Trends in mussel cover, density and size at exploited and unexploited intertidal reefs in eastern South Africa

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The brown mussel *Perna perna* is the dominant indigenous mussel along the east coast of South Africa, where it is harvested by recreational and subsistence fishers. High fishing pressure near metropolitan areas has led to declining abundance, and closure of some reefs to fishing in 1998. We estimated trends in mussel population dynamics at exploited and unexploited sites over a 27-year period (1993–2019) along fixed transects. Trends in recreational fishing effort were inferred from yearly permit sales and existing catch statistics. At high fishing effort, short-term trends in mussel cover and densities were inversely related to fishing effort at three of four sites, while a fourth site was influenced by intermittent breaching of a nearby estuary. Mussel size was inversely related to densities. The effects of longer term harvesting bans were partially obscured by sharp declines in fishing effort across the entire recreational fishery. Seasonal and interannual patterns in cover and density were partially synchronised among sites, indicating environmental forcing at similar time-scales. The long-term dataset was invaluable in disentangling the relative effects of fishing and environmental factors on mussel population dynamics and should be continued as a baseline for assessing future climate-induced effects on rocky shore biota.

Keywords: closed areas, environmental factors, mussel population dynamics, *Perna perna,* recreational fishery

Introduction

Declines in intertidal mytilids (mussels) caused by unsustainable fishing pressure and environmental change have been reported from many locations worldwide and harvesting restrictions to allow stocks to recover have had mixed results (Dankers et al. 2001; Carranza et al. 2009; Sorte et al. 2017). For example, depleted blue mussel *Mytilus edulis* in sheltered parts of the Wadden Sea re-established over a 2-year period (Dankers et al. 2001), but some historic mussel beds in the region recovered slowly or not at all, attributed to unusually warm winters and increased predation on recruits (Beukema and Dekker 2007). Recovery of the so-called Mediterranean mussel *Mytilus galloprovincialis* only occurred where predation by fish was controlled (Rius and Zabala 2008). Several South American mytilids exhibited large ecosystem-level effects at local scales, and about a third of fisheries appeared to be vulnerable to overexploitation (Carranza et al. 2009). Mussel populations are dynamically influenced by habitat suitability (Erlandsson et al. 2005; Nicastro et al. 2008), recruitment (McQuaid and Lindsay 2005; Reaugh-Flower et al. 2011), mortality (Zardi et al. 2008) and growth rates (McQuaid and Lindsay 2000). Disentangling the effects of fisheries and environmental change on mussel populations is a key aspect of developing coastal management strategies (Carranza et al. 2009).

The brown mussel *Perna perna* (Linnaeus, 1758) is the dominant indigenous mussel species found on rocky intertidal reefs along the eastern coast of South Africa. Towards the south (eastern part of Western Cape) brown mussels are mainly confined to the lower intertidal zone because of competition with the invasive mussel *M. galloprovincialis* in the upper zone (Bownes and McQuaid 2006). More centrally (Eastern Cape Province) they are heavily exploited by subsistence fishers (Dye et al. 1997), with poor recovery attributed to low primary productivity, biological limitations, competitive interactions and sparsity of facilitating species (Dye 1992; Erlandsson et al. 2006; Reaugh-Flower et al. 2011). Further to the north (KwaZulu-Natal Province [KZN]), brown mussels are patchily distributed on intertidal reefs, with dense mussel beds interspersed with areas denuded of mussels because of variable recruitment success, unfavourable reef conditions or exploitation pressure (Berry 1978; Tomalin and Kyle 1998). Mussels in KZN are exploited by a widespread recreational fishery (Steyn 2016; Steyn et al. 2019) and localised subsistence fisheries (Tomalin and Kyle 1998; Harris et al. 2007; WIOFish 2013).

Steyn et al. (2019) described trends in the recreational fishery for mussels in KZN based on postal, telephone and online surveys. The fishery is managed by national authorities and fishers must buy a collection permit, adhere to a daily bag limit, and use only a narrow blade as a collection tool, to reduce damage to mussel beds. Opportunities to fish for mussels are naturally limited to only 3–4 outings per quarter year by tidal cycles (reefs emerge fully only during spring low tides) and adverse sea conditions (Steyn et al. 2019). Recreational fishing effort and mussel landings were much higher in the past (1980–1998) than at present, based on trends in permit sales and a reduction in the allowed daily bag limit after 1998 (Tomalin and Kruger 2000; Steyn and Schleyer 2014; Steyn et al. 2019). Nevertheless, recreational fishing effort remains high in the densely populated Durban metropole and surroundings in central KZN (Figure 1).

Mussel surveys undertaken during the 1980s suggested overexploitation in central KZN with potential stock collapse on some reefs (De Freitas et al. 1987, 1988, 1989; Tomalin and Kyle 1998). Mussel harvesting was banned on several heavily exploited reefs in eMdloti on a trial basis in 1995 and 1997, and was formally closed in 1998, following the proclamation of a no-take mussel conservancy (Figure 1). The spatial proximity of mussel beds on reefs: (i) within the conservancy (unexploited since 1998); (ii) next to the conservancy boundary (uninterrupted exploitation); and (iii) away from the boundary offered a natural laboratory for studying long-term trends in mussel cover, density and size structure relative to fishing pressure and environmental factors.

The aims of this study were to: (i) estimate trends in mussel cover, density and size at exploited and unexploited sites in central KZN over a 27-year period (1993–2019) and at which regular sampling of fixed transects had been undertaken; (ii) estimate mussel removals by recreational fishers at individual sites; (iii) infer the relative influences of mussel removals and environmental factors on trends in mussel populations; and (iv) evaluate the effects of a no-take conservancy – as a management tool – on local mussel populations. We demonstrate the value of long-term mussel monitoring data in disentangling the effects of fishing and environmental factors on the dynamics of mussel populations.

Materials and methods

Study area and field sampling

Intertidal mussel populations along a 4-km stretch of the central KZN coast at eMdloti (previously Umdloti) were sampled at four sites (Figure 1). The northernmost site at eMdloti (Um) covered a high-profile rocky outcrop exposed to high wave action. Newsell North (NN) covered low-profile reefs, partially sheltered from wave action by an offshore ridge, and Newsell South (NS) was on a flat high-profile reef with intermediate exposure to waves. Peace Cottage (PC) was located <500 m from the mouth of the uMhlanga River, and comprised low-profile reefs exposed to strong wave action. The Um, NN and NS sites are easily accessible to recreational fishers, whereas PC is 2.5 km to the south without road access. Recreational fishing for mussels at Um and NN ceased in 1998 when a no-take mussel conservancy was established that included these two sites. The conservancy, now existing in terms of a municipal bylaw, was still in place at the time of writing (2021) (Figure 1). NS is located outside the conservancy, adjacent to its southern boundary. Recreational fishing at NS and PC continued uninterrupted over the study period.

A fixed 20-m transect line was attached to the reef at each site, parallel to the shore in the middle of the mussel bed (mid-bed transects). Transects were sampled biannually during autumn (March–May) and spring (September–November) between 1993 and 2019 at spring low tide. Quarterly sampling took place between 1993 and 2000. Strong wave action and sanding-over of mussel beds occasionally prevented sampling. Mussel cover was sampled visually in 0.25 m^2 quadrats set at 1-m intervals along the 20-m mid-bed transect lines and expressed as percentage cover. Three replicate mussel samples were harvested from a 0.01 m^2 quadrat set in mid-bed areas with 100% mussel cover during each sampling event. All mussels in each quadrat were removed down to the rock bed. Samples were processed in a laboratory to determine mussel count (ind. m^{-2}) and size distribution (longest antero-posterior shell distance, mussels grouped in 5-mm size classes).

Data analysis

The data were derived from 196 sampling events between 1993 and 2019, stratified by site and season. No data were available for 2007, but with a few exceptions (mainly at PC), data for two seasonal sampling events per reef were available for all other years. Sampling of the Um site only began in 1995. Mussels were categorised into recruits (<35 mm length) and post-recruits (≥35 mm) with the latter assumed to be >6 months old (Reaugh-Flower et al. 2011). Subsequent analyses focussed on mussel cover, count and the mean length of post-recruits. The mean mussel length per sampling event was estimated as:

$$\text{Mean length}_{\text{post recruit}} = \frac{\sum_{\text{size class}}^{\text{Max}} ((n_{\text{size class}}) \times \text{size class mid–length})}{N}$$

where n is the number of mussels per 5-mm size class and N is the total number of mussels ≥35 mm.

Trends in mussel cover, count and mean length were analysed with generalised linear mixed models (GLMMs). GLMMs are appropriate for analysis of data from unbalanced sampling designs (Baayen et al. 2008), and data from all sampling events could therefore be used. R 4.0.2 (R Core Team 2020) and the statistical software packages 'glmmTMB' (Brooks et al. 2017), 'car' (Fox and Weisberg 2019), 'dplyr' (Wickham et al. 2020) and 'performance' (Lüdecke et al. 2021) were used to perform the GLMMs. The Template Model Builder (Kristensen et al. 2016) and maximum likelihood estimation were used to fit the models to the data. Independent variables used in the models were site (Site), survey year (Y), season (S), count (Count; only used in mean length models), mean length (meanL; only used in count models) and conservation status (CS) (Table 1). Conservation status had three levels: open to mussel fishing (all sites 1993–1994 and 1996; PC 1993–2019); boundary fishing (NS 1995, 1997–2019) and closed to mussel fishing (Um and NN 1995,1997–2019). A dummy transect variable was used as a unique identifier (site and date combined). The transect variable nested within Site was included as a random effect to compensate for spatial and temporal pseudo-replication in the data. The full factorial nested variable (Site + Site:Tran) and reduced model without Site as main effect (Site:Tran) were both tested. Model intercepts were set to 1993, autumn and open to fishing.

Final models were selected using a stepwise approach, by modelling combinations of error structure, link functions and explanatory variables. Models were compared using likelihood ratio tests, and those 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 beta error structure and a logit link function were selected to model mussel cover after converting percentage cover to proportions and adding an offset of plus or minus 1.0×10^{-13} to values of zero and one. GLMMs with a gamma error structure and a log link function were selected to model mussel count and mean length. Estimated mussel density along transects (number of mussels ≥35 mm m^{-2}) was determined *post hoc*, by multiplying model-estimated mussel cover by count.

Estimates of mussel removals by recreational fishers

Mussel removals by recreational fishers (annual mussel catches expressed as *F*-Index; 1993–2019) were estimated from permit sales and catch and effort data in voluntary catch reports (1996–1998; Tomalin and Kruger 2000) and offsite postal and telephone questionnaire surveys (1994–1995, 1999–2019; Steyn et al. 2019). For each site, the *F*-index incorporated the relative effects of four permit types used: annual and temporary mussel permits; and annual and temporary bait permits (Table 2). On average, only 57% of annual mussel permits are actively used for conducting at least one mussel outing (Steyn et al. 2019). All temporary mussel permits are presumably used, as each permit is purchased for a planned collection trip and used to conduct twice as many outings in a month as an annual permit (Tomalin and Kruger 2000). However, temporary permits may be used for only one month as opposed to the collection of mussels over a 12-month period with an annual permit; hence, a temporary mussel permit holder collects only 30% of the total catch of an annual permit holder. Voluntary catch returns made by shellfish collectors (1982–1998) indicated that, on average, annual and temporary bait permit holders collected respectively, 28% and 6% of the catch of annual mussel permit holders (Tomalin and Kruger 2000).

Based on catch reports, 0.7% of all mussels removed by recreational fishers in KZN province originated from PC (1993–2019; Tomalin and Kruger 2000; Steyn and Schleyer 2014). Low spatial resolution of catch reports necessitated the grouping of catches from the other three sites; in combination they accounted for 13.5% of KZN mussel removals prior to 1998 (Tomalin and Kruger 2000). To estimate removals at each of these three sites, ease of access was used as a criterion, measured as the distance from the car park to individual sites (–15% per 500 m interval away from the car park). After 1998, collection was only allowed at NS, where 5.2% of KZN mussel removals were made, according to catch reports (Steyn and Schleyer 2014). The decrease in allowed bag limit from 50 to 30 mussels per day after 1998, and closure of Um and NN sites to mussel harvesting in 1995 and 1997, was also incorporated into the *F*-index (Table 2). The estimates relied on consistent individual recreational fishing effort over the past two decades expressed as avidity (proportion of permit holders that go fishing), effort (number of outings per permit holder) and catch per unit effort (number of mussels caught per outing), as determined by Steyn et al. (2019).

Results

Population structure

Mussel recruits (<35 mm shell length; <6 months old) dominated the combined sample (51% of 48 811 mussels), followed by 20% in the 35–59 mm category (6 months to 1 year old) and 22% in the 60–89 mm category (1–2 years old) (Figure 2). Only 8% of mussels were ≥90 mm, or older than two years. The population structure differed among sites, with a higher proportion of recruits at PC than at other sites (Chi-square test, $p < 0.01$). Mussels ≥90 mm length were proportionally most abundant at NN and least abundant at Um (Chi-square test, $p < 0.01$).

Mussel cover

Mussel cover at Um and NN was moderately fragmented prior to the formal establishment of the conservancy in 1998, but became more uniform thereafter. The two sites showed broadly similar temporal trends – with lower mussel cover during the first than the second part of the 27-year time-series and peaks in cover in 1996, 2000 and 2010–2014 (Figure 3a). Rapid mussel cover recovery (+222%) was noted at NN during 1995 (trial closure), followed by large decreases in mussel cover during 1996 (open for harvesting) at Um (–50%) and NN (–45%). The largest increase in mussel cover in a single season was in 1999 (Um: +136%; NN: +105%)

and the largest decrease was in 2014 (Um: –55%). Mussel cover at NS outside the conservancy boundary remained more uniform than in the conservancy. Lowest mussel cover at NS occurred in 1995–1998, during the trial closures of Um and NN, with peaks in 1994 and 1999 and high but variable cover after 2011. The largest increase and decrease in a single season at NS occurred in 1994 (+38%) and in 1995 (–34%; Um and NN trial closure), respectively. Mussel cover increased slightly during 1996 (+15%) when Um and NN were open for harvesting. Mussel cover at PC was highly fragmented, lower, and more variable than at the other three sites, repeatedly cycling between roughly 5 and 80% cover. Peak cover was recorded in 1996, 2010, 2011 and 2019, with troughs in 1993–1994, 1997–2003 and 2013–2016. Sanding events at the PC site were recorded in late 1996, September 2011 and May 2012, preceding periods of low mussel cover. The largest increase and decrease in a single season at PC occurred in 1999 (+419%) and in 1998 (–91%).

Year, conservation status and the nested random transect (Site:Tran) were retained in the best-fitting mussel cover model (Table 3). In addition, there were strong interactions of the time factor and conservation status of the four areas ($p < 0.05$). This resulted in estimated increases in mussel cover of 195% at the conservancy sites and 70% at the boundary site, and a decline of 25% in cover at the exploited site (Figure 3b).

Mussel count and estimated density (post-recruits)

Mussel count was highly variable at all sites between 1993 and 2000 but stabilised at a lower level of around 2 000–4 000 ind. m^{-2} after 2000 (Figure 4a). Year, season, mean mussel length and the nested random transect (Site:Tran) were retained in the best-fitting model (Table 3). Count declined significantly over time, by an average of 3% per year. By season, count was significantly lower during spring than other seasons, by 11–13%. Count was inversely related to mean mussel length (Figure 4b), decreasing by 2% for every 1 mm increase in mean length.

Estimated density (mussel cover × mussel count; ind. m^{-2}) was highly variable at all sites with the highest densities occurring during the 1990s (Figure 4a). The highest and lowest densities were estimated for the PC site, respectively in 1996 (~6 200 ind. m^{-2}) and 2014 (~200 ind. m^{-2}). Estimated densities at PC were generally lower than at the other sites after 1999 and followed the same cyclical pattern as cover, indicating that counts varied relatively little in relation to cover. Low densities (<500 ind. m^{-2}) were estimated at PC in 1998, 2001–2003 and 2013–2015, followed by recoveries in 2005–2010 and 2018–2019. Even so, densities remained below 2 000 ind. m^{-2} after 1997. Estimated densities at the Um, NN and NS sites ranged between 500 and 4 000 ind. m^{-2}, except in 1998 when density at NS peaked at 5 600 ind. m^{-2}. Densities at NN increased by 48% during 1995 (trial closure) followed by large decreases at Um (–67%) and NN (–60%) during 1996 (open for harvesting). In contrast, a large decrease (–51%) in density during a single season in 1995 was recorded at NS, followed by recovery in 1996 (+43%).

Mean mussel length (post-recruits)

The mean mussel length of post-recruits varied between 50 and 90 mm during the study period (Figure 5a). Only count and the full factorial nested random transect variable (Site+Site:Tran) were significant in the best-fitting model. Mean mussel length was inversely related to count, decreasing by 0.4% per increase of 100 ind. m^{-2} (Table 3; Figure 5b).

Fishing effort and mussel removals by recreational fishers

The number of annual mussel permits sold decreased by 60% from approximately 11 000 permits in 1993 to 4 000 permits per year between 1999 and 2019, and the sale of temporary mussel permits decreased from about 5 000 in 1993 to <100 per year between 2010 and 2019 (Figure 6a). Between 1993 and 1998, means of 13 700 (SE 300) annual bait permits and 2 200 (SE 170) temporary bait permits were sold each year. Mussel removals by bait permit holders made up only 26% of the total recreational catch, with mussel permit holders collecting the rest (74% of mussels removed). Mussel removals decreased by 74% between 1998 and 1999 and thereafter remained at <20% of initial 1993 removals for the rest of the study period. Mussel removals aligned well with the numbers of annual mussel permits sold.

Questionnaire surveys (Steyn and Schleyer 2014) and catch returns (Tomalin and Kruger 2000) indicated that, on average, 13 (SE 5) % of mussel permit holders in KZN fished at Um, NN and NS combined prior to 1998; thereafter only 5 (SE 3) % of permit holders fished at NS. Only 0.7 (SE 0.1) % of permit holders in KZN fished for mussels at PC between 1993 and 2019, and consequently removals at PC would have been 13% of those at Um, NN and NS combined (Figure 6b). We estimated that fishing effort and mussel removals at the boundary site at NS would have increased by >245% during 1995 and 1997, when recreational mussel fishers were excluded from the conservancy area on a trial basis. However, the simultaneous reduction in the daily bag limit by 40% and a steep decline in the numbers of permits sold after 1998 reduced overall fishing effort, including the anticipated shift of fishing effort from conservancy to open sites at NS and PC.

Discussion

We used short- and long-term trends in mussel cover, counts and size at exploited- and unexploited sites to disentangle the effects of fishing pressure and environmental change on mussel beds at a geographical scale of <5 km of coastline. Short-term harvesting bans at the Um and NN sites during the mid-1990s, when recreational mussel collection effort in KZN province was high, resulted in rapid increases in mussel cover and estimated densities, but gains at these two sites were reversed immediately after reopening them to fishing in the following years (Figure 6b). In direct contrast, mussel cover and density at the adjacent NS site, which remained open to fishing, decreased rapidly when fishing effort shifted there upon the closure of the Um and NN sites. Resumption of fishing at Um and NN in the following years had the opposite effect – cover and estimated densities at those two sites declined rapidly, but increased at NS when fishing effort shifted back to Um and NN. An inverse relationship between mussel removals and mussel cover was therefore demonstrated at high levels of fishing effort, with short recovery periods.

The short recovery periods of exploited mussel beds found in our study agree with the findings of De Freitas et al. (1987), that brown mussels along the KZN coast have fast recovery rates and are able to increase cover to 50% after total clearance in three to four years under favourable conditions. In contrast, brown mussels along the southern and eastern Cape coasts of South Africa may require more than eight years to recover because of low reproductive potential, the simultaneous exploitation of grazers by subsistence fishers and competition for space with the invasive mussel *Mytilus galloprovincialis* (Dye et al. 1997; Erlandsson and McQuaid 2004; Erlandsson et al. 2006). Genetic differences (Zardi et al. 2011) and environmental factors (higher water temperatures and primary productivity) also contribute to faster growth rates and a higher reproductive potential on the KZN coast (Dye 1992; Robertson 2003). Furthermore, regulations in KZN promote the individual picking of mussels, with collectors targeting larger mussels (Tomalin and Kyle 1998), as opposed to the clearing of reef patches by subsistence fishers (Lasiak and Dye 1989). Successful recolonisation of cleared reefs appears to be slower because of mussel settlement preferences and post-settlement processes (Lasiak and Barnard 1995; Erlandsson and McQuaid 2004; Erlandsson et al. 2008, 2011; Reaugh-Flower et al. 2011). Brown mussel beds increase through encroachment of neighbouring mussels (De Freitas et al. 1987; Erlandsson et al. 2006), and hence fragmented beds can recover more rapidly than denuded areas after exploitation (Tomalin and Kyle 1998).

The effects of longer-term harvesting bans were more difficult to discern and were partially confounded by a decline in fishing effort across the entire recreational fishery in KZN, measured as numbers of permits sold (Steyn et al. 2019). Lower overall fishing pressure reduced the contrast between exploited and unexploited sites, with gradual increases in mussel cover observed at both closed (Um and NN) and boundary sites (NS). Strong cyclical patterns in cover and thus estimated density were synchronised among sites, both seasonally and interannually, suggesting that environmental forcing affected the sites similarly.

The site at PC was anomalous, with highly variable mussel cover and densities despite low fishing effort. Berry (1978) reported severe depletion of formerly large mussel beds in this area, followed by recovery two years after an unusually high settlement event in KZN. Three prolonged sanding events during the study period (1996, 2001 and 2012) clearly affected mussel populations at PC. Sanding events followed breaching of the adjacent uMhlanga Lagoon, and the deposition of sand near the mouth of the estuary (including at PC), which may persist for several weeks (Tomalin and Schleyer 1998). The frequency of breaching has increased since the 1980s because wastewater is now channelled into the upper estuary (Begg 1984; Zietsman 2004; Forbes and Demetriades 2008). Mussel mortalities at PC caused by smothering / sand scouring have resulted in a highly fragmented mussel bed, with lower cover and densities than at the other three sites, despite low fishing pressure. Even so, a rapid recovery of mussel cover at PC took place between 2015 and 2018, when redbait pods *Pyura stolonifera* colonised the mussel zone. Redbait pods facilitate the survival of mussel recruits (Fielding et al. 1994), and by 2019 mussels had overgrown the pods at PC (ES, pers. obs,).

Apart from sanding, wave action can influence mussel population dynamics (Griffiths 1981; McQuaid and Lindsay 2000, 2005) and in the extreme, storm surges can dislodge mussels, clearing large patches in mussel beds (Paine and Levin 1981). High wave action increases growth rates and mean sizes through improved feeding efficiency (McQuaid and Lindsay 2000), while decreasing density by means of wave-induced mortalities (Griffiths 1981). Intense competition for space often causes the upward forcing of older, larger mussels by those that are near the substrate (Griffiths 1981; McQuaid et al. 2015). This weakens the attachment of large mussels to the substrate, and they are then more easily dislodged during high wave action (Griffiths 1981; Nicastro et al. 2008). The synchronised reduction in mussel cover at our study sites where sanding does not take place (i.e. Um and NS) were most likely the result of severe storms.

Intertidal brown mussel populations on the KZN coast consist mainly of two or three year-classes, with more than half of the population being <1 year old (Figure 2, Berry 1978). Settlement and post-settlement processes therefore have a large impact on adult abundance. Peak settlement occurs during spring and summer (Berry 1978; Harris et al. 1998; Reaugh-

Flower et al. 2011) with high mortality of recruits and sub-adults during the first year (Tomalin 1995; McQuaid and Lindsay 2000), and with the older year-classes approaching 2 and 3 years old, respectively. The lower mussel count in spring than other seasons can therefore be explained by a preponderance of recruits in the population at that time, but lower post-recruit numbers because of cumulative mortalities of the older size classes over the foregoing year.

Primary productivity has been postulated as a strong indicator of mussel settlement intensity in South Africa (Harris et al. 1998; Reaugh-Flower et al. 2011). Compared to the highly productive west coast of South Africa, productivity is comparatively low and highly variable in the study area where it is dependent on the variable cyclonic Durban Eddy with inconsistent effects on productivity (Guastella and Roberts 2016) and riverine nutrient-input associated with summer rainfall intensity (Schleyer 1981; Fennessy et al. 2016; Pretorius et al. 2016). The formation of the Durban Eddy and the frequency and intensity of summer rainfall are both influenced by the prevailing Agulhas Current system (Walker 1990; Jury et al. 1993; Guastella and Roberts 2016), which has warmed (Rouault et al. 2009; Sweijd and Smith 2020) and broadened over recent decades because of increased mesoscale eddy activity and variability (Beal and Elipot 2016; Halo and Raj 2020). Changes in sea surface conditions in the Agulhas Current and southwest Indian Ocean (Reason and Mulenga 1999; Jury 2015) and an increase in extreme *El Niño*-Southern Oscillation events (Ratnam et al. 2014; Wang et al. 2019) have contributed to a warmer and drier climate in KZN since the 1960s (Ndlovu et al. 2021). The variable mussel counts in our study are thus not surprising and can be partially explained by the influences of a more variable regional climate on productivity.

Fishing effort for mussels declined sharply during the mid-1990s, driven by increased permit fees, changes in permitting systems, and a 40% reduction in the allowed daily bag limit (Tomalin and Kruger 2000; Steyn et al. 2019). A decrease in fishing effort is corroborated by fishery compliance patrols in KZN that reported large declines in recreational effort and in catches of all marine invertebrate species between 1996 and 2004, with numbers of mussel fishers declining by 42% (Kruger and Schleyer 2005). Aerial surveys revealed a 23% reduction in the recreational shore-based linefishing effort in KZN from the 1990s to the present (Mann and Mann-Lang 2020). Access and opportunity to participate in recreational fisheries in KZN therefore appear to have shrunk. Likely factors are a ban on beach-driving since 2002, which limits access to remote areas, an increased crime rate during the 1990s, and lifestyle changes associated with post-industrialisation, such as less free time and a larger choice of leisure activities (Mann et al. 2008; Arlinghaus et al. 2014; Mann and Mann-Lang 2020). Nevertheless, stability in mussel permit sales, catch and effort statistics since 2000 (Steyn et al. 2019) indicate that fishing effort for mussels has stabilised at a lower level compared to the

1980s and 1990s. The lower participation of younger people (<30 years old; Steyn et al. 2019) suggests that recreational fishing effort may decline further, although this is not certain. The mussel conservancy remains an important conservation tool in central KZN, given the present uncertainty associated with climate-induced environmental change.

In conclusion, brown mussel populations at three of four study sites recovered within a short time-frame (3 to 4 years) when fishing pressure was reduced, but population trends at the fourth site could better be explained by changes in reef habitat suitability. Overall recreational fishing effort has declined drastically over the past two decades; and over a longer term, there was little difference between the unfished populations within the conservancy, compared to the fished site outside and adjacent to the conservancy boundary. Although not specifically monitored, the influence of environmental factors on mussel populations was highlighted by similarly timed peaks and troughs in mussel populations at these three sites, irrespective of trends in fishing effort. The 27-year mussel monitoring dataset was invaluable in disentangling the effects of recreational fishing and environmental factors on the dynamics of mussel populations. Monitoring should be continued, and expanded by also measuring abiotic variables (sea surface temperature, primary productivity, turbidity) to track climate-induced impacts on the biota of rocky shores, an environment highly exposed to the effects of global climate change (Harley et al. 2006).

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Figure legends

Figure 1: Map of study site at eMdloti, north of Durban in central KwaZulu-Natal, South Africa, showing survey sites and mussel conservancy

Figure 2: Population structure (shell length) of mussels sampled at eMdloti (Um), Newsell North (NN), Newsell South (NS) and Peace Cottage (PC) in central KwaZulu-Natal, South Africa, between 1993 and 2019, showing new recruits <6 months old (<35 mm) and post-recruit categories. Inset shows 5-mm-size-class size frequencies from all sites combined

Figure 3: (a) Mussel cover along transects at eMdloti (Um), Newsell North (NN), Newsell South (NS) and Peace Cottage (PC) sites between 1993 and 2019 in central KwaZulu-Natal, South Africa. (b) Temporal trends in mussel cover at open, boundary and closed sites as predicted by the best-fitting model, with 95% confidence intervals

Figure 4: (a) Mussel counts (post-recruits ≥35 mm m^{-2}, in mid-bed with 100% cover) and estimated density (mussel count × mussel cover) in transects at the eMdloti, Newsell North, Newsell South and Peace Cottage sites in central KwaZulu-Natal, South Africa. (b) Predicted effects of year, mean length and season on mussel counts, based on the best-fitting model. Error bars represent SE

Figure 5: (a) Mean mussel length at transects at the eMdloti, Newsell North, Newsell South and Peace Cottage sites in central KwaZulu-Natal, South Africa, between 1993 and 2019. (b) A significant relationship between mean mussel length and mussel count (post-recruits ≥35 mm m^{-2}, in mid-bed with 100% cover) predicted by best-fitting model, shows density-dependent size

Figure 6: (a) Number of annual and temporary mussel permits (Ma, Mt) and bait permits (Ba, Bt) sold in KwaZulu-Natal (KZN), South Africa, from 1993 to 2019. The KZN *F*-Index estimates mussel collection effort relative to 1993, with and without the reduction in bag limit after 1998 (arrow). (b) *F*-Index of mussel collection at eMdloti (Um), Newsell North (NN), Newsell South (NS) and Peace Cottage (PC)

from 1993 to 2019 relative to 1993. The effects of trial closures of Um and NN in 1995 and 1997 (marked with X) and reduction in bag limit in 1999 (arrow) are shown. The mussel conservancy (Um and NN) was formalised in 1998

Table 1: Independent variables tested in mussel cover, count and mean mussel length models using the mussel survey data collected in the eMdloti area, KwaZulu-Natal, for the period 1993–2019

Independent variables	Type	Description
Site (survey site)	Categorical	Four levels: eMdloti (Um), Newsell North (NN), Newsell South (NS), Peace Cottage (PC)
Y (year)	Continuous	1993–2019
S (season)	Categorical	Four levels: summer (Dec–Feb), autumn (Mar–May), winter (Jun–Aug), spring (Sep–Nov)
CS (conservation status)	Categorical	Three levels: closed to fishing; open to fishing; open and located on the conservancy boundary
Count (number)	Continuous	Number of mussels ≥35 mm length per 0.01 m^2 quadrat sampled in mid-bed with 100% cover. Used in mean length models
meanL (mean mussel length)	Continuous	Excludes mussels <35 mm. Used in count models
Site:Tran (unique identifier for each sample time and site; transect nested in site)	Categorical	175 samples in mussel cover models; 196 samples in count models; 196 samples in mean length models. Transect nested in site interaction term used in mussel cover and count models. Interaction term and site main effect used in mean length models

Table 2: Factors considered in mussel removal estimates (*F*-Index) per site for the recreational fishery between 1993 and 2019. Estimates relied on the numbers of permits sold for use in KZN ($Permits_{KZN}$), fishing effort and catch data sourced from voluntary catch reports (1996–1998; Tomalin and Kruger 2000) and offsite postal and telephone questionnaire surveys (1994–1995,1999–2019; Steyn and Schleyer 2014; Steyn et al. 2019). Um = eMdloti; NN = Newsell North; NS = Newsell South; PC = Peace Cottage. P_{PC} and P_{Group} refer to the proportion of permits used at respectively Peace Cottage and the three eMdloti sites.

Factor	Rationale	Equation
Permit type	Ratios of mussel removals per permit type was estimated as: – annual mussel permits (Ma): 1.0 – temporary mussel permits (Mt): 0.3 – annual bait permits (Ba): 0.28 – temporary bait permits (Bt): 0.06 Bait permits were discontinued after 1998 (Tomalin and Kruger 2000; Steyn et al. 2019)	$F\text{-Index}_{1993–1998} = Ma + 0.3Mt + 0.28Ba + 0.06Bt$
Daily bag limit	Daily bag limit reduced from 50 to 30 mussels/permit/day in 1999	$F\text{-Index}_{1999–2019} = 0.6(Ma + 0.3Mt)$
Site effects; distance from parking (1993–1998)	Catch reports distinguished permits used at PC (P_{PC}) but grouped the other three sites (P_{Group}). We assumed that the *F*-Index decreased by 15% at 500-m intervals away from the carpark. – Um: adjacent – NN: 500 m – NS: 1 km – PC: known proportion	$F\text{-Index}_{Um\ 1993–1998} = (P_{Group} \times Permits_{KZN}) / 2.55$ $F\text{-Index}_{NN\ 1993–1998} = 0.85\ F\text{-Index}_{Um\ 1993–1998}$ $F\text{-Index}_{NS\ 1993–1998} = 0.7\ F\text{-Index}_{Um\ 1993–1998}$ $F\text{-Index}_{PC} = P_{PC} \times Permits_{KZN}$
Site effects; closure of Um and NN to mussel collection in 1998	All permits previously used at Um and NN shift to NS – Um = 0 – NN = 0	$F\text{-Index}_{NS\ 1999–2019} = P_{Group} \times Permits_{KZN}$

Table 3: Best-fitting generalised linear mixed models (GLMMs) used to describe mussel cover, count and mean mussel length in the eMdloti area, KwaZulu-Natal, showing the factors retained, analysis performed, error structure, link functions used, Akaike's information criterion (AIC) and the numbers of observations (*n*). Parameter estimates marked with an asterisk (*) were significantly different from the intercept ($p < 0.05$). Y = year; S = season; CS = conservation status; meanL = mean mussel length; Um = eMdloti; NN = Newsell North; NS = Newsell South; PC = Peace Cottage

	Mussel cover	Count	Mean mussel length
Factors	Y × CS + random(Site:Tran)	Y + S + meanL + random(Site:Tran)	Y + Count + random(Site+Site:Tran)
Analysis	GLMM	GLMM	GLMM
Error	Beta	Gamma	Gamma
Link	Logit	Log	Log
AIC	–17 106	4 003	3 930
n	3 474	569	569
Data	20-m transects	All 0.25-m^2 quadrats; mussels >35 mm	All 0.25 m^2 quadrats; mussels >35 mm
	Estimate (SE)	Estimate (SE)	Estimate (SE)
(Intercept)	0.36 (0.03)*	3 943.33 (257.97)*	78.41 (1.66)*
CS: closed	+0.19 (0.04)*		
CS: boundary	+0.34 (0.04)*		
Year	–0.06 (0.05)	–101.65 (12.39)*	
Year × CS: closed	+0.43 (0.06)*		
Year × CS: boundary	+0.34 (0.08)*		
S: summer		–72.28 (298.78)	
S: winter		–120.26 (303.70)	
S: spring		–529.49 (187.12)*	
Mean mussel length		–1 141.79 (81.83)*	
Count			–0.28 (0.03)*
random(Site): Um			–3.62 (0.08)
random(Site): NN			+2.46 (0.05)
random(Site): NS			+1.86 (0.04)
random(Site): PC			–0.79 (0.02)
random(Site:Tran)	+0.02(<0.01)	+106.88 (0.62)	+0.20 (<0.01)