# Ecosystem change in a South African marine reserve (1960–2009): role of seagrass loss and anthropogenic disturbance

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ABSTRACT: Seagrass ecosystems are disappearing throughout the world, raising several concerns for ecosystem functioning and biodiversity. In the present study we document changes in intertidal sandflat ecosystems over the last 5 decades in Langebaan Lagoon, a marine reserve on the west coast of South Africa, following large-scale losses of seagrass *Zostera capensis*. Aerial photography and GIS revealed a 38% loss of seagrass at sites in Langebaan Lagoon between 1960 and 2007. Long-term monitoring of one particular site, Klein Oesterwal, indicated a major shift in invertebrate communities between 1983, when *Z. capensis* was abundant, and 2009, when *Z. capensis* had virtually disappeared. Abundance and species richness of invertebrates declined significantly over this period. Seagrass-associated species such as the limpets *Siphonaria compressa* and *Fissurella mutabilis*, and the starfish *Parvulastra exigua*, declined almost to extinction locally. Generalists such as the gastropod *Assiminea globulus* also declined in abundance. However, sandflat species, particularly burrowers, increased in abundance and vertical range. Wading birds also appeared to be affected by changes in seagrass cover. The terek sandpiper, which depends on *Z. capensis* for feeding, showed 3 local population crashes, each corresponding to periods of seagrass collapse. Abundance of wading birds that were not dependant on this seagrass was more stable. The loss of seagrasses in the system, together with anthropogenic disturbance such as bait harvesting and trampling, may have had severe impacts on invertebrates, the most significant being the virtual extinction locally of the critically endangered limpet *S. compressa*. Cascading effects on wading birds, possibly through changes in availability of invertebrate prey, were also evident.

KEY WORDS: Invertebrates · Habitat loss · GIS · Wading birds · South Africa

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## INTRODUCTION

Human activities are responsible for the destruction and loss of structurally complex habitats in marine ecosystems across the globe, collectively representing one of the main threats to marine biodiversity (Gray 1997, Airoldi & Beck 2007, Airoldi et al. 2008). Despite this, the consequences of habitat loss have not been well studied in marine habitats relative to terrestrial ones, due to ignorance of the extent and significance of these losses (Airoldi et al. 2008). Increased development along coasts, destructive harvesting and fishing methods, along with deteriorating water quality, are the foremost causes of habitat destruction, which collectively result in the loss of resident species, energetic resources, and ecosystem functions, jointly leading to biotic and environmental homogenisation (McKinney & Lockwood 1999, Airoldi et al. 2008).

Seagrass meadows are prime examples of structurally complex marine ecosystems threatened by anthropogenic activities (Hemminga & Duarte 2000, Orth et al. 2006, Airoldi et al. 2008, Waycott et al. 2009). Seagrasses can exist as continuous beds, spanning tens to hundreds of m² in area, or as mosaics of smaller patches

interspersed amongst unvegetated sandflats, thereby enhancing local heterogeneity (Hemminga & Duarte 2000). They can also function as ecosystem engineers, as their root/rhizome systems act to stabilise sediments, while their 3-dimensional leaf canopies modify local hydrodynamics, trapping organic and inorganic nutrients, thus providing nutrient-rich, sheltered habitats for resident communities, which are often unique in comparison to unvegetated sand (Kikuchi & Peres 1977, Whitfield 1989, Hemminga & Duarte 2000, Coleman & Williams 2002, Ward et al. 2003). Seagrasses are also food for megaherbivores, such as manatees, dugongs, and turtles, and function as nurseries for many fish and invertebrates (Heck et al. 2003, Orth et al. 2006). All of these features interact to enhance biomass, richness, and abundance of fauna in seagrass beds relative to surrounding bare sand (Hemminga & Duarte 2000, Hughes et al. 2002, Baden et al. 2003).

Seagrass meadows are, however, extremely sensitive to environmental perturbations, and are declining around the world (Short & Wyllie-Echeverria 1996, Hemminga & Duarte 2000, Orth et al. 2006, Waycott et al. 2009), culminating in these ecosystems being listed as worthy of protection in the Rio Reclaration (Duarte 1995). A recent synthesis showed a 29% loss of seagrass cover globally between 1879 and 2006, roughly equivalent to an area of 3370 km$^2$. This rate of seagrass loss is comparable to those reported for mangroves, coral-reefs, and tropical rainforests, placing seagrass meadows among the most threatened ecosystems on the planet (Waycott et al. 2009).

Although natural factors such as 'wasting disease' played a role in seagrass declines, anthropogenic activities are considered to be primarily responsible (Hemminga & Duarte 2000, Waycott et al. 2009). Coastal eutrophication is frequently implicated in the disappearance of seagrasses, as elevated nutrient loads enhance microalgal growth, which limits light available to these plants, smothers them, or uproots them due to the gas present in microalgal mats (Short & Burdick 1996, Hemminga & Duarte 2000, Baden et al. 2003). The over-exploitation of predatory fish through fishing can also intensify the effects of eutrophication, as intermediate predators thrive in the absence of top predators, potentially reducing abundance of grazers such as shrimp and other molluscs, thus allowing epiphytic to proliferate on seagrasses (Burkepile & Hay 2006, Baden et al. 2010).

Coastal developments, such as dredging and harbour construction, can also modify sediment dynamics, often to the detriment of seagrass meadows (Cabaço et al. 2008, Cyrus et al. 2008), principally because they are smothered, suffer a reduction in light availability, or because enhanced nutrient levels are associated with sedimentation (Terrados et al. 1999, Hemminga &

Duarte 2000). Collectively, anthropogenic activities can lead to the irreversible elimination of seagrasses from coastal ecosystems (Duarte 2002).

Loss of seagrasses can have important repercussions for marine ecosystems and communities (Coleman & Williams 2002). The decimation of seagrass meadows in the North Atlantic in the 1930s due to wasting disease, for example, was associated with the collapse of a scallop fishery, a major decline in abundance of waterfowl, and the extinction of an eelgrass limpet (Carlton et al. 1991, Orth et al. 2006). Despite growing concern regarding the loss of such ecosystems, few studies directly report on the consequences of such losses, with a shortage of historical data being a particular hindrance (Dayton et al. 1998, Jackson et al. 2001, Airoldi et al. 2008). Most evidence gathered is based on comparisons between areas with and without the habitat of interest, or on experimental manipulation, which usually cannot replicate the large spatiotemporal scales characteristic of habitat loss (Airoldi et al. 2008, Waycott et al. 2009).

Given the strong role seagrasses play in structuring marine communities, the first aim of the present study was to quantify changes in coverage of the seagrass *Zostera capensis* in Langebaan Lagoon (Fig. 1), a marine reserve on the west coast of South Africa, using GIS and aerial photographs of the system from 1960 until 2007. This is especially pertinent in view of the recommendation by the Rio Declaration that marine ecosystems with high biodiversity, especially seagrasses, be mapped (Baden et al. 2003). Secondly, historical monitoring data were used to document changes in invertebrate communities in an intertidal sandflat in the lagoon known as Klein Oesterwal (Fig. 1) between 1983, when *Z. capensis* was present, and 2009, when *Z. capensis* had virtually disappeared. To link these changes in invertebrate communities to losses in *Z. capensis*, we compared macrofauna in seagrass beds and unvegetated sandflats in Klein Oesterwal in 1983. The rationale was that if similar patterns were obtained from (1) comparisons of seagrass beds and bare sandflats, and (2) between 1983 and 2009, this would provide strong circumstantial evidence linking changes in invertebrate communities with seagrass loss. Lastly, we used long-term bird count data between 1978 and 2007 to assess the possible effects of changes in seagrass coverage on intertidal wading birds in Langebaan Lagoon.

## MATERIALS AND METHODS

**Study site.** Langebaan Lagoon (located between 33° 11' 27" S, 18° 07' 37" E and 33° 03' 54" S, 17° 58' 07" E) is a marine-dominated lagoon on the
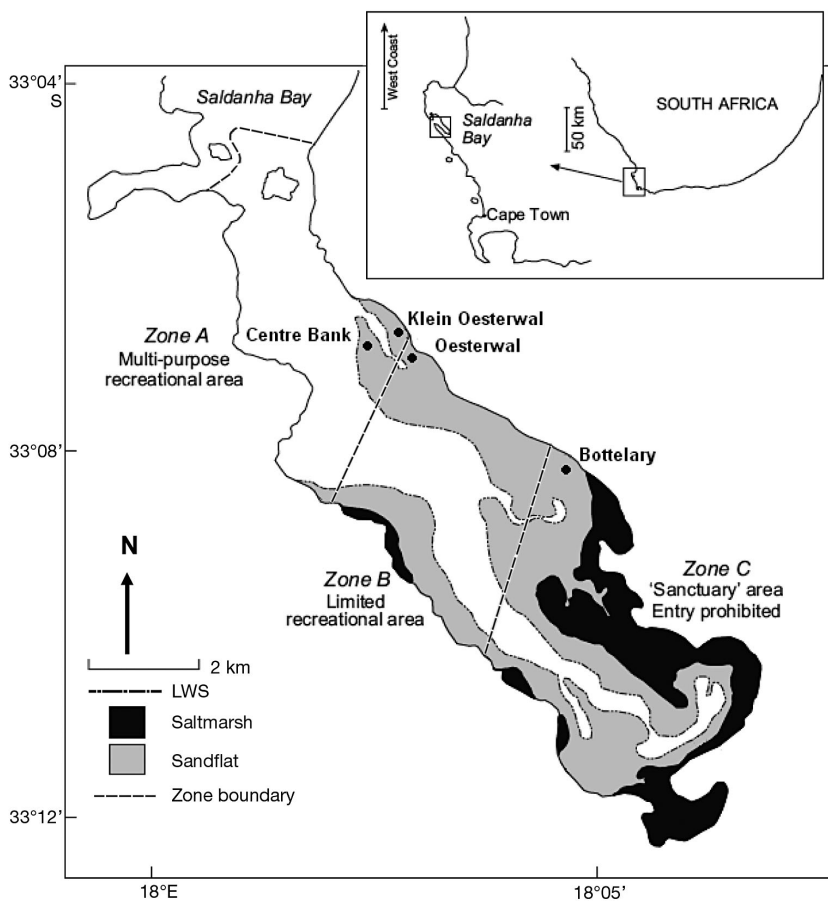
Fig. 1. Langebaan Lagoon, showing its geographic position on the South African coastline, as well as sampling sites and park zones. Tidal rage at sampling sites is approximately 1.8 m. LWS: low water spring

west coast of South Africa. The system was declared a national park in 1985, is registered as a wetland of international importance in terms of the Ramsar Convention, and is recognized by BirdLife International as an Important Bird Area. The lagoon is divided into 3 zones with varying recreational and harvesting activities (Fig. 1). Zone A is a general recreational area where angling and bait harvesting, principally for sandprawns *Callianassa kraussi* and mudprawns *Upogebia africana* are permitted. Zone B permits limited recreational activity, mainly sailboating and windsurfing, but bait collecting is prohibited. Zone C is a sanctuary, with entry prohibited without a valid permit. The tidal range at sampling sites is roughly 1.8 m.

**Historical changes in seagrass cover in Langebaan Lagoon.** Orthophotos of Langebaan Lagoon in 1960, 1968, 1977, 1988, 2000, and 2007 were obtained from the South African Department of Land Affairs: Surveying and Mapping, and geo-referenced to a 1:50000 topographical map using ArcGIS version 9. Coverage of *Zostera capensis* was estimated for Klein Oesterwal,

Oesterwal, Centre Bank, and Bottelary in Langebaan Lagoon (Fig. 1) by digitizing seagrass beds from georeferenced photos at a scale of 1:5000 for each time period. Additional seagrass data were obtained from Angel et al. (2006) in which the coverage of *Z. capensis* beds was documented annually for the period 1972 until 2006 at Klein Oesterwal.

**Macrofauna sampling.** Samples of macrofauna were collected during spring low tides in March of 1983 and 2009 at Klein Oesterwal during spring low tides. Transects were run perpendicular across the shore and sampling stations established every 20 m from the high-water level down to the low-water mark. This method yielded 10 sampling stations in 1983 and 9 in 2009. Sediment at each sampling station was dug out of quadrats ($0.25 \times 0.25$ m) down to a depth of 0.2 m, sieved through a 1 mm mesh, and the retained organisms sorted and identified. Six replicate transects were sampled in 1983 and 5 in 2009. In a separate comparison of macrofauna between beds of *Z. capensis* and unvegetated sandflats, single samples were collected from 12 seagrass beds and 12 unvegetated regions in Klein Oesterwal in 1983, at the levels of both high- and low-shore *Zostera* beds and processed as stated above.

**Surveys of wading birds.** Surveys of waterbirds were conducted at Langebaan Lagoon bi-annually, in midsummer and midwinter, between 1978 and 2007. The surveys were conducted under the auspices of the Western Cape Wader Study Group, and incorporated into the Coordinated Waterbirds Count project of the Animal Demography Unit, University of Cape Town, South Africa. Survey methods were described by Underhill (1987a). In brief, the lagoon was divided into 10 count sections, and the waterbirds at roosting sites in each section were counted by experienced birders at high tide over a 3 h period. Population trends were assessed for terek sandpiper *Xenus cinereus*, which is dependant on seagrass for feeding, and for ringed plover *Charadrius hiaticula*, common whimbrel *Numenius phaeopus*, greenshank *Tringa nebularia*, and bartailed godwit *Limosa lapponica*, which are not dependant on seagrasses (Hockey et al. 2005).

**Statistical analyses.** All multivariate analyses were performed using PRIMER version 6 (Plymouth Routines in Multivariate Ecological Research). Non-metric

multidimensional scaling (MDS) and cluster-analysis were used to visually assess differences in macro-faunal assemblages between 1983 and 2009. MDS was also employed to assess differences in macrofauna between sites with and without *Zostera capensis* in 1983, and differences in community structure of ma-crofauna between high-, mid-, and low-shore positions in 1983 and 2009. MDS ordinations were constructed from resemblance matrices generated from Bray-Curtis similarities, with untransformed and un-standardised abundance data. Permutational multi-variate analysis of variance (PERMANOVA) was employed to test the effect of time (1983 vs. 2009), shore position, and their interaction on invertebrate assemblages. Two-way ANOVA was used to assess the effect of year (1983 vs. 2009) and shore-position on total macrofaunal abundance and richness. Parametric *t*-tests were used to assess differences in abundance of individual species of macrofauna between 1983 and 2009. Linear regressions were performed between counts of wading birds (actual counts and 5 yr moving medians) and sampling years. Correlation analyses were performed between wader species and seagrass coverage. Seagrass data from Angel et al. (2006) were used for the latter analyses, as these data were col-lected annually between 1974 and 2006 at Klein Oesterwal and provide a better temporal match with wader data than those obtained by GIS, which have 8 to 12 yr gaps. Normality and homogeneity of vari-ance required for parametric testing were assessed using the Kolmogorov-Smirnov and Levene's tests respectively. In instances where these assumptions were not met, data were transformed (log $x + 1$) and then subjected to parametric analyses. In cases where abundance of a given species was zero for all samples in one treatment, no statistical tests were run because the absence of variance precluded valid statistical comparisons.

## RESULTS

### Changes in seagrass coverage between 1960 and 2007

The total area of *Zostera capensis* declined by 38% at all sampling sites in Langebaan Lagoon between 1960 and 2007, representing a total loss of roughly 0.22 km$^2$ of seagrass over this period. Losses were most severe at Klein Oester-wal, where 98.6% of seagrass was lost over this period (Fig. 2). *Z. capensis* formed dis-tinct high-, low-, and mid-shore beds in Klein Oesterwal in 1988 (Fig. 3a), but had

virtually disappeared by 2007, with no evidence of such zonation (Fig. 3b). At Oesterwal, 81.6% of *Z. ca-pensis* was lost between 1960 and 2007, followed by Bottelary (44.9% loss for 1968–2007) and Centre Bank (18% loss for 1960–2007, Fig. 2). Coverage of *Z. capen-sis* on the Centre Bank was most variable, declining by 39% between 1960 and 1977, increasing by 42% between 1977 and 1988, and then decreasing again by 21.8% between 1988 and 2007, despite an increase in the northern portion evident in Fig. 3b.

### Changes in macrofauna between 1983 and 2009

MDS ordinations indicated that macrofaunal com-munities in Klein Oesterwal differed significantly between 1983, when *Zostera capensis* was abundant, and 2009, when it had all but disappeared (Fig. 4). PERMANOVA also indicated significant effects of time ($F_{1,85} = 12.9$, p = 0.0001), zone ($F_{9,85} = 4.62$, p = 0.0001), and their interaction ($F_{9,85} = 3.25$, p = 0.0001) on macro-faunal assemblages.

Macrofaunal species richness (Fig. 5a,b) was signifi-cantly influenced by year (1983 vs. 2009; $F_{2,85} = 19.9$, p < 0.0001) and shore position ($F_{2,85} = 16.3$, p < 0.0001), but not by their interaction ($F_{2,85} = 19.9$, p > 0.1). Rich-ness was greater in 1983 (11.2 ± 1.23 SE) than in 2009 (8.2 ± 1.3 SE), and was generally lower in the higher shore. Macrofaunal density (Fig. 5c,d) also differed significantly between years ($F_{1,85} = 10.5$, p < 0.01), but was not affected by shore position ($F_{2,85} = 1.2$, p > 0.1) or their interaction ($F_{2,85} = 2.1$, p > 0.1). Density was significantly greater in 1983 (5000 ± 698 ind. m$^{-2}$) than in 2009 (1532 ± 236 ind. m$^{-2}$). Three peaks in macro-faunal abundance were observed in 1983 (Fig. 5c), roughly corresponding with the high-, mid-, and low-shore *Zostera* beds present at the time (Fig. 3a). Macrofaunal abundance was more uniform in 2007,
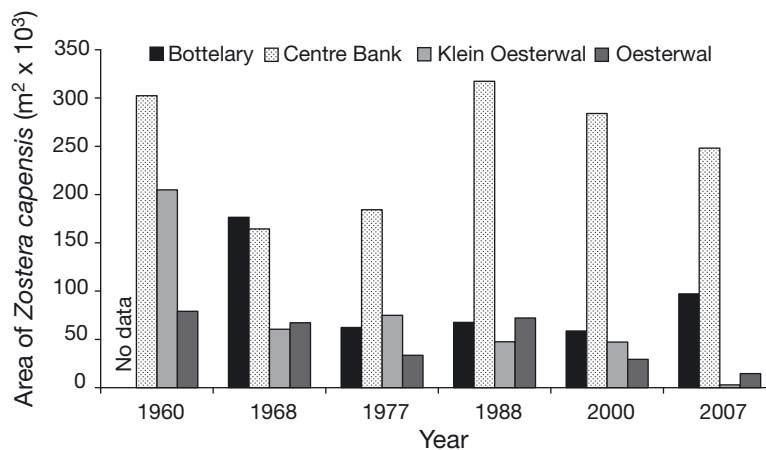
Fig. 2. *Zostera capensis*. Changes in total areas of the seagrass at 4 sites in Langebaan Lagoon analysed between 1960 and 2007
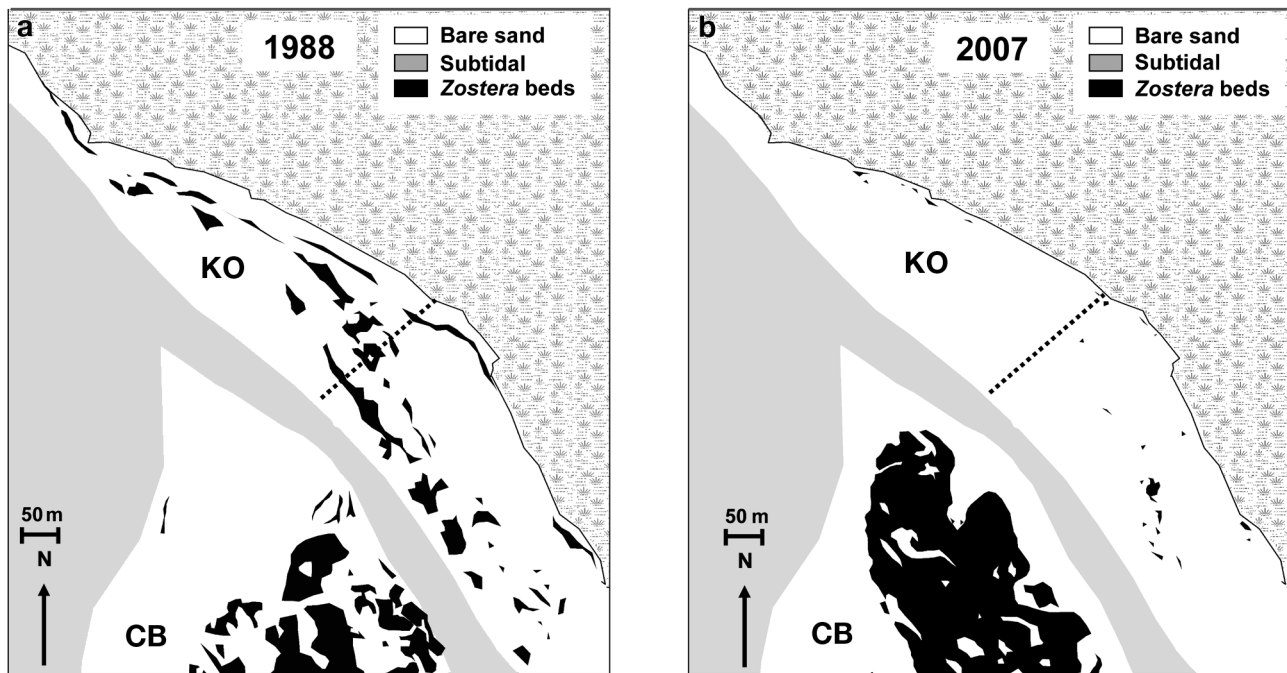
Fig. 3. *Zostera capensis*. Changes in total areas of the seagrass at Klein Oesterwal (KO) and Centre Bank (CB) between (a) 1988 (b) and 2007. Dashed lines indicate approximate transect positions. Maps are based on orthophotos with digitised seagrass beds
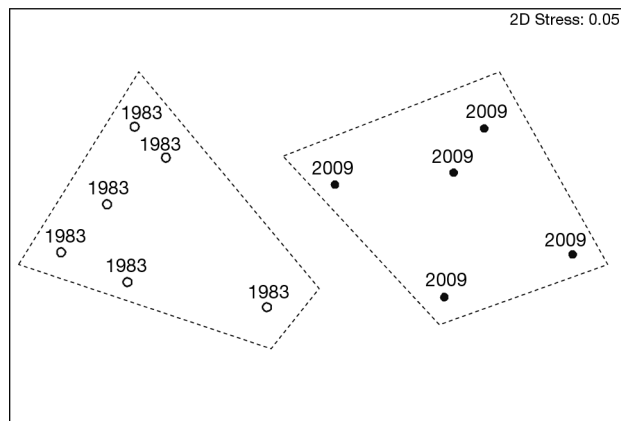


Fig. 4. Non-metric multidimensional scaling (MDS) ordination showing differences in macrofaunal assemblages at Klein Oesterwal between 1983 (○) and 2009 (●). Each sample represents a single transect with pooled data from all stations between high- and low-water marks. Dashed lines indicate clusters formed at a 30% similarity

probably due to habitat homogenization following the loss of *Zostera capensis* in the area (Fig. 5d).

A number of macrofaunal taxa differed in density between 1983 and 2009 (Fig. 6). The general pattern was that species that occurred predominantly with *Zostera capensis*, such as the starfish *Parvulastra exigua* and the limpets *Siphonaria compressa* and *Fissurella mutabilis*, or generalist surface dwellers such as

the gastropods *Assiminea globulus*, *Littorina saxatilis*, and *Hydrobia* sp., declined in abundance over this period. In contrast, species that burrowed predominantly in unvegetated sand, such as the amphipod *Urothoe grimaldii* and the polychaetes *Scoloplos johnstonei* and *Orbinia angrapequensis*, increased in density.

The zonation of macrofauna between the high- and low-water marks also changed between 1983 and 2009 at Klein Oesterwal (Fig. 7). The gastropod *Assiminea globulus* contributed between 86 and 96% to total abundance in the high shore in 1983, but its contribution dropped to 13% in 2009. The gastropod *Protomella capensis*, which was the major contributor in the mid-shore in 1983, contributing 35 to 60% to total density, shifted dominance to the low-shore in 2009, where it contributed 13 to 41%. The amphipod *Urothoe grimaldii* and the polychaete *Orbinia angrapequensis* increased their numerical contributions in 2009 across the entire shore, and *Euclymene lumbricoides* did so in the upper shore.

MDS ordinations indicated unique macrofaunal assemblages in the high-, mid-, and low-shore zones of Klein Oesterwal in 1983 ($p < 0.01$; Fig. 8a) but not in 2009 ($p > 0.1$; Fig. 8b). This is probably indicative of the structuring role played by *Zostera capensis* in the high, mid, and low shore where it was present in 1983, and of habitat homogenisation in 2009, following the loss of *Z. capensis* beds.
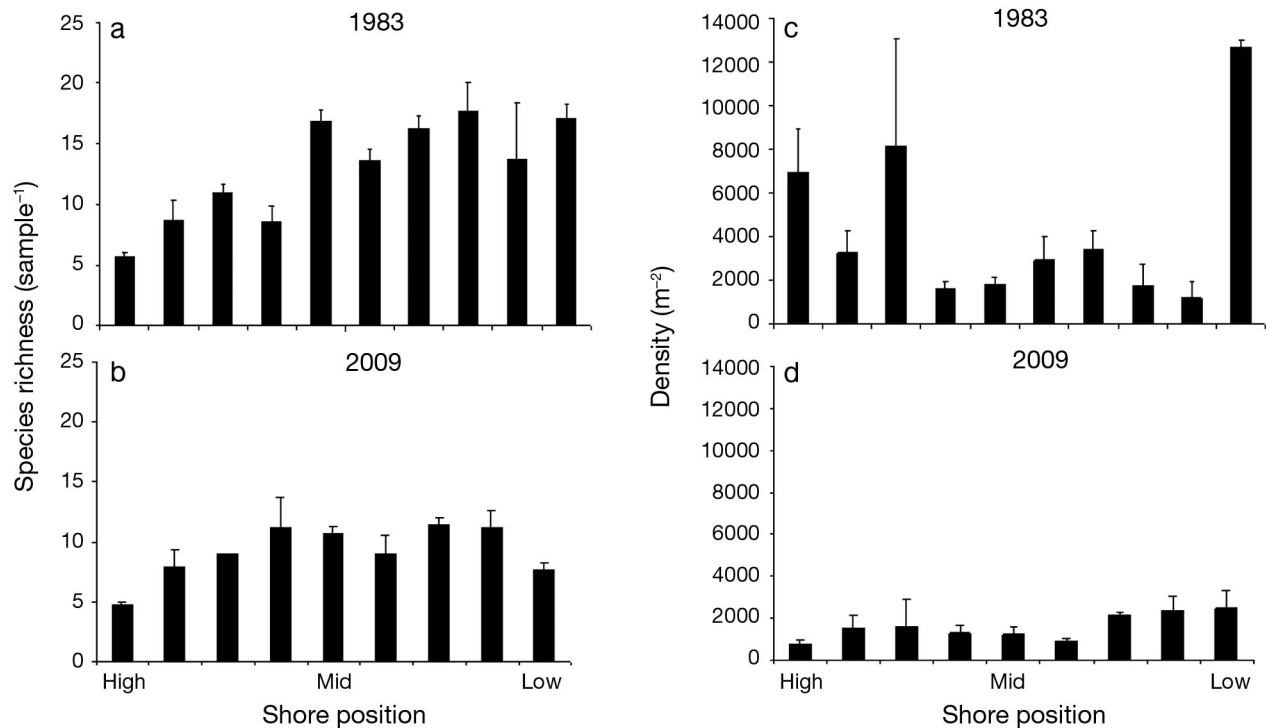
Fig. 5. Differences in (a,b) species richness (per sample) and (c,d) density (scaled to m$^{-2}$) of macrofauna at Klein Oesterwal in 1983 and 2009 between high- and low-tide marks. Means +1 SE are shown
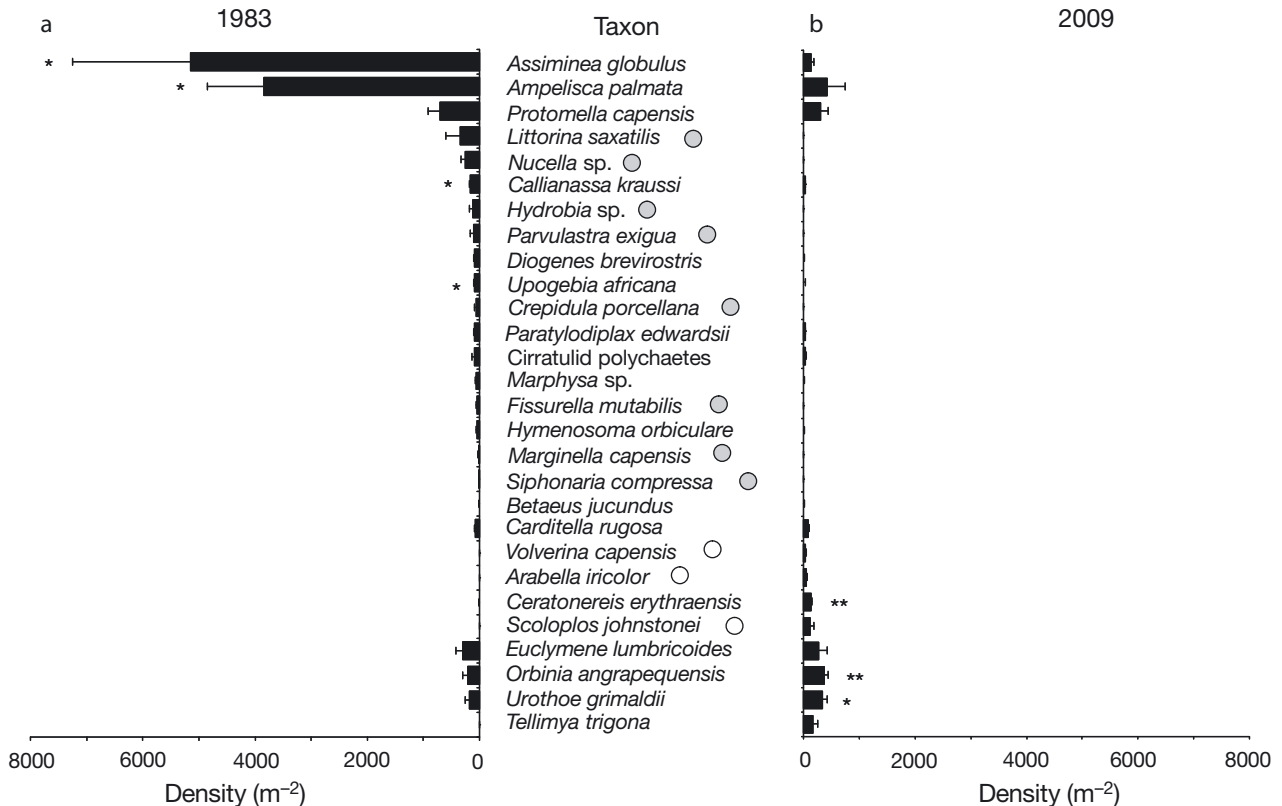


Fig. 6. Differences in density (mean +1 SE) of macrofauna at Klein Oesterwal between (a) 1983 and (b) 2009; ○: species that increased from 0 in 1983; ◐: species that declined to 0 in 2009. Asterisks indicate significant differences: *p < 0.05, **p < 0.01
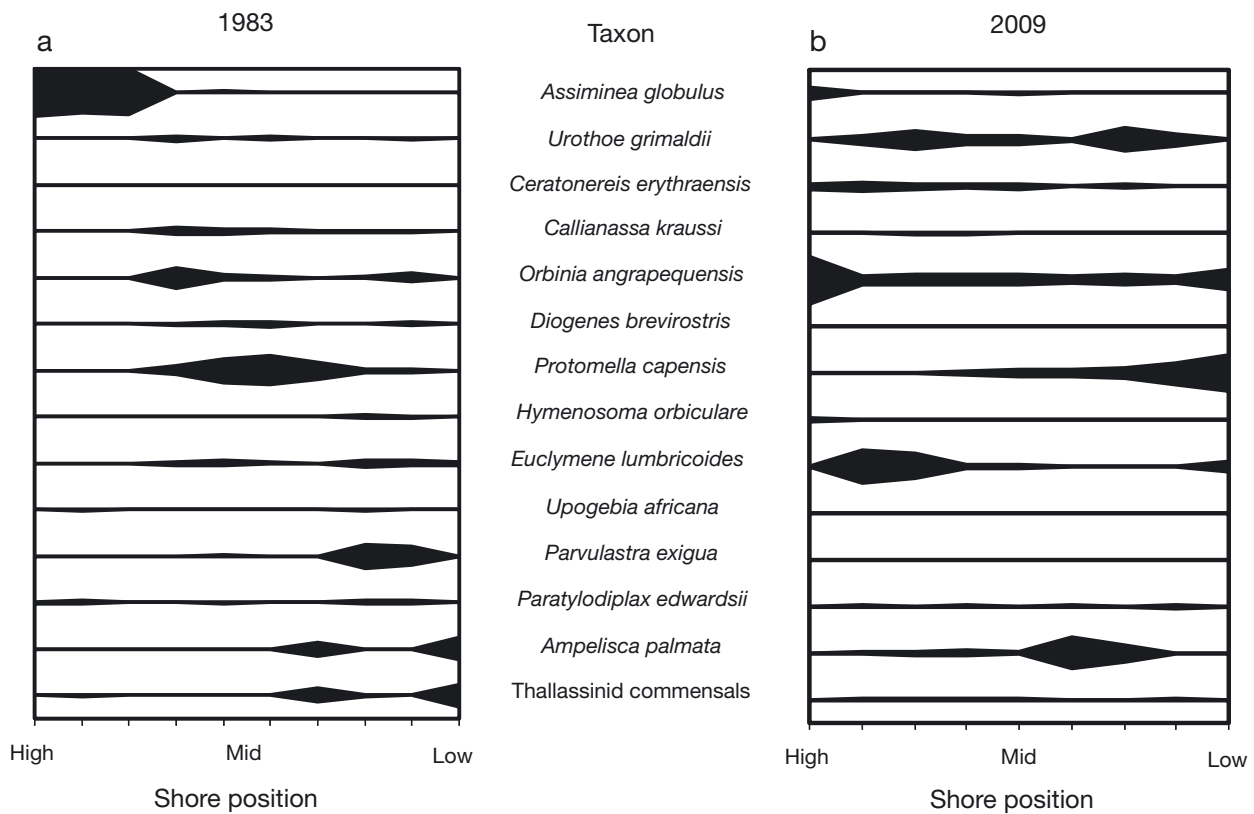
Fig. 7. Relative abundance (% composition) and distribution of macrofauna between high- and low-water marks at Klein Oesterwal in (a) 1983 and (b) 2009
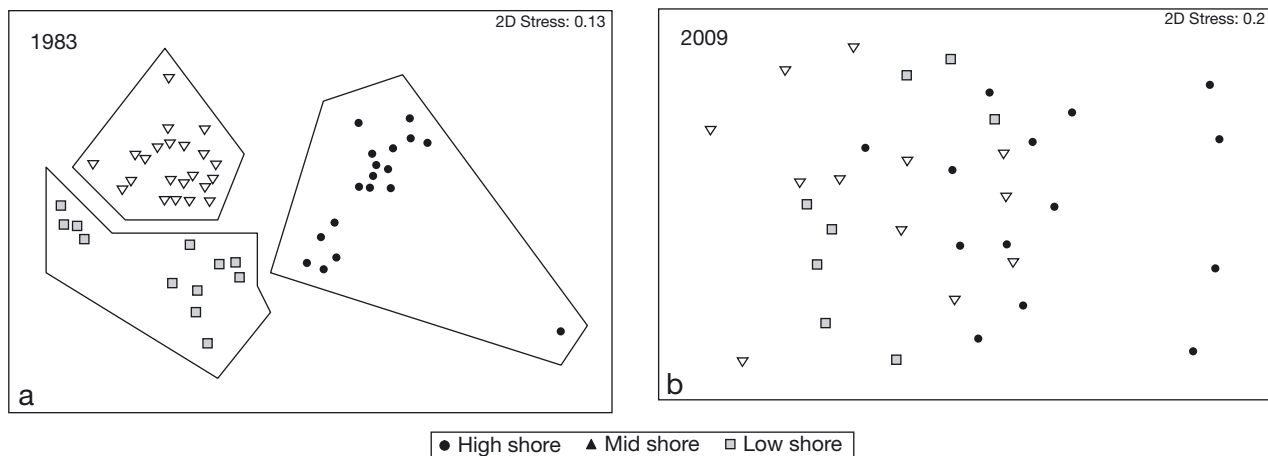


Fig. 8. MDS ordination showing macrofaunal assemblages in high-, mid- and low-shore zones of Klein Oesterwal in 1983 and 2009. Lines indicate clusters formed between 10 and 20% similarity. Each point represents data from an individual quadrat

## Differences in macrofauna between *Zostera capensis* beds and unvegetated sandflats

Macrofaunal assemblages differed significantly between *Zostera capensis* beds and unvegetated sandflats in 1983 in both the high and low shore (p = 0.001 for both shore positions, Fig. 9). High-shore *Z. capensis* beds were dominated by the surface-dwelling gastropods *Assiminea globulus* and *Hydrobia* sp., the limpet *Siphonaria compressa*, and the crab *Paratylodiplax edwardsii* (Fig. 10). The gastropod *Littorina saxatilis*, the mudprawn *Upogebia africana*, the starfish

Fig. 9. MDS ordination showing differences in macrofaunal assemblages between beds of *Zostera capensis* and unvegetated sandflats in high- and low-shore zones of Klein Oesterwal in 1983. Lines indicate clusters formed between 10 and 20% similarity. Each point represents data from an individual quadrat

*Parvulastra exigua* and the hermit-crab *Diogenes brevirostris* were recorded only in high *Z. capensis* beds and not in bare sandflats. The burrowing polychaete *Orbinia angrapequensis* was significantly more abundant in high-shore sandflats than *Z. capensis* beds. Three other burrowers, viz. the sandprawn *Callianassa kraussi*, the amphipod *Urothoe grimaldii* and the polychaete *Notomastus laticereus*, were not recorded in high-shore *Z. capensis* beds.

Low-shore *Zostera capensis* beds were dominated by the hermit-crab *Diogenes brevirostris* and the limpets *Fissurella mutabilis* (the latter generally attached to shells occupied by *D. brevirostris*) and *Crepidula porcellana*, whereas the sandprawn *Callianssa kraussi*, the amphipod *Urothoe grimaldii* and the polychaete *Euclymene lumbricoides* were more abundant in sandflats. The polychaete *Notomastus latiriceus* and the amphipod *Ampelisca palmata* were not recorded in low shore *Zostera* beds.

## Changes in abundance of wading birds between 1978 and 2007

Total counts ($R^2 = 0.45$, $p < 0.001$) and 5 yr moving medians ($R^2 = 0.88$, $p < 0.0001$) showed a linear decline in abundance of wading birds in Langebaan Lagoon between 1978 and 2007 (Fig. 11a). A total of 35 848 wading birds was counted in Langebaan Lagoon in 1978, but this dropped to 21 531 in 2009. Curlew sandpiper *Calidris ferruginea*, which is a generalist feeder and accounts for roughly 60% of wading birds in Langebaan Lagoon, also showed a corresponding decline in abundance over time (Fig. 11b; $R^2 = 0.66$, $p < 0.0001$). Wading birds with contrasting reliance on seagrass showed opposing population trends over time (Fig. 11). The abundance of terek sandpiper, which feeds exclusively in seagrass beds, was erratic between 1978 and 2007 (coefficient of variance CV = 64%), with population crashes coinciding with periods when cover of *Zostera capensis* declined in Klein Oesterwal (Fig. 11b). Waders that do not feed in seagrass beds, such as the ringed plover *Charadrius hiaticula* (CV = 28%), common whimbrel *Numenius phaeopus* (CV = 27%), greenshank *Tringa nebularia* (CV = 19%), and bar-tailed godwit *Limosa lapponica* (CV = 37%) were comparatively more stable, and did not exhibit declines that matched periods of *Z. capensis* collapse (Fig. 11c). Correlation analysis indicated a significant relationship between *Z. capensis* cover and abundance of terek sandpiper ($p = 0.041$, $R^2 = 0.33$) but not with counts of ringed plover ($p = 0.92$, $R^2 = 0.019$), common whimbrel ($p = 0.76$, $R^2 = 0.06$), greenshank ($p = 0.093$, $R^2 = 0.11$), and bar-tailed godwit ($p = 0.79$, $R^2 = 0.052$).

## DISCUSSION

The decline in cover of *Zostera capensis* in Langebaan Lagoon between 1960 and 2007 is consistent with other studies reporting declines in seagrasses over the last century (Hall et al. 1999, Hemminga & Duarte 2000 and references cited therein, Hughes et al. 2002, Waycott et al. 2009). The exact reason for the loss of *Z. capensis* in Langebaan Lagoon is unclear, but Angel et al. (2006) reported 2 major declines in abundance of this seagrass in Klein Oesterwal in 1976 and 2003, the first coincident with blasting and dredging operations in the adjacent Saldanha Bay, but there is no obvious explanation for the second decline (Angel et al. 2006). Dredging is known to increase suspended sediment loads and nutrient levels in marine systems (Riemann & Hoffmann 1991), often to the detriment of seagrasses (Hemminga & Duarte 2000, Baden et al. 2003, Waycott et al. 2009).

Smaller-scale losses of *Zostera capensis* may have been caused by human disturbance associated with trampling and bait collecting. *Z. capensis* was virtually eliminated by 2007 at Klein Oesterwal, a site where recreational harvesting of mud- and sandprawns is common. At the adjacent Oesterwal, where no such harvesting is permitted, *Z. capensis* is still present, albeit at a much lower abundance than in 1960, and it staged a recovery at Bottelary, which is located in the sanctuary area. Mud- and sandprawns are usually collected using a hand-held prawn pump, which turns over sediment cores from roughly 90 cm deep to the sediment surface. Wynberg & Branch (1992) estimated that each bait collector turns over 175 to 297 kg of sedi-
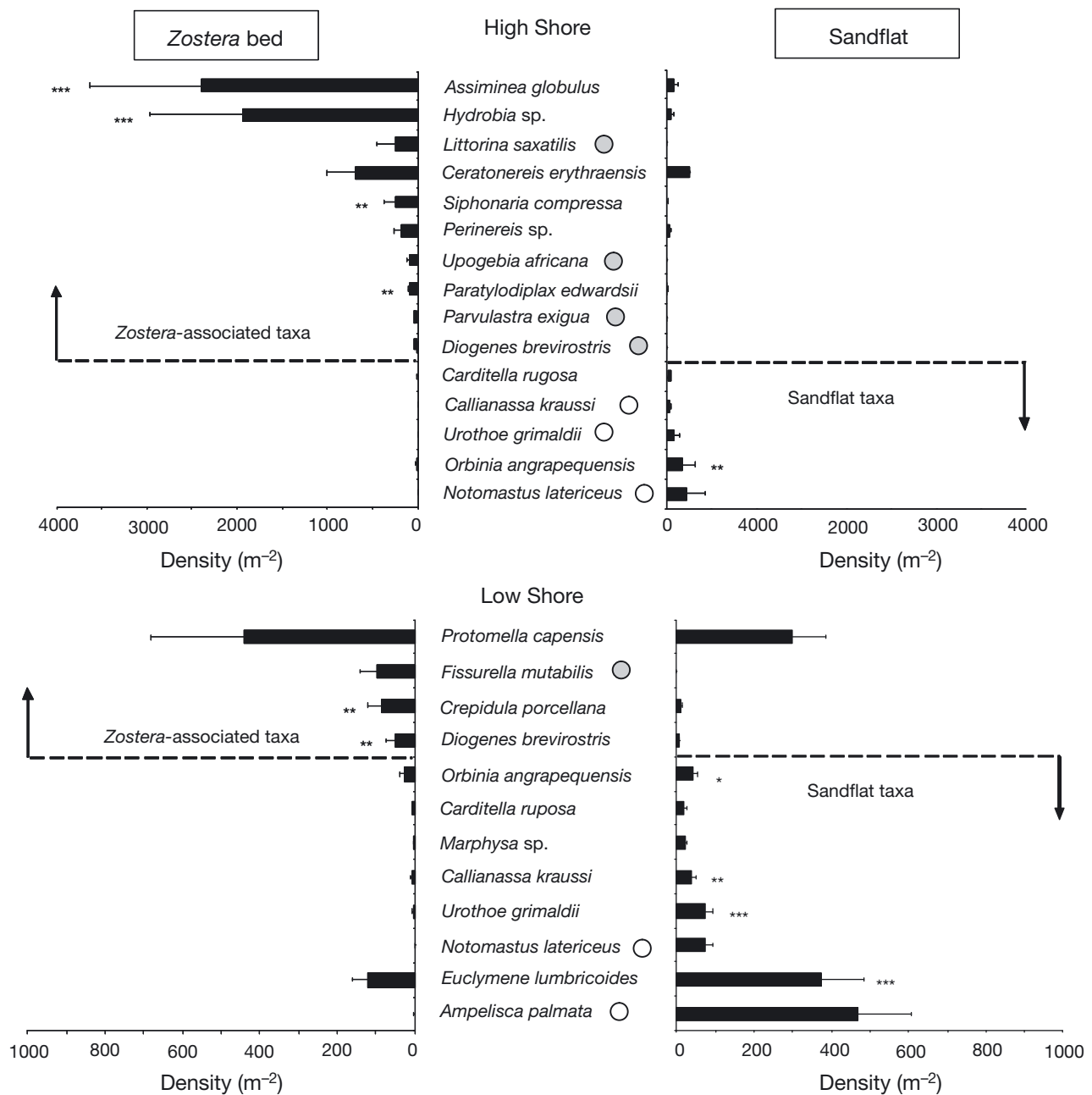
Fig. 10. Differences in density (mean +1 SE) of macrofauna between beds of *Zostera capensis* and unvegetated sandflats in the high- and low-shore zones of Klein Oesterwal in 1983; ○: species that were recorded in sandflats only; ◐: species that occurred in *Z. capensis* beds only. Asterisks indicate significant differences: *p < 0.05, **p < 0.01

ment to collect a quota of 50 prawns per day, resulting in roughly 4840 tons of sediment being turned over annually in the lagoon. In view of the susceptibility of seagrasses to sedimentation and burial (Cabaço et al. 2008), it is probable that such disturbance has contributed to the demise of *Z. capensis* at Klein Oesterwal.

The decline in seagrass cover at Centre Bank between 1960 and 2007 was less severe than in other areas of Langebaan Lagoon, even though this site is

also utilised by recreational harvesters for bait collecting (Wynberg 1991). It is possible that *Zostera* coverage at this site was overestimated from orthophotos during our analysis due to confusion with beds of the alien mussel *Mytilus galloprovincialis* present at times, thereby underestimating seagrass decline at this site (Robinson & Griffiths 2002).

While the reasons for the decline in *Zostera capensis* cover in Langebaan Lagoon remain speculative, our
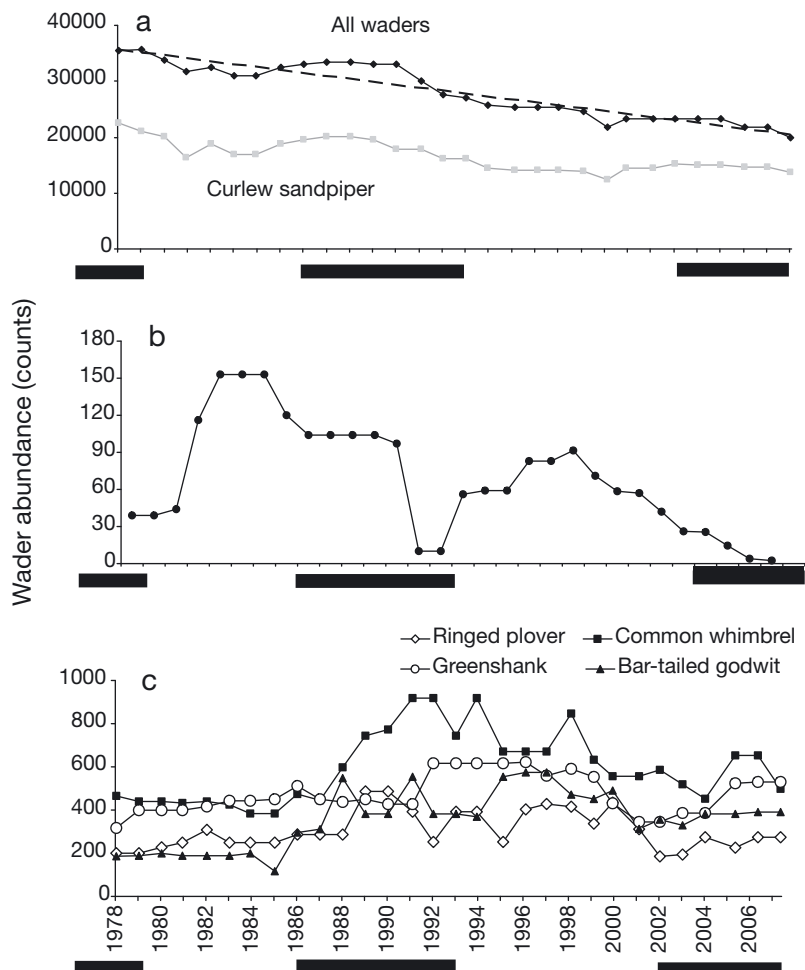
Fig. 11. Overall changes in abundance of (a) all intertidal wading birds and curlew sandpiper, (b) terek sandpiper, and (c) ringed plover, common whimbrel, greenshank, and bar-tailed godwit, in Langebaan Lagoon between 1978 and 2007. Five year moving medians are shown. Black bars indicate periods of seagrass collapse. (Seagrass data obtained from Angel et al. 2006). Linear trendline (dashes) shown in (a)

monitoring data from Klein Oesterwal point to important cascading effects on biota following these losses. The transformation in invertebrate communities in this sandflat between 1983 and 2009, the underlying mechanisms involved and cascading effects on higher trophic levels are summarised in Fig. 12. One of the biggest changes over this period was the reduction in invertebrate richness by roughly 20 to 50%, and abundance by 20 to 70% at this site. This is consistent with other studies highlighting the effect of seagrass loss in reducing invertebrate richness and abundance (Orth et al. 2006, Airoldi et al. 2008). Total abundance of invertebrates showed 3 peaks across the shore in 1988, roughly corresponding to the high, middle, and low *Z. capensis* beds present at that time. By 2009 no such peaks were evident, probably due to the scarcity of *Zostera* in the region.

Based on our comparisons made in 1983 of macrofaunal species between beds of *Zostera capensis* and adjacent bare sandflats, many of the species that declined in abundance between 1983 and 2009 are exclusively or predominantly associated with *Z. capensis*. The most significant change that occurred over this period from a conservation point of view was the near local extinction of the limpet *Siphonaria compressa* in Klein Oesterwal. This species is currently listed as critically endangered by the International Union for the Conservation of Nature (IUCN) and occurs exclusively on blades of *Z. capensis*, where it feeds on epiphytic films (Allanson & Herbert 2005). There are only 2 known systems where this species occurs, Knysna Lagoon and Langebaan Lagoon, which are also known to sustain dense beds of *Z. capensis* (Allanson & Herbert 2005). Intolerance to salinity changes is another reason for extreme habitat restriction by *S. compressa* and for its decline after floods in Knysna Lagoon (Wilson et al. 2009).

The conservation of *Siphonaria compressa* is thus critically linked to the conservation and proper management of seagrass meadows in Langebaan Lagoon. Angel et al. (2006) documented how *S. compressa* approached localised extinction in Langebaan Lagoon on both occasions when major declines in density of *Zostera capensis* occurred. Further warning signals for *S. compressa* arise from the reported extinction of the eelgrass limpet *Lottia alveus*, following an attack of the wasting disease on eelgrasses in the north Atlantic (Carlton et al. 1991).

Other species that are largely associated with *Zostera capensis* and virtually disappeared from Klein Oesterwal between 1983 and 2009 are the surface-dwelling limpet *Fissurella mutabilis*, the shell-occupying limpet *Crepidula porcellana*, and the starfish *Parvulastra exigua*. The role of *Z. capensis* in supporting these species is indicative of its capability to increase heterogeneity in otherwise homogeneous sedimentary habitats (Hemminga & Duarte 2000).

Other macrofaunal species that decreased in abundance between 1983 and 2009 do not occur exclusively with *Zostera capensis*, but are generalists, and are known to occur in sandflats without *Z. capensis* in Langebaan Lagoon. Examples include the gastropod
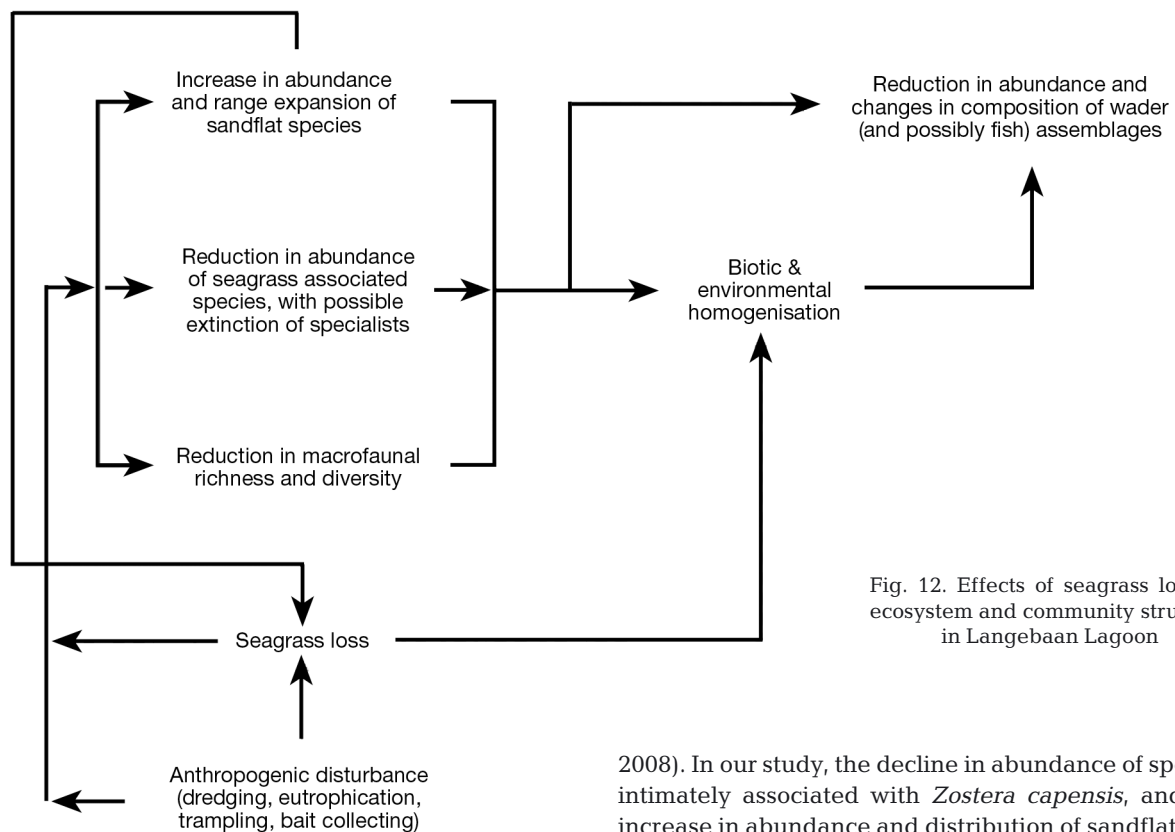
Fig. 12. Effects of seagrass loss on ecosystem and community structure in Langebaan Lagoon

*Assiminea globulus* and the crabs *Diogenes brevirostris* and *Hymenosoma orbiculare*. It is probable that these species were positively affected by the enhanced food availability and shelter provided by beds of *Z. capensis* in 1983, relative to bare sand in 2009.

Although the loss of *Zostera capensis* resulted in the demise of species intimately linked with it, it promoted species that preferred bare unvegetated sandflats. Polychaetes such as *Orbinia angrapequensis* and *Scoloplos johnstonei*, and the amphipod *Urothoe grimaldii*, all increased in density over this period. These are all burrowing infaunal species that may be negatively affected by the complex root systems of seagrasses because of physical hindrance to burrow construction (Brenchley 1982, Siebert & Branch 2005a). In addition, *O. angrapequensis* and *U. grimaldii*, which were patchily distributed along the shore in Klein Oesterwal in 1983 when *Z. capensis* beds were abundant, increased their horizontal range across almost the entire shore when *Z. capensis* had virtually disappeared.

Airoldi et al. (2008) hypothesised that the demise of complex ecosystems would result in the loss of resident species that have narrow distributions and occur almost exclusively in the habitat concerned. Conversely, it would also free up space for new species with broader habitat requirements, leading to an increase in abundance of such colonisers (Airoldi et al.

2008). In our study, the decline in abundance of species intimately associated with *Zostera capensis*, and the increase in abundance and distribution of sandflat species, serves as supportive evidence for this hypothesis.

Airoldi et al. (2008) also proposed that new colonisers may intensify and accelerate habitat loss, and may prevent the re-establishment of these habitats. In the case of our study, one species capable of these effects is the burrowing sandprawn *Callianassa kraussi*. This ecosystem engineer turns over sediment at prodigious rates (Branch & Pringle 1987), and its bioturbative activities are powerful structuring agents of marine communities (Siebert & Branch 2005a,b, 2006, 2007, Pillay et al. 2007a,b,c, 2008). Bioturbation by this sandprawn negatively affects the abundance of *Zostera capensis*, and consequently the invertebrates intimately linked to it (Angel et al. 2006, Siebert & Branch 2007). Although the abundance of *C. kraussi* declined in Klein Oesterwal between 1988 and 2007, probably due to bait collecting and trampling (Wynberg & Branch 1997, Contessa & Bird 2004), one cannot dismiss the possible role of *C. kraussi* bioturbation in the demise of *Z. capensis*.

While we have highlighted the possible role of losses of *Zostera capensis* beds on macro-invertebrates in Langebaan Lagoon, physical disturbance associated with bait collecting may have also played a secondary role. Wynberg & Branch (1992) showed that a maximum of 386 kg of macrofauna is incidentally turned over per year during sandprawn harvesting, of which 80 % is preyed upon by birds. Changes to sedimentary

properties induced by prawn pumping may also negatively affect macrofauna, as shown by Peterson (1976), who reported a decline in density of the commensal bivalve *Cryptomya californica* due to harvesting of *Callianassa californiensis*. Lastly, trampling during bait harvesting can also have severe negative effects on macrofauna (Wynberg & Branch 1997).

The reductions in cover of *Zostera capensis* beds in Langebaan Lagoon and the associated changes to macro-invertebrates may have serious repercussions for higher trophic levels in the system. Our data show a linear decline in counts of wading birds in Langebaan Lagoon between 1978 and 2007, with wader species that feed in these seagrass beds showing population crashes at times corresponding to periods of seagrass decline (Angel et al. 2006). Wading birds that do not feed in seagrass beds were more stable over time. These results indicate that losses of seagrass ecosystems, and the associated changes in invertebrates in the system, may be responsible for declines in seagrass-associated waders. However, it is difficult to be certain of this, as extrinsic factors may also be involved. Curlew sandpiper *Calidris ferruginea* numbers and age structure in Langebaan Lagoon, for example, are correlated with lemming numbers in the arctic tundra, the nesting grounds of *C. ferruginea* (Underhill 1987b). It is hypothesised that when lemmings are scare, arctic foxes feed on nesting birds, thereby influencing adult population structure. Nevertheless, losses of seagrass meadows in Langebaan Lagoon may decrease the attractiveness of the lagoon for seagrass-associated wading species and represent a significant management concern, given the lagoon's RAMSAR status and importance for birdlife.

Large-scale losses of seagrass beds in Langebaan Lagoon are also likely to negatively impact fish assemblages. We could not directly address this issue due to the unavailability of comparable fish data, but several studies have reported greater richness and abundance of fish in seagrass meadows compared with unvegetated sandflats, due to greater prey availability and protection from predators (Hanekom & Baird 1984, Whitfield et al. 1989, Hemminga & Duarte 2000). Hughes et al. (2002) demonstrated that reductions in coverage of the seagrass *Zostera marina* between 1988 and 1999 in estuaries in the USA were linked to reductions in richness, abundance, and biomass of fish, with biomass and abundance of 11 of the 13 common species declining. Pihl et al. (2006) also demonstrated a shift in fish community structure in Swedish waters following large-scale losses of *Z. marina*.

Taken collectively, our analyses indicate that loss of seagrass beds, together with anthropogenic disturbance from bait collecting and trampling, may have been pivotal in transforming invertebrate assemblages in

Klein Oesterwal. Cascading reductions in seagrass-associated waders and fish are also possible due to reductions in richness and abundance of invertebrate prey. The threat posed by further seagrass loss to the critically endangered eelgrass limpet *Siphonaria compressa* and intertidal wading birds are important conservation concerns. The present study thus raises awareness of the critical roles seagrasses play and the need for appropriate management to protect remaining seagrass meadows in Langebaan Lagoon and elsewhere.

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