Table 3. Representation of accessions in different clusters

Cluster	Accession	Location	State
A	CIMAP/PA5	Mundiyanakau, Arcot	Tamil Nadu
	CIMAP/PA39	Kumbakonam	Tamil Nadu
	CIMAP/PA26	Palayamkottai	Tamil Nadu
	CIMAP/PA28	Attyapuram, Tuticorin	Tamil Nadu
	CIMAP/PA120	Panipat	Punjab
	CIMAP/PA140	Shakti Nagar	Karnataka
B	CIMAP/PA6	Ullundurpet, Arcot	Tamil Nadu
	CIMAP/PA11	Adivaran, Salem	Tamil Nadu
	CIMAP/PA23	Vallioor, Tirunelveli	Tamil Nadu
	CIMAP/PA74	Momealli	Assam
	CIMAP/PA30	Paramakudi	Tamil Nadu
	CIMAP/PA78	CFTRI Campus, Mysore	Karnataka
	CIMAP/PA76	GKVK, Bangalore	Karnataka
	CIMAP/PA98	Dhaiadam	Karnataka
	CIMAP/PA77	Sanakana	Karnataka
	CIMAP/PA84	Harnahatti	Karnataka
C	CIMAP/PA37	Pudukkottai	Tamil Nadu
	CIMAP/PAC	Lucknow	Uttar Pradesh
D	CIMAP/PA25	Kanyakumari	Tamil Nadu
	CIMAP/PA80	Kusal Nagar	Karnataka
E	CIMAP/PA53	Sepahijala Wildlife Sanctuary	Tripura
F	CIMAP/PA2	Tinisular, Chennai	Tamil Nadu
	CIMAP/PA54	Barjalu, Jirania	Assam
	CIMAP/PA21	Thirumangalam, Madurai	Tamil Nadu
	CIMAP/PA117	Karnal	Haryana
	CIMAP/PA 22	Kayathar, Tirunelveli	Tamil Nadu
	CIMAP/PA135	Rishra	West Bengal
	CIMAP/PA144	Agra	Uttar Pradesh
	CIMAP/PA112	Ferozpur Jhinka, Gurgaon	Maharashtra
	CIMAP/PA111	Gurgaon	Maharashtra
	CIMAP/PA134	Kalmegha	West Bengal
	CIMAP/PA136	Bithur	Uttar Pradesh
G	CIMAP/PA145	Aghar	Gujarat

(west India) and Tripura (northeast India) outgrouped from the rest, forming distinct clusters (E and G) according to expectation, as they are from two entirely different geographical locations. Though *P. amarus* has distinct characters to substantiate the species status and constant chromosome number[11], the RAPD profiles display vast genetic variation indicative of the evolving nature of the taxa.

1. Webster, G. L., Synopsis of the genus and suprageneric taxa of Euphorbiaceae. *Ann. Mo. Bot. Gard.*, 1994, **81**, 33–144.
2. Webster, G. L., A monographic study of the west Indian species of *Phyllanthus*. *J. Arnold Arboric. Harv. Univ.*, 1957, **39**, 49–100.
3. Mitra, R. L. and Jain, S. K., Concept of *Phyllanthus niruri* (Euphorbiaceae) in Indian Floras. *Bull. Bot. Surv. India*, 1987, **27**, 161–176.
4. Chowdhury, L. B. and Rao, R. R., Taxonomic study of herbaceous species of *Phyllanthus* L. (Euphorbiaceae) in India. *Phytotaxonomy*, 2002, **2**, 143–162.
5. Virk, P. S., Ford-Lloyed, B. V., Jackson, M. T. and Newbury, H. J., Use of RAPD for the study of diversity within plant germplasm collections. *Heredity*, 1995, **74**, 170–179.
6. Shaanker, R. U. and Ganeshaiah, K. N., Mapping genetic diversity of *Phyllanthus emblica*: forest gene bank as a new approach for *in situ* conservation of genetic resources. *Curr. Sci.*, 1997, **73**, 163–168.
7. Khanuja, S. P. S., Shasany, A. K., Darokar, M. P. and Sushil Kumar, Rapid isolation of PCR amplifiable DNA from the dry and fresh samples of plants producing large amounts of secondary metabolites and essential oils by modified CTAB procedure. *Plant Mol. Biol. Rep.*, 1999, **17**, 74.
8. Khanuja, S. P. S., Shasany, A. K., Srivastava, A. and Sushil Kumar, Assessment of genetic relationships in *Mentha* species. *Euphytica*, 2000, **111**, 121–125.
9. Nei, M. and Li, W. H., Mathematical model for studying genetic variation in terms of restriction endonucleases. *Proc. Natl. Acad. Sci. USA*, 1979, **76**, 5269–5273.
10. Mathew, K. M., *Flora of Tamil Nadu Carnatic*, St. Joseph's College, Tiruchirapalli, 1983.
11. Brunel, J. F. and Roux, J., South-East Asian *Phyllanthus* II. Some *Phyllanthus* of subsect. *Swartziani. Nord. J. Bot.*, 1984, **4**, 469–473.

Pattern of species succession of soft-bottom macrofauna in the estuaries of Goa, west coast of India

Sadanand N. Harkantra* and Nimi R. Rodrigues

Biological Oceanography Division, National Institute of Oceanography, Dona Paula, Goa 403 004, India

Multivariate techniques, chord normalized expected species shared (CNESS) and principal component analyses of hypergeometric probability of species matrices (PCA-H) were applied to soft-bottom macrofauna data of Goa estuaries, west coast of India, to assess the pattern of species succession at different sites. These analyses revealed three groups of species that produced three-stages or triangular species succession pattern, corresponding to the three seasons, namely post-, pre- and southwest monsoon. Each site exhibited a different pattern of species succession and compostion. A total of 58 species were recorded among which 18 were new to the local fauna. Dominant species that controlled the orientation of this succession were Polychaetes (*Prioniospio pinnata*, *Clymene annandalei*, *Nereis capensis*), Bivalves (*Meretrix casta*, *Cardium flavum*), Amphipoda (*Urothoe platydactyla*), Echiurida (*Thalassema* sp.) and Nema-

*For correspondence. (e-mail: sadanand@darya.nio.org)

toda at different sites. Species succession was mainly influenced by the southwest monsoon and the local biotic and abiotic factors at specific sites.

A number of hypotheses of soft-bottom faunal species succession have been discussed[1–14]. Ecological succession consists of the sequence of changes in community structures that occur after a site has been disturbed[11]. It can be considered as a local progression of species invasion and occupancy[12]. Rhoads and Boyer[9] defined soft-bottom benthic succession as a significant directional change in pattern of animal–sediment interaction, rather than changes in species composition. Clements'[12] view is that succession was driven by changes in external environment. Species succession largely depends on the life-history strategies and recruitment process[2]. Species which have r-selected and opportunistic traits will be found during early stages, while species which have less opportunistic and k-selected traits will be found at later stages[2]. Based on many views, Connell and Slayter[13] have formulated three models of succession – facilitation, tolerance and inhibition. Facilitation is based on biotic habitat modification by each group of species that enhances the settlement of subsequent groups. The tolerance mechanism centres on differences in species resource-utilization pattern and life histories. Inhibition involves suppression of settlement and/or growth of other species by those already established in the disturbed area.

This fundamental ecological process of species-succession models of facilitation, tolerance and inhibition has been studied in a number of soft-bottom environments in temperate waters[1–14]. Though there are some studies on soft-bottom macrofauna in Indian estuaries[15–19], no such approach was made. The multivariate techniques, chord normalized expected species shared (CNESS) and principal component analyses of hypergeometric probability of species matrices (PCA-H) were applied to soft-bottom macrofauna data of Goa estuaries to assess the pattern of species succession at different sites, in order to examine the various hypotheses mentioned above.

The Mandovi and Zuari estuarine system of Goa is located on the central west coast of India (Figure 1). Spatio-temporal variations in abiotic and biotic parameters in this estuarine system are affected by tropical southwest monsoon; riverine and tidal flows make them ecologically complex ecosystems[15–17,20,21]. The average annual rainfall of Goa is about 3000 mm, of which nearly 80% occurs during the southwest monsoon period (June–September), while relatively stable conditions prevail during post-monsoon (October–January) and pre-monsoon (February–May) periods. The study sites M1, M2 and Z1, Z2 are located upstream of Mandovi and Zuari estuaries, respectively (Figure 1). The depth varied between 3.5 and 4.5 m, whereas salinity varied from 1.5 to 33.0 psu. The substrata were sandy in Mandovi sites and muddy in Zuari sites. The organic carbon values ranged
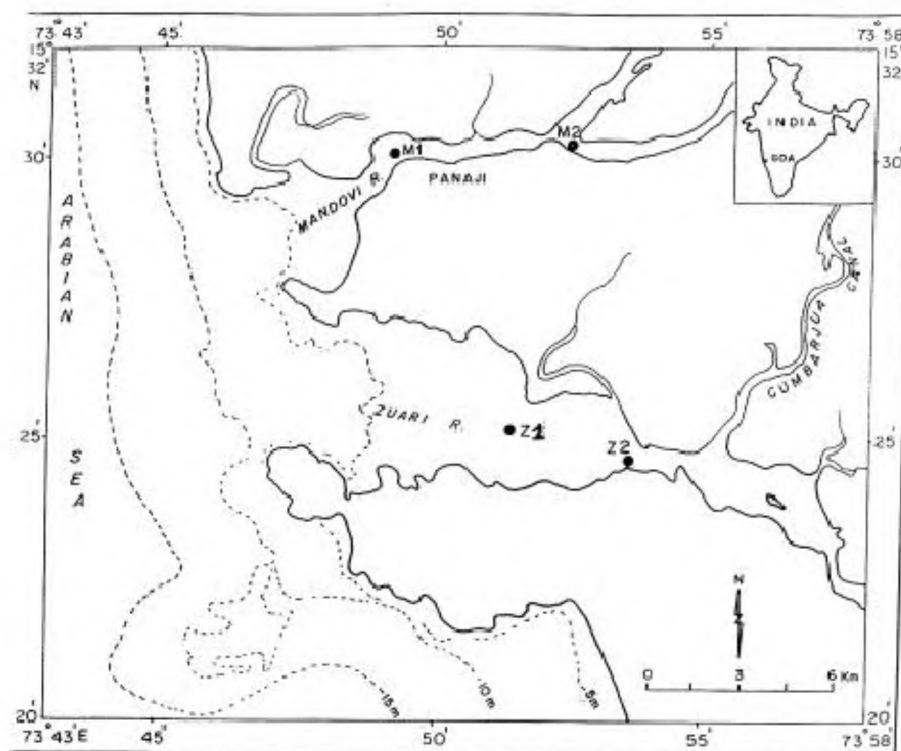

Figure 1. Map showing location of the study area.

Table 1. Species density $n/0.04$ m^2 (average of triplicate samples) at different sites and months, which has contributed more than 2% of the sample. First column and row indicate species code (refer figure code) and month respectively

	O	N	D	J	F	M	A	M	J	J	A	S
M1												
Dn	4.0	0.0	17.3	1.0	6.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nc	3.0	7.0	15.0	0.0	6.0	2.5	16.5	2.0	2.0	3.0	12.0	35.0
Mc	0.0	5.0	0.3	0.0	0.0	3.0	0.0	0.0	0.0	4.5	6.0	0.0
Pm	0.0	3.0	0.0	0.0	3.0	0.0	4.5	3.0	6.0	0.0	0.0	6.0
Up	1.0	0.0	1.6	0.3	115.5	0.0	16.5	14.0	0.0	1.0	1.0	0.0
N	0.0	2.0	0.3	0.0	0.0	12.0	0.5	2.0	1.0	0.0	0.0	8.0
Th	0.0	2.0	0.3	0.3	0.0	0.5	3.5	0.0	0.5	0.0	2.0	467.0
M2												
Pp	4.5	0.0	0.3	0.0	0.0	0.0	0.0	1.5	2.5	0.5	0.0	16.5
Ga	0.5	0.0	0.6	1.0	1.0	5.0	1.0	0.5	0.0	0.5	0.0	0.0
Nc	0.0	0.0	1.0	2.0	0.0	0.0	0.0	2.0	0.0	0.0	6.5	4.5
Mc	3.5	1.3	21.3	0.0	4.0	30.5	0.0	238.0	0.0	17.5	16.5	4.0
Cfl	0.5	1.0	0.0	0.0	0.0	0.0	25.0	0.0	1.0	0.0	0.0	0.0
Up	0.0	0.6	0.0	1.0	1.5	0.0	0.0	0.0	0.0	0.5	0.0	6.5
Z1												
Pp	20.0	3.0	5.3	20.0	6.5	12.0	9.0	0.0	0.5	2.0	13.5	46.5
Ni	1.5	1.6	0.3	0.0	0.0	0.0	0.0	0.0	1.0	0.0	1.0	5.5
Sc	0.5	0.0	4.3	5.0	7.0	9.0	8.0	0.0	0.0	0.0	0.0	0.0
Ga	2.0	0.6	0.6	10.0	0.5	4.0	3.0	0.5	2.5	0.0	0.0	0.0
Cc	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	4.5	1.0
Ca	0.5	0.6	3.6	9.0	8.0	0.0	0.0	6.0	13.0	0.0	0.0	2.0
Up	0.5	1.0	0.0	0.0	4.0	4.0	1.0	0.5	0.0	0.5	0.5	0.3
N	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	24.5	0.0
Th	0.0	0.0	0.0	0.0	1.5	0.0	4.0	1.0	1.0	0.0	0.0	1.0
Cf	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	8.5	0.0
Z2												
Pp	1.0	7.0	4.3	28.0	8.5	54.0	0.0	5.0	0.5	1.0	2.0	2.5
Ni	0.0	0.0	0.0	2.0	0.0	0.0	0.0	2.0	0.0	6.0	0.0	2.0
Ga	0.0	2.0	13.0	2.5	9.0	1.0	0.0	1.5	0.0	0.0	0.0	0.0
Cc	1.0	3.0	0.0	0.0	0.5	13.0	1.0	4.0	0.0	0.0	3.0	18.5
Ca	6.5	7.0	0.0	24.0	0.0	2.0	8.0	22.0	10.0	12.0	9.5	4.0
N	0.0	9.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Th	0.0	3.0	0.0	3.0	1.5	0.0	0.0	0.5	0.5	0.0	0.0	2.0

from 0.15 to 3.5% and showed higher values at sites in the Zuari estuary.

Four sites were sampled monthly, from October 1997 to September 1998 (Figure 1). Sites positions were noted by hand-held GPS ($\pm$ 15). Triplicate samples were obtained at each site with a 0.04 m^2 van Veen grab up to the depth of 15–20 cm. Sediment samples from the grab were preserved in a 10% sea-water formalin and Rose Bengal stain mix. Later, these samples were sieved through 0.5 mm mesh sieve, with samples retained on the sieve, being transferred to plastic containers and preserved in 5% sea-water formalin[22]. Macrofauna were identified to species level and each species was counted under a stereo zoom microscope. Population density was converted to 0.04 m^2. Food and feeding habits of the species were ascertained from the literature. New faunal distance matrices, CNESS and PCA-H were used[14,23]. Succession of species was analysed using the Combinatorial Polythetic Agglomerative Hierarchial Clustering 96 (COMPAH 96)

software of Gallagher[23]. Species versus month matrices were arranged for each site, as there was significant difference in environmental parameters and community structure (ANOVA test). Actual mean density data (Table 1) and species which contributed more than 2% of the samples were considered for this analysis[14,23]. Sample size (m) was determined as half of the minimum total population in a sample[14,23–25]. These techniques are similar to nonmatrix multidimensional scaling (NMDS) of chord distance, which was found to be the best among the eight procedures tested for ecological data[24]. Details about this analysis and techniques have been described elsewhere[14,23].

A total of 58 species was recorded (Table 2), among which 19 were new to the local benthic fauna. Species density varied from sites to months, with highest density being of Echiurida, *Thalassema* sp. 467/0.04 m^2, which was recorded in the month of September 1998 at site M1 (Table 1). Polychaetes formed the dominant taxa follo-
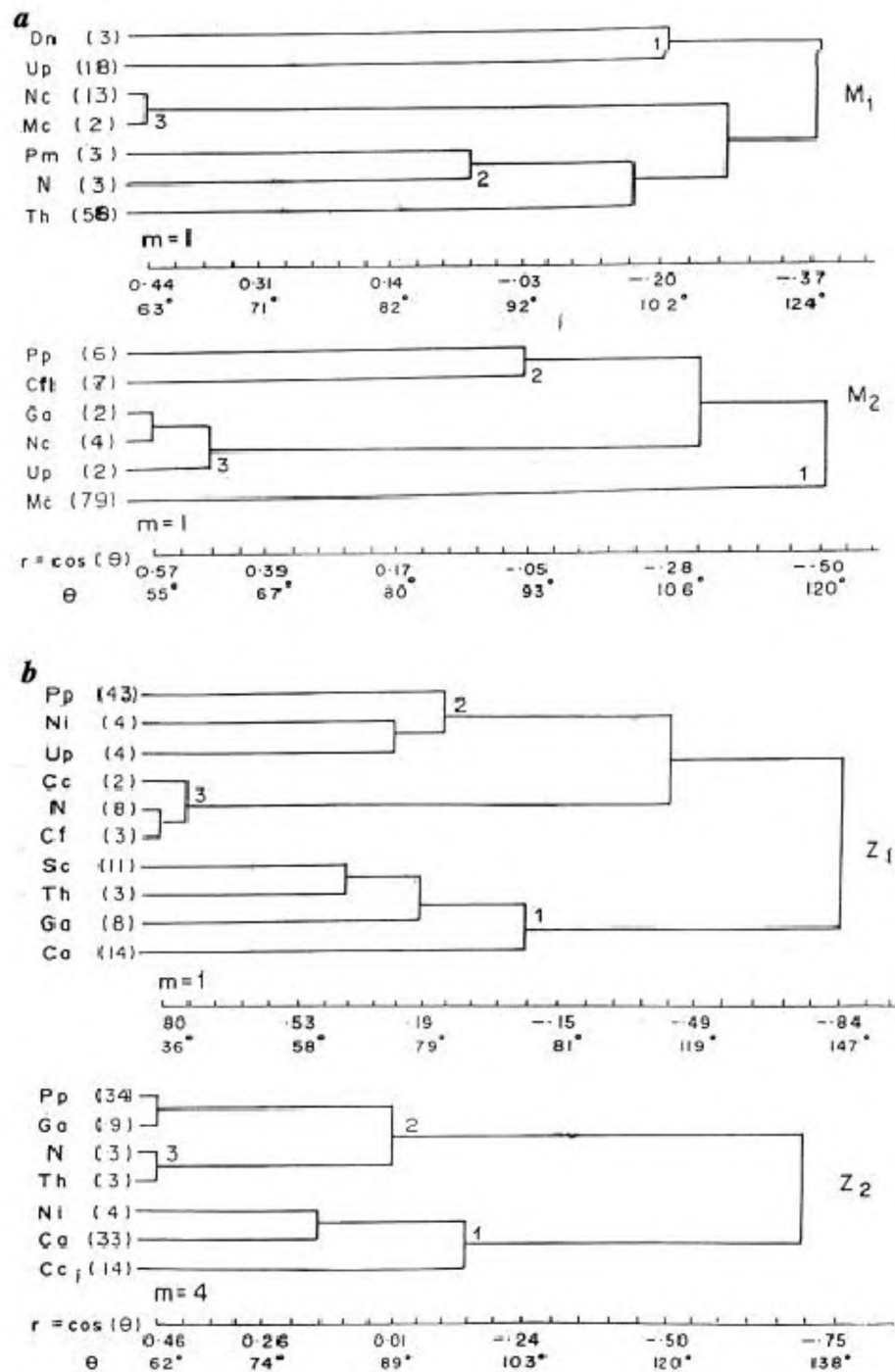
Figure 2 a and b. Single linkage clustering of columns of the hypergeometric probability (H) matrices at different sites, indicating species with frequencies at $m = 1, 4$ using Pearson's r. Clustering with Pearson's r is mathematically equivalent to clustering the species vectors displayed in Figure 3 using $\cos\phi$ similarity, where ϕ is the angle between species vectors in 12-dimensional ordination space. The three successional stages 1, 2 and 3 and the $\cos\phi$ (= Pearson's r) and ϕ value at which these clusters fuse are indicated. Numbers in parantheses are the percentage of contribution of species to CNESS analyses. Ca, *Clymene annandalei*; Cc, *Cossura coasta*; Cfl, *Cardium flavum*; Cf, *Cerethedia fluviatalis*; Dd, *Dendrostomum* sp.; Dn, *Diopatra neapolitana*; Th, *Thalassema* sp.; Ga, *Glycera alba*; Mc, *Meretrix casta*; N, Nematoda; Nc, *Nereis capensis*; Ni, *Nephthys inermis*; Pp, *Prionospio pinnata*; Sc, *Sternaspis scutata*; Up, *Urothoe platydactyla*.

wed by molluscs and crustaceans. Figure 2 a and b shows clusters of species based on the $\cos\phi$ between the species vectors in the Gabriel covariance plot. Only 6–10 species

contributed to more than 2% of the CNESS variation among the samples of 58 species recorded (Tables 1 and 2; Figures 2 and 3). The stages of succession of species

formed three distinct clusters of the species vector shown as 1, 2 and 3. Stages 1, 2 and 3 represent post-, pre- and southwest monsoon season species samples. The orientation of the species vectors in 12-dimensional sample space was seen in three groups, each oriented at different angles between 36 and 147° to others (Figure 2 a and b). These three groups indicate three stages of succession, which produced the triangular pattern of seasonal samples (Figure 2 a and b). Cluster analyses also describe the composition of the three successional stages and show the percentage of proportional contribution of each species to CNESS distance among the samples. Stages 1, 2 and 3 were composed of different species at different sites (Figure 2 a and b). The most important species that controlled the orientation of the samples were the grazer amphipod, *Urothoe platydactyla* (18%) at site M1, filter feeder bivalve, *Meretrix casta* (79%) at site M2 and head-down burrowing sub-surface deposit feeder, *Clymene annandalei* at sites Z1 (14%) and Z2 (33%) during succession stage 1 of the post-monsoon season. Onset of succession was largely due to the first stage of recruitment which occurred after the southwest monsoon disturbance and re-establishment in stability of the environment. The first shift in the successional topology was from stage 1 to stage 2. Stage 1 species do not facilitate or inhibit stage 2 in this sequence, because their population has declined before stage 2 species recruit. The cause for this shift in succession to topology was the

pre-monsoon second stage of recruitment state. The important species that controlled the orientation of stage 2-premonsoon period were Echiurida, *Thalassema* sp. (58%) at site M1, filter feeder bivalve, *Cardium flavum* (7%) at site M2 and *Prionospio pinnata* at site Z1 (43%) and Z2 (34%). Defaunation of macrofauna occurred largely due to a sudden decline in salinity and sediment disturbance during stages 2 and 3, which was brought about by the southwest monsoon. Stage 3, southwest monsoon succession was distinguished from stage 2 primarily by the presence of low salinity-tolerant species. The important species that controlled the orientation of stage 3 were the polychaete, *Nereis capensis* at site M1 (13%) and M2 (4%), Nematoda at site Z1 (8%) and Z2 (3%). These three important species each formed by a different successional stage 1, 2 and 3, account for 89% at site M1, 90% at site M2, 65% at site Z1 and 70% at site Z2 of the total variation in CNESS distance among the samples. Apart from this, other species also contributed in controlling the orientation of different stages (Figures 2 a and b). High percentage composition of different species at different sites and seasons (Figure 2 a and b) also indicates the spawning periodicity and recruitment process.

The species association was better analysed with a covariance bi-plot (Figure 3) and shows three groups of species vectors, indicated by 1, 2 and 3. The species vectors do not form a continuum, but fall into three discrete groups. The species vectors gives a picture of the association among the succession of species. In the PCA-H analyses (Figure 3), the variation in CNESS was explained by the first two axes (as percentage). Axis 1 depicts the difference between the post- and pre-monsoon sampling months, with dominant species primarily contributing to the orientation of the axis. Similarly, axis 2 was formed by the difference between the pre- and southwest monsoon season sample months. The estuarine soft-bottom species succession varied both temporally and spatially, and showed three distinct seasonalities over a period of 12 months. No two stages were similar, each site exhibited different species succession and composition (Figures 2 and 3).

The patterns of benthic faunal succession found in this study exhibit elements of each of the models mentioned earlier. A variety of abiotic and biotic factors like hydrodynamic, salinity, sediment properties, competition for food and space, spawning period, recruitment process, prey–predator relationship might have affected this pattern, including human perturbation[1–14]. For example, the initial establishment of population by early colonizing species or opportunistic species with r-selected traits *C. annandalei* (Polychaete, Maldanidae, head-down burrowing sub-surface deposit feeder) was followed by increase in dominance of less opportunistic species or k-selected traits, *P. pinnata* (Polychaete, Spionidae, surface-deposit feeder) at sites Z1 and Z2, and was a tolerance model[13].

Table 2. List of species recorded in the study sites

Polychaetes – *Prionospio pinnata* Ehlers; *P. cirrifera* Wiren; **Nephthys inermis* Ehlers; **N. dibranchis* Grube; **N. oligobranchia* Southern; *Glycera alba* Rathke; **Goniada emerita* Audouin & Milne-Edwards; *Lumbriconereis heteropoda* Marenzeller; **Clymene annandalei* Southern; **Heteromastus similis* Southern; **Maldane sarsi* Malmgren; *Nereis capensis* Willey; *Diopatra neapolitana* Delle Chiaje; **Onuphis eremita* Audouin & Milne-Edwards; **Sabella melanostigma* Schmarda; **Terebella ehrenbergi* Grube; **Cossura coasta* Kitamori; **Scoloplos marsupialis* Southern; *Eunice tentaculata* Quatrefages; **Sternaspis costata* Marenzeller; **Magelona rosea* Moore; **Arabella iricolor* Montagu; **Cirratulus filiformis* Keferstein

Molluscs – *Meretrix casta* (Chemnitz); *Paphia malabarica* (Chemnitz); *P. textile* (Gmelin); *Perna viridis* Linne; *P. indica* (Hanley); *Cardium flavum* Linne; **Gafrarium tumidum* Roding; *Tellina bruguieri* Hanley; **Lutraria arcuata* Deshayes; *Cerithidea fluviatilis* (Potiez & Michaud); *Turritella attenuata* Reeve; *Villorita cyprinoides* (Grey); *Arca granosa* Lamarck; *Solen truncatus* Wood

Crustaceans – *Metapenaeus dobsoni* (Miers); *Sphaeroma annandalei* Stebbings; *S. Walkeri* Stebbings; *Gastrasoccus simulans* W. H. Tattersall; *Ampelisca brevicornis* (Costa); **Urothoe platydactyla* Rabindranath; *Diogene affinis* Henderson; *Portunus sanguinolentus* (Herbst); *Paradiastylis* sp., *Eurydice* sp., *Cyathura* sp., *Scottolana* sp.

Others – *Boleopthalmus dussimieri* Cuv. & Val.; *Edwardsia tinctrix* Annandale; *Cavernularia* sp., *Sertularia* sp., *Nemertea* sp., *Dendrostomum* sp., *Ophiothrix* sp., *Thalassema* sp., Nematoda

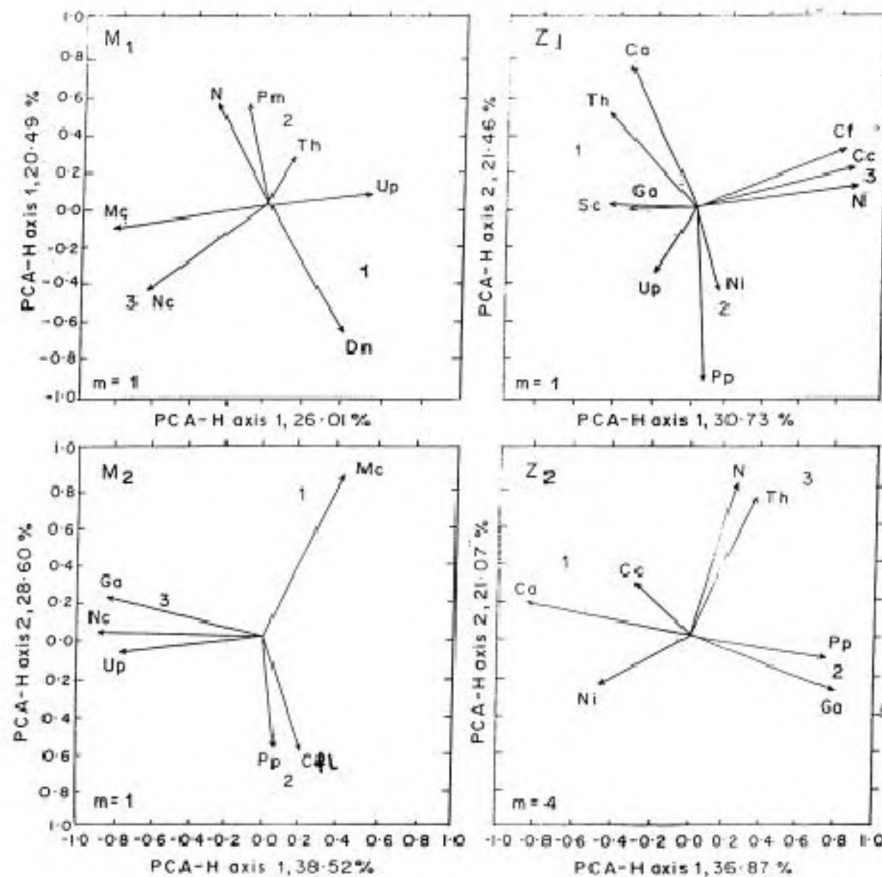Asterisk indicates new species to the local fauna.

Figure 3. Three-dimensional covariance plot of species vectors. Angles between vectors indicate the temporal association among species, with acute angle indicating species with frequencies at $m = 1, 4$ that are highly correlated in time. Three groups of species comprising successional stages 1, 2 and 3 are labelled.

This was mainly due to the use of different level of food resources and different life-history strategies[2,7,8,25–28]. If the decline of the initial colonizers (*C. annandalei*) was due to resource depletion and intra-interspecific competition, then the subsequent domination by a different species (*P. pinnata*) was mainly due to more efficient exploitation of food and/or space resources[5,9,26–28]. Biotic habitat modification by earlier species may also enhance the settlement of subsequent species, which suggests that facilitative mechanisms of succession can occur in soft-bottom communities[5,7,8]. However, the extent to which these interactions shape successional patterns has to be tested by manipulative experiments[5,7,8]. Similarly, early succession of grazer Amphipoda, *U. platydactyla* and later by deposit feeder Echiurida, *Thalassema* sp. at site M1 can be explained by tolerance and facilitative models[5,7,8]. The model of inhibition[5,7,8] holds good at site M2, where we observed a succession by the filter feeder bivalves, *M. casta* and *C. flavum* during post- and pre-monsoon. These species can occupy all niches and keep-off all the later-arriving species[29]. Species succession of *N.*

capensis at M1 and M2 sites and Nematoda at sites Z1 and Z2 during southwest monsoon was largely due to presence of earlier stage tolerant species and defaunation of other non-tolerant species. This succession was not a fresh recruitment[29]. Defaunation was mostly due to adult/larval mortality or migration to nearby areas, physical disturbance, etc. Some of the other explanations could be sudden changes in the environmental parameters such as lowering of salinity that may trigger gonadal release from the benthic invertebrates[30] in the water column, thereby increasing the larval abundance. Larval forms may also undergo adaptive strategies like cyst formation, post-ponement of larval settlement, etc. during these severe conditions[29–31]. These larvae will settle once the condition is favourable[29–31]. Though the seasonality was clear at all the sites, species composition differed among sites and seasons (Figures 2 and 3). This was mainly due to a significant difference in environmental parameters and benthic community structure among the sites and seasons. It is clear from the foregoing account that the species succession was mainly brought about by the southwest

monsoon and local abiotic and biotic factors, which largely agrees with the concept of Rhoads and Boyer[9], Clements[12], and Connel and Slatyer[13].

The pattern of succession differed from season to site in the Mandovi and Zuari estuarine complex. The study was limited to 12 months, with three seasons. Whether seasonality of species succession repeats in a similar pattern has to be ascertained from the long-term monitoring of the macrobenthos. Manipulative experiments are needed to understand the species interactions and influence of biotic factors. Based on our study, we designate *C. annandalei*, *M. casta*, *U. platydactyla* as opportunistic or *r*-selected species. *P. pinnata*, *C. flavum*, *Thalassema* sp. are considered as equilibrium or *k*-selected species and *N. capensis* and Nematoda as stress-tolerance species and taxa, respectively.

1. McCall, P. L., Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. *J. Mar. Res.*, 1977, **35**, 221–226.

2. Grassle, J. F. and Grassle. J. P., Opportunistic life histories and genetic systems in marine benthic polychaetes. *J. Mar. Res.*, 1974, **32**, 253–284.

3. Pearson, T. H. and Rosenberg, R., Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Annu. Rev.*, 1978, **16**, 229–311.

4. Rhoads, D. C., Aller, R. C. and Goldhaber, M. B., In *Ecology of Marine Benthos: The Influence of Colonizing Benthos on Physical Properties and Chemical Diagenesis of the Estuarine Seafloor* (ed. Coull, B. C.), University of South Carolina Press, Columbia, 1977, pp. 113–138.

5. Thistle, D., Natural physical disturbance and communities of marine soft-bottoms. *Mar. Ecol. Prog. Ser.*, 1981, **6**, 223–228.

6. Whitlach, R. B., Pattern of resource utilization and co-existence in marine intertidal deposit feeding communities. *J. Mar. Res.*, 1980, **38**, 743–765.

7. Zajac, R. N. and Whitlatch, R. B., Response estuarine infauna to disturbance. I. Spatial and temporal variation of recolonization. *Mar. Ecol. Prog. Ser.*, 1982, **10**, 1–14.

8. Zajac, R. N., Robert, R. B. and Whitlatch, R. B., Response estuarine infauna to disturbance. II. Spatial and temporal variation of succession. *Mar. Ecol. Prog. Ser.*, 1982, **10**, 15–27.

9. Rhoads, D. C. and Boyer, L. F., In *Animal–Sediment Relations: The Effects of Marine Benthos on Physical Properties of Sediments – A Successional Perspective* (eds McCall, P. L. and Tevesz, M. J. S.), Plenum, 1982, pp. 3–52.

10. McCook, L. J., Understanding ecological community succession: casual models and theories, a review. *J. Vegetation Sci.*, 1994, **110**, 115–147.

11. Paine, R. T. and Levin, S. A., Intertidal landscapes: disturbance and dynamics of pattern. *Ecol. Monogr.*, 1981, **51**, 145–178.

12. Clements, F. E., *Plant Succession: An Analysis of the Development of Vegetation*, Carnegie Institute of Washington DC, USA, 1916, Publication No. 242.

13. Connell, J. H. and Slayter, R. O., Mechanism of succession in natural communities and their role in community ability and organisation. *Am. Nat.*, 1977, **111**, 119–144.

14. Trueblood, D. D., Gallagher, E. D. and Gould, D. M., Three stages of succession on the Savin Hill Cove mudflat, Boston Harbour. *Limnol. Oceanogr.*, 1994, **44**, 1430–1454.

15. Harkantra, S. N., Benthos of Kali estuary, Karwar. *Mahasagar-Bull. Natl. Inst. Oceanogr.*, 1975, **8**, 53–58.

16. Parulekar, A. H., Dhargalkar, V. K. and Singbal, S. Y. S., Benthic studies in Goa estuaries: Part III- Annual cycle of macrofauna dis-

17. tribution, production and tropic relations. *Indian J. Mar. Sci.*, 1980, **9**, 189–200.

17. Harkantra, S. N. and Parulekar, A. H., Community structure of sand dwelling macrofauna of an estuarine beach in Goa, India. *Mar Ecol. Prog. Ser.*, 1985, **30**, 291–294.

18. Mathew, Annie and Govindan, K., Macrobenthos in the nearshore coastal system of Bombay. *Proc. Natl. Acad. Sci. India*, 1995, **65**, 411–430.

19. Nandan, B. S. and Aziz, P. K. A., Benthic polychaetes in the anoxic sulphide biomes of the retting zones in the Kodinamkulam, Kayal. *Indian J. Environ. Prot.*, 1995, **16**, 12–22.

20. Qasim, S. Z. and Sen Gupta, R., Environmental characterstics of the Mandovi-Zuari estuarine system in Goa. *Estuar. Coast. Shelf Sci.*, 1981, **13**, 557–578.

21. Shetye, S. R., Gouveia, A. D., Singbal, S. Y., Naik, C. G., Sundar, D., Michael, G. S. and Nampoothiri, G., Propagation of tides in the Mandovi-Zuari estuarine network. *Proc. Indian Acad. Sci. (Earth Planet. Sci.)*, 1995, **4**, 667–682.

22. Eleftheriou, A. and Holme, N. A., In *Methods for the Study of Marine Benthos: Macrofauna Techniques* (eds Holme, N. A. and McIntyre, A, D.), Blackwell Scientific, London, 1984, pp. 140–216.

23. Gallagher, E. D., Combinatorial Polythetic Agglomerative Hierarchial Clustering (COMPAH96) documentation, 1996, http://www.es.umb.edu/edgwebp.htm

24. Kenkel, N. and Orloci. L., Applying metric and nonmetric multidimensional scaling to ecological studies. *Ecology*, 1986, **67**, 919–928.

25. Grassle, J. F. and Smith, W., A similarity measures sensitive to the contribution of rare species and its use in the investigation of variance in marine benthic communities. *Oecologia*, 1976, **25**, 13–25.

26. Santos, S. L. and. Simon, J. L., *Mar. Ecol. Prog. Ser.*, 1980, **2**, 235–241.

27. Jumars, P. A. and Fauchald, K., In *Ecology Marine Benthos: Between-Community Contrasts in Successful Polychaete Feeding Strategies* (ed. Coull, B. C.), University of South Carolina Press, Carolina, 1977, pp. 1–20.

28. Peterson, C. H., Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. *Mar. Biol.*, 1977, **43**, 343–359.

29. Richer, W. and Sarnthein, M., In *Biology of Benthic Organisms: Molluscan Colonization of Different Submerged Platforms in the Western Baltic Sea* (eds Keegen, B. F., Ceidigh, P. O. and Boaden P. J. S.), Pergamon Press, New York, 1977, pp. 465–477.

30. Kinne, O., In *Marine Ecology: Environmental Factors–Salinity: Animal–Invertebrates* (ed. Kinne, O.), John Wiley, New York, 1977, vol. 1, pp. 821–996.

31. Osman, R. W., The establishment and development of a marine epifauna community. *Ecol. Monogr.*, 1977, **47**, 37–63.