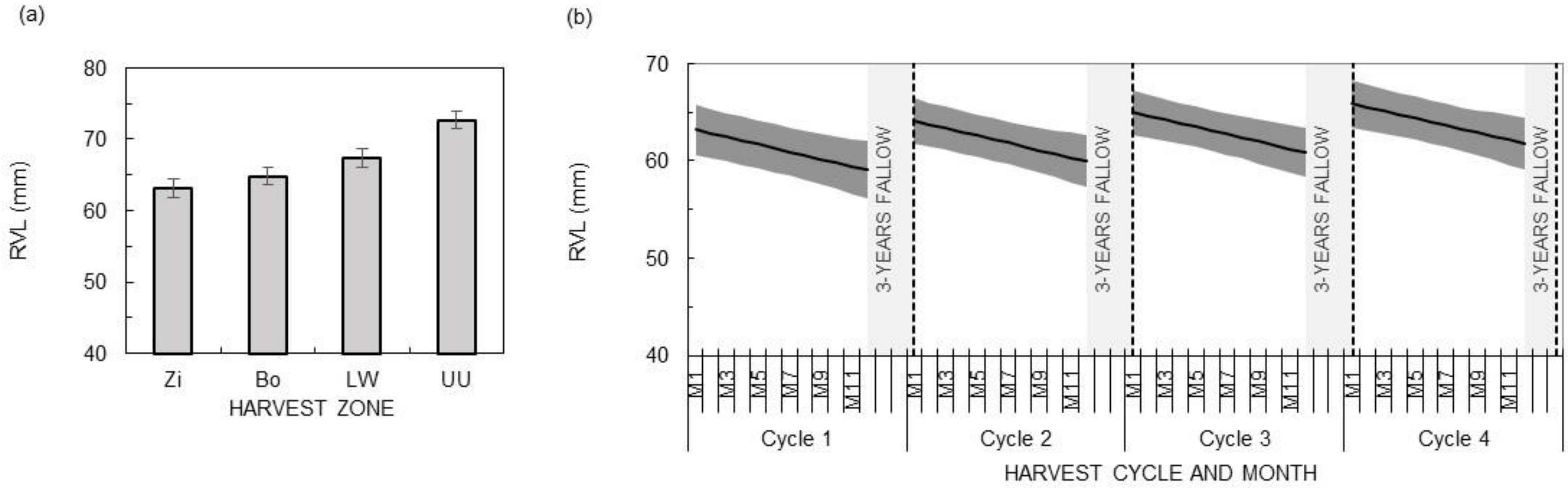

Figure 6: Predicted effects of (a) harvest zone (cycle 1 and month 1 as reference) and (b) harvest cycle and month in zone (M) on mean oyster right valve length (mean RVL, mm) at Zinkwazi, based on the best fitting model. (a) Standard error (bars) and (b) 95% confidence intervals (shaded area) are shown.

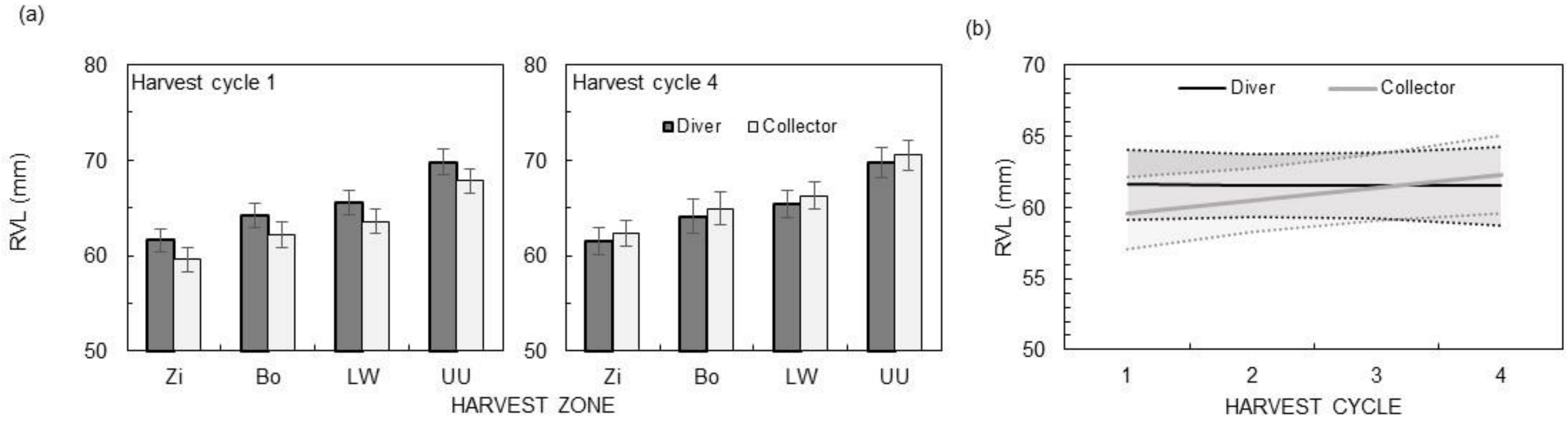

Figure 7: Predicted effects of (a) harvest zone and (b) harvest cycle on mean oyster right valve length (mean RVL, mm) at Zinkwazi based on the best fitting model. (a) Standard error (bars) and (b) 95% confidence intervals (shaded area) are provided. For (a), harvest cycles 1 and 4 are shown.