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Published:


**In Press:**


**Communicated:**


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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-II) 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 composition. 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 (*Prionospio pinnata, Clymene annandalei, Nereis capensis*), Bivalves (*Meretrix casta, Cardium flavum*), Amphipoda (*Urothoe platydactyla*), Echiurida (*Thalassemia sp.*) and Nema-

*For correspondence. (e-mail: sadanand@darya.nioc.org)
A number of hypotheses of soft-bottom faunal species succession have been discussed. Ecological succession consists of the sequence of changes in community structures that occur after a site has been disturbed. It can be considered as a local progression of species invasion and occupancy. Rhoads and Boyer defined soft-bottom benthic succession as a significant directional change in pattern of animal–sediment interaction, rather than changes in species composition. Clemente's view is that succession was driven by changes in external environment. Species succession largely depends on the life-history strategies and recruitment process. 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. Based on many views, Connell and Slayter 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. Though there are some studies on soft-bottom macrofauna in Indian estuaries, 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. 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...
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 (± 15). Triplicate samples were obtained at each site with a 0.04 m² 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 formalin²². Macrofauna were identified to species level and each species was counted under a stereo zoom microscope. Population density was converted to 0.04 m². Food and feeding habits of the species were ascertained from the literature. New faunal distance matrices, CNESS and PCA-H were used¹⁴. Succession of species was analysed using the Combinatorial Polythetic Agglomerative Hierarchial Clustering 96 (COMPAH 96) software of Gallagher²³. 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 analysis¹⁴. Sample size (m) was determined as half of the minimum total population in a sample¹⁴. 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 data²⁴. Details about this analysis and techniques have been described elsewhere¹⁴,²³.

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 m², which was recorded in the month of September 1998 at site M1 (Table 1). Polychaetes formed the dominant taxa follo-

<table>
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RESEARCH COMMUNICATIONS
Figure 2a 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 cosθ similarity, where θ is the angle between species vectors in 12-dimensional ordination space. The three successional stages 1, 2 and 3 and the cosθ (= Pearson’s r) and θ value at which these clusters fuse are indicated. Numbers in parentheses are the percentage of contribution of species to CNESS analyses. Ca, Clymene annandalei; Cc, Cossura costa; Cf, Cardium flavum; Cf, Cerethedia flaviatilis; Dd, Dendrostomum sp.; Dn, Diopatra neapolitana; Th, Thalassema sp.; Ga, Glyceria 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 2a and b shows clusters of species based on the cosθ 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 platydictyla (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-pre-monsoon period were Echiuriida, Thalassema sp. (58%) at site M1, filter feeder bivalve, Cardium flavum (7%) at site M2 and Priospongia 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 give 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 perturbation1-14. For example, the initial establishment of population by early colonizing species or opportunistic species with r-selected traits C. annandalei (Polychaeta, 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 model13.

Table 2. List of species recorded in the study sites

| Polychaetaes – Priospongia pinnata Ehlers; P. cirrifer a Wigen; *Nephthys inermis Ehlers; *N. dibranchia Grube; *N. oligobranchia Southern; Glycera alba Rathke; *Goniada emerita Audoun & Milne-Edwards; Lumbriciceris heteropoda Marenzeller; *Clymene annandalei Southern; *Heteromastus similis Southern; *Maldane sarsi Malmgen; Nereis capensis Willey; Diopatra nepolitana Delle Chiaje; *Onuphis eremita Audoun & Milne-Edwards; *Sabella melanostigma Schmarda; *Terebella ehrenbergi Grube; *Cassura coasta Kitamori; *Scallopis marniphius Southern; Eunice tentaculara Quatrefages; *Sternaspis costata Marenzeller; *Magelona rosea Moore; *Arabella tricolor Montagia; *Cirularus filiformis Kerferstein |
| Mulluscs – Meretrix casta (Chernitz); Paphila malabarica (Chernitz); P. textile (Gmelin); *Perna viridis Linne; P. indica (Hanley); Cardium flavum Linne; *Gafrarium tumidum Roding; Tellina brugueleri Hanley; *Lutraria arcuata Deshayes; Cerithidea flavilisit (Potez & Michaud); Turricula attenuata Reeve; Villorita cyprinoides (Grey); Arcia granosa Lamarc; Solen truncatus Wood Cystaceans – Metapenebus dobboni (Miers); Sphaeroma annandalei Stebbings; S. Walkeri Stebbings; Geastracous similans W. H. Tat tersall; Ampelisca brevicornis (Costa); *Urhothoe platydictyla Rabingradnath; Diogene affinis Henderson; Portunus sanguinolentus (Herbst); Paradystylis sp., Eurydice sp., Cyathara sp., Scotolana sp. |
| Asterisk indicates new species to the local fauna. |
This was mainly due to the use of different level of food resources and different life-history strategies. 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. 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. However, the extent to which these interactions shape successional patterns has to be tested by manipulative experiments. Similarly, early succession of grazer Amphipoda, U. platyocyla and later by deposit feeder Echiurida, Thalassema sp. at site M1 can be explained by tolerance and facilitative models. The model of inhibition 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. 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. 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 in the water column, thereby increasing the larval abundance. Larval forms may also undergo adaptive strategies like cyst formation, postponement of larval settlement, etc. during these severe conditions. These larvae will settle once the condition is favourable. 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, Clements, and Connel and Slattery.

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. platydictyla as opportunistic or r-selected species. P. pinnata, C. flavum, Thalassasema sp. are considered as equilibrium or k-selected species and N. capensis and Nematoda as stress-tolerance species and taxa, respectively.

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


ACKNOWLEDGEMENTS. - We thank Dr E. Desa, Director, NIO, Goa for encouragement and facilities. The work was carried out under the Indo-US project on Trophic Dynamics funded by Office of Naval Research, Washington. We also thank Dr Y. K. Somayajulu for help during various stages of this work. N.R.R. thanks CSIR, New Delhi for award of a Senior Research Fellowship. This is NIO contribution no 3848.

Received 1 February 2003; revised accepted 25 August 2003