

Spatial synchrony of population changes in rocky shore communities in Shetland

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ABSTRACT:

Rocky shore monitoring around the Sullom Voe Oil Terminal in Shetland has produced a 20-year dataset of population fluctuations for 40-plus species at 15 to 20 sites separated by distances up to 30km. Synchrony in population changes was quantified by correlation among series of abundance categorised on quantitative scales. Two periods were analysed separately, pre- and post-1992, following changes in methods and extent of monitoring. Positive average correlations among sites were found for 10 out of 16 species pre-1992 and for 23 out of 26 post-1992, statistically significant for 4 and 8 species for the two periods respectively. The intertidal barnacle *Semibalanus balanoides* showed most synchrony among sites for both periods, while dogwhelks *Nucella lapillus* and macroalgae (*Fucus vesiculosus*, *F. serratus*, *Mastocarpus stellatus*) had very low average correlations among sites. *Littorina saxatilis* was the only other species with significant positive correlation among sites in both periods. Corallinaceae, *Verrucaria maura* and *V. mucosa*, and *Littorina neglecta* were less synchronised pre-1992 than post-1992, while *Littorina obtusata* showed less synchrony post-1992.

Differences in reproductive biology and ecology failed to explain patterns of synchrony among species. Species with planktonic larvae were no more likely to be synchronised than those without. There was a tendency for species living higher on the shore to be more synchronised post-1992, but species predominant on wave-exposed shores were no more synchronous than sheltered-shore species. The more synchronised species in this study need to be monitored at relatively few sites to detect change, whereas more sites may be needed for species where change occurs

on a local scale. Population synchrony also suggested usefulness of species as indicators of large-scale change: the barnacle *Semibalanus balanoides* is the best indicator among species in the study area.

KEY WORDS: Population synchrony, Rocky shore communities, monitoring methods.

INTRODUCTION

While explicit studies of population synchrony in marine species have been rare (but see Higgins et al. 1997), rocky shore ecologists have long been aware of the spatial scale of temporal changes in intertidal communities. Spatial scales of change have emerged from long-term monitoring of intertidal biota at yearly and less frequent intervals. Although examples of such studies are well known and the causes of patterns well understood, no particular scales of change have emerged that are consistent among taxa. For example, changes in barnacle populations in southwest England from abundant *Semibalanus balanoides* in the 1930s to predominantly *Chthamalus stellatus* in the 1950s were found to extend over a broad area of western Britain and Ireland (Southward & Crisp 1954, 1956). Subsequent changes were closely associated with changes in temperature (Southward 1967, 1980, 1991, Southward et al. 1995). The 'Torrey Canyon' oil spill and cleanup caused another broad-scale community-level change (Southward & Southward 1978, Hawkins & Southward 1992) in the same region. Both these examples suggest large-scale synchrony of community change. On Australian shores, in contrast, changes

in algae on the low and mid shore appear idiosyncratic (Chapman & Underwood 1998, Underwood & Chapman 1998), with no two sites showing similar changes. In South Africa, however, some similarities in long-term trends have been seen among sites separated by up to 240km (Dye 1998a). In the latter study, and some others (Kendall et al. 1985, Svane 1984) the degree of similarity in temporal change among sites was determined by correlation among time series. The use of correlation to determine spatial synchrony in population changes among spatial networks of sites has been the focus of many recent studies (see Koenig 1999 for review). Such studies address the nature of the pattern of response over a geographical scale rather than the environmental factors producing change, and may cast new light on studies of long-term change in marine communities. Not least, the method offers an objective index of synchrony that may be compared among different taxa and spatial scales.

There are thought to be two major causes of spatial synchrony in populations (Koenig 1999, Ranta et al. 1995, 1997). The first is when a spatially autocorrelated density-independent factor ('disturbance') synchronizes fluctuations that are controlled by a common density-dependent structure (the 'Moran effect', Moran 1953, Ranta et al. 1997). The second is dispersal between neighbouring areas. Dispersal makes synchrony decline with distance in a way that depends on the scale of dispersal (Bjørnstad & Bolker 2000). Another possible cause of synchrony may be roaming predators that switch between areas with high densities of prey (Koenig 1999).

Notwithstanding the causes, the degree of synchrony among spatially separate populations has obvious consequences for environmental monitoring. Where

population changes occur simultaneously over a broad spatial scale, just one or two monitoring sites will indicate the status of the entire area. Where synchrony is limited to areas within sites or to closely grouped sites, a broad spatial network of monitoring sites will be needed to determine the status of species over a wide area.

Regular monitoring of rocky shore populations in and around Sullom Voe, Shetland has provided the opportunity to access long time series of population changes for a spatial network of monitoring sites. After early broad-scale surveys starting in 1976 (Hiscock 1981), the present set of 15 core sites have been surveyed every year since 1981 (Fig. 1). Another 5 sites were added in 1993 that were beyond 10km from the Terminal to aid discrimination of changes in the vicinity of the potential impact sites from those occurring over a broader geographical scale. The survey methodology involved assigning abundance of the conspicuous species to logarithmic or semi-logarithmic categories. Precision was thereby sacrificed to allow typically 30 to 50 species to be assessed at five shore levels at each site, yet producing data that is still amenable to numerical analysis. The resulting data set is an unparalleled collection of spatially referenced time series of abundance for a broad range of contrasting species.

In this study we analyse the Sullom Voe rocky shore survey data for synchrony of population changes in a wide range of contrasting species. Established information on biology and dynamics of populations of the species involved can be used with the synchrony measured here to deduce the most likely causes. Consequences for monitoring rocky shore communities are discussed.

METHODS

Field surveys

Sites were originally chosen to detect change in rocky shore communities around the Oil Terminal in Sullom Voe (Fig. 1). After a survey of many sites over a broad geographical area (Hiscock 1981), a core set of 15 sites around the Terminal were chosen for annual monitoring in August of each year. This core set of sites was visited from 1981 until 1992. Reconsideration of the power of the sampling scheme to detect and discriminate natural from anthropogenic change (at the Terminal) led to the addition of more distant sites to the core set (Fig. 1). It was felt that the concentration of effort less than 10km distant from the potential source of effects was not the best use of resources, given that no sites could be considered as control sites in a before-after control-impact design (Underwood & Peterson 1988). The full set of 15 core sites and 5 reference sites was visited yearly from 1993 to 2000.

Each site survey consisted of a fixed transect relocated in the same position each year (Moore et al. 1995). Stations were set up along the transect line at 20cm vertical intervals. The abundance of the major animal and plant species were estimated at five of these stations at each site, lower shore (LS), lower middle shore (LMS), middle shore (MS), upper middle shore (UMS) and upper shore (US), corresponding approximately to MLWS, MLWN, MTL, MHWN and MHWS. Before 1992, abundances were also recorded at every 20cm interval on the transect line.

Abundance was scored on seven-point scales of abundance appropriate to each taxon (Hiscock 1981, modified from Crisp & Southward 1958, Table 1). These scales provide rapid estimates of population density based on limited quadrat counts.

Category intervals are similar on logarithmic scales, and are sufficiently well spaced to be not easily misjudged. Use of these scales by different workers during different phases of the study may have contributed to some variability in abundance estimates. Such effects have not been accounted for in subsequent analyses.

Data analysis

As a result of the added sites and the reduced number of stations per site from 1993, the time series was divided into two periods for analysis: 1981 to 1992 and 1993 to 2000. All abundance scores were replaced by the mid-point value on the appropriate scale (Table 1). Thus a score of 'Common' for barnacles, corresponding to 10-99 per 0.01m², was converted to a value of 50 per 0.01m². These values were converted log base 10. Where abundance was zero for a station at a site in a particular year this was interpreted either as absence if the species were found at other stations at the site, or as a missing value if the species were not recorded at all at the site on that visit. Absence was valued as a population density an order of magnitude less than the minimum defined in the appropriate scale. Average log-transformed abundance was calculated over all five shore levels at each site to provide a single time series for each species at the site.

Selection of species for analysis of spatial synchrony depended on two criteria: that the species were sufficiently ubiquitous (present at > 75% of sites), and was recorded in at least half the years surveyed. Twenty-six species met these criteria for the period 1993 to 2000, while 16 qualified for the period 1981 to 1992.

Synchrony was quantified by correlation among all the time series for each species. The effects of distance on synchrony were determined by linear regression

of correlation coefficients on the distance between each site. Because the same sets of data were used many times in calculations, the correlation coefficients could not be considered to be independent of each other. This non-independence of data invalidated standard statistical tests of significance. Therefore, as in similar studies (Paradis et al. 2000, Swanson & Johnson, 1999), for each species the statistical significance of the average correlation among sites and the linear regression coefficient of correlation on distance were determined using bootstrap methods (Efron & Gong, 1983). Selecting 20 sites from the original set with replacement produced a bootstrap sample of the original 20 sites. Correlation coefficients between sites in the bootstrap sample were used to calculate an average correlation and a linear regression of correlation versus distance. This process was repeated 500 times for each species and time period. The mean and standard error of the resulting 500 values of correlation and regression coefficients were used in *t*-tests to determine whether mean values were significantly different from zero.

RESULTS

For the period from 1981 to 1992, 10 of the 16 species had positive average coefficients of correlation among sites (Table 2) with 4 significant values. For 1993 to 2000, 23 out of 26 species had positive average correlation coefficients, of which 8 were significantly different from zero.

Four taxa showed much greater synchrony among sites in the 1990s than in the 1980s: Corallinaceae, *Verrucaria maura* and *V. mucosa*, and *Littorina neglecta*, while *Littorina obtusata* showed less synchrony in the 1990s than in the 1980s. The remaining taxa had consistent levels of synchrony in both decades. *Semibalanus*

balanoides, the dominant barnacle species in the area, showed the strongest synchrony of all species in both the 1980s and 1990s with averages significantly different from zero in both periods. The degree of synchrony is evident from plots of time series from a subset of the sites. Abundance of *S. balanoides* declined to and increased from a minimum in 1993 at all sites (Fig. 2a). *Littorina saxatilis* was the only other taxon with significant positive averages in both periods (Fig. 2b), with maxima at a number of sites evident in the late 1980s and again in the mid 1990s. Adult limpets (*Patella* sp.) were intermediate in the strength of synchrony, with little evidence for clear changes across all sites, albeit with a slight increase from 1980s to 1990s (Fig. 2c). The pattern of changes in abundance of *L. obtusata* showed similar maxima and minima to that of *L. saxatilis* (Fig. 2d).

Several species showed low or no apparent overall correlation among sites. Dogwhelks, *Nucella lapillus*, and the algae *Fucus vesiculosus*, *F. serratus* and *Mastocarpus stellatus* had very low average correlation coefficients. As expected, for these species no changes in abundance over time were discernible that were common to all sites (Figs. 2e, 2f).

Synchrony in population changes was expected to decline with the distance separating the sites compared. A declining trend in synchrony with distance was indeed evident in the most synchronised species, *Semibalanus balanoides* (Fig. 3). However, none of the bootstrap estimates of regression slope were significantly different from zero, out of the 16 and 26 calculated for 1981-1992 and 1993-2000 periods respectively. Neither was there a tendency for regression slopes to be

negative. Ten regression slopes out of 16 for 1981-1992 and 10 of 26 for 1993-2000 were negative, frequencies not significantly different from an expectation of 50:50.

Associations of synchrony with species characteristics

The association of species synchrony with species abundance, aspects of vertical distribution, whether animal or plant species, and approximations of the length of dispersal phase effects was measured by simple correlation (Table 4). Taking the average correlation across the range of sites as the measure of synchrony, it can be seen that species present at more sites in more years were more likely to have larger average correlation. The duration of the larval phase had no significant consistent effect on synchrony for the whole set of species. Some species with planktonic larvae showed very little synchrony (*Littorina littorea*) while others (*S. balanoides*) were strongly synchronised. Animals were more synchronised than plants during the 1980s, but this effect was not seen in the second time period.

In the second time period, species living higher on the shore, with a greater vertical range and with an upper limit near the top of the shore, tended to be synchronised across the sites. Thus species living lower on the shore in narrower zones were less synchronous. The height of the lower limit of the species had little effect. Finally, certain species in the set were more abundant at wave-exposed sites while others were more typical of sheltered sites. To quantify this tendency, a principal components analysis was done on the average abundance for species in Table 2 at each site over the 20 years of data (1981-2000). The first principal component explained 36.5% of the total variance and was strongly correlated with the exposure rating of the site as originally defined on the Ballantine (1961) scale

(Kendall's tau b = -0.78493, n=20, P<0.0001). Thus the factor loading for each species for the first principal component was a good measure of affinity for wave exposure or shelter (Table 3). Species more common on wave-exposed shores were not more synchronous than those more common in shelter.

DISCUSSION

In this study changes in abundance of most species were positively correlated among sites, with 25% (4 of 16) and 31% (8 of 26) significantly greater than zero. Given that many previous studies have identified large-scale changes in abundance and distribution of barnacles (see Introduction), it was perhaps not surprising that *Semibalanus balanoides* was the most synchronised of all species examined (1981-1992: 0.27, 1993-2000: 0.35). This species is one of the few intertidal species for which population synchrony has previously been quantified. Peak settlement counts of *S. balanoides* from 1975 to 1981 in North Yorkshire (Kendall et al. 1982) were very strongly correlated among sites ($r=0.6-0.95$) along a 60km stretch of linear coast, while over the same period along a complex coastline in Northwest Scotland a wider range of correlation was seen (-0.16 to 0.98). Reduced synchrony along a complex coastline may be due to differences in orientation and coastal configuration among sites, resulting in a greater range of environmental conditions among sites separated by similar distances (Kendall et al. 1982), and potential supply of wind-driven dispersal stages (Hawkins & Hartnoll 1982). Large-scale synchrony of changes in barnacle populations has also been seen in *Tetraclita serrata* in South Africa (Dye 1998a).

By contrast with *S. balanoides*, the dogwhelk *Nucella lapillus* showed very little synchrony. The species has very limited dispersal, producing egg capsules and having a high degree of microgeographic genetic variability (Day 1990, Kirby et al. 1997). Populations in the vicinity of the Oil Terminal in Sullom Voe have advanced tributyltin-induced imposex from the antifouling paints used on large ships (Davies & Bailey 1991, Harding et al. 1997). Decline, extinction and subsequent partial recovery of dogwhelk populations in this area can be seen in the time series (Fig. 2f). The localised effect reduced the correlation among the populations in the whole area. Possible consequences for other species of changes in dogwhelk populations (Moore et al. 1995) were not investigated.

From the above examples it is tempting to draw generalities as to the influence of the characteristics of particular species on degree of synchrony. Species with broad-scale dispersal of long-lived larvae would seem predisposed to show synchronized changes across a broad range of sites, while those with limited dispersal such as macroalgae (Reed et al. 1988, Sousa 1984) might be more likely to synchronised over shorter distances. Analysis of association of degree of synchrony with species characteristics showed no effect of the mode and degree of dispersal. *Littorina littorea* also has an extended pelagic larval phase, yet showed no significant synchrony among the sites in either period. The general conclusion that widely dispersed species are more synchronised is therefore not supported by the present set of species and sites.

The nature and causes of synchrony may be specific to particular spatial scales. Synchrony on very small scales (1m to 100m) may be due to the dynamics of

community patches, driven by patchy disturbance and recovery (Sousa, 1984) species interactions (Johnson et al. 1998, Burrows & Hawkins 1998, Johnson 2000). Where spatial interaction effects ensure that adjacent patches cycle out of phase with each other this may account for positive trends of spatial autocorrelation with distance at small scales (Heino et al. 1997). Small-scale variation in abundance due to patchiness may influence yearly site values when fixed study sites are used, as in this study.

At larger spatial scales (typically beyond 10s km) spatially autocorrelated disturbance (the Moran effect) and dispersal are the dominant causes of synchrony. In terrestrial systems spatial synchrony of population fluctuations over 100s of km is common: in the UK butterflies (Pollard 1991) and birds (Paradis et al. 2000) have been shown to be dominated by widespread factors. Separating the Moran effect from that of dispersal-induced synchrony requires more thorough understanding of the density dependence of the populations involved (Swanson & Johnson 1999). Both effects may act. Density-dependent cycles in red grouse and rock ptarmigan populations are synchronised by weather (the Moran effect), but dispersal plays some part in entraining changes in adjacent areas (Watson et al. 2000).

For those marine species with planktonic larvae, such as sessile invertebrates (Roughgarden et al. 1988, Underwood & Fairweather 1989) or teleost fishes (e.g. plaice, Ziljstra & Witte 1985), population fluctuations are thought to be driven by variation in larval supply. While this may imply that dispersal should be an important influence on synchrony, it may be that vulnerability of early life stages to environmental conditions varying on large scales is the dominant cause. Evidence

for the latter is to be found in the often strong association of synchronous changes with environmental conditions. Plaice recruitment time series around the UK over the last 20 to 40 years are strongly correlated (Fox et al. 2000), with a common signal correlated with sea temperature. Barnacles in SW England (Southward et al. 1995) also follow temperature, while wide-scale synchrony in California is driven by interannual variation in coastal upwelling affecting offshore advection of larvae (Roughgarden et al. 1988).

For some species there may be an influence of wider geographical distributions. Those species operating near limits may rely on sporadic successful recruitment events (Lewis et al. 1982). Successive failure of recruitment may ultimately lead to local extinction and thus a change in distribution. This phenomenon may produce synchrony through a Moran effect operating on dispersal stages but not through dispersal itself. *S. balanoides* is also strongly temporally synchronised, with the synchronous release of larvae occurring over a wide area (Kendall et al. 1985) possibly to coincide with the presence of food species in the plankton (Barnes 1956)

At the level of whole rocky shore communities, long-term studies produce inconsistent conclusions as to the spatial scale of temporal change. Large-scale long-term changes may dominate variation in abundance and community composition, and are thought to be associated with oceanographic processes (Shanks 1983, Caffey 1985, Gaines et al. 1985, Underwood et al. 1983, Dayton et al. 1999). Where these changes have been analysed statistically, major shifts in community structure have been found to be due to changes in a subset of species. On South African shores, changes in community composition common to distant sites were mostly due to

changes in the barnacle species (Dye 1998b). This group shows a similar degree of spatial synchrony in this and other studies (Caffey 1985, Judge et al. 1988). Similarly, lack of synchrony in low shore algal species in this study has also been found elsewhere (Chapman & Underwood 1998, Underwood & Chapman 1998, Menconi et al. 1999). Low shore algae may be more susceptible to direct effects of local factors, such as anthropogenic disturbance (Benedetti-Cecchi et al. 2001) or grazing (Benedetti-Cecchi et al. 2000). Where these effects are consistent over large scales, large-scale changes may result (Benedetti-Cecchi et al. 2001). More often it seems that processes affecting low shore algae are idiosyncratic to particular conditions prevailing at each site.

The spatial extent of population synchrony has obvious implications for monitoring strategies. Such is the degree of synchrony in *S. balanoides*, for example, that changes at a single site adequately reflect changes over the whole of the southwest of England (Southward et al. 1995). More sites will be needed to estimate large-scale changes in species with weaker synchrony among sites.

Long-term study of rocky shore communities has shown that some of the dominant species are good indicators of ecosystem responses to climatic change (Southward et al. 1995). This study indicates that species other than barnacles common on rocky shores show relatively low correlation among time series, and therefore may be less sensitive indicators. Climate change should affect all sites similarly. However, most of the sites in this study were over a very limited spatial scale (0-30km) in a semi-enclosed area that may be more prone to local effects, such as the effects of the Oil Terminal on dogwhelks, rather than climatic effects. This

contrasts with the choice of open coastal sites for monitoring programmes intended to detect climatic influences (such as COST 47: Lewis 1984). The complexity of the local coastline may also mitigate broad-scale synchrony driven by climate.

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Table 1. Numerical equivalents for categorical estimates of abundance following Hiscock (1981) definitions. Categories are A, Absent; R, Rare; O, Occasional; F, Frequent; C, Common; A, Abundant; S, Super Abundant, Ex, Extremely Abundant. Values chosen are midpoints between scale limits, with Absent on the scale replaced by the lower limit of the Rare scale.

Species	Scale	Unit	Abundance Class							
			A	R	O	F	C	A	S	Ex
Live barnacles, <i>Littorina neritoides</i> , <i>L. neglecta</i>	1	0.01m ²	0.001	0.005	0.5	5	50	200	400	600
<i>Balanus perforatus</i>	2	0.01m ²	0.001	0.005	0.05	0.5	5	55	200	350
<i>Patella</i> adults, <i>L. littorea</i> , <i>L. mariaae/obtusata</i> , <i>Nucella lapillus</i> (<3mm)	3	0.1m ²	0.01	0.05	0.25	0.75	2.5	7.5	15	30
<i>L. 'saxatilis'</i> , <i>Patella</i> (<10mm)	4	0.1m ²	0.01	0.05	0.5	2.5	7.5	15	35	60
<i>Nucella lapillus</i> (>3mm), <i>Gibbula</i> sp.	5	0.1m ²	0.1	0.25	0.5	2.5	7.5	25	75	130
<i>Mytilus edulis</i>	6	%	0.01	0.1	1	2.5	12	35	65	90
<i>Pomatoceros</i> sp	7	0.01m ²	0.001	0.005	0.05	0.5	25	60		
Spirorbinidae	8	0.1m ²	0.001	0.005	0.05	0.5	50	150		
Sponges, hydroids, bryozoans	9	%	0.01	0.1	1	2.5	12	25		
Lichens, lithothamnia	10	%	0.01	0.1	0.5	2.5	10	35	65	90
Algae	11	%	0.01	0.2	1	2.5	17	45	75	95

Table 2. Average correlations (r_{boot}) between time series of average abundance at monitoring sites around Sullom Voe. Estimated averages and standard errors (SEr_{boot}) were determined through bootstrap resampling of the set of sites (N_S) where the species occurred to select from the set of correlations between sites (N_C). Values significantly different from zero are shown by an asterisk ($P<0.05$). Values are sorted in descending order for the 1993-2000 period.

Species	S	1981-1992				1993-2000			
		N_C	N_S	r_{boot}	SEr_{boot}	N_C	N_S	r_{boot}	SEr_{boot}
<i>Semibalanus balanoides</i>	1	210	15	0.2664	0.0489 *	400	20	0.3511	0.0973 *
Corallinaceae	10	110	12	0.0299	0.0962	324	19	0.2951	0.0824 *
<i>Hildenbrandia</i> spp.	10					400	20	0.2872	0.0895 *
<i>Porphyra</i> spp.	11					252	18	0.2728	0.1115 *
<i>Fucus</i> spp. (sporelings)	11					361	20	0.2582	0.0801 *
<i>Verrucaria maura</i>	10	178	15	-0.0381	0.0552	400	20	0.2339	0.0693 *
<i>Littorina neglecta</i>	1	142	15	-0.0213	0.0855	287	19	0.1761	0.1150
<i>Littorina saxatilis</i>	4	210	15	0.3274	0.0596 *	400	20	0.1717	0.0751 *
<i>Bowerbankia</i> sp.	9					359	19	0.1652	0.0706 *
<i>Cladophora</i> spp.	11					308	18	0.1391	0.0787
<i>Verrucaria mucosa</i>	10	182	15	-0.0505	0.0513	400	20	0.1318	0.0865
<i>Corallina</i> sp.	11					196	15	0.1211	0.0919
<i>Pelvetia canaliculata</i>	11					167	18	0.1150	0.1366
<i>Patella</i> spp. (<10mm)	4	100	13	0.1725	0.1081	349	20	0.1115	0.0894
<i>Patella</i> spp. (all)	3	210	15	0.1067	0.0419 *	400	20	0.1018	0.0547
<i>Ceramium</i> spp.	11					144	15	0.0550	0.0991
<i>Mytilus edulis</i>	6	180	15	0.1336	0.0717	386	20	0.0424	0.0610
<i>Littorina obtusata</i>	3	156	13	0.2649	0.0819 *	337	20	0.0294	0.0900
<i>Enteromorpha</i> spp.	11					370	20	0.0257	0.0875
<i>Fucus vesiculosus</i>	11	154	14	0.0675	0.0700	287	18	0.0172	0.0730
<i>Halichondria panicea</i>	9					169	17	0.0145	0.1032
<i>Nucella lapillus</i>	5	176	15	0.0246	0.0564	169	15	0.0116	0.1063
Spirorbidae	8	52	11	-0.0571	0.1286	279	19	0.0107	0.0763
<i>Littorina littorea</i>	3	90	13	0.1072	0.1063	221	16	-0.0076	0.0900
<i>Fucus serratus</i>	11	152	15	-0.0445	0.0684	314	19	-0.0153	0.0683
<i>Mastocarpus stellatus</i>	11	130	15	-0.0295	0.0629	320	20	-0.0328	0.0622

Table 3. Species characteristics. As in Table 2, species are arranged in descending order of synchrony for the period 1993-2000. Abbreviations: D, duration of dispersal phase; K, kingdom (A, animal; P, plants /lichens); P10, P90, 10th, 90th percentiles; PC1, factor loading from PCA ranging from -1 for sheltered-shore species to +1 for exposed-shore species.

Species	Dispersal mode	D (d)	K	Mean Shore level	Level range	P10 Upper	P90 Lower	PC1
<i>Semibalanus balanoides</i>	Planktonic	28	A	1.0	3.3	MTL	MLWS	0.65
Corallinaceae	Zoospore	2	P	0.6	0.6	MLWN	MLWS	0.36
<i>Hildenbrandia</i> spp.	Zoospore	2	P	1.1	0.7	MHWN	MLWS	-0.32
<i>Porphyra</i> spp.	Zoospore	2	P	0.9	0.7	MHWN	MLWS	0.54
<i>Fucus</i> spp. (sporelings)	Zoospore	2	P	1.1	1.0	MHWN	MLWS	-0.72
<i>Verrucaria maura</i>	Spore	2	P	2.1	0.9	MHWS	MHWN	0.58
<i>Littorina neglecta</i>	Live-bearing	0	A	1.2	2.0	MTL	MLWN	0.82
<i>Littorina saxatilis</i>	Live-bearing	0	A	1.5	1.9	MHWS	MLWN	-0.56
<i>Bowerbankia</i> sp.	Lecithotrophic	2	A	1.0	0.1	MHWN	MLWN	-0.36
<i>Cladophora</i> spp.	Zoospore	2	P	0.7	0.3	MTL	MLWS	0.63
<i>Verrucaria mucosa</i>	Spore	2	P	1.5	1.0	MHWS	MLWN	-0.01
<i>Corallina</i> sp.	Zoospore	2	P	0.5	0.4	MLWN	MLWS	0.68
<i>Pelvetia canaliculata</i>	Zoospore	2	P	1.9	0.5	MHWS	MHWN	-0.18
<i>Patella</i> spp. (<10mm)	Planktotrophic	7	A	0.6	0.5	MLWN	MLWS	0.80
<i>Patella</i> spp. (all)	Planktotrophic	7	A	0.9	0.9	MTL	MLWS	0.87
<i>Ceramium</i> spp.	Zoospore	2	P	0.6	0.3	MLWN	MLWS	0.77
<i>Mytilus edulis</i>	Planktonic	21	A	0.6	0.5	MLWN	MLWS	0.71
<i>Littorina obtusata</i>	Encapsulated	0	A	0.9	0.7	MTL	MLWS	-0.82
<i>Enteromorpha</i> spp.	Zoospore	2	P	0.9	0.8	MHWN	MLWS	0.03
<i>Fucus vesiculosus</i>	Zoospore	2	P	1.0	1.2	MTL	MLWS	-0.85
<i>Halichondria panicea</i>			A	0.5	0.2	MLWS	MLWS	0.24
<i>Nucella lapillus</i>	Encapsulated	0	A	0.8	1.0	MTL	MLWS	0.81
Spirorbidae	Planktonic	14	A	0.5	0.7	MLWN	MLWS	-0.39
<i>Littorina littorea</i>	Planktonic	28	A	0.8	0.5	MTL	MLWS	-0.80
<i>Fucus serratus</i>	Zoospore	2	P	0.5	0.5	MLWN	MLWS	-0.53
<i>Mastocarpus stellatus</i>	Zoospore	2	P	0.5	0.3	MLWS	MLWS	0.22

Table 4. Associations of species synchrony with species characteristics measured by correlation. Values shown are Pearson correlation coefficients, with significant values shown by asterisks ($P < 0.05$).

	1981- 1992	1993- 2000		1981- 1992	1993- 2000
Number of species	16	26		16	26
<u>Abundance</u>			<u>Vertical distribution</u>		
Number of observations	0.360	0.455 *	Average shore height	0.030	0.394 *
Number of sites	0.034	0.310	Vertical range (SD height)	0.405	0.470 *
Number of coefficients	0.384	0.400 *	Upper limit (90 th percentile height)	0.171	0.450 *
Duration of planktonic phase (square root days)	0.130	0.003	Lower limit (10 th percentile height)	-0.218	0.214
Kingdom (Animal = 1, Plant/Fungus = 0)	0.571 *	-0.173	Wave exposure (PC1)	-0.127	0.196

FIGURE LEGENDS

Fig. 1. Location of sites around Sullom Voe, Shetland. Sites are distinguished by a decimal code, where the integer portion denotes the wave exposure determined on the Ballantine (1961) biologically defined exposure scale. Outlying sites (6.11, 3.4, 2.9, 6.14, 3.12) were monitored from 1993 onwards. Symbols used as Fig. 2.

Fig. 2. Time series of average abundance at 10 out of the 20 monitored sites. Only alternate sites are shown for clarity. Symbols and decimal site codes as Fig. 1.

Plots are arranged in descending order of degree of synchrony for 1993-2000 (a) *Semibalanus balanoides*, $r_{boot} = 0.35$ (b) *Littorina saxatilis*, 0.17 (c) *Patella* sp. adults, 0.11 (d) *Littorina obtusata*, 0.03 (e) *Fucus vesiculosus*, 0.02 (f) *Nucella lapillus*, 0.01.

Fig. 3. Population synchrony as the correlation between time series versus distance between pairs of sites, for the period 1993-2000.



Fig. 1 Burrows et al



