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Dynamics of Rocky Intertidal Communities: Analyses of Long Time Series from South African Shores

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The abundance of benthic invertebrates in undisturbed and experimentally cleared quadrats on three rocky shores on the east coast of South Africa was monitored quarterly for 13 years. Most of the 11 commonly occurring species exhibited significant seasonal cycles and, although interannual variability was high, there was evidence of biennial cycles in abundance. Long-term trends were evident for many species. Limpets generally decreased in abundance, while periwinkles and rock oysters increased. The two numerically dominant barnacles exhibited an inverse relationship over time, and at some sites one species was replaced by the other. There was a high degree of both inter- and intraspecific correlation at small scales, but this was attenuated at scales of tens to hundreds of kilometres. Many of the time series exhibited significant discontinuities in which changes in abundance of up to three orders of magnitude were evident. Such discontinuities usually marked the start of periods of altered interannual variability lasting for 3–4 years. In some cases, this resulted in time series divided into phases with completely different underlying dynamics. After an initial recovery period of up to 3 years, the cleared areas exhibited many of the same characteristics as the controls, but with a tendency for increased interannual variability. An interesting finding was that areas cleared in spring and summer did not exhibit the biennial cycles characteristic of undisturbed areas, while those cleared in autumn and winter retained this characteristic. Fluctuations in abundance of intertidal invertebrates clearly exhibit complex dynamics, which are discussed in terms of possible external forcing functions.

Keywords: intertidal invertebrates; biennial cycles; complex dynamics; South Africa

Introduction

Many studies have shown that one of the most important characteristics of rocky shore communities is their great spatial and temporal variability which arises from a combination of biotic and physical factors (Dayton, 1971; Menge, 1976; Denley & Underwood, 1979; Hawkins & Hartnoll, 1982, 1983; Hawkins, 1983; Dethier, 1984; Menge & Sutherland, 1987; Raimondi, 1990, 1991). Manipulative experiments have led to an appreciation of the importance of species interactions, such as grazing, predation and competition, in spatial structuring of intertidal communities (Connell, 1961; Menge, 1976; Peterson, 1979; Underwood, 1980; Dungan, 1986; Menge *et al.*, 1986; Petraitis, 1990; Dye & White, 1991; Dye, 1992*a*, 1993*a*, 1995; Lasiak & White, 1993). Spatial and temporal variations in settlement and recruitment have also been shown to play an important role in establishing and maintaining the often complex mosaics associated with such communities (Lewis, 1976; Bowman & Lewis, 1977; Caffey, 1985; Gaines *et al.*, 1985; Kendall *et al.*, 1985; Raimondi, 1988; Dye, 1988, 1990, 1992*b*, 1993*b*). Human impacts on rocky shores have also received increasing attention, which has demonstrated the often devastating effects of trampling (Beauchamp & Gowing, 1982), and of exploitative activities such as shellfish collection (Duran *et al.*, 1987; Castilla & Bustamente, 1989; Lasiak & Dye, 1991; Underwood, 1993; Lasiak & Field, 1995).

Although short- to medium-term experiments will continue to be valuable in furthering our understanding of intertidal community interactions, they can shed little light on underlying long-term processes which may affect their outcome (Garrity & Levings, 1981; Connell, 1985; Fairweather, 1988). Long-term studies (≈10 years or more) are important not only in providing a background against which short-term studies can be assessed, but also because many important processes may occur over such long periods that they could never be detected within the usual time span of intertidal field experiments (Southward, 1967, 1991; Underwood, 1984; Paine, 1986; Butler & Chesson, 1990; Barry *et al.*, 1995; Southward *et al.*, 1995). Furthermore, because the prior state of the system is known, long-term studies can shed light on the effects of unusual events which could not be

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Table 1. Species recorded in the mid- and upper-littoral zones at Mazeppa, Dwesa and Mkambati

	Mazeppa		Dwesa			Mkambati		
Species	LZ	LB	LZ	UB	LB	LZ	UB	LB
Barnacles								
Chthamalus dentatus	—	—	—	√√	√√	—	√√	√√
Octomeris angulosus	—	√√	—	√	√√	—	√	√√
Tetraclita serrata	—	√√	—	√√	√√	—	√√	√√
Bivalves								
Saccostrea cucullata	—	—	—	√√	√√	—	√√	√√
Perna perna	—	√√	—	—	√	—	—	—
Polychaetes								
Pomatoleios kraussi	—	√	—	√	√	—	—	—
Limpets								
Cellana capensis	—	√√	—	√√	√√	—	√√	√√
Patella granularis	—	√√	—	√√	√√	—	√√	√√
Patella concolor	—	√	—	—	—	—	—	—
Patelloida profunda	—	√√	—	√	√	—	√	√
Siphonaria capensis	—	√	—	—	—	—	—	—
Siphonaria concinna	—	√√	—	√√	√	—	√	√
Fissurella natalensis	—	√	—	√	√	—	—	√
Periwinkles								
Nodilittorina africana	√√	√√	√√	√√	√√	√√	√√	√√
Oxystele tabularis	—	√√	—	√√	√√	—	√√	√√
Whelks								
Nerita albicilla	—	—	—	—	√	—	—	—
Burnupena lagenaria	—	√	—	√	√	—	√	√
Nucella dubia	—	√	—	—	√	—	√	√

LZ, Littorina zone; UB, Upper Balanoid; LB, Lower Balanoid; √√, common; √, rare; —, absent.

predicted, or simulated experimentally (Lewis, 1976; Hawkins & Hartnoll, 1983; Foster & Schiel, 1993; Francis & Evans, 1993). Finally, the time series resulting from long-term studies may in themselves be useful tools for refining experimental designs and statistical procedures employed in estimating natural variability and assessing the effects of disturbance (McArdle *et al.*, 1990; Underwood, 1994) and for investigating non-linear phenomena such as chaos (Turchin & Taylor, 1992; Ellner & Turchin, 1995).

Despite their obvious utility (Lively *et al.*, 1993; Southward *et al.*, 1995) there have been relatively few long-term studies of rocky intertidal systems (Barnes, 1956; Southward, 1967; Luckins, 1976; Caffey, 1985; Kendall *et al.*, 1982, 1985; Judge *et al.*, 1988). The present paper is the first to report on a long-term study of rocky shores in South Africa. The initial hypothesis was that temporal and spatial fluctuations in the abundance of species would be highly stochastic and therefore independent of each other, and of the scale on which they were measured. The objective was therefore to establish the nature and extent of natural fluctuations in mid- and upper intertidal communities at large spatial and temporal scales, both to test this hypothesis, and as a background to the interpretation of experimental data on community interactions and human impacts on the south-east coast of South Africa. Studies on low-shore communities and human impacts in this area have been reported on elsewhere (Lasiak, 1991; Lasiak & Dye, 1989; Lasiak & Field, 1995).

Material and methods

Benthic populations in the mid- and upper-littoral zones were monitored from November 1982 at two sites, Mazeppa Bay (28°06′E, 32°41′S) and Dwesa (28°50′E, 32°18′S), and from May 1983 at a third site, Mkambati (30°E, 31°16′S). The region experiences mainly summer rainfall with an annual mean of 1100 mm. Air temperature ranges from 13 °C to 35 °C with a mean of 20 °C. Prevailing winds are from the south-west but frequent easterlies also occur. Sea temperature varies from 10 °C, during occasional upwelling, to 24 °C, with a mean of 18 °C. Tides are semi-diurnal with an amplitude of approximately 2 m and all sites experience continuous moderate to heavy wave action, mainly from the south-west.

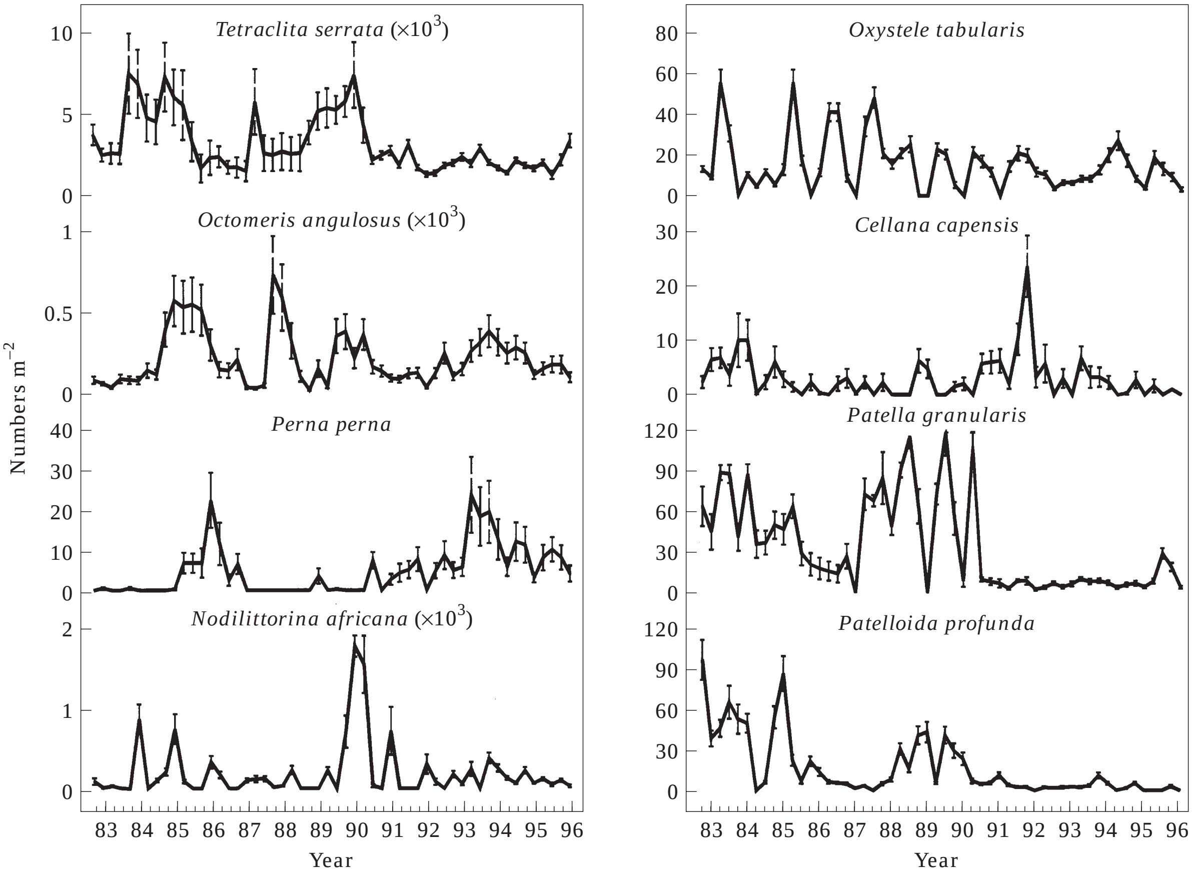

FIGURE 1. Long-term fluctuations in mean abundance (± SE) of the eight most common species in undisturbed quadrats in the Lower Balanoid zone at Mazeppa.

The shore at Dwesa is approximately 100 m wide and consists of a series of shale platforms backed by a narrow sandy beach below vegetated dunes. At Mkambati the shore, 60 m in width, consists of a series of quartzitic sandstone platforms backed by vegetated dunes. Both sites are located in marine reserves and four tidal zones are distinguishable (Branch & Branch, 1981). On the high-shore, the Littorina zone is dominated by the periwinkle *Nodilittorina africana*, a small but numerous grazing gastropod rarely exceeding 5 mm in length. Approximately 60 cm below this is the upper balanoid zone, characterized by the rock oyster, *Saccostrea cucullata*, which reaches the southern limit of distribution in this region, and the barnacle *Chthamalus dentatus*. Extending below this to about 30 cm above the low spring tide level is the lower balanoid zone, characterized by the barnacles *Tetraclita serrata* and *Octomeris angulosus*. Finally the low-shore zone extends down to the spring low water level and in marine reserves supports *inter alia* large numbers of the brown mussel *Perna perna*, various patellid limpets and numerous species of algae. There are no marine reserves in the vicinity of Mazeppa Bay, which lies to the south of the limit of rock oyster distribution, and has a steep profile, approximately 30 m wide, consisting of dolorite steps. As a consequence of shellfish harvesting by the local population, the low-shore supports few mussels or limpets and is covered by barnacles and patches of coralline algae.

At Dwesa and Mkambati, quarterly estimates of abundance were based on 16 monochrome photographs of $0{\cdot}25^2$ quadrats located within an approximately 5 × 20 m area parallel to the sea in the littorina zone, as well as in the upper and lower balanoid zones. The photographs were taken through a plastic frame divided into 100 50 × 50 mm squares. To reduce background noise and to enable data to be collected for recruitment and growth studies (Dye, 1989, 1990, 1992*b*, 1993*b*), the quadrats, which were chosen initially at random, were marked either with steel pegs or screws to facilitate accurate placement of the frame on each sampling occasion. Although this procedure reduced the independence of replicates within tidal levels, this was considered to be an acceptable compromise in terms of the objectives of the study. Owing

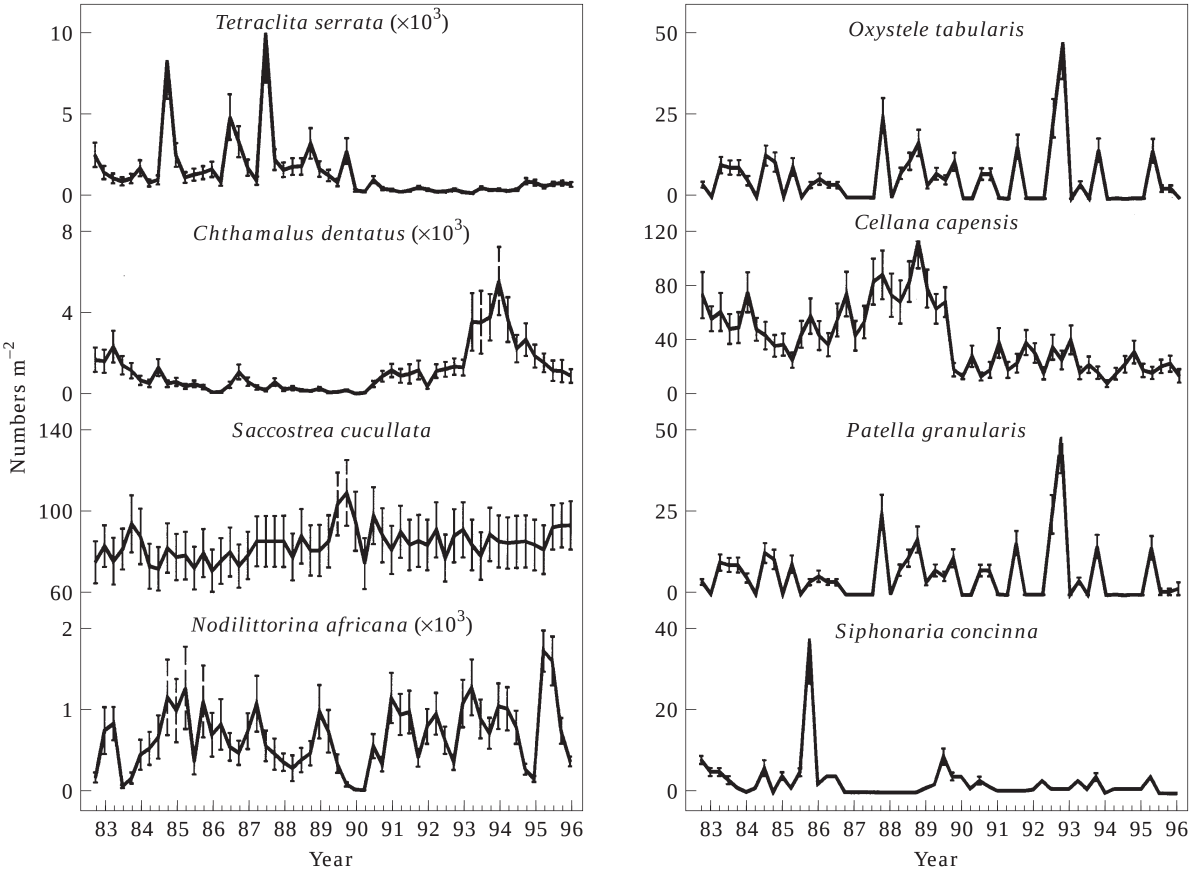

FIGURE 2. Long-term fluctuations in mean abundance (± SE) of the eight most common species in undisturbed quadrats in the Upper Balanoid zone at Dwesa.

to the narrow intertial and the absence of rock oysters, only the Nodilittorina and lower balanoid zones were monitored at Mazeppa.

In order to create a clearly defined pulse disturbance to act as a reference point for the recolonization aspect of the study, areas adjacent to the undisturbed quadrats were denuded experimentally and their recovery monitored. At quarterly intervals during the first 12 months of the study, four contiguous 0·25 m^2 quadrats were cleared of all macro-organisms by scraping with a paint scraper. Data on species composition and abundance were obtained photographically as described above. The working hypothesis, given the relatively short longevity of most of the species, was that recovery would be rapid, and that the cleared areas would converge on the control condition within a relatively short time.

Since many of the resulting time series contained strings of zeros, analyses were based on data transformed to $\log_{10}$ $(x+1)$. All abundance data are expressed as mean number m^{-2} (± SE). To reduce Type I error rates, all multiple comparisons were tested at the 99% confidence level.

Results

A total of 18 species were recorded during the study (Table 1). *N. africana* was the only species recorded in the littorina zone at Mazeppa and Dwesa, while at Makambati low numbers of *C. dentatus* were also recorded. The most abundant species in the upper balanoid zone at Dwesa and Mkambati were barnacles and *N. africana*. Rock oysters (*S. cucullata*) were also abundant in this zone and limpets (*Siphonaria concinna* and *Cellana capensis*) were common. Apart from *N. africana* the only other common periwinkle was *Oxystele tabularis*. A similar group of species were found in the lower balanoid zone. The only molluscan predators were the whelks *Burnupena lagenaria* and *Nucella dubia* which occurred occasionally.

Undisturbed quadrats

Figures 1 to 5 show the long-term fluctuations in mean abundance of the 11 most common species recorded during the study. The remainder are not plotted as they occurred too sporadically for

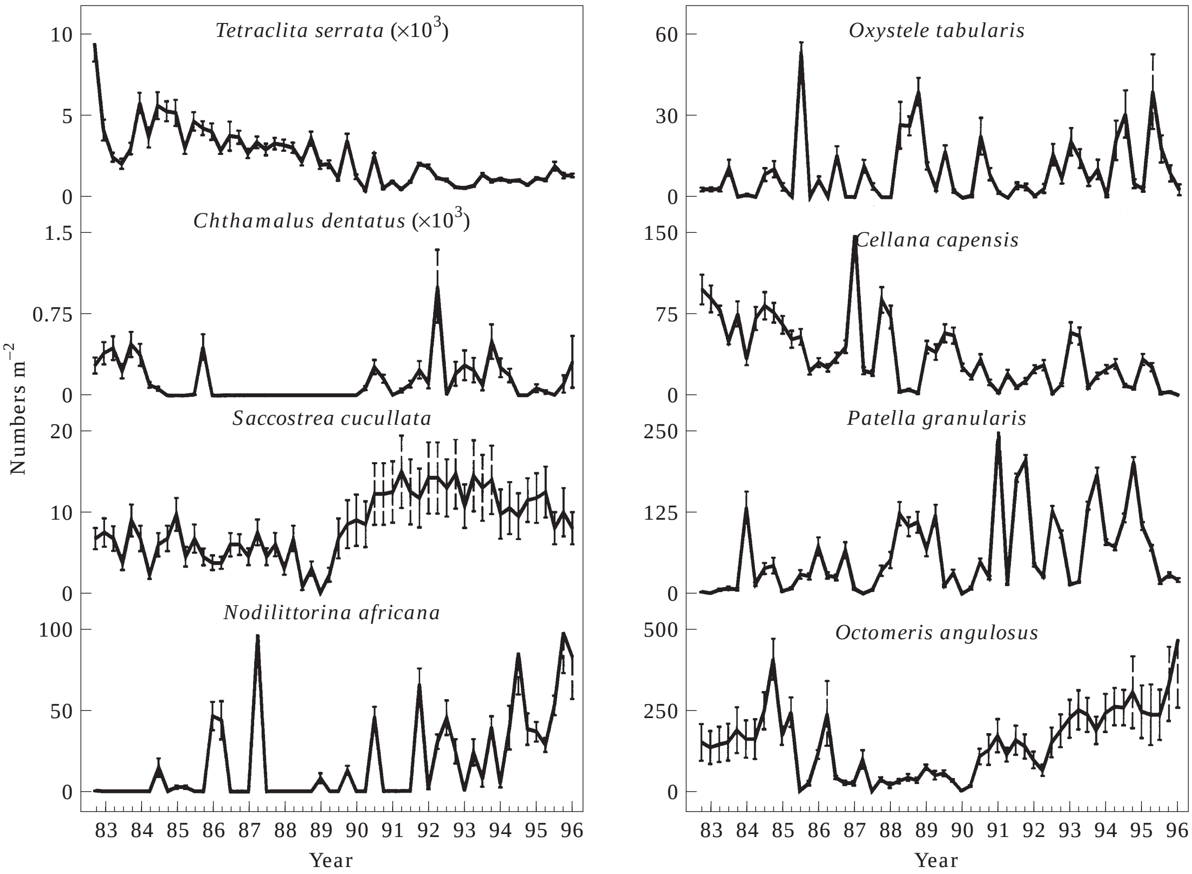

FIGURE 3. Long-term fluctuations in mean abundance (± SE) of the eight most common species in undisturbed quadrats in the Lower Balanoid zone at Dwesa.

meaningful univariate analysis. The most striking features of almost all of these time series are their variability and strong degree of seasonality. Analysis revealed moderate to strong first order autocorrelation which, in most cases, could be removed by lag-1 differencing (Chatfield, 1989). Subsequent Fourier transformation of the detrended series revealed significant annual cycles ($f=4$) in 83% of the series. At Mazeppa, 83% of the species which showed annual cycles in abundance also showed biennial cycles ($f=8$). In the upper balanoid zone at Dwesa, 75% of species with annual cycles had biennal cycles, while 78% exhibited biennal cycles in the lower balanoid zone. At Mkambati, in contrast, only 43% of species in both zones showed biennial cycles, although 83% showed annual cycles. Although some evidence of cycles with frequencies of 12 and 15 (3 and 5 years, respectively) emerged these should be treated with caution because of the limited length of the series (Jassby & Powell, 1990).

Many of the time series showed discontinuities or abrupt changes in abundance and temporal variability, which occurred at about the same time over vastly different spatial scales. One of the most widespread discontinuities occurred between mid 1989 and mid 1990. During this period, the abundance of *T. serrata* declined sharply at all sites, sometimes by over an order of magnitude. At Mazeppa and Dwesa, these changes have persisted until the present. In contrast the abundance of other species, such as *C. dentatus*, *O. angulosus*, *P. perna* and *S. cucullata* started to increase at this time, in some cases by up to three orders of magnitude.

Apart from the above, other, more subtle, changes in the nature of the time series can be discerned. An interesting example is *P. granularis*. At Mazeppa, this limpet exhibited three distinct types of fluctuation. Initially, the population varied between 60 and 90 m^2, but declined from 1985 to almost zero by 1987. At that point, the population suddenly increased and started oscillating annually between 120 and close to zero m^{-2} for the next 3·5 years. This apparently chaotic behaviour ceased abruptly in mid 1990 when abundance declined to about 5 m^{-2} where, with the exception of a peak of 24 m^{-2} in 1995, it has remained. The same species at Dwesa appears to

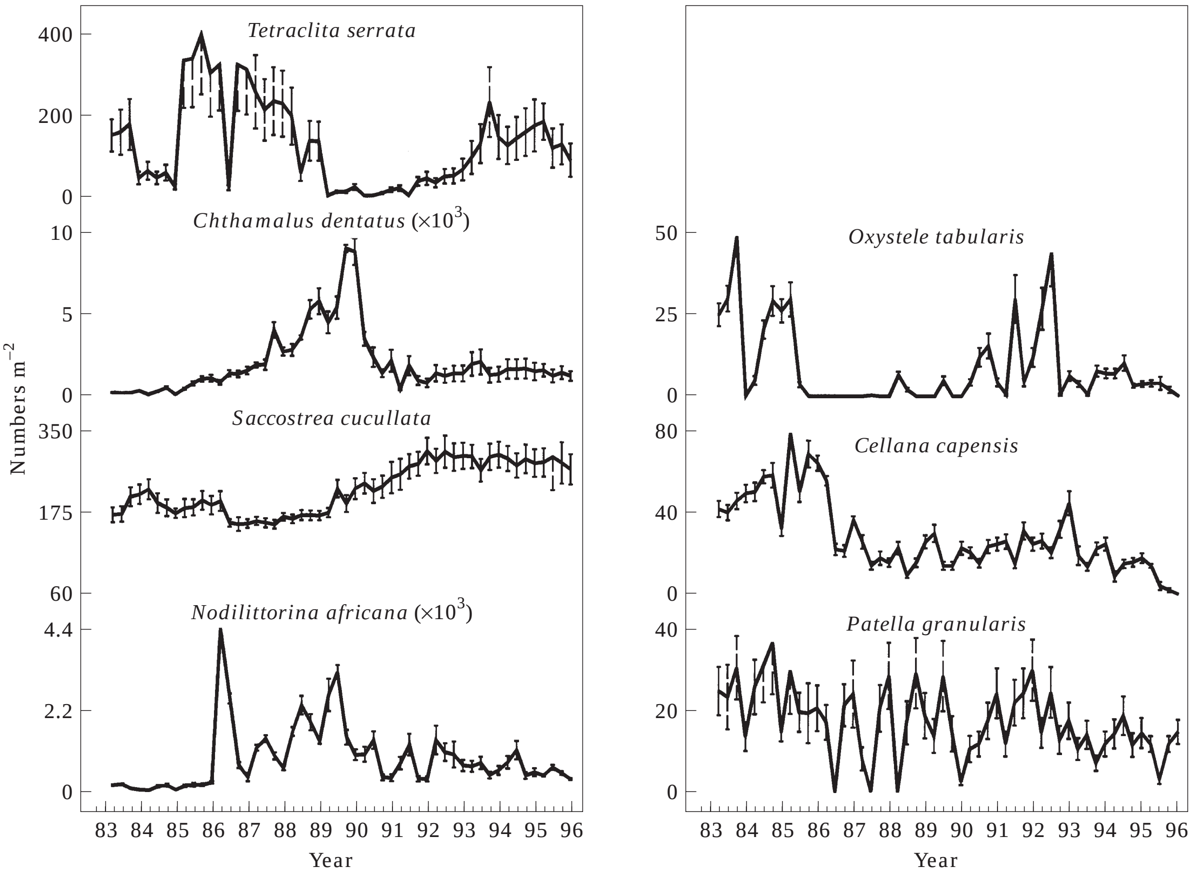

FIGURE 4. Long-term fluctuations in mean abundance (± SE) of the seven most common species in undisturbed quadrats in the Upper Balanoid zone at Mkambati.

exhibit the opposite trend, with variability increasing after 1990. Other species such as *C. dentatus*, *O. tabularis*, *N. africana* and *C. capensis*, also exhibit changes in temporal variability of the type describe above.

Apart from cyclic variations in abundance, long-term trends were evident in most of the species studied. There was a decrease in the abundance of *T. serrata* at most sites during the study period, while the abundance of *C. dentatus* and *S. cucullata* increased. There were long-term decreases in the abundance of the most common grazers, *C. capensis*, *P. granularis*, *P. profunda*, *S. concinna* and *O. tabularis*, with only *N. africana* exhibiting long-term increases in abundance.

The extent to which long-term fluctuations in abundance correlate spatially within and between species is shown in Table 2. Although many correlations were significant ($P \leq 0{\cdot}01$) a large number had low correlation coefficients. For clarity, therefore, only those which accounted for at least 50% of the covariance are given. At Mazeppa, 15% of the within-site comparisons were significant (Table 2) and, of these, 50% were positive. Although no clear patterns emerged, limpets tended to correlate positively with *T. serrata*, which is the dominant space-occupier. Approximately one-third of the possible correlations at Dwesa were significant and, of these, all of the intraspecific correlations were positive, compared with half of the interspecific correlations. There were more significant correlations within the lower balanoid zone than within the upper balanoid. The clearest pattern was a tendency for *T. serrata* to correlate negatively with other sessile species, but positively with limpets. Fluctuations in the abundance of conspecifics were generally positively correlated across tidal levels. Within-site comparisons revealed much the same picture at Mkambati, were 42% of possible correlations were significant. Conspecifics correlated positively both within and between tidal levels. Limpets tended to correlate negatively with most sessile species, but there were no significant correlations with *T. serrata*. In contrast to Dwesa, fluctuations in the abundance of different species tended to correlate more frequently in the upper balanoid zone than in the lower balanoid.

Only 15% of possible comparisons in species abundance between the upper balanoid zones at Dwesa

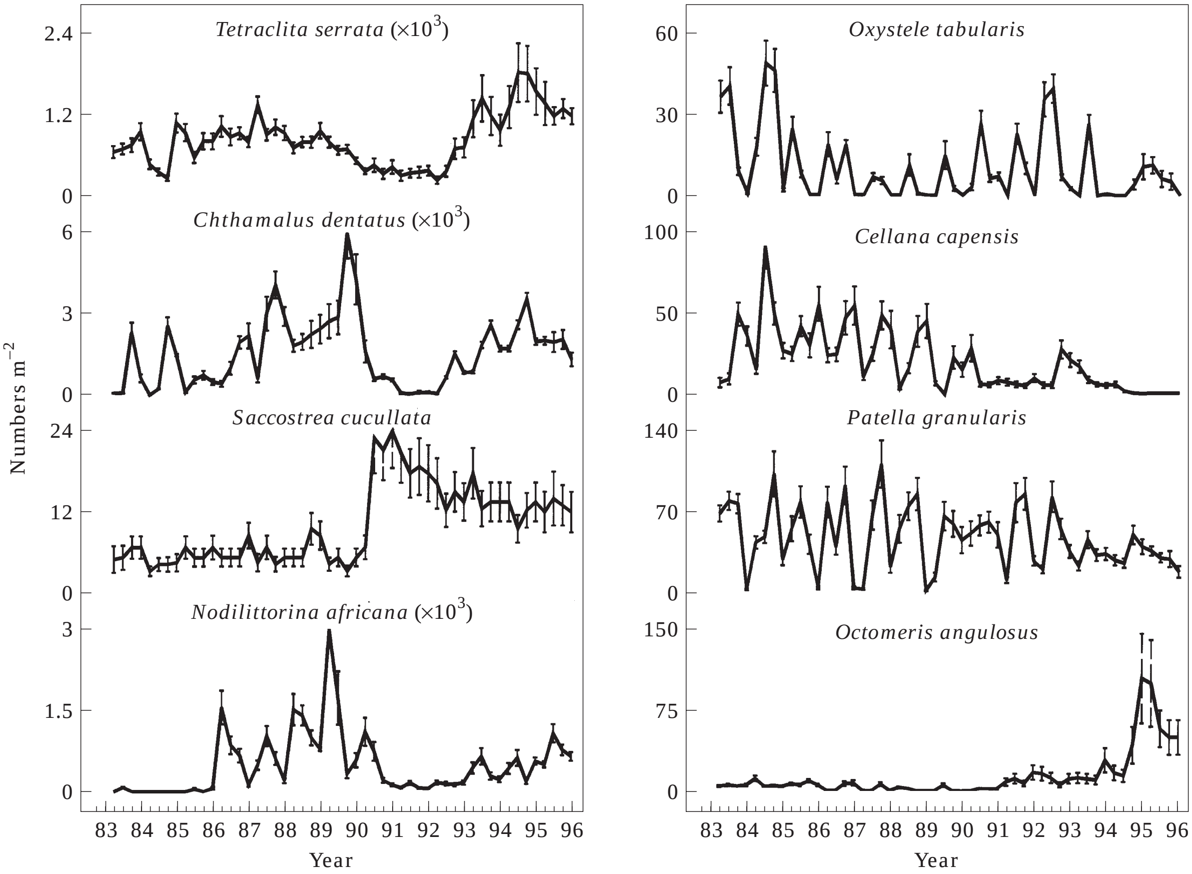

FIGURE 5. Long-term fluctuations in mean abundance (± SE) of the eight most common species in undisturbed quadrats in the Lower Balanoid zone at Mkambati.

and Mkambati were significant, and no clear pattern was discernible. Similarly, only 5% of possible comparisons between the lower balanoid zones at Mazeppa and Dwesa and between Mazeppa and Mkambati were significant. In contrast, a higher frequency of significant correlations emerged in comparisons between the lower balanoid zones at Dwesa and Mkambati. In this case, one-third of all possible correlations were significant and 80% of the intraspecific correlations were positive. Fluctuations in the abundance of *T. serrata* at Dwesa tended to correlate negatively with other sessile species and positively with limpets at Mkambati. Fluctuations in abundance of *N. africana* on the high-shore at Mazeppa were found to correlate positively ($r = 0{\cdot}299$, $n = 54$) with those of *N. africana* on the high-shore at Dwesa, while those at Dwesa correlated positively in turn with those at Mkambati ($r = 0{\cdot}368$, $n = 51$). There was, however, no significant correlation between high-shore *N. africana* at Mazeppa and those at Mkambati.

Overall, the number of significant intraspecific correlations within and between shore levels and sites decreased logarithmically with increasing spatial scale ($y = 42{\cdot}28–29{\cdot}916\log_{10}x$; $r^2 = 0{\cdot}659$; $P \leq 0{\cdot}05$). Within tidal levels, on scales of less than 10 m, 85% of intraspecific correlations were significant, while at larger scales only 20–40% of the correlations were significant.

The predominant cycles in percentage cover at all sites were annual and biennial. In the upper balanoid at Dwesa cover generally decreased from an initial average of 60% in 1983 to 15% in 1990, after which it increased to its present level of 25%. In contrast, cover in the upper balanoid at Mkambati was initially low (15%), but increased from 1987 to reach 50% by 1990. Cover has since fluctuated between 25 and 50%. Up to 1990, percentage cover on the low shore at Mazeppa exhibited cyclic fluctuations, ranging between 30 and 60% over periods of 4 years. In 1990, cover began to decrease and apart from peaks in 1994 and 1995, continued to decline to its present level of 25%. Cyclic fluctuations, although still evident, are of shorter periods. The highest cover was found on the lower balanoid at Dwesa, where from 1983 to 1989, cover varied between 80 and 90%. Over the following 2 years cover decreased sharply to about 45% after

TABLE 2. Pearson correlation coefficients for inter- and intraspecific within-site comparisons of abundance time series ($\log_{10}(x+1)$) from undisturbed quadrats in the Lower Balanoid (LB) zone at Mazeppa ($n=54$) and in the Lower Balanoid (LB) and Upper Balanoid (UB) zones at Dwesa ($n=54$) and Mkambati ($n=51$). Only significant correlations ($P \leq 0{\cdot}01$) for which $r \geq |0{\cdot}500|$ are shown

Species comparisons	Correlation coefficient r
Mazeppa	
T. serrata (LB): *P. perna* (LB)	− 0·500
C. capensis (LB): *P. profunda* (LB)	0·527
Dwesa	
T. serrata (UB): *C. capensis* (UB)	0·531
T. serrata (UB): *T. serrata* (LB)	0·818
T. serrata (UB): *C. dentatus* (LB)	− 0·500
C. dentatus (UB): *C. dentatus* (LB)	0·518
C. capensis (UB): *P. profunda* (UB)	0·637
C. capensis (UB): *N. africana* (LB)	− 0·500
P. profunda (UB): *T. serrata* (LB)	0·501
P. profunda (UB): *N. africana* (LB)	− 0·500
Mkambati	
T. serrata (UB): *T. serrata* (LB)	0·633
T. serrata (UB): *C. dentatus* (LB)	0·810
C. dentatus (UB): *C. capensis* (UB)	− 0·636
C. dentatus (UB): *N. africana* (UB)	0·792
C. dentatus (UB): *O. tabularis* (UB)	− 0·509
C. dentatus (UB): *N. africana* (LB)	0·794
S. cucullata (UB): *O. anglosus* (LB)	0·706
S. cucullata (UB): *S. cucullata* (LB)	0·702
N. africana (UB): *C. capensis* (UB)	− 0·587
N. africana (UB): *N. africana* (LB)	0·855
C. capensis (UB): *N. africana* (LB)	− 0·706
C. capensis (UB): *C. capensis* (LB)	0·731
O. tabularis (UB): *O. tabularis* (LB)	0·673
T. serrata (LB): *C. dentatus* (LB)	0·563
O. angulosus (LB): *S. cucullata* (LB)	0·648
P. granularis (LB): *O. tabularis* (LB)	0·609

which it gradually increased to its present level of 50%. At this site, the period from 1991 to the present has been characterized by much greater temporal variability than before. Until 1993, the lower balanoid zone at Mkambati had the lowest cover of all sites (22%). Between 1993 and 1995, cover increased to 70% before declining again to its present level of 25%.

Cleared quadrats

Long-term fluctuations in mean abundance of the common species following clearance at Mazeppa, Dwesa and Mkambati are shown in Figures 6 to 10. In each case, data from four treatments, representing clearance in different seasons, i.e. spring (A), summer (B), autumn (C) and winter (D), are shown. In almost all cases there was a tendency for areas cleared in autumn and winter to be recolonized more rapidly than those cleared in spring and summer. After the second year, however, the effect of season became less obvious. Some species such as *P. perna* and *P. profunda* at Mazeppa, *O. angulosus* and *S. cucullata* in the upper balanoid zone at Dwesa and *S. cucullata* in the upper and lower balanoid zones at Mkambati, took several years to recolonize the cleared areas. As in the undisturbed quadrats, the majority of species exhibited annual cycles of abundance. The influence of season of clearance became evident, however, when the proportions of species which also exhibited biennial cycles was calculated. At Mazeppa, 92% of species cleared in autumn and winter subsequently exhibited biennial cycles, as opposed to only 29% of those cleared in spring and summer. At Dwesa, the relevant proportions were 64 and 25% in the upper balanoid zone and 57 and 35% in the lower balanoid zone. At Mkambati, all species cleared in the upper balanoid zone in autumn and winter showed subsequent biennial cycles in abundance, as opposed to only 10% of those cleared in spring and summer. In the lower balanoid, the relative proportions were 85 and 45%, respectively.

Apart from rock oysters, which gradually increased in abundance, there was little evidence of long-term trends, although large fluctuations in abundance of up to three orders of magnitude were recorded for a number of species. Almost all of the time series exhibited the discontinuities shown by the undisturbed populations, particularly around 1990.

After the initial recovery period of 1–2 years, there was a high level of correlation between fluctuations in abundance of conspecifics cleared in different seasons (treatments) (Table 3). At Mazeppa, 67% of the species were positively correlated, 60% of which had correlation coefficients of 0·50 or higher. All conspecifics correlated positively between treatments in the upper balanoid zone at Dwesa, while 74% correlated positively in the lower balanoid zone. Over 75% of the correlation coefficients were 0·50 or higher. At Mkambati, all conspecifics correlated positively in both the upper and lower balanoid zones with over 96% having correlation coefficients better than 0·50.

Table 4 gives Pearson correlation coefficients for intraspecific between-site comparisons of abundance time series from disturbed quadrats. There were generally fewer significant correlations between sites than within sites. In the upper balanoid zones at Dwesa and Mkambati only three species exhibited significant correlations in abundance over time, these were

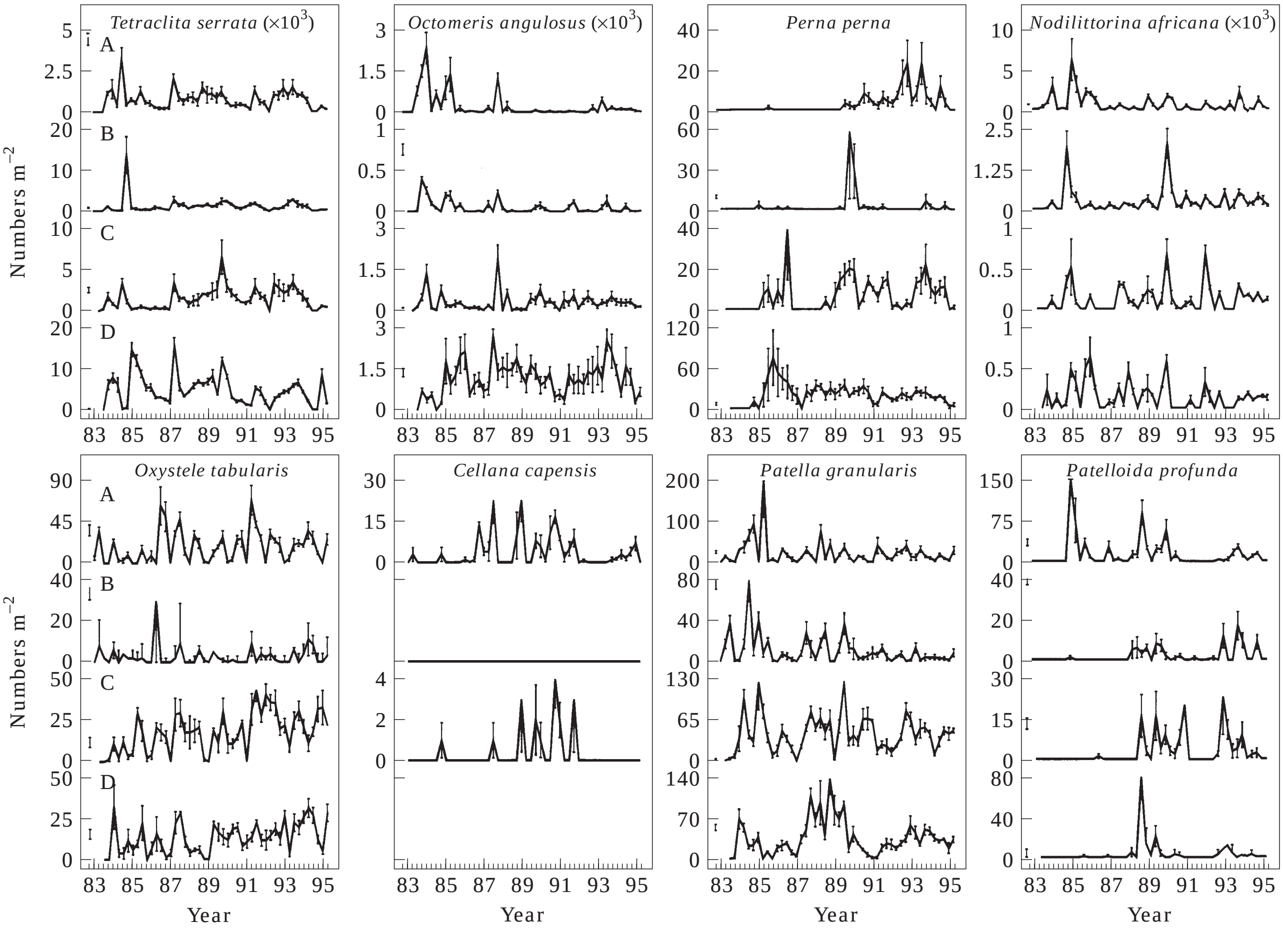

FIGURE 6. Long-term fluctuations in mean abundance (± SE) of the eight most common species following clearance in the Lower Balanoid zone at Mazeppa. (A, spring; B, summer; C, autumn; D, winter). Arrows at the start of each time series indicate initial abundances.

C. dentatus, *N. africana* and *C. capensis*. Approximately half of the species in the lower balanoid zones at Mazeppa, Dwesa and Mkambati showed significant correlations in temporal abundance. *T. serrata*, *C. dentatus* and *P. granularis* correlated most strongly across sites. There was no relationship between season of clearance and the degree of temporal correlation.

Pearson correlation coefficients for interspecific within-site comparisons of abundance time series from disturbed quadrats are given in Table 5. Although only 30% of possible correlations were significant, over 90% of these were positive. There was a tendency for species within areas cleared in summer to correlate less than those in areas cleared in other seasons. Barnacles correlated most often with other species in the lower balanoid zones at all sites, while in the upper balanoid zones at Dwesa and Mkambati, rock oysters and barnacles correlated most frequently with other species, particularly grazers. The same trend as in the undisturbed quadrats, namely that interspecific correlations were less common than intraspecific correlations, was evident in the cleared areas.

Intraspecific within-site Pearson correlation coefficients for comparisons between disturbed and undisturbed quadrats are given in Table 6. At all sites there was generally a high degree of correlation between species in cleared and uncleared quadrats. The highest degree of correlation (80%) was between the controls and areas cleared in spring, while the lowest (65%) occurred between controls and areas cleared in autumn.

The number of intraspecific correlations decreased logarithmically with increasing spatial scale ($y = 99{\cdot}87 - 83{\cdot}41\log_{10}x$; $r^2 = 0{\cdot}901$; $P \leq 0{\cdot}001$). As with the undisturbed quadrats, 76% of intraspecific correlations were significant on small scales. At larger scales of 10 m, however, 48% of intraspecific correlations were significant, while at scales of 10^4 m (between

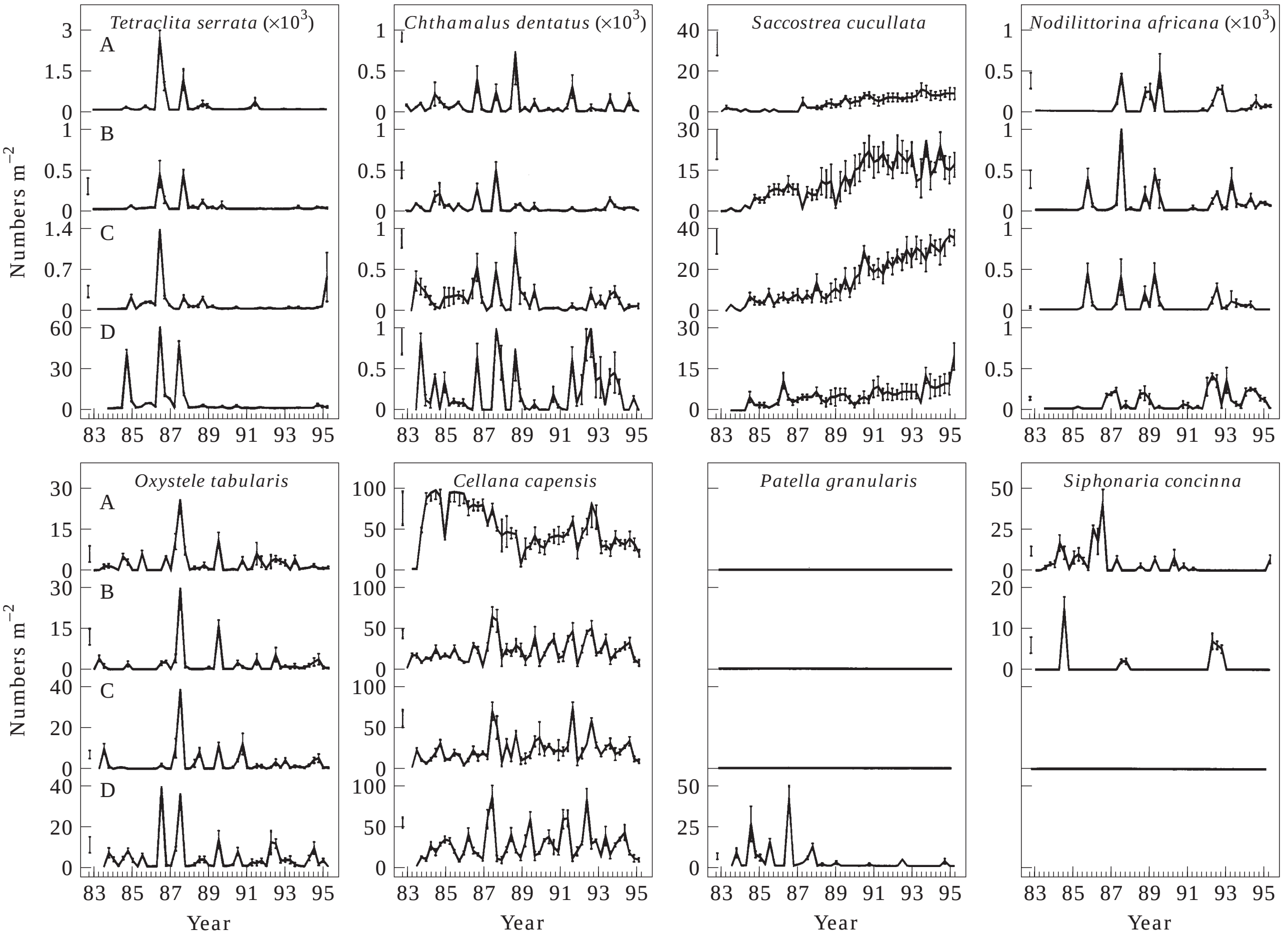

FIGURE 7. Long-term fluctuations in mean abundance (± SE) of the eight most common species following clearance in the Upper Balanoid zone at Dwesa. (A, spring; B, summer; C, autumn; D, winter). Arrows at the start of each time series indicate initial abundances.

juxtaposed sites), 30% were significant, and at 10^5 m (the geographic extremes), only 3% of correlations were significant.

As with undisturbed quadrats, percentage cover in cleared areas at all sites exhibited annual cycles, after an initial lag of varying duration. Areas cleared in autumn and winter also exhibited biennial cycles. Cover remained below the initial level in all treatments in the upper balanoid zone at Dwesa. Only in areas cleared in winter did cover approach the initial value, but even in this case, a subsequent decline was evident. At Mkambati, however, cover exceeded the initial level in all treatments in the upper balanoid zone, albeit after an initial delay of 3 years. From mid 1994, a sharp decline in cover was apparent. In general, areas cleared in the lower balanoid zones recovered more quickly and to a greater extent than those in the upper balanoid. An exception was the lower balanoid at Dwesa where cover only approached the initial level during the mid to late 1980s, thereafter declining to about half of the original level. Once again, a discontinuity around 1990 was evident in most of the time series.

Discussion

The mid-littoral zone of rocky shores on the east coast of South Africa is dominated, both numerically and spatially, by micro-algal grazers and filter-feeders (Dye, 1993*a*, 1995). Mid-shore macro-algal and mussel communities are absent. As a consequence of this, and the mild climate with relatively small seasonal changes, the dynamics of mid-shore populations would be expected to depend primarily on variations in larval supply. Autumn (March/April) and early winter (June/July) are the main periods of settlement for most of the intertidal species, and seasonal cycles tuned to these periods would therefore comprise a large proportion of the high frequency signal in long time series of abundance. That this is indeed the case,

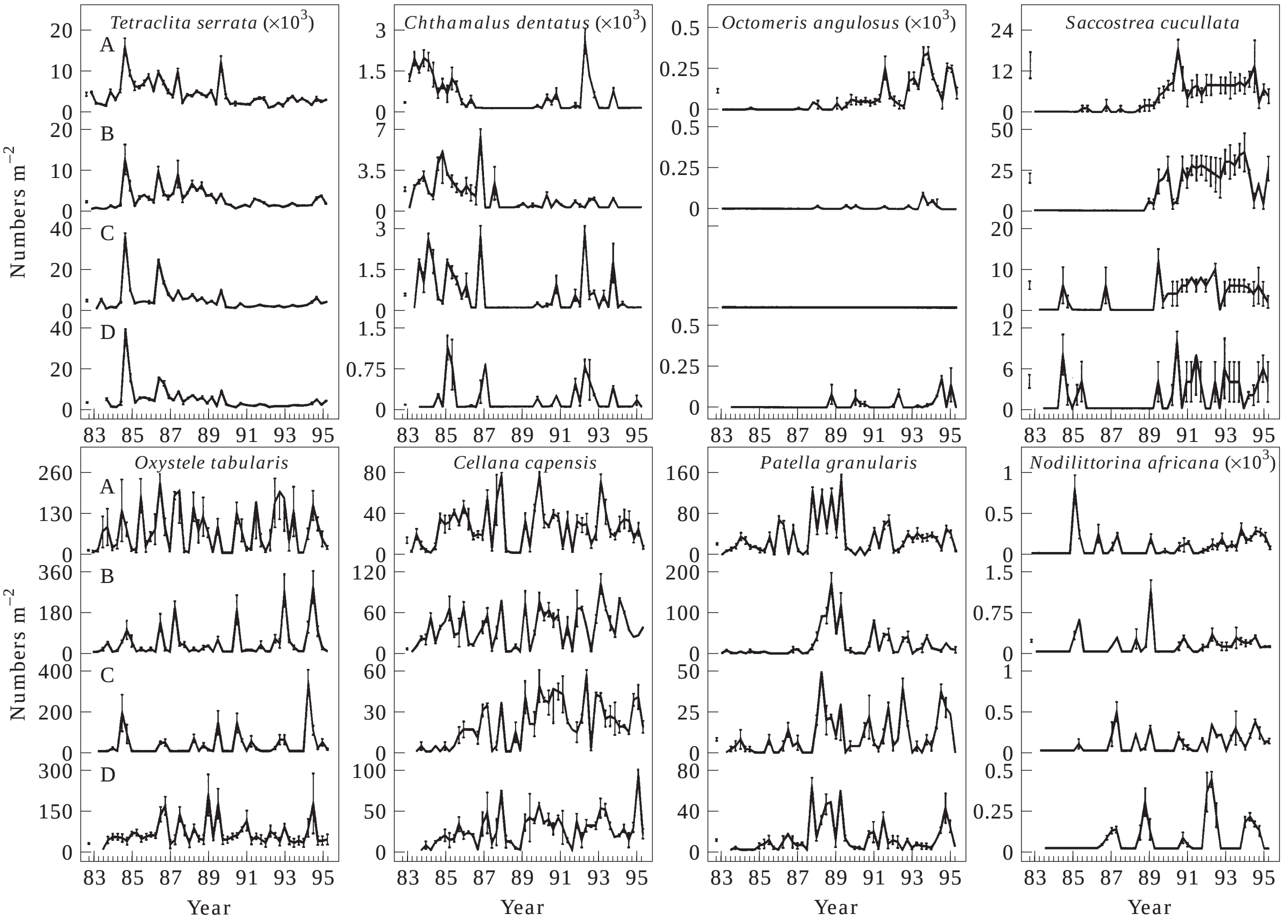

FIGURE 8. Long-term fluctuations in mean abundance (± SE) of the eight most common species following clearance in the Lower Balanoid zone at Dwesa. (A, spring; B, summer; C, autumn; D, winter). Arrows at the start of each time series indicate initial abundances.

even at large spatial scales, is therefore no surprise. What is surprising and less easy to explain are the significant biennial cycles of abundance characteristic of many of the time series. For short-lived species, such as limpets and littorinids, for which the life span is 2–3 years, these cycles are probably a superposition of recruitment and mortality cycles which are at times constructive and at others destructive, but which, over the long-term, resonate with a period of approximately 2 years. For longer lived species, such as barnacles and particularly rock oysters, which may live for up to 20 years (Dye, 1989), biennial cycles are less clear or absent. Instead, a variety of longer-term cycles from 4 to 8 years or more may be evident. While the same explanation could be invoked in this case, the relatively short length of the time series makes it difficult to establish the significance of longer cycles (Jassby & Powell, 1990) and precludes further development of this idea.

The presence of abrupt changes in abundance or variability which persist for varying periods of time, may shed light on the underlying interactions between species. The fact that different species are involved and that the fluctuations occur, if not simultaneously then within a narrow time period across sites, suggests an extrinsic cause. The first event, which occurred in early 1985, was characterized by a significant decline in the abundance of the limpet *C. capansis*. This coincided with a decline in the abundance of *T. serrata* and was followed soon thereafter by increases in the abundance of *C. dentatus* and *S. cucullata*. A similar event of greater magnitude occurred between mid 1989 and mid 1990. Unfortunately, in the absence of additional environmental data for this area, it is impossible to say what could have caused the decline in limpets at these times. As all of these species have a planktonic phase in their life cycle and all breed at approximately the same time, it is unlikely that variation in larval supply was the cause, as this would presumably have affected all the species in the same way, either enhancing recruitment or reducing it.

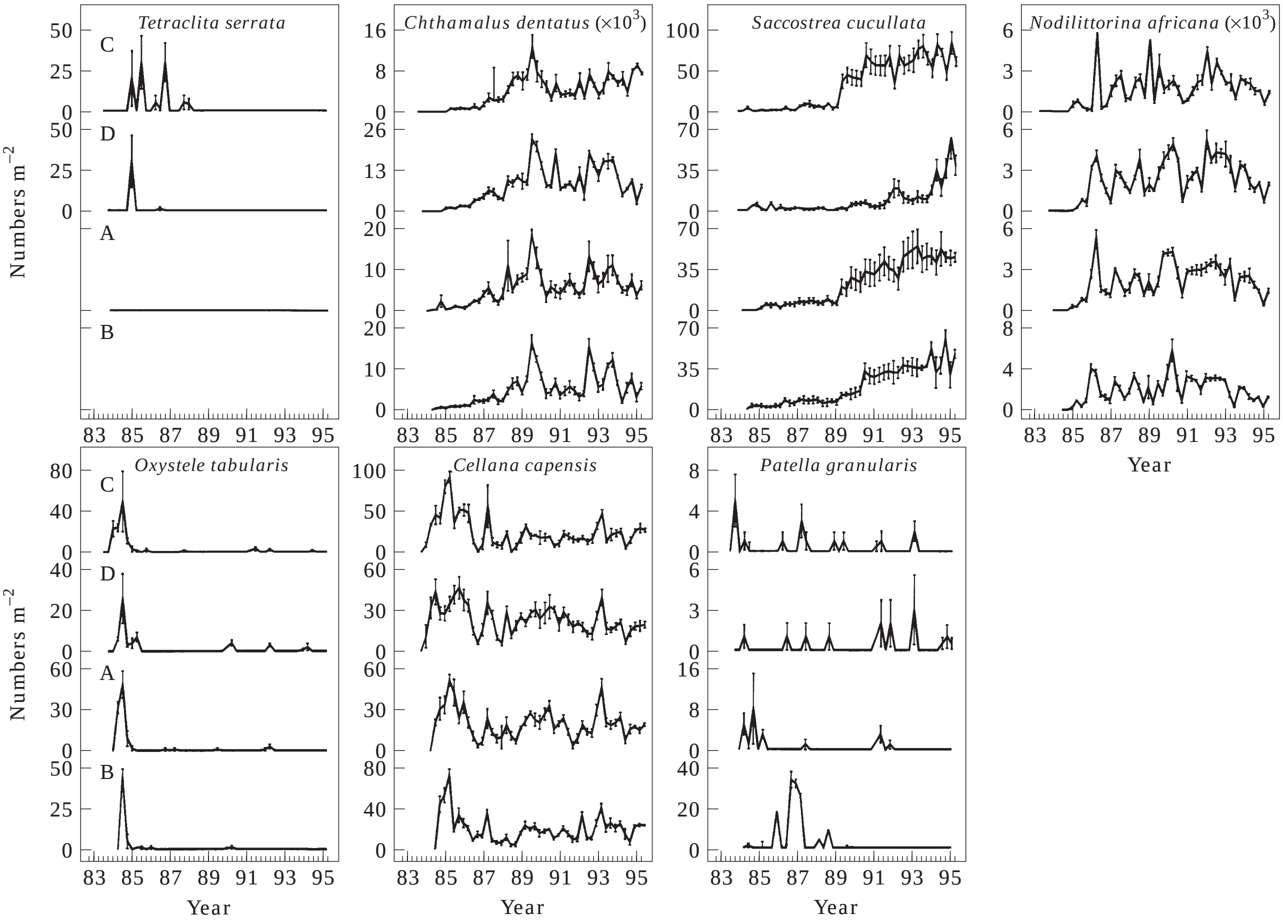

FIGURE 9. Long-term fluctuations in mean abundance (± SE) of the seven most common species following clearance in the Upper Balanoid zone at Mkambati. (A, spring; B, summer; C, autumn; D, winter). Arrows at the start of each time series indicate initial abundances.

These examples of sudden changes in abundance with persistent effects must be seen against the background of long-term changes in the species composition of grazers and sessile filter-feeders. *C. capensis*, for example, decreased in abundance by 80–90% between 1983 and 1996, while *P. granularis* decreased by between 50 and 90% over the same period. Only at one site was there an increase in the abundance of this species. Even more striking were the increases in *N. africana* of between 2- and 100-fold over the 13-year period.

There are two explanations which may account in part for the apparent relationship between the decline in abundance of limpets and subsequent fluctuations in the abundance of other species. Firstly, it is known that limpets can affect barnacle recruitment by ‘ bulldozing ’ new recruits off the rock while grazing (Denley & Underwood, 1979; Branch, 1981; Hawkins, 1983). While a decline in the number of limpets and their possible bulldozing effect could account for the increase in *C. dentatus*, and possibly *S. cucullata*, it is difficult to see how this could account for a decline in *T. serrata*. An alternative explanation is that the decline in limpet numbers, and hence grazing pressure, could have altered the composition and abundance of micro-flora in such a way as to inhibit the recruitment of *T. serrata*. A number of studies have shown that reducing the grazing pressure of limpets results in increased abundance of micro- and macro-algae (Jones, 1948; Southward, 1964; Hawkins, 1981; Underwood, 1980; Bertness *et al.*, 1983; Levings & Garrity, 1984; Dye & White, 1991; Dye, 1995). Total elimination of grazers is unusual in natural situations and it may be that subtle changes in the biofilm covering the rock surface favoured one barnacle over the other, resulting in the observed species replacement. It is, of course, possible that changes in the micro-flora occurred first, causing a decrease in grazers with subsequent effects on other species. The increase in *N. africana* noted above may

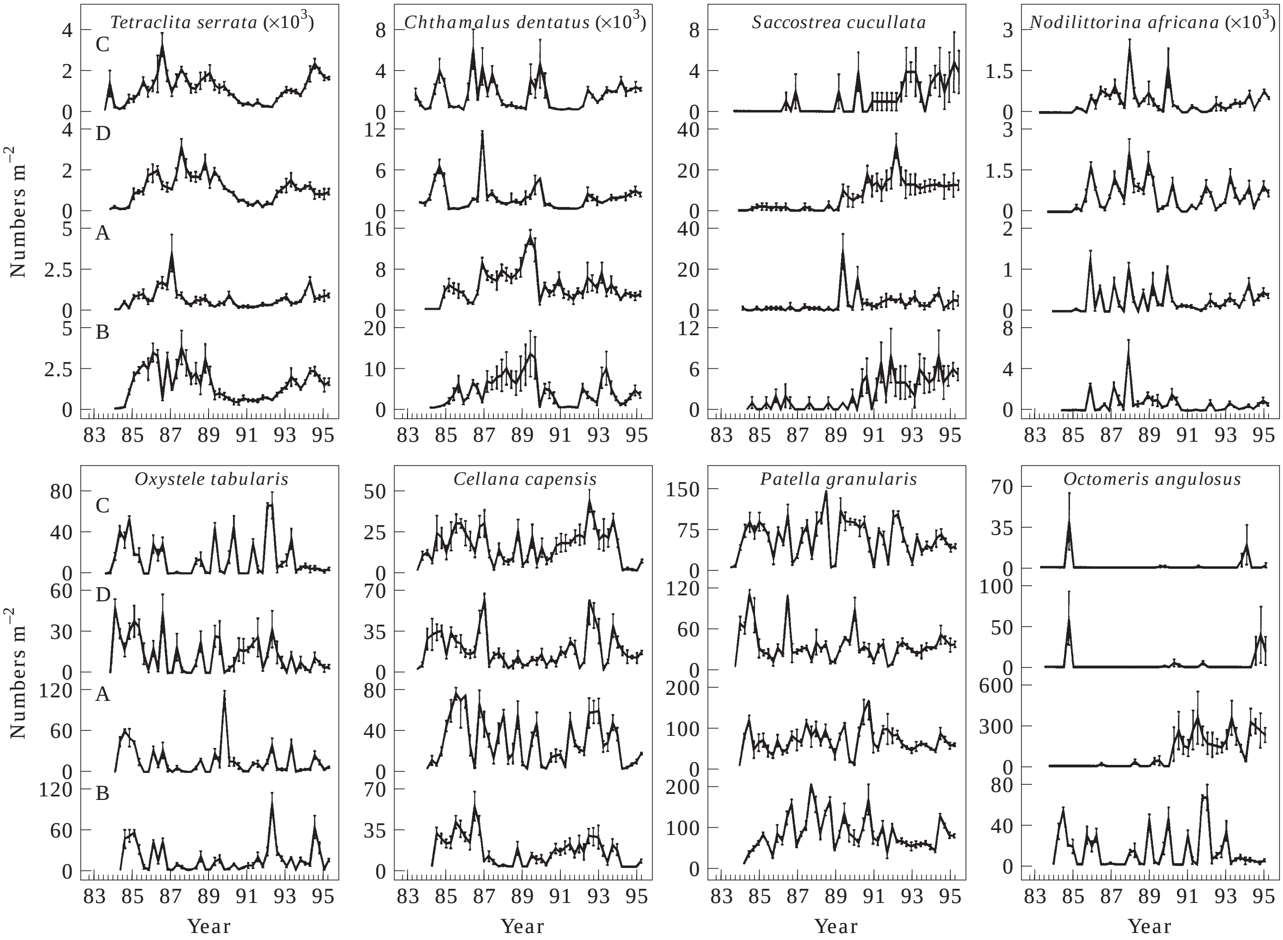

FIGURE 10. Long-term fluctuations in mean abundance (± SE) of the eight most common species following clearance in the Lower Balanoid zone at Mkambati. (A, spring; B, summer; C, autumn; D, winter). Arrows at the start of each time series indicate initial abundances.

result from the increase in abundance of *C. dentatus* and *S. cucullata*, both of which seem to be associated with large numbers of juveniles of this species. Since *N. africana* migrate upshore as they grow, this could explain the temporal increase in abundance of this species on the high shore.

Discontinuities in the time series were often followed by changes in the variability of grazer populations. In some cases, interannual fluctuations were reduced and populations appeared to be more stable, while the opposite occurred in other cases. The variance of population estimates also changed following discontinuities, a fact that can be accounted for by the well-known direct relationship between mean and variance (McArdle *et al.*, 1990).

While the temporal dynamics of many species are similar at scales of 100 km or more, there are still substantial differences between sites in both absolute abundance and proportional changes in abundance over time. These differences arise from a variety of sources, such as variations in settlement and recruitment (Kendall *et al.*, 1982, 1985; Connell, 1985; Gaines *et al.*, 1985; Raimondi, 1990), differences in the degree of competition, local disturbances and space occupancy (Dayton, 1971), and the density of existing populations (Dye, 1990, 1992*b*, 1993*b*). It would be expected that the high frequency spectra of time series derived from adjacent populations will correlate more strongly than with those from more distant populations, and that the degree of correlation will be higher between conspecifics from adjacent areas. The extent to which this occurs, however, may depend on coastal topography. In a study of settlement dynamics of *Balanus balanoides* Kendall *et al.* (1982) found high correlations (± 0·80) in settlement between sites on the relatively straight North Yorkshire coast of England compared to very low correlations, except at nearby sites, on the incised west coast of Scotland. In studies of barnacle abundance at eleven sites in the Transkei region on the east coast of

TABLE 3. Pearson correlation coefficients for intraspecific comparisons of abundance time series ($\log_{10}(x+1)$) between disturbed quadrats within the Lower Balanoid (LB) zone at Mazeppa and within the Upper Balanoid (UB) and Lower Balanoid (LB) zones at Dwesa and Mkambati

Seasonal comparisons	Sp/Su	Sp/Au	Sp/Wi	Su/Au	Su/Wi	Au/Wi
Mazeppa	$n=53$	52	51	52	51	51
T. serrata (LB)	0·764	0·826	0·817	0·846	0·884	0·869
O. angulosus (LB)	0·530	0·475	NS	NS	NS	0·535
P. granularis (LB)	NS	0·461	NS	NS	NS	0·623
O. tabularis (LB)	NS	0·520	NS	0·520	0·550	0·752
N. africana (LB)	0·295	0·605	0·658	0·661	NS	0·650
P. profunda (LB)	0·511	NS	0·495	0·572	0·465	0·668
P. perna (LB)	NS	0·480	NS	0·487	NS	0·524
C. capensis (LB)	NS	0·647	NS	NS	NS	NS
Dwesa						
T. serrata (UB)	0·704	0·560	0·525	0·743	0·516	0·549
O. tabularis (UB)	0·596	0·579	0·599	0·689	0·563	0·575
N. africana (UB)	0·676	NS	0·678	0·755	0·697	0·338
S. cucullata (UB)	0·583	0·689	0·532	0·892	NS	0·851
C. dentatus (UB)	0·592	0·473	NS	0·595	NS	0·554
C. capensis (UB)	0·557	0·575	0·511	0·719	0·688	0·784
T. serrata (LB)	0·586	0·607	0·597	0·721	0·795	0·831
O. tabularis (LB)	0·699	0·485	0·687	0·539	0·511	0·585
N. africana (LB)	0·801	0·730	NS	0·841	NS	NS
C. dentatus (LB)	0·664	0·757	NS	0·600	0·271	0·485
C. capensis (LB)	0·773	0·589	0·687	0·564	0·507	0·648
P. granularis (LB)	0·636	0·378	NS	0·611	0·611	0·508
N. africana (LB)	0·801	0·730	NS	0·841	NS	NS
O. angulosus (LB)	0·644	NS	NS	NS	0·238	NS
S. concinna (LB)	NS	NS	NS	0·862	NS	NS
Mkambati	$n=50$	49	48	49	48	48
O. tabularis (UB)	0·666	0·777	0·584	0·739	0·583	0·706
S. cucullata (UB)	0·725	0·938	0·916	0·723	0·808	0·955
C. dentatus (UB)	0·946	0·840	0·854	0·855	0·881	0·981
C. capensis (UB)	0·659	0·635	0·579	0·822	0·667	0·776
T. serrata (LB)	0·814	0·763	0·741	0·901	0·923	0·929
O. tabularis (LB)	0·691	0·843	0·537	0·829	0·514	0·587
C. dentatus (LB)	0·764	0·339	0·531	NS	0·556	0·851
C. capensis (LB)	0·670	0·727	0·784	0·678	0·623	0·626
S. cucullata (LB)	0·628	0·635	0·578	0·824	0·813	0·648
P. granularis (LB)	0·785	0·632	0·511	0·722	0·567	0·782

NS, not significant ($P \leq 0{\cdot}01$). Season of clearing: Sp, spring; Su, summer; Au, autumn; Wi, winter.

South Africa, which is characterized by numerous embayments and headlands, Dye (1992*b*, 1993*b*) found that recruitment was related to adult population size and concluded that larval dispersal was localized and limited by the topography of the coastline. With increasing scale on rugged coastlines, there should therefore be rapid attenuation in the degree of correlation of temporal variability both within and between species. This is supported by the results of the present study in which a 50% decrease in correlation at scales of 10–100 km compared with 1–10 m was found, thus disproving the original hypothesis of no correlation. Given this, it is clear that only large-scale forcing variables, such as winds, rainfall, and insolation, will affect all sites simultaneously. Further analyses of the time series in relation to data on these factors should reveal the extent to which they influence intertidal population dynamics.

The above discussion has focussed on the dynamics of mid-shore populations in undisturbed areas and provides a background against which to interpret the effects of experimental disturbance. Apart from one or two exceptions (*S. cucullata* and *P. perna*), the time series from disturbed areas, following an initial 2-year recovery period, are similar to those from undisturbed areas. Comparable cycles and discontinuities are evident and yet there are subtle differences. One explanation for this is that grazers did not exhibit the same

TABLE 4. Pearson correlation coefficients for intraspecific between-site comparisons of abundance time series ($\log_{10}(x+1)$) from disturbed quadrats

Species	Lower Balanoid MZ *vs* DW[a]	Lower Balanoid MZ *vs* MK[b]	Lower Balanoid DW *vs* MK[b]	Upper Balanoid DW *vs* MK[b]
T. serrata				
Sp	0·448	0·726	NS	NS
Su	0·686	0·679	NS	NS
Au	0·667	NS	NS	NS
Wi	0·810	NS	NS	NS
N. africana				
Sp	NS	NS	NS	0·334
Su	0·383	NS	NS	NS
Au	NS	NS	NS	0·408
Wi	NS	NS	NS	0·411
O. tabularis				
Sp	NS	NS	0·357	NS
Su	NS	NS	NS	NS
Au	NS	NS	NS	NS
Wi	NS	NS	NS	NS
C. capensis				
Sp	NS	NS	NS	0·425
Su	NS	NS	NS	NS
Au	NS	NS	NS	0·472
Wi	NS	NS	0·284	0·653
P. granularis				
Sp	NS	NS	NS	NS
Su	NS	NS	NS	NS
Au	NS	0·617	NS	NS
Wi	NS	NS	0·466	NS
C. dentatus				
Sp			NS	0·574
Su			NS	0·392
Au			0·549	NS
Wi			NS	NS

[a] Sp: $n=54$; Su: $n=53$; Au: $n=52$; Wi: $n=51$.
[b] Sp: $n=51$; Su: $n=50$; Au: $n=49$; Wi: $n=48$.
MZ, Mazeppa; DW, Dwesa; MK, Mkambati. NS, not significant ($P \leq 0{\cdot}01$). Seasons of clearance: Sp, spring; Su, summer; Au, autumn; Wi, winter.

decrease in abundance characteristic of undisturbed areas. In fact grazer abundance was often higher in cleared areas and in many cases remained so throughout the study. The exception was at Mkambati where low-shore grazer abundance was the same in each treatment. Increased space for grazing probably contributed to the increased abundance of grazers, which in turn may explain the lower number of barnacles present in cleared areas compared with controls. This effect is striking and even at the end of the study, the cleared areas were still visually different from undisturbed areas.

Studies on the long-term effects of disturbances such as oil spills have shown that recovery usually requires a period of time longer than the longevity of the key species (Southward, 1976). With the exception of the rock oyster *S. cucullata* (Dye, 1989), all of the species in the present study have average life spans of less than 5 years and so at least two generations of organisms have recruited and died during the study. The fact that convergence to the undisturbed state has not yet occurred indicates that the initial disturbance has in some fundamental way altered the dynamics of the system on both the species and community level (Dye, unpubl. data), disproving the original hypothesis of rapid convergence.

Although recolonization was fairly rapid in most cases, the season of clearance had subtle and long-lasting effects on cleared areas. Given that peak recruitment is in early winter, it is not surprising that recovery was fastest in areas cleared at this time, as replacement of lost organisms would have occurred almost immediately, compared with at least a 6-month delay in areas cleared in spring. During this

TABLE 5. Pearson correlation coefficients for interspecific within-site comparisons of abundance time series ($\log_{10}(x+1)$) from disturbed quadrats in the Lower Balanoid (LB) zone at Mazeppa and in the Lower Balanoid (LB) and Upper Balanoid (UB) zones at Dwesa and Mkambati. Only significant correlations ($P \leq 0{\cdot}01$) for which $r \geq |0{\cdot}500|$ are shown

Species comparisons		Correlation coefficient *r*
Mazeppa LB		
Summer ($n=53$)	*O. angulosus* : *P. perna*	0·544
Winter ($n=51$)	*O. angulosus* : *P. perna*	0·723
Dwesa UB		
Spring ($n=54$)	*S. cucullata* : *S. concinna*	−0·602
	O. tabularis : *N. africana*	0·534
Autumn ($n=52$)	*S. cucullata* : *C. capensis*	0·633
Winter ($n=51$)	*T. serrata* : *S. cucullata*	0·500
	T. serrata : *C. capensis*	0·644
	S. cucullata : *N. africana*	0·565
	S. cucullata : *C. capensis*	0·624
Dwesa LB		
Summer ($n=53$)	*C. dentatus* : *S. concinna*	0·504
Winter ($n=51$)	*T. serrata* : *C. capensis*	0·500
Mkambati UB		
Spring ($n=51$)	*C. dentatus* : *O tabularis*	0·622
	C. dentatus : *N. africana*	0·968
	O. tabularis : *N. africana*	−0·633
Summer ($n=50$)	*C. dentatus* : *S. cucullata*	0·753
	C. dentatus : *C. capensis*	0·546
	C. dentatus : *N. africana*	0·825
	S. cucullata : *N. africana*	0·802
	S. cucullata : *O. tabularis*	−0·506
	O. tabularis : *N. africana*	−0·621
Autumn ($n=49$)	*C. dentatus* : *S. cucullata*	0·793
	C. dentatus : *C. capensis*	0·661
	C. dentatus : *N. africana*	0·832
	S. cucullata : *N. africana*	0·713
Winter ($n=48$)	*C. dentatus* : *N. africana*	0·904
	C. dentatus : *S. cucullata*	0·748
	C. dentatus : *O. tabularis*	−0·747
	S. cucullata : *N. africana*	0·665
	O. tabularis : *N. africana*	−0·712
Mkambati LB		
Spring ($n=51$)	*C. dentatus* : *P. granularis*	0·545
	P. granularis : *O. tabularis*	0·573
Summer ($n=50$)	*T. serrata* : *C. dentatus*	0·686
	T. serrata : *P. granularis*	0·508
Autumn ($n=49$)	*T. serrata* : *C. dentatus*	0·707
	T. serrata : *P. granularis*	0·656
	C. dentatus : *P. granularis*	0·548
Winter ($n=48$)	*P. granularis* : *O. tabularis*	0·596

TABLE 6. Pearson correlation coefficients for intraspecific within-site comparisons of abundance time series ($\log_{10}(x+1)$) from disturbed with those from undisturbed quadrats in the Lower Balanoid (LB) zone at Mazeppa and in the Lower Balanoid (LB) and Upper Balanoid (UB) zones at Dwesa and Mkambati. Only significant correlations ($P \leq 0{\cdot}01$) for which $r \geq |0{\cdot}500|$ are shown

Disturbed *vs* undisturbed		Correlation coefficient *r*
Mazeppa LB		
Summer ($n=53$)	*N. africana*	0·642
	O. tabularis	0·500
Winter ($n=51$)	*P. perna*	0·503
Dwesa LB		
Spring ($n=54$)	*P. granularis*	0·693
	O. tabularis	0·552
	N. africana	0·720
Summer ($n=53$)	*P. granularis*	0·553
	O. tabularis	0·582
	N. africana	0·718
Autumn ($n=52$)	*N. africana*	0·647
Winter ($n=51$)	*O. tabularis*	0·528
Mkambati UB		
Spring ($n=51$)	*C. dentatus*	0·857
	S. cucullata	0·719
	N. africana	0·874
Summer ($n=50$)	*C. dentatus*	0·825
	S. cucullata	0·668
	N. africana	0·879
Autumn ($n=49$)	*C. dentatus*	0·801
	S. cucullata	0·654
	N. africana	0·891
Winter ($n=48$)	*C. dentatus*	0·798
	S. cucullata	0·613
	N. africana	0·884
Mkambati LB		
Spring ($n=51$)	*T. serrata*	0·515
	C. dentatus	0·820
	C. capensis	0·593
	O. tabularis	0·704
	P. granularis	0·680
	S. cucullata	0·576
Summer ($n=50$)	*C. dentatus*	0·606
	S. cucullata	0·771
	O. tabularis	0·579
Autumn ($n=49$)	*S. cucullata*	0·601
	O. tabularis	0·624
Winter ($n=48$)	*C. dentatus*	0·627
	S. cucullata	0·734
	C. capensis	0·530

delay, any number of factors could have altered the conditions necessary for successful settlement and recruitment, particularly of sessile species. One interesting effect of spring/summer clearing was the substantial decrease in biennial cycles in subsequent time series of abundance. The persistence of this effect is striking and suggests that the system is unable to ‘ reset ’ following a disturbance if it should occur outside the main recruitment period. Populations which returned after clearing tended to exhibit greater interannual variability than those in undisturbed areas, although this did not appear to be related to season of clearance. This and the previous observation suggest that populations in the disturbed areas are less stable than their undisturbed counterparts and a more detailed analysis of the underlying dynamics of the undisturbed populations has confirmed this (Dye, unpubl. data).

As with undisturbed areas there were also considerable differences between sites in abundance and proportional change in abundance in areas that had been cleared. This resulted once again in a rapid attenuation of intra- and interspecific correlation at larger spatial scales. In this case, however, the attenuation was more rapid than in the undisturbed areas, possibly reflecting the relative instability of populations in disturbed areas.

While changes affecting short-lived species may disappear rapidly unless reinforced, those which affect long-lived species can persist for several years. During this time, the system may be susceptible to other factors which may not have had significant effects previously. For example, an increase in the cover of barnacles will reduce space for grazing by limpets and lead to long-term changes in the composition of micro-flora and primary production. Although many of the consequences of a particular change, whether natural or experimentally induced, may be predictable, the ultimate cause of the natural changes themselves usually are not. It may, however, be possible to improve this situation by meta-analyses of data from wide geographic scales. More information is required on meteorological and oceanographic factors to establish the linkages between atmosphere, ocean and intertidal zone necessary to permit reasonable predictions of events that may affect intertidal populations.

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