

The Response of Mobile Intertidal
Invertebrates to Subsistence Harvesting in
Northern KwaZulu-Natal

Derek Morgan

HANS 2000
KD MORG

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.



Abstract

The Response of mobile intertidal invertebrates to subsistence harvesting in Northern KwaZulu Natal was investigated. Spatial scale comparisons were made between as well as within harvested and non-harvested locations. The difference in three population variables was investigated; i) abundance of species groups, ii) size structure of each organism and iii) community structure of mobile organisms. Abundance analysis revealed no significant difference between harvested and non-harvested regimes for most species groups, excepting Snails and Chitons. Snails were more abundant and chitons less abundant at harvested sites. A significant difference between locations was however noted, for all species groups, suggesting that variation in abundance within is more prominent than between harvesting regimes. Size structure analysis revealed significantly larger sizes for most species at non-harvested locations, with only *Morula granulata* and *Scutellastra exusta* showing a significantly larger size structure at non-harvested locations. Community structure analysis revealed no clear distinction between or within harvested locations.

A decrease in size structure with no corresponding density effect may be a function of the preference of harvesters for larger individuals, thereby favouring juvenile populations. The possibility also exists that density effects have been masked due to the use of size instead of biomass data. Converting to size data to biomass, using wet mass *versus* size regressions, may be a more appropriate analysis method. The observed differences in community structure between as well as within locations indicates that the intertidal communities are inherently heterogenous in this area. In order to determine the impact of exploitation, spatial scale comparisons between harvesting regimes thus ideally need to be conducted at each location. In this study

there was also a lack of representative control sites, as unharvested locations are in reality impacted by fisherman and tourists. A possible strategy would be to demarcate "no-go" areas in harvested and non-harvested areas, to serve as both controls and provide brooding stocks for adjacent ledges. It is however recommended that more research emphasis be placed on the user in evaluating the effects of human impact on intertidal resources.

Introduction

Subsistence utilization of the intertidal zone in South Africa has a long and persistent history dating back 50 000 years (Volman 1978, Siegfried 1988, Siegfried *et al.* 1994). This tradition of collecting organisms as a basic source of nutrition and medicine is still practiced today, for the most part along the coastlines of northern KwaZulu-Natal (KZN) (Dye *et al.* 1994, Kyle *et al.* 1997a, 1997b) and in the area of the Eastern-Cape formerly known as the Transkei (Bigalke 1973, Branch 1975, Siegfried *et al.* 1985, Hockey and Bosman 1986, Hockey *et al.* 1988, Lasiak 1991, 1992, 1993, Dye *et al.* 1997). Recently however, a debate has developed regarding the sustainability of subsistence harvesting of intertidal invertebrates, particularly in the northern region of KZN (Maputaland).

Two key arguments justify concerns that stocks are being depleted, biodiversity compromised and that effective mechanisms of control are needed. The first is that the pressure of human harvesting on mussels as well as limpet populations in the Transkei has resulted in a decrease of density as well as maximum size of these animals. The impact is so severe that mussel beds are no longer present in exploited areas, with only sporadically distributed clumps or individuals surviving the coastline (Hockey and Bosman 1986, Hockey *et al.* 1988, Lasiak and Dye 1989, Lasiak 1991, Siegfried *et al.* 1994, Branch and Odendaal in press). A second argument is that recent biodiversity studies along the northern KZN coastline (K. Sink unpublished data), show that compared to stock surveys from the 1970s (Jackson 1976), the intertidal

mussel bands have shifted seaward into the infratidal, and have consequently been replaced by algal belts.

To compound this, there are no *de facto* control structures in place with regards to intertidal harvesting in the Maputaland area. The coastline of northern KZN has been divided into two marine restricted areas. The Maputaland Marine Reserve (MMR) stretches 72 km from the Mozambique border along the coastline of the Kosi lake system to 20km north of Sodwana Bay. The St Lucia Marine Reserve (SLMR) borders the MMR and stretches south as far as Cape Vidal. By law harvesters are required to carry permits to collect organisms inside the reserves, and are only authorized to harvest in certain restricted zones. However, because of previously ineffective control methods, as well as an established history of utilization in the MMR, these and other regulations have been all but ignored.

To counter calls for stricter regulatory systems, it has been argued that it is not reasonable to compare Maputaland to the Transkei, as they are two distinct biogeographic regions. Jackson (1976) describes a well-defined biogeographic break at Cape Vidal between the northern tropical and southern subtropical faunal assemblages. It is also argued that Maputaland has an exploitation history dissimilar to that in the Transkei, and that although there has been continued extensive harvesting in the Maputaland area, the level and effect of harvesting appears to have continued at a sustainable level (Kyle *et al.* 1997a, 1997b, Tomalin and Kyle 1998).

In 1988 a long-term monitoring project was initiated to evaluate the sustainability of intertidal harvesting along a 30km stretch of coastline within the MMR (see Kyle *et*

al. 1997a and 1997b for details). Effort as well as off-take was recorded for a number of harvested species groups including mussels (*Perna perna*), red bait (*Pyura stolonifera* (Heller)), oysters and limpets. Effort was calculated as the number of women collecting from each per day ($\text{women}\cdot\text{day}^{-1}$). However because the Maputaland coastline comprises predominantly sandy beaches (90%), harvesters are forced to walk great distances (on average 4 hours) to harvest the rocky shore resources. Over the survey period roughly 200 women collected regularly, directly supplying food for approximately 1200 people. There was also a small component of medicinal collectors, but this group made up less 1% of the total collecting effort.

Over the 7-year period, the study demonstrated that the catch per unit effort (CPUE) of the primary target species mussels and redbait as well as oysters remained constant. However there was evidence to suggest that the CPUE of the secondarily harvested species, specifically limpets but also urchins, whelks and chitons (including the endemic *Chiton salihafui*) declined significantly. In this paper I investigate these animals further with the aim of ascertaining whether subsistence harvesting in the Maputaland area is having a significant impact on these secondarily harvested, mobile, invertebrate populations.

Three central questions are posed: 1) Are mobile intertidal invertebrates more abundant at non-harvested than at harvested locations? 2) Do these animals have a different size structure at locations that are non-harvested? 3) Is there a distinct divergence in community structures between harvested and non-harvested regimes?

The results from these questions, in association with current research being conducted in this area, should give an insight into the sustainability of intertidal harvesting in Maputaland and from this, if necessary, new and effective management strategies can be initiated.

Methods

Study sites

The study region spanned an area of more than 120km stretching from Botelier Point in the MMR to Cape Vidal in the SLMR (32° 54'E, 26° 50'S to 32° 16'E, 28° 10'S) along the northern KwaZulu coast of South Africa (Fig 1). The shoreline constitutes approximately 10% intermittent quaternary sandstone rocky shore and 90% sandy beaches (Jackson and Lipschitz 1984). Eight separate intertidal rock ledges were sampled, four of which experience regular subsistence harvesting and four are supposedly protected from harvesting. Three of the non-harvested locations (Cape Vidal, Sodwana and Adlins) are situated within the St Lucia Marine reserve, which is strictly patrolled by the KwaZulu Natal Nature Conservation Services (Tomalin and Kruger 1997, Tomalin and Kyle 1998), while the fourth location, Island rock, is situated further north, and is mostly inaccessible to local harvesters as it is separated from the mainland by a fairly deep channel. Kyle (*pers comm*) states that harvesters gain access to the island once every few years during especially low spring tides. The four harvested locations (Black Rock, Botelier Point, Mabibi and Rabbit Rock) are all situated within the MMR. All sampling was conducted during three spring low tides, between the period 17 March 2000 to 21 April 2000.

Sampling Method

At each location two separate sites were selected that best characterized the intertidal rock ledge. The sites were positioned a minimum of 60m apart and labeled North and South. Each site was 20m wide, and extended from the mean low water spring (MLWS) to the mean high water spring mark (MHWS). The sites were divided into four equidistant horizontal zones; low, mid, high and top, excepting Island rock, which was divided into two zones (low and mid), as it lacked the upper two zones. Zonation was assigned spatially rather than ecologically to accommodate for the possible shift in zonation patterns due to harvesting (Fig. 2).

Abundance was recorded using two separate sampling methods, (*A* & *B* below) at all sites, in order to accommodate the wide-ranging densities, sizes and visual impacts of the different species (Fig. 2). In sampling method *A*, each zone was surveyed on two transects, each consisting of five 1m X 0.5m sampling quadrats spaced 4m apart. The transects were positioned parallel to the shore, equidistant from the zone's two neighbouring borders and to each other. All harvested mobile intertidal invertebrates were recorded per quadrat as a total per m². Sampling method *B* was more extensive so as to obtain a representative sample of the larger and more scarce species, and therefore excluded the more abundant species such as limpets (*Cellana capensis*, *Fissurella* spp., *Scutellastra aphanes*, *Scutellastra exusta*, *Scutellastra oblecta* and *Siphonaria* spp.) and small whelks (*Morula granulata* and *Thais savignyi*) (see Table 1). Species were recorded using four replicate belt transects per zone, 1m wide and 20m long, placed at 45° to the shoreline. Abundance was expressed in terms of numbers per m².

Size structure was determined by measuring the total body length of all recorded specimens within each zone, but limited to a maximum of $N = 30$ and minimum of $N = 10$ measurements per species per zone, due to time constraints.

Data analyses

To establish the effects of harvesting on exploited population and/or communities, many studies have made spatial comparisons between exploited and non-exploited localities (Moreno *et al.* 1984, Hockey and Bosmann 1986, Oliva and Castilla 1986, Duran *et al.* 1987, Castilla and Bustamente 1989, Lasiak 1991). However these studies have been criticised owing to a lack of within-site replication (Fairweather 1991, Lasiak and Field 1995). Underwood (1989) states that without sufficient intra-spatial replication it is unrealistic to attempt to determine a statistical effect of inter-spatial factors, such as human harvesting. I therefore evaluated the influence of exploitation by formulating comparisons between as well as within harvesting and non-harvesting regimes.

For abundance data species were grouped according to basic taxonomic resemblances. 'Large Limpets' included *Cellana capensis*/*Helcion concolor*, *Fissurella* spp. and *Scutellastra exusta* (formerly *Patella pica*) while 'Small Limpets' included *Scutellastra aphanes*, *Scutellastra obtecta* and *Siphonaria* spp. The data for *Cellana capensis* and *Helcion concolor* have been combined in this study due to an initial mis-identification. The 'Large Whelks' group consisted of *Mancinella alouina*, *Purpura panama* and *Thais bufo*, while *Morula granulata*, *Thais savignyi* and *Nucella*

squamous were classed as 'Small Whelks'. All polyplacophora were grouped as 'Chitons' and the category 'Snails' included *Littoraria glabrata*, *Mitra litterata*, *Nerita* spp. and *Turritella* spp. All grouped data were log transformed ($\log_{10}(x + 1)$) to improve homogeneity of variance. The experimental design was a three-way nested analyses of variance, with two harvesting regimes (harvested and non-harvested), four locations within each harvesting regime and two sites per location. Because of nesting, interactions of the nested factor with the factor/s in which it was nested could not be evaluated (Zar 1974). Consequently only the interaction between harvesting regime and site could be considered.

The null hypotheses being tested were: H1: Harvested (x) = Non-harvested (x) for all x . H2: No significant difference in density between locations within either harvesting regime, H3: North (x) = South (x) for all (x) at every location, and H4: The interaction between harvesting regime and site has no significant difference for all (x), where (x) represents the total density of species groups at each site.

With regards to size structure analysis, a Kolmogorov-Smirnov two sample test was applied to test the null hypothesis H5: Harvested (x) = Non-harvested (x) for all x_i where (x) represent the size frequency distribution at all locations within each harvesting regime. Due to the irregular distribution of most species it was not possible to do size structure analysis between and within locations. For accuracy, analysis was also limited to species with $n > 10$ size measurements.

Community structure was analysed after root-root transformation of abundance data for all species (see Lasiak 1999 for transformation justification). Bray-Curtis

similarity coefficients were derived between all fits (for details of techniques see Field *et al.* 1982, Clarke 1993), by employing CLUSTER, a program in the PRIMER software package (Plymouth Marine Laboratory, U.K.). The results were plotted on a Bray-Curtis similarity dendrogram.

Results

The percentages of the total number of species and the densities of species found at each of eight locations are summarised in Tables 2 and 3 respectively. Six species (*Cellana capensis*, *Helcion concolor*, *Scutellastra exusta*, *Siphonaria* spp., *Morula granulata* and *Thais savignyi*) constituted more than 80% of all animals recorded. Species groups that were poorly represented included echinoderms (0.66%), cones (0.86%) and cowries (0.14%). There was also unevenness in species diversity at different locations, with Black Rock being the most diverse location, containing 23 of the 31 species recorded. The diversity at Island Rock (17 species) should also be seen in light of the fact that its elevation is low so that only low and mid shore zones are present.

The results for the nested analysis of variance for the six most abundant species groups are shown in Table 4. H1 (Harvested (x) = Non-harvested (x) for all x) is accepted for all species groups excepting chitons and snails, where a significant difference between the harvested and non-harvested regimes was revealed ($F = 10.236$, $df(1,215)$ $P < 0.005$ and $F = 1.821$, $df(1,215)$ $P < 0.0005$ respectively). Snails were more abundant and chitons less abundant at harvested sites. Overall, this signifies limited effect of harvesting on abundance. Additionally, there was a

significant difference in the interaction between harvesting regime and site ($F = 4.899$, $df(4,215)$ $P < 0.0001$) for chitons, thus rejecting H4 (The interaction between harvesting regime and site has no significant difference for all x), implying that the significant variance between harvesting regimes cannot be considered in isolation but needs to be examined in conjunction with inter-site variation. H2 (No significant difference in density between locations within either harvesting regime) is rejected for all species groups, which suggests that the variation in abundance between locations was more prominent than between harvesting regimes. In two instances, this was compounded by inter-site differences, which were significant for small limpets ($F = 11.601$, $df(4,576)$ $P < 0.0001$) and small whelks ($F = 6.983$, $df(4,215)$ $P < 0.005$).

To further evaluate the significant inter-location variations, means and standard deviations were plotted for the six species groups at each location (see Fig. 3). There were no consistent spatial patterns discernable among the different species groups, although a marginal bias in abundance towards Island Rock and Black Rock was evident. Large limpets, large whelks, small whelks and chitons were all well represented at these two locations. Mabibi too had considerable representation by all species groups, in particular snails and small limpets.

The Kolmogorov-Smirnov test results for size structure analyses revealed conspicuous differences between harvesting regimes. Table 5 shows that H5 (Harvested (x) = Non-harvested (x) for all x) is rejected for all species, excepting *Morula granulata* and *Scutellastra exusta*, which had a significantly greater size distribution in the harvested regime ($P < 0.001$ and $P < 0.025$ respectively), implying that harvesting caused a decrease in the size composition for most of the exploited

species. Frequency distribution plots of these species (Fig. 4) corroborated these results and illustrate that the overall size composition for harvested species was always less than that of non-harvested species, excepting for the above two mentioned species. Note that for these plots, number of observations is arbitrary as measurements were limited to $n = 30$ in each zone.

Community structure similarities between sites are represented by the dendograms in figure 5. It is evident that neither site, location or harvesting regime cluster together. This indicates that for mobile organism community structure there appears to be more variation within sites and locations, than between harvesting regimes.

Discussion

Human impact on intertidal resources is not a recent phenomenon. Several researchers have provided evidence that harvesting well before historic times may have influenced both size structure and densities of various intertidal species (Anderson 1979, Brownell and Stevely 1981, Yesner 1984). In more recent times however, there is concern that the degree of exploitation has dramatically intensified with expanding human coastal populations and as resources have acquired economic value. In Maputaland these factors are especially relevant owing to the severe level of unemployment. As a consequence resources supplement diets as well as household incomes.

Frequently the most immediate impact of over-exploitation is a change in density and size structure of the exploited species. In reality even in areas where there is limited

access, exploitation can cause a shift in both size structure and abundance of the harvested organisms (McLachlan and Lombard 1980, Branch and Moreno 1994). Furthermore the effects of over-exploitation are not limited to population dynamics. There can be indirect interspecific effects, where the harvesting of one species affects the dynamics of another, as well as ripple effects that spill throughout the intertidal community (Branch and Moreno 1994).

Direct effects

Tables 2, 3 & 4 show minimal evidence that harvesting contributes to density shifts for the majority of the species groups. A significant difference between harvested and non-harvested regimes was only detected for chitons and snails ($p < 0.005$ and $p < 0.0005$ respectively). To compound this, species density results (Fig. 3) suggests that there is no obvious pattern discernable between harvested and non-harvested regimes, even for chitons and snails, which display opposite trends with chitons less abundant snails more abundant in harvested areas. However in light of the growing concern (Kyle et al 1997b) that harvesting may be placing the endemic population of the Polyplacophora *Chiton salihafui* at risk, these results need to be discussed in more detail.

Chitons typically inhabit shaded areas, such as rock crevices or vertically shaded rock outcrops (Branch *et al.* 1994). Chitons were most abundant at four locations: Island Rock, Black Rock, Mabibi and Adlims (Fig. 3). These four locations share a common feature in that they all, to varying degrees, provide shaded, sheltered microhabitats, whether through rock crevices and outcrops or through extensive barnacle covering

(see below). In comparison the other four locations (Cape Vidal, Sodwana, Rabbit Rock and Botelier Point) all have relatively homogenous horizontal rock shelves.

The low- to mid-shore of Island Rock was almost completely dominated by large adult barnacles (*Octomeris angulosa* and *Tetraclita squamosa rufotincta*). Both *Chiton salihafui* and *Onithochiton literatus* were most often found residing in shadows created by barnacle shells (*pers. obs.*). At Black Rock chitons were found interspersed between barnacles in the low zone, but were also found resident in the higher mid zone and to some extent in the high zone. The rock profile in the mid- to high-shore of Black Rock is effectively vertical with several shading projections and overhangs. At Mabibi and Adlims, there are shaded vertical rock surfaces in the low to mid shore at both locations.

A comparable argument for habitat preference could be applied to snails. The two locations where snails were most abundant were Mabibi and Black Rock (Fig. 2). Two species of snails were largely responsible for these high densities, *Nerita* spp. and *Littoraria glabrata* respectively (Table 2). Juvenile *L. glabrata* are well adapted to desiccation stress, and as a result are often widespread on the high shores. Branch *et al.* (1994) state that *Nerita* spp. also favours the high shore although preferably in shaded crevices. Mabibi and Black Rock, which harbour several shallow cracks transversing the length of the high shore rock ledge, provide the characteristic habitats for these animals.

Because the greater densities of chitons and snails were not consistent over all unharvested sites, but occurred at ledges that appear to provide specific habitat

preference, it is possible that the observed significant differences are rather a consequence of habitat requirements than of harvesting pressure. However, this does not imply that there is no effect of harvesting. It is quite possible that harvesting may be masked by habitat preferences. To determine if harvesting has impacted these populations, more rigorous, either temporal or more localised spatial comparisons need to be made. Better still, sections of harvested areas could be closed to harvesting and the consequences monitored

A further potential direct impact of harvesting is an adjustment in size structure. Harvesting often reduces the cumulative size composition of species, as predominantly larger animals are selected for (Lasiak 1991). This has been demonstrated for intertidal grazers in South Africa where, along the Transkei coast, subsistence harvesting of the limpets *Helcion concolor* and *Cellana Capensis* (Branch 1975a) and *Cymbula oculus* (Branch and Odendaal in press) resulted in a marked shift in size structure. Similarly, I found consistently lower cumulative size-frequency distributions, for most species at harvested sites (Fig. 4). This implies that harvesting has impacted on the collective size structure of the majority of the intertidal mobile animals.

Of the 14 species analyzed for size structure variation, only the limpet *Scutellastra exusta* and whelk *Morula granulata* had a significantly greater cumulative frequency distribution in a harvested regime. Furthermore even the results for *S. exusta* seem contestable as this particular limpet grows to the largest size of all the intertidal limpets in Maputaland (Kilburn 1942), making it probably the most desirable species. However analysis of the biology of *S. exusta* shows that the zone of preference of this

animal is the sublittoral fringe, often growing alongside barnacle and mussel patches (Kilburn 1942). Because most of the intertidal grazers are opportunistically harvested while the collectors wait for the tide to ebb (Kyle pers. comm.), it is quite probable that in the brief period when the tide is at its lowest, the harvesters are more engaged in their primary catch, mussels and red bait, than in limpets.

As Branch and Moreno (1994) state, changes in size structure and abundance are only symptoms of an unhealthier syndrome. The power relationship between flesh mass and size implies that a decrease in size composition causes a far more substantial reduction in flesh weight. To illustrate, harvesting of *Patella concolor* in the Transkei caused a 35% decrease in size structure, but this translates into a 72% decrease in maximum flesh mass (Branch and Moreno 1994). The unsettling consequence of this relationship is that more, smaller animals need to be harvested in order to attain an equivalent biomass.

With decreased densities and/or size structure, there is also a possible consequential decrease in reproductive output, which in turn can feed back to a decrease in density. However, this is not universal, as previous exploitation studies have shown a range of consequences on recruitment success (Creese 1981, Creese 1982, Quinn 1988, Branch and Odendaal in press). Success of recruitment varies depending on, among other factors, larval dispersal distances, adult influence on settlement habitat, as well as competition for food and space with adults and other species.

There may also be positive implications of a reduction in abundance and size composition. Growth rates of intertidal grazers are often inversely proportional to

density (Underwood 1978, Eekhout et al. 1992, Branch and Moreno 1994). Studies have also indicated occurrences of earlier maturation, and higher recruitment with decreasing abundance (Branch 1975b). But these conclusions too are not unanimous. In surveys dealing specifically with the impact of human harvesting on limpet populations (*C. oculus* in the Transkei, Branch and Odendaal (in press) and *Siphonaria gigas* in Costa Rica, Ortega 1987) maturation and growth rates remained unaltered following exploitation.

It is nevertheless evident that size structure and density are intimately related. Therefore it seems perplexing to some extent that a general decrease in size structure was observed in this study but not a corresponding decrease in abundance. Analysis of biomass, rather than abundance may have yielded a different picture. This can be amended by reanalyzing the density data through converting size to biomass using wet mass *versus* size regressions. Furthermore a shift in size composition with no subsequent density effect does not necessarily imply that reproductive output has not been affected. Branch and Odendaal (in press) have demonstrated that harvesting of *C. oculus*, decreased abundance of large individuals but favoured juveniles, so that total density remained unchanged.

However it is also possible that the results are accurate, in that harvesting has only effected size composition. This inference is potentially consequential, in that if density is not effected by harvesting, coupled with the fact that harvesting has been carried out in this area for generations, it is quite possible that harvesting is being conducted at a sustainable, if not maximum level.

Indirect effects

Interspecific interactions such as grazing are often crucial in intertidal communities, as these animals serve an important role in regulating the settlement of competitive dominants. Ample evidence demonstrates that the most frequent result of removing intertidal grazers is an increase in either algal or sessile organism cover (Paine and Vadas 1969, Branch 1981, 1985, Branch and Moreno 1994). Interspecific interactions are in addition seldom executed in isolation. Often the effects on secondary species in turn impact on other species, consequently cascading throughout the community. This is manifest in an example in Chile where harvesting of the grazing keyhole limpets (*Fissurella* spp.) and 'locos' (*Concholepas concholepas*) have triggered a complete intertidal community restructuring, resulting in the algae *Iridaea laminarioides* competitively dominating the low shore (Oliva and Castilla 1986, Duran and Castilla 1989). However when humans were prevented from harvesting, the grazer populations were restored and consequently the abundance of *I. laminarioides* dwindled. This shift created space for barnacle settlement and the return of competitively subordinate algae species, such as *Ulva* and *Porphyra*.

Added to this ripple effect is the fact that subsistence harvesting is seldom a single species fishery. Thus a common occurrence in harvested areas is a convergence in community structure towards a similar (often inedible) assemblage, with a corresponding increase in diversity through intermediate disturbances. (Hockey and Bosman 1986, cited in Branch and Moreno 1994, Lasiak and Field 1995). Thus the underlying reasoning in similarity community analysis is that areas that experience

similar harvesting stresses are likely to show convergence in community assemblages compared with those areas that are unexploited.

In the present sites however, Bray-Curtis similarity plots yielded insufficient clustering to separate the two harvesting regimes (Figure 4). This could be translated as negligible harvesting effect on community structure, except that the analysis only incorporated mobile invertebrates and was thus not truly representative of the entire intertidal community. Further analysis, which integrates a more representative sample of the intertidal community, is required before any meaningful conclusions can be reached regarding transformation of community structure.

Nonetheless, one important inference can be made from densities presented in Tables 2 & 3 and from personal observations. Menge & Branch (in press) state that one of the key physical variables affecting intertidal species composition is wave action. As an example, at more exposed sites, the mid zone is often dominated by barnacles and foliose algae while the low zone often includes bands of mussels. These mussels in turn create microhabitats for other species, particularly juvenile limpets, and prevent competitively dominant algae from suffocating other low-shore animals. This increases overall species diversity. At less exposed sites there are fewer mussels, which are replaced by algae and barnacles. As a consequence there is often lower species diversity (Menge and Farrell 1989). Two most diverse locations in terms of mobile invertebrates were Island Rock and Black Rock (Table 2). Both the low zones of Island Rock and Black Rock had substantial mussel clumps, rarely observed at the other six sites. To compound this, of the eight locations, Island Rock and Black Rock are the only two sites which are classified as very exposed to wave action (K. Sink

unpublished data.). Wave action may thus play a fundamental role in the Maputaland intertidal community assemblages. The implications of this are that further analysis will need to consider whether the degree to which wave action effects community structures, should be controlled for in order to interpret the impact of harvesting.

Management implications

Underwood (1989) emphasizes the importance of replication in spatial scale comparisons. In this study, analysis of variance as well as similarity analysis indicated that there was significant variability not only between locations but also between sites within locations. The reasons for this variability are twofold. Firstly there is obvious heterogeneity along the rock ledges with regards to physical variables such as ledge profile and wave exposure. Secondly there are different levels of exploitation at the different locations. To compound this, Kyle *et al.* (1997b) have illustrated a distinct spatial (location) separation in effort directed at the various harvested organisms. For example, 78% of all mussels harvested were from the intertidal ledges known as Dog Point and Black rock, 40% of red bait was gathered from Kosi Mouth and in particular 52% of all limpets harvested were from a single location, Rabbit Rock.

An additional component that has not been included in my analysis is the impact of recreational fishermen and tourist activity, particularly on the ledges at Cape Vidal and Sodwana, in addition to Adlims and Mabibi. There is an ever-growing congregation of both resident and seasonal recreational fishermen who in theory are not permitted to collect organisms in a protected area but in practice use a range of invertebrates, including limpets and whelks, for bait (J. Porter, Nature Conservator of

Cape Vidal, *pers. comm.*). It is obvious that if organisms are being collected from both harvested and non-harvested locations, the above comparisons are invalid. Recent surveys have also indicated that although tourist activity is mainly seasonal, it can be particularly damaging through trampling effects, to both the invertebrate and algal populations present on rocky shores (Keough and Quinn 1998, Schiel and Taylor 1999).

In order to incorporate the impact of these groups into the analysis, comparative-use values between local harvesters and tourists\fishermen could be determined by simultaneous spot surveys. The abundance and size structure data between the two harvesting regimes could then be adjusted accordingly. These comparative-use values could also give an indication of the severity of impact on intertidal communities by these tourists\fishermen group, and if necessary, management regulations can be implemented.

In order to reap the benefits of marine protected areas it is essential that there are representative sections in the reserve that remain completely undisturbed. However because of the heterogeneity of the Maputaland area, selecting a representative site as a control location is almost impossible. Ideally an effective strategy would be to demarcate replicated "no-go" areas at each of the main rock ledges. This would ensure a control for each location as well as serve as a brooding stock for many of the organisms. Realistically however this would be difficult to implement, particularly in the areas used by subsistence harvesters. It may be possible to assure local harvesters of the advantages a brooding stock, as they are more dependent on the resource. However they would need to sacrifice some of their catch without the sure guarantee

of improved densities or diversity. Another approach is to use protected areas as a means of demonstrating the impact of harvesting. This method has been successfully implemented on the intertidal ledges of Sokhulu, a region directly south of SLMR (J. Harris unpublished). The ledge is divided into a number of zones, each subject to a different intensity of exploitation. Ultimately the resultant range in invertebrate densities and community structure serves both as a visual demonstration of the impact of harvesting and as a means for determining the maximum sustainable yield for the organisms.

For tourists\fishermen "no-go" area may be more achievable as there are already policing structures in place. Either a complete section of a ledge can be demarcated as "no-go", or alternatively people could be given access only on designated walkways. The latter may be a more effective approach as it would not exclude people from the ledge but would create a sense of awareness to the vulnerability for the intertidal communities.

People have over many decades become an integral part of the intertidal environment in this region, and will continue have an influence over the foreseeable future. It is often assumed that as human population numbers expand, so their impact on natural resources will intensify. This is true for tourists and fishermen, where in the foreseeable future their numbers can only multiply. In order for effective management, emphasis on their future impacts has to be realistically evaluated. Conversely, it is possible that the impact of subsistence harvesting may subside in the future as a subsistence lifestyle becomes less and less favoured, particularly

among the youth (Kyle *pers. comm.*). In effect a shift in focus from the resource to the user in terms of both research and management may be a more prudent way forward.

Acknowledgements

Firstly would like to thank Dr. Jean Harris for her supervision and organization of this project. I doubt whether it would have been such an accomplishment without her input. Secondly I would like to thank Ronnie Breiton-Styles, Mabongi Mashlango and James Rawlinson for their assistance data collection, often in extremely uncomfortable and pressurized conditions. I would also like to thank Prof. George Branch for his sensible advice and for always making time available for discussion. Thanks also to Barry Clarke, Anthony Richards and Jackie Sommerville for their assistance in data analysis.

The National Research Foundation (NRF), Marine and Coastal Management (MCM) and South African Center Oceanographic Research (SANCOB), all provided funding in the form of grants to G.M. Branch. Likewise thanks to KwaZulu Natal Nature Conservation Services for their logistic support in terms of accommodation and vehicles.

Finally thanks to my family for their continuous support.

Reference list

- Anderson, A.J. 1979. Prehistoric exploitation of marine resources at Black Rocks Point, Palliser Bay. In Leach, B.F., Leech, M.M. editors. *Prehistoric man in Palliser Bay*. *Bull Natl Mus NZ*. 21: 49-65
- Bigalke, E.H. 1973. The exploitation of shellfish by coastal tribesmen of the Transkei. *Annals of the Cape Province Museum*. 9: 159-175.
- Branch, G.M. 1985. Limpets: Their role in littoral and sublittoral community dynamics. In Moore, P.G.; Seed, R.A. editors, *The ecology of rocky shores*. Hodder and Stoughton Educational, London, pp 97-116.
- Branch, G.M. 1981. The biology of limpets: Physical factors, energy flow, and ecological interactions. *Oceanography and marine biology: an annual review*. 19: 235-379
- Branch, G.M. 1975a. Notes on the ecology of *Patella concolor* and *Cellana capensis*, and the effects of human consumption on limpet populations. *Zool. Afr.* 10: 75-85
- Branch, G.M. 1975b. Interspecific competition in *Patella cochlear*. *Born. J. Anim. Ecol.* 44: 263-282
- Branch, G.M.; Odendaal, F. In Press. Marine protected areas and wave action: Effects on a South African limpet, *Cymbula oculus*. *Ecological Applications*
- Branch, G.M.; Griffiths, C.L.; Branch, M.L.; Beckley, L.E. 1994. *Two oceans. A guide to the marine life of southern Africa*. David Philip; Cape Town (South Africa), 359 pp
- Branch, G.M.; Moreno, C.A. 1994. Intertidal and subtidal grazers. In R.W. Siegfried, editor. *Rocky Shores: Exploitation in Chile and South Africa*. Springer-Verlag, New York. pp. 75-100
- Brownell, W.N.; Stevely J.M. 1981. The biology, fisheries and management of the queen conch, *Strombus gigas*. *Mar Fish Rev* 43: 1-12
- Castilla, J.C.; Bustamante, R.H. 1989. Human exclusion from rocky intertidal of Las Cruces, central Chile: Effects on *Durvillaea antarctica* (Phaeophyta, Durvilliales) *Mar. Ecol. (Prog. Ser.)* 50 (3): 203-214
- Clarke, K.R. 1993. Non-parametric multivariate analysis of changes in community structure. *Australian J. of Ecol.* 18:117-143
- Creese, R.G. 1981 Patterns of Growth, Longevity and Recruitment of Intertidal Limpets in New South Wales. *J. Exp. Mar. Bio. & Ecol.* 51:145-171
- Creese, R.G. 1982 Distribution and Abundance of the Acmaeid Limpet, *Patelloida latistrigata*, and its Interaction With Barnacles. *Oecologia* 52: 85-96

Duran, L.R.; Castilla, J.C. 1989. Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. *Mar. Bio.* 103: 555-562

Duran, L.R.; Castilla, J.C.; Oliva, D. 1987. Intensity of human predation on rocky shores at Los Cruces in central Chile. *Environ. Cons.* 14: 143-149

Dye, A. H.; Lasiak, T. A.; Gabula, S. 1997. Recovery and recruitment of the brown mussel, *Perna perna* (L.), in Transkei: implications for management. *S. Afr. J. Zool.* 32: 118

Dye, A.H.; Schleyer, M.H.; Lambert, G.; Lasiak, T.A. 1994. Intertidal and subtidal filter-feeders in Southern Africa. In R.W. Siegfried, editor. *Rocky Shores: Exploitation in Chile and South Africa*. Springer-Verlag, New York. pp. 57-74

Eckhout, S.; Raubenheimer, C.M.; Branch, G.M.; Bosman, A.L.; Bergh, M.O. 1992. A holistic approach to the exploitation of intertidal stocks: Limpets as a case study. *S. Afr. J. Mar. Sci.* 12: 1017-1029

Fairweather, P.G. 1991. A conceptual framework for ecological studies of coastal resources: An example of a tunicate collected for bait on Australian seashores. *Ocean shoreline manage* 15: 125-142.

Field, J.G.; Clarke, K.R.; Warwick, R.M. 1982. A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. (Prog. Ser.)* 8: 37-52

Hockey, P.A.R.; Bosman, A.L.; Siegfried, W.R. 1988. Patterns and correlates of shellfish exploitation by coastal people in Transkei: An enigma of protein production. *J. Appl. Ecol.* 25: 353-363

Hockey, P.A.R.; Bosman, A.L. 1986. Man as an intertidal predator in Transkei: Disturbance, community convergence and management of a natural food resource. *Oikos* 46: 3-14

Jackson, L. F. 1976. Aspects of the intertidal ecology of the east coast of south africa. *S. Afr. Assoc. Mar. Biol. Res. Invest. Rep. No.* 46. 72p.

Keough, M.J.; Quinn, G.P. (1989) Effects of periodic disturbances from trampling on rocky intertidal algal beds. *Ecol. Appl. Publ. Ecol. Soc. Amer.* 8(1): 141-16

Kilburn, R. 1982. Sea shells of Southern Africa. Macmillan. South Africa. Beaverton

Kyle, R.; Robertson, W.D.*; Birnie, S.L. 1997a. Subsistence shellfish harvesting in the Maputaland Marine Reserve in northern KwaZulu-Natal, South Africa: Sandy beach organisms. *Biol Cons.* 82: 173-182

Kyle, R.; Pearson, B.; Fielding, P.J.; Robertson, W.D.; Birnie, S.L. 1997b. Subsistence shellfish harvesting in the Maputaland Marine Reserve in northern KwaZulu-Natal, South Africa: Rocky shore organisms. *Biol Cons.* 82: 183-192.

- Lasiak, T. 1999. The putative impact of exploitation on rocky infratidal macrofaunal assemblages: a multiple-area comparison. *J. Mar. Biol. Assoc. U.K.* 79: 23-34.
- Lasiak, T. 1993. Temporal and spatial variations in exploited and non-exploited populations of the intertidal limpet *Cellana capensis*. *J. Moll. Stud.* 59: 295-307.
- Lasiak, T. 1992. Contemporary shellfish-gathering practices of indigenous coastal people in Transkei: Some implications for interpretation of the archaeological record. *S. Afr. J. Sci.* 88: 19-27.
- Lasiak, T. 1991. The susceptibility and/or resilience of rocky littoral molluscs to stock depletion by the indigenous coastal people of Transkei, Southern Africa. *Biol. Cons.* 56: 245-264.
- Lasiak, T.A.; Field, J.G. 1995. Community-level attributes of exploited and non-exploited rocky infratidal macrofaunal assemblages in Transkei. *J. Exp. Mar. Bio. Eco.* 185: 33-53.
- Lasiak, T.; Dye, A. 1989. The ecology of the brown mussel *Perna perna* in Transkei, Southern Africa: Implications for the management of a traditional food resource. *Biol. Cons.* 47: 245-257.
- McLachlan, A.; Lombard, H.W. 1980. Growth and reproduction in exploited and unexploited populations of a rocky shore gastropod, *Turbo sarmaticus*. *Veliger* 23: 221-230.
- Menge, B.A. and Branch, G.M. In press. Rocky intertidal communities. Chapter In: *Marine Community Ecology*. Eds. Bertness, M.D., Gaines, S. & Hay, M.E. Sinauer Associates, Sunderland.
- Menge, B. A. and T. M. Farrell. 1989. Community Structure And Interaction Webs. In *Shallow Marine Hard-Bottom Communities: Tests Of An Environmental Stress Model*. *Adv. Ecol. Res.* 19: 189-262.
- Moreno, C.A.; Sutherland, J.P.; Jara, H.F. 1984. Man as a predator in the intertidal zone of southern Chile. *Oikos* 42: 155-160.
- Oliva, D.; Castilla, J.C. 1986. The effect of human exclusion on the population structure of key-hole limpets *Fissurella crassa* and *F. limbata* on the coast of central Chile. *Mar. Ecol.* 7: 201-217.
- Ortega, S. 1987. The effects of human predation on the size distribution of *Siphonaria gigas* (Mollusca: Pulmonata) on the Pacific coast of Costa Rica. *Veliger* 29: 251-225.
- Paine, R.T.; Vadas R.L. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnol. Oceanogr.* 14: 710-719.
- Quinn, G.P. Effects of conspecific adults, macroalgae and height on the shore on recruitment of an intertidal limpet. *Mar. Ecol. (Prog. Ser.)* 48: 305-308.

- Schiel, D.R.; Taylor, D.I. 1999 Effects of trampling on a rocky intertidal algal assemblage in southern New Zealand. *J. Exp. Mar. Biol. Ecol.* 235 : 213-235
- Siegfried, W.R. 1988. Shellfish: Food for potentates and peasants. *Afr. Wildlife* 42: 33-38
- Siegfried, W.R.; Hockey, P.A.R.; Branch, G.M. 1994. The exploitation of intertidal and subtidal biotic resources of rocky shores in Chile and South Africa: an overview. In R.W. Siegfried, editor. *Rocky Shores: Exploitation in Chile and South Africa*. Springer-Verlag, New York. pp. 1-15
- Siegfried, W.R.; Hockey, P.A.R.; Crowe, A.A. 1985. Exploitation and conservation of brown mussel stocks by coastal people of Transkei. *Environ. Cons.* 12: 303-307.
- Tomalin, B.J.; Kyle, R. 1988. Subsistence and recreational mussel (*Perna perna*) collecting in KwaZulu-Natal, South Africa: fishing mortality and precautionary management. *S. Afr. J. Zool.* 33: 12-22
- Underwood, A.J. 1989. The analysis of stress in natural populations. *Biol. J. of the Linn. Soc.* 37: 51-78
- Underwood, A.J. 1978 An experimental evaluation of competition between three species of intertidal gastropods. *Oecologia* 33(2): 185-202
- Volman, I.P. 1978. Early archeological evidence for shellfish collecting. *Science* 201: 911-913
- Yesner, D.R. 1984. Population pressure in coastal environments: an Archaeological test. *World Archaeol.* 16 (1):108-127
- Zar, J. H. 1974. *Biostatistical analysis* 2nd ed. Prentice-Hall Inc. New Jersey, U.S.A.

Table 1 Species lists for each of two sampling techniques. (A & B)

Sampling Method A		Sampling Method B	
Echinodermata		Echinodermata	
Echinoidea	<i>Echinometra mathaei</i>	Echinoidea	<i>Echinometra mathaei</i>
	<i>Stomopneustes variolaris</i>		<i>Stomopneustes variolaris</i>
Holothuroidea	<i>Holothuria</i> spp.	Holothuria	<i>Holothuroidea</i> spp.
Mollusca		Mollusca	
Gastropoda		Gastropoda	
Prosobranchia	<i>Cellana capensis/ Helcion concolor</i>	Prosobranchia	<i>Conus ebraeus</i>
	<i>Conus ebraeus</i>		<i>Conus sponsalis</i>
	<i>Conus sponsalis</i>		<i>Cypraea annulus</i>
	<i>Cypraea annulus</i>		<i>Cypraea caputserpentis</i>
	<i>Cypraea</i>		<i>Cypraea felina</i>
	<i>caputserpentis</i>		<i>Drupa ricinus</i>
	<i>Cypraea felina</i>		<i>Littoraria glabrata</i>
	<i>Drupa ricinus</i>		<i>Mancinella alouina</i>
	<i>Fisurella</i> spp.		<i>Mitra litterata</i>
	<i>Littoraria glabrata</i>		<i>Nerita</i> spp.
	<i>Mancinella alouina</i>		<i>Nucella squamous</i>
	<i>Mitra litterata</i>		<i>Purpura panama</i>
	<i>Morula granulata</i>		<i>Thais bufo</i>
	<i>Nerita</i> spp.		<i>Trivia pellucidula</i>
	<i>Nucella squamous</i>		<i>Turritella</i> spp.
	<i>Purpura panama</i>	Opisthobranchia	<i>Aplysia</i> spp.
	<i>Scutellastra aphanes</i>		<i>Haminoea natalensis</i>
	<i>Scutellastra exustra</i>	Polyplacophora	<i>Acanthochiton gamoti</i>
	<i>Scutellastra oblecta</i>		<i>Chiton salihafui</i>
	<i>Thais bufo</i>		<i>Onithochiton litteratus</i>
	<i>Thais savignyi</i>		
	<i>Trivia pellucidula</i>		
	<i>Turritella</i> spp.		
Opisthobranchia	<i>Aplysia</i> spp.		
	<i>Haminoea natalensis</i>		
Pulmonata	<i>Siphonaria</i> spp.		
Polyplacophora	<i>Acanthochiton gamoti</i>		
	<i>Chiton salihafui</i>		
	<i>Onithochiton litteratus</i>		

Table 2: Species abundance summarised as a percentage of the total number of organisms recorded at each of eight location in two harvesting regimes. The four harvested locations were Rabbit Rock Botelier Point., Mabibi and Black Rock, while the four non-harvested locations were Sodwana, Cape Vidal, Adlims and Island Rock.

		Sodwana	Cape Vidal	Adlims	Island Rock	Rabbit Rock	Botelier Point	Mabibi	Black Rock
Echinodermata									
Echinoidea	<i>Echinometra mathaei</i>	0.28							
	<i>Stomopneustes variolaris</i>			1.81	0.28			0.52	0.34
Holothuroidea	<i>Holothuria</i> spp.								0.06
Mollusca									
Gastropoda									
Prosobranchia									
	<i>Cellana capensis/ Helcion concolor</i>	23.68	9.34	3.63	3.16	4.63	4.83	4.14	56.04
	<i>Conus ebraeus</i>	0.97		0.24	0.56		0.59		0.06
	<i>Conus sponsalis</i>	0.69			0.74		0.12		0.34
	<i>Cypraea annulus</i>								0.06
	<i>Cypraea caputserpentis</i>			0.12					0.06
	<i>Cypraea felina</i>								0.06
	<i>Drupa ricinus</i>				0.28			0.09	0.11
	<i>Fisurella</i> spp.	1.25	1.03		1.30	0.30	0.47	0.89	1.24
	<i>Littoraria glabrata</i>		0.62				0.24		2.36
	<i>Mancinella alouina</i>		0.51	2.06	2.23	0.50	0.12		7.70
	<i>Mitra litterata</i>	0.55			0.74	0.10			
	<i>Morula granulata</i>	43.35	12.94	15.72	27.70	3.02	39.69	5.73	3.49
	<i>Nerita</i> spp.		0.10			4.63	0.24	30.69	1.41
	<i>Nucella squamous</i>								0.06
	<i>Purpura panama</i>	0.55	0.51	0.85	2.97	0.70	0.35	2.35	0.22
	<i>Scutellastra aphanes</i>		0.21						
	<i>Scutellastra exustra</i>	15.10	1.85	22.97	27.51	3.62	16.37	5.92	4.89
	<i>Scutellastra obtecta</i>		6.47	0.97	1.12	0.40	0.59	0.09	0.34
	<i>Thais bufo</i>	0.69	0.51	1.93	0.09	0.30	2.71	0.75	0.22
	<i>Thais savignyi</i>	1.80	13.35	5.44	0.28	5.43	6.48	2.07	14.50
	<i>Trivia pellucidula</i>						0.12		
	<i>Turritella</i> spp.					0.91			
Opisthobranchia	<i>Aplysia</i> spp.								0.11
	<i>Haminoea natalensis</i>					1.91			
Pulmonata	<i>Siphonaria</i> spp.	10.94	52.26	35.43	0.93	73.54	27.09	43.33	
Polyplacophora									
	<i>Acanthochiton garnoti</i>		0.31						
	<i>Chiton salihafui</i>	0.14			7.71			0.23	0.84
	<i>Onithochiton literatus</i>			8.83	22.40			3.20	5.51
Total number of species		13	14	13	17	14	15	14	23

Table 3: Average species density (per m²) over total shore recorded at each of eight location in two harvesting regimes. The four harvested locations were Rabbit Rock, Botelier Point Mabibi and Black Rock, while the four non-harvested locations were Sodwana, Cape Vidal, Adlims and Island Rock.

		Sodwana	Cape Vidal	Adlims	Island Rock	Rabbit Rock	Botelier Point	Mabibi	Black Rock
Echinodermata									
Echinoidea	<i>Echinometra mathaei</i>	0.013							
	<i>Stomopneustes variolaris</i>			0.050	0.019			0.034	0.021
Holothuroidea	<i>Holothuria</i> spp.								0.003
Mollusca									
Gastropoda									
Prosobranchia									
	<i>Cellana capensis/Helcion concolor</i>	1.069	0.615	0.188	0.425	0.288	0.256	0.550	6.391
	<i>Conus ebraeus</i>	0.022		0.007	0.038		0.017		0.003
	<i>Conus sponsalis</i>	0.016			0.050		0.003		0.021
	<i>Cypraea annulus</i>								0.003
	<i>Cypraea caputserpentis</i>			0.003					0.003
	<i>Cypraea felina</i>								0.003
	<i>Drupa ricinus</i>				0.019			0.006	0.007
	<i>Fisurella</i> spp.	0.056	0.068		0.175	0.019	0.025	0.119	0.141
	<i>Littoraria glabrata</i>		0.019				0.007		0.145
	<i>Mancinella alouina</i>		0.016	0.057	0.150	0.017	0.003		0.472
	<i>Mitra litterata</i>	0.013			0.050	0.003			
	<i>Morula granulata</i>	0.978	0.394	0.433	1.863	0.100	1.123	0.381	0.214
	<i>Nerita</i> spp.		0.003			0.153	0.007	2.041	0.086
	<i>Nucella squamosus</i>								0.003
	<i>Purpura panama</i>	0.013	0.016	0.023	0.200	0.023	0.010	0.156	0.014
	<i>Scutellastra aphanes</i>		0.014						
	<i>Scutellastra exusta</i>	0.681	0.122	1.188	3.700	0.225	0.869	0.788	0.558
	<i>Scutellastra oblecta</i>		0.426	0.050	0.150	0.025	0.031	0.013	0.038
	<i>Thais bufo</i>	0.016	0.016	0.053	0.006	0.010	0.077	0.050	0.014
	<i>Thais savignyi</i>	0.041	0.406	0.150	0.019	0.180	0.183	0.138	0.890
	<i>Trivia pellucidula</i>						0.003		
	<i>Turritella</i> spp.					0.030			
Opisthobranchia	<i>Aplysia</i> spp.					0.063			
	<i>Haminoea natalensis</i>								0.007
Pulmonata	<i>Siphonaria</i> spp.	0.494	3.439	1.831	0.125	4.569	1.438	5.763	
Polyplacophora									
	<i>Acanthochiton garnoti</i>		0.020						
	<i>Chiton salihafui</i>	0.003			0.519			0.016	0.052
	<i>Onithochiton literatus</i>			0.243	1.506			0.213	0.338
Total number of species			14	13	17	14	15	14	23

Table 4: Analysis of abundance data for six species groups, examining the null hypotheses of H_1 : No difference between harvesting regimes, H_2 : No difference between locations within harvesting regimes, H_3 : No difference between sites within locations and H_4 : No difference in the interaction between harvesting regime and site.

	df	MS	F	p-level		df	MS	F	p-level
Large Limpets					Large Whelks				
Harvesting Regime	1	0.229	1.087	0.298	Harvesting Regime	1	0.059	0.463	0.497
Location	6	3.234	15.343	<0.0001	Location	6	0.692	5.406	<0.0001
Site	4	0.395	1.873	0.114	Site	4	0.148	1.156	0.331
Harvesting/Site Interaction	4	0.106	0.504	0.733	Harvesting/Site Interaction	4	0.129	1.012	0.402
Small Limpets					Small Whelks				
Harvesting Regime	1	0.017	0.074	0.786	Harvesting Regime	1	0.099	0.300	0.585
Location	6	4.105	17.848	<0.0001	Location	6	2.257	6.856	<0.0001
Site	4	2.668	11.601	<0.0001	Site	4	2.299	6.983	<0.0001
Harvesting/Site Interaction	4	0.029	0.128	0.972	Harvesting/Site Interaction	4	0.783	2.379	0.053
Snails					Chitons				
Harvesting Regime	1	2.397	14.609	<0.0005	Harvesting Regime	1	0.297	10.236	<0.005
Location	6	0.532	3.244	<0.005	Location	6	0.538	18.531	<0.0001
Site	4	0.326	1.988	0.097	Site	4	0.004	0.138	0.968
Harvesting/Site Interaction	4	0.299	1.822	0.126	Harvesting/Site Interaction	4	0.142	4.899	<0.001

Table 5: Kalmogorov-Smirnov Test results for species with a minimum of $n = 10$ size measurements in both the Harvest and Non-harvest regimes. Underlined values indicate where Harvest is significantly greater than Non-harvesting.

	p	n		Mean (mm)		Standard Deviation	
		Harvest	Non-Harvest	Harvest	Non-harvest	Harvest	Non-harvest
<i>Chiton salihafui</i>	$p < .05$	32	65	25.34	28.88	7.45	8.07
<i>Onithochiton literatus</i>	$p < .001$	152	110	24.80	29.41	6.48	6.51
<i>Morula granulata</i>	$p < .001$	330	536	<u>16.81</u>	<u>16.26</u>	<u>2.93</u>	2.47
<i>Purpura panama</i>	$p < .001$	70	63	33.17	40.30	9.86	14.76
<i>Mancinella alouina</i>	$p < .001$	124	91	26.94	32.36	5.93	6.96
<i>Thais bufo</i>	$p < .025$	47	35	28.43	31.83	7.78	7.63
<i>Thais savignyi</i>	$p < .001$	356	170	15.68	20.55	3.81	4.13
<i>Scutellastra exustra</i>	$p < .025$	207	289	<u>28.95</u>	<u>26.88</u>	6.96	7.21
<i>Scutellastra obtecta</i>	$p > .10$	16	59	15.50	14.95	5.29	4.54
<i>Cellana capensis</i>	$p < .001$	332	240	15.10	16.88	4.27	5.76
<i>Siphonaria spp.</i>	$p < .001$	402	274	12.56	13.97	5.81	4.74
<i>Fisurella spp.</i>	$p > .10$	40	33	20.35	20.33	8.28	7.66
<i>Stomopneustes variolaris</i>	$p < .001$	22	27	41.50	117.59	20.11	40.32
<i>Conus sponsalis</i>	$p < .05$	10	14	14.78	17.36	3.63	3.10

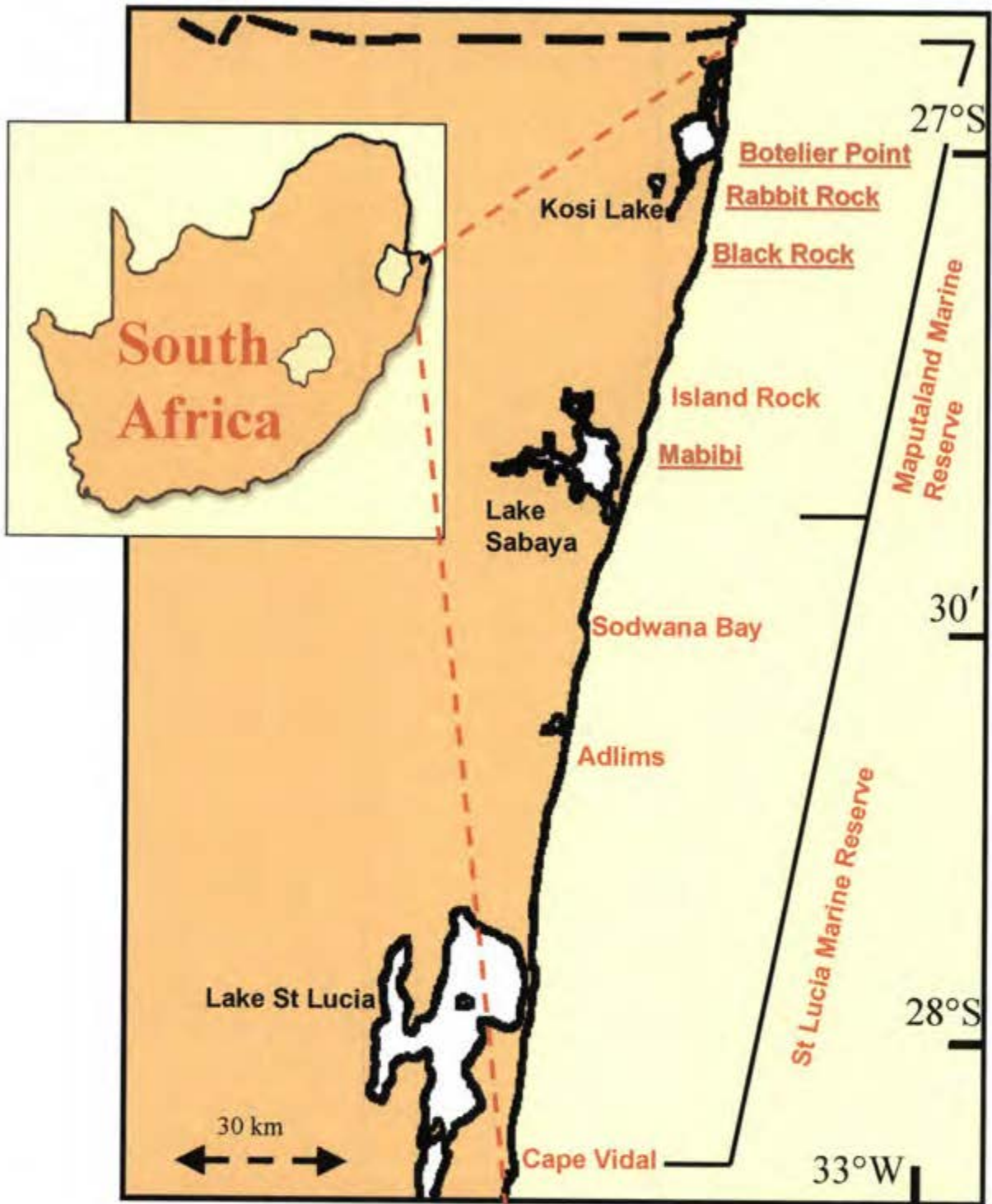


Figure 1: The Northern Kwa-Zulu coastline, illustrating four underlined harvested locations; Botelier Point, Rabbit Rock, Black Rock and Mabibi, and four non-harvested locations; Island Rock, Sodwana Bay, Adlims and Cape Vidal.

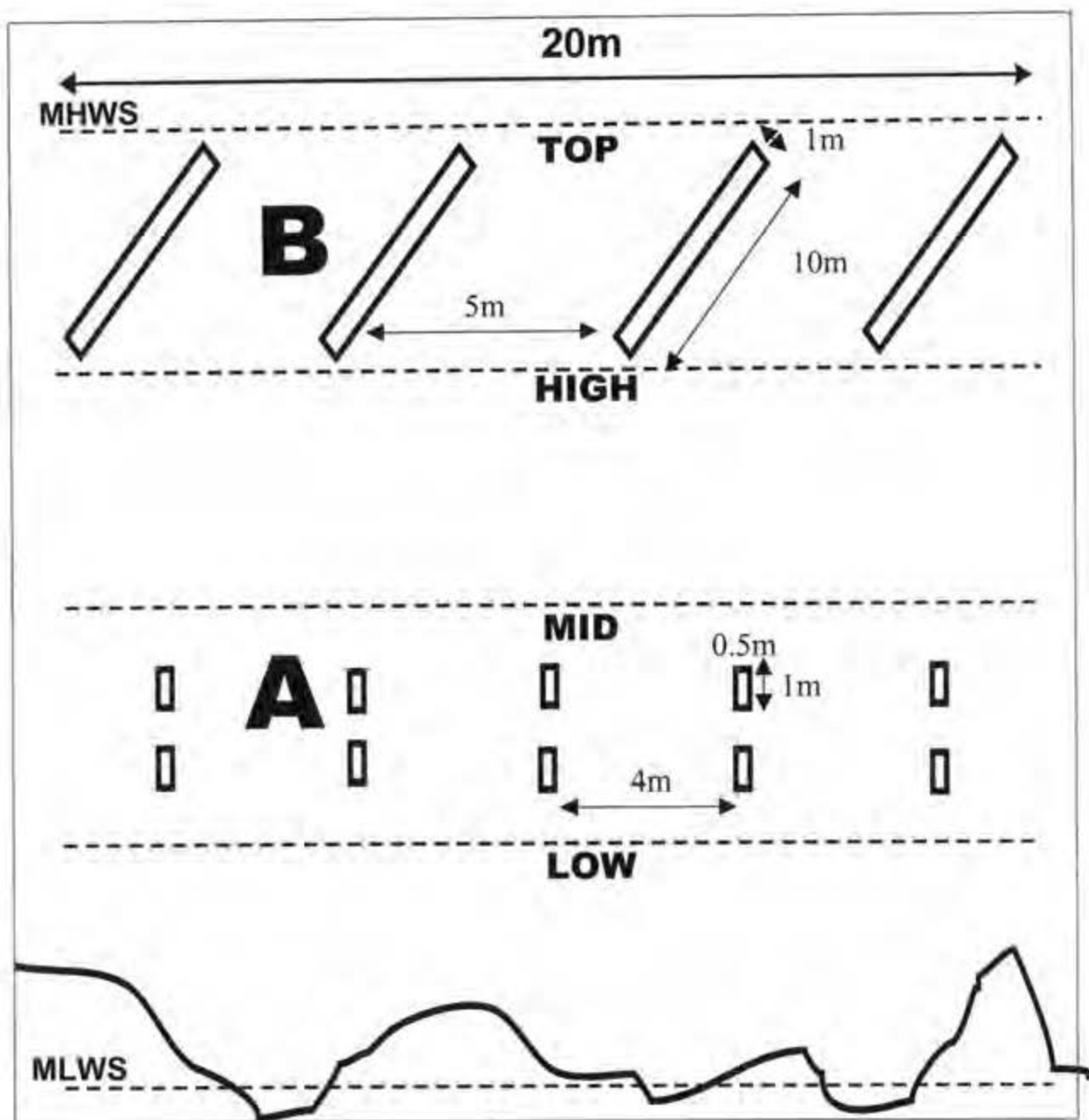


Figure 2: Schematic diagram of 2 different mobile intertidal invertebrate sampling techniques. In sampling method *A*, each zone was surveyed by two transects consisting of five 1m X 0.5m sampling quadrats spaced 4m apart. In sampling method *B*, species were recorded using four replicate belt transects per zone, 1m wide and 20m long, placed at 45° to the shoreline.

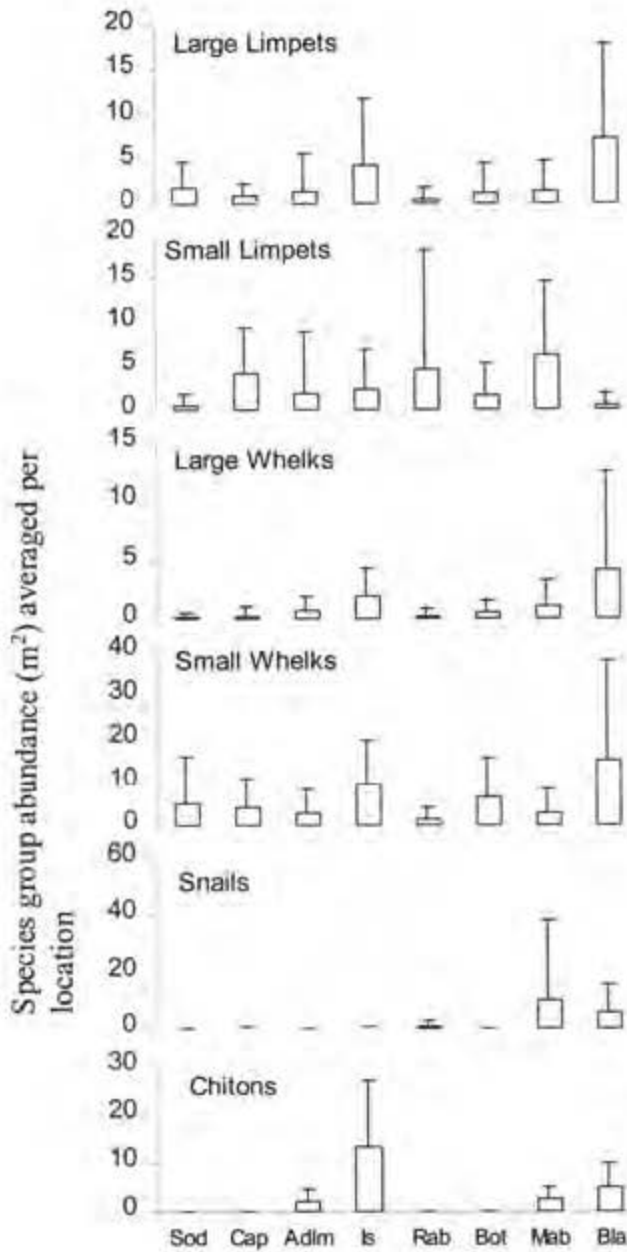
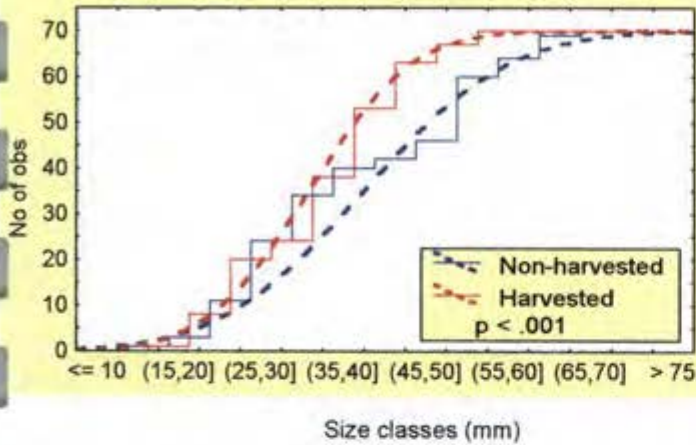
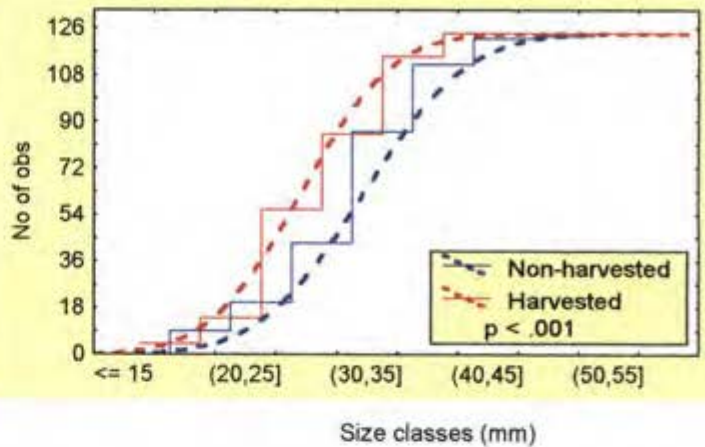


Figure 3: Mean and Std Dev. values for species groups at four harvested locations; Sodwana (Sod), Cape Vidal(Cap), Adlms (Adlm), Island Rock (Is) and four non-harvested locations Rabbit Rock (Rab), Botelier Point (Bot), Mabibi (Mab) and Black Rock (Bla).

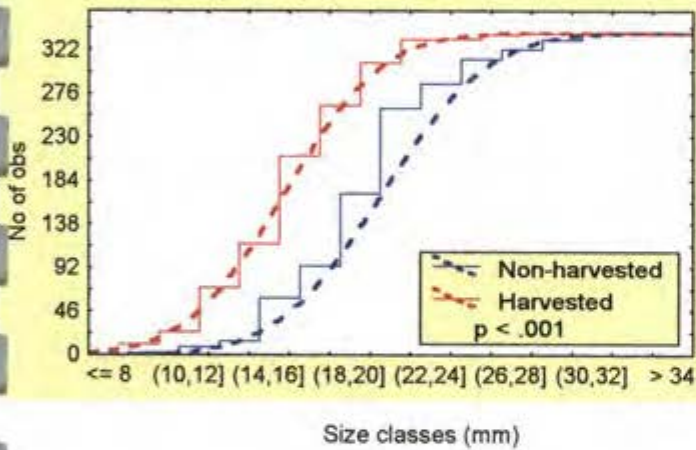
A) *Purpura panama*



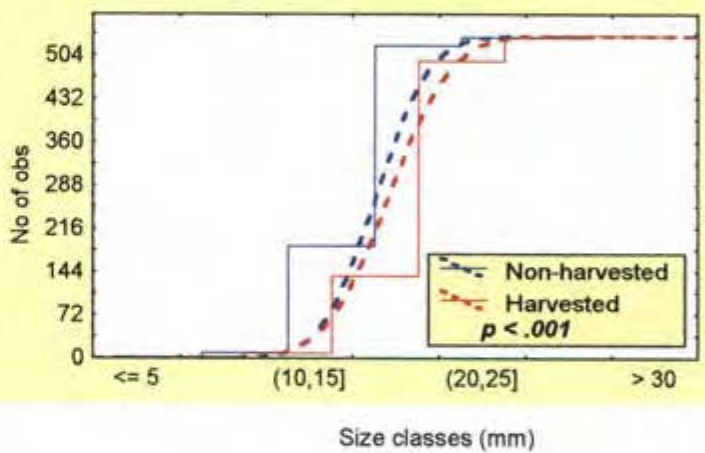
B) *Mancinella aliuona*



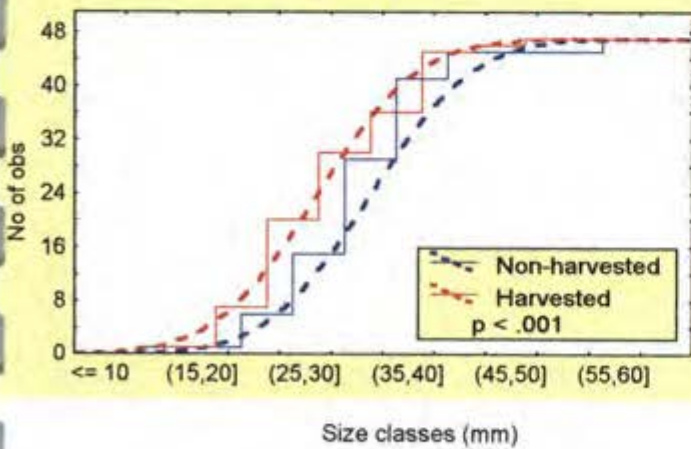
C) *Thais savignyi*



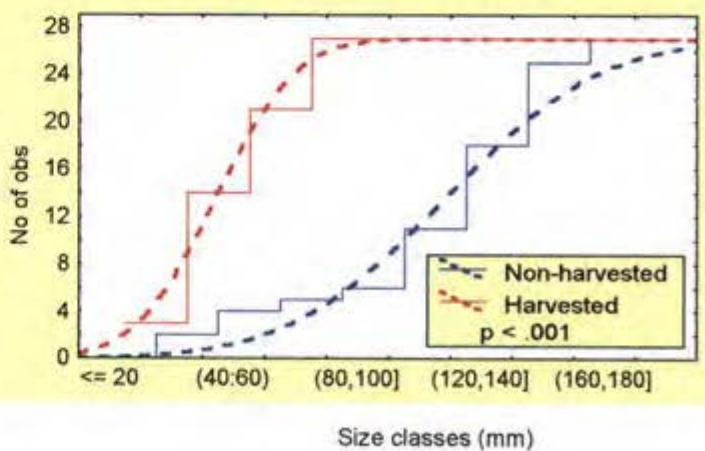
D) *Morula granulata*



E) *Thais bufo*



F) *Stomopneustes variolaris*



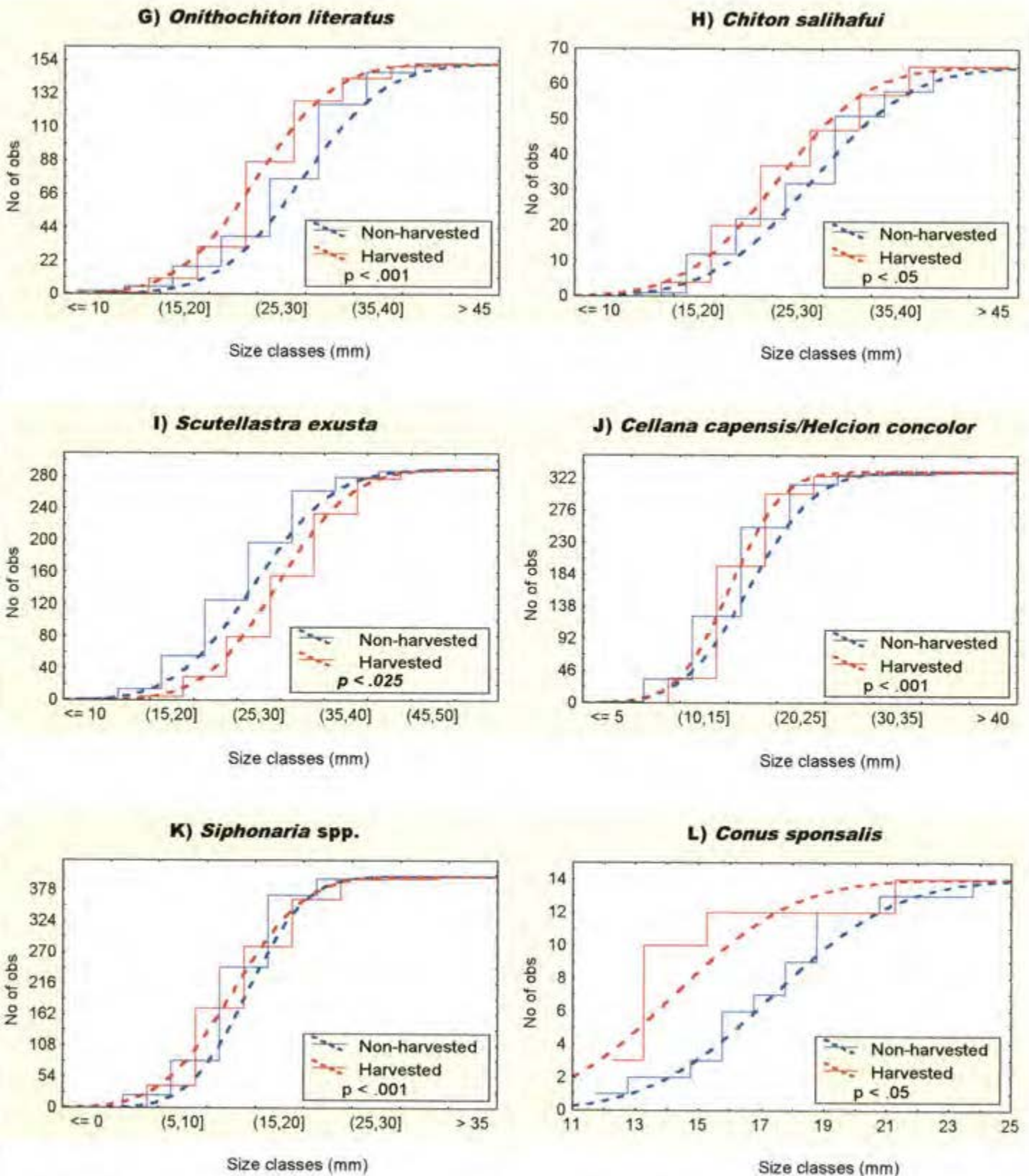


Figure 4: Size-class step plots with cumulative fit frequency distributions (25% smoothing) equating 4 harvested and 4 non-harvest localities for: a) *Pupura panama*, b) *Mancinella alouina*, c) *Thais savignyi*, d) *Morula granulata*, e) *Thais bufo*, f) *Stomopneustes variolaris*, g) *Onithochiton literatus*, h) *Chiton salihafui*, i) *Scutellastra exusta*, j) *Cellana capensis*, k) *Siphonaria* spp. and l) *Conus sponsalis*. Significant differences obtained from Kalmogorov-Smirnov Test are indicate by p values in legend. Italicized p values indicate that size distribution in harvesting is significantly greater that non-harvesting regimes.

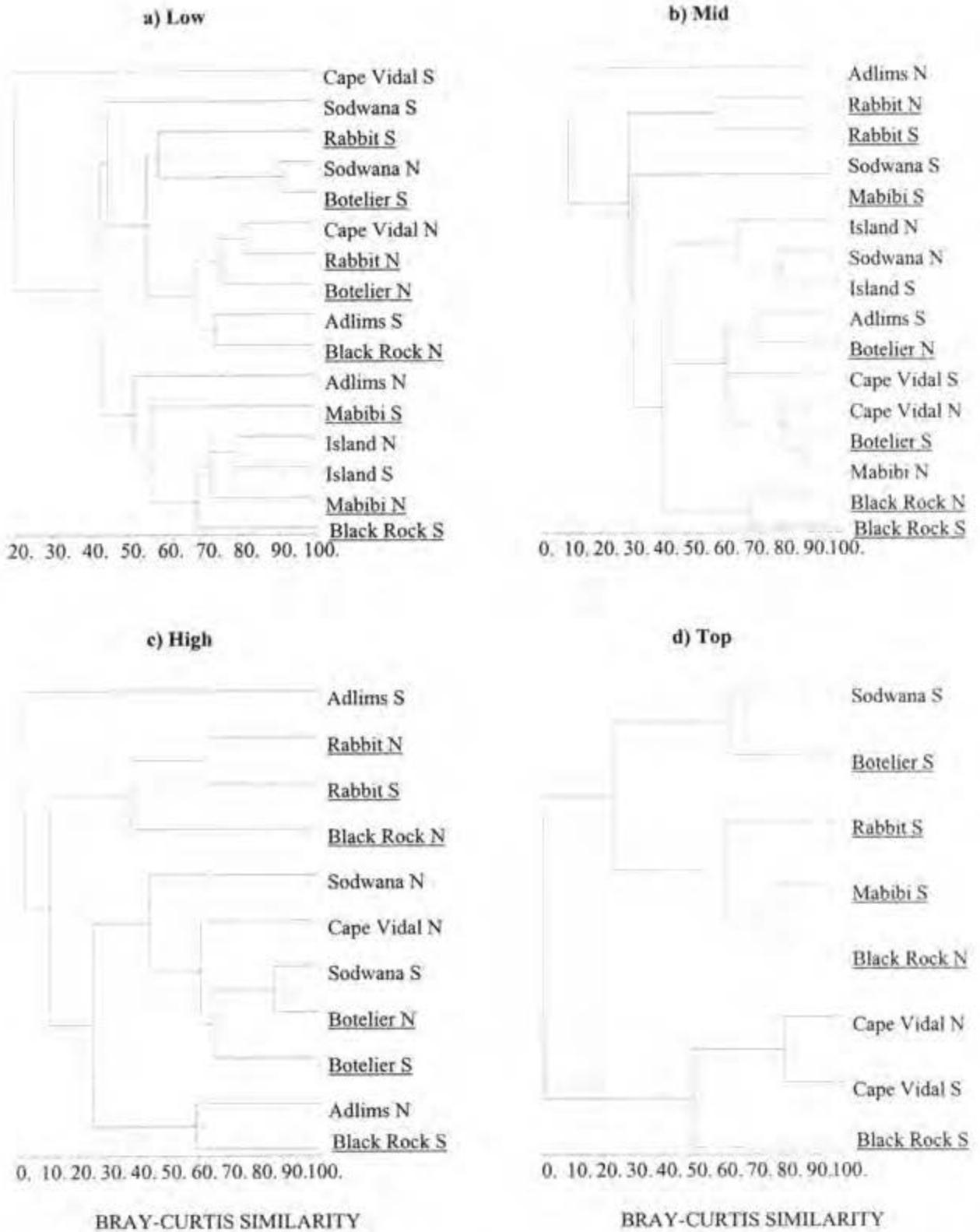


Figure 5: Bray-Curtis similarity plots for a) Low, b) Mid, c) High and d) Top zones, where underlined names indicate harvested location and N and S indicates North or South sites respectively within each location.