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SPATIO-TEMPORAL DISTRIBUTION OF ASSEMBLAGES OF BRACHYURAN CRABS AT LAAMU ATOLL, MALDIVES

BY

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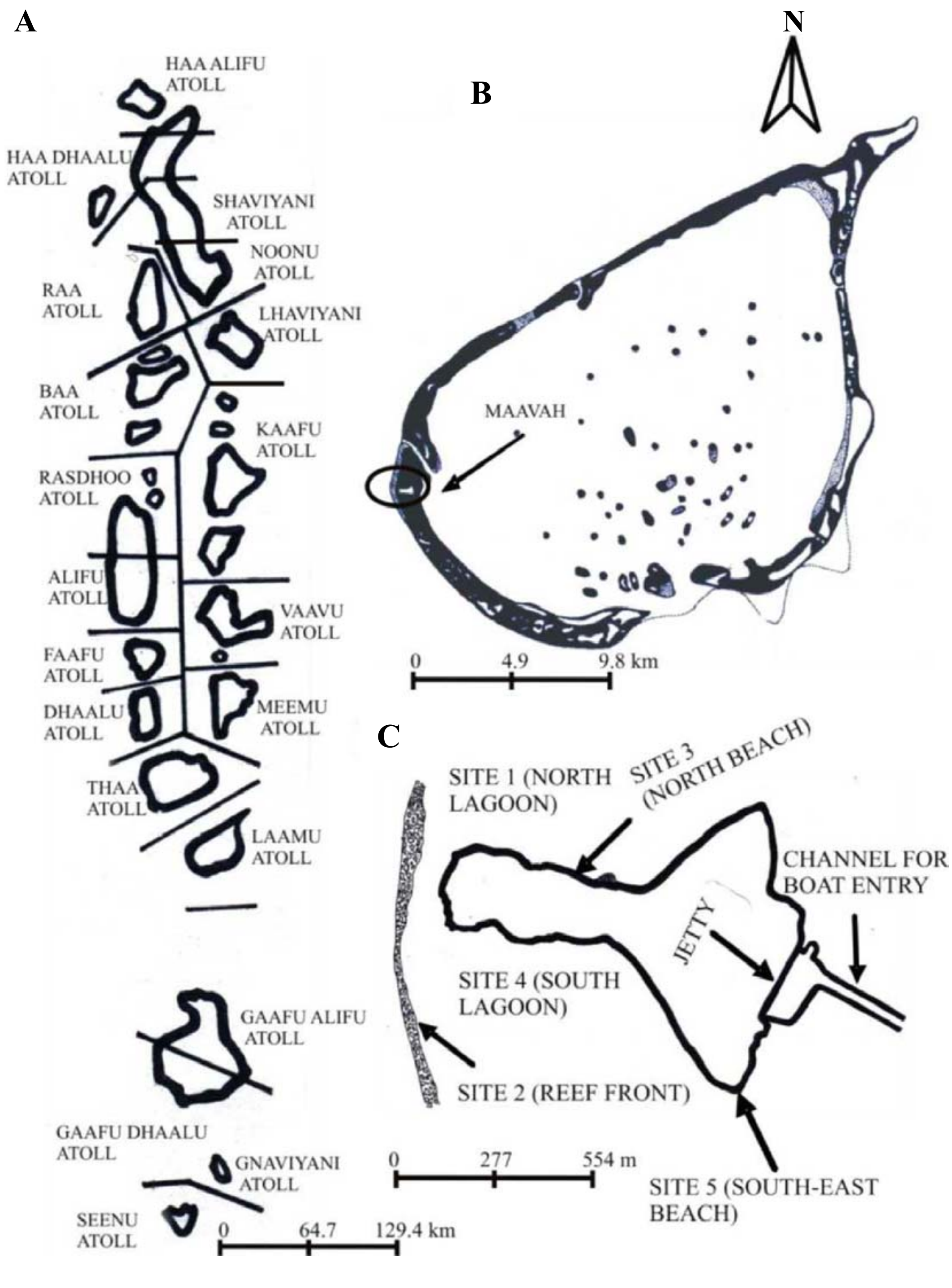

Figure l. A) The Maldives (7°10′N and 0°4′S and 72°30′ and 73°40′E) showing Laamu atoll; **B)** Laamu atoll (2°08′N and 1°47′N) showing Maavah (inside the circle); **C**) Maavah (1°53′08.92″N and 73°14′35.61″E) showing the study sites.

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ABSTRACT

A spatio-temporal study of the brachyuran assemblages at five marine habitats at Maavah Island, Laamu atoll, Maldives, was conducted for a period of two years from April 2001 to March 2003. Forty-seven species and a sub-species were collected from the study sites. An analysis of the species diversity of the study sites revealed that distributions of families and species were site-specific although some species have wider distributions than others and that there were seasonal variations at some of the sites. The highest species richness (S = 32) and the highest diversity index was shown by a site at north lagoon, which has complex and heterogeneous habitats. The south-east beach brachyuran community, which was low in species richness, exhibited the lowest evenness. An analysis of the constancy index of the different brachyuran communities revealed that the ratio of the species number and abundance of the constant species were considerably higher than the accessory and accidental species. To get a clearer idea about the taxocenosis of the brachyuran fauna of the atoll, the brachyuran fauna of the study sites were compared to the Laamu atoll collections of Borradaile in 1903.

INTRODUCTION

Spatial heterogeneity and temporal variability are the major characteristics of ecological systems (Leveque and Mounolou, 2003). The biodiversity of one place is not fixed and temporal factors play major roles in altering the community structure of a habitat. The community structure of one habitat may be different between two seasons. Owing to this, spatio-temporal studies are indispensable to a better understanding of the biodiversity of a habitat as a whole.

Several studies have focused on the seasonal movements of economically viable crab species such as those of the portunid swimming crab genus *Callinectes* (Orth and Van Montfrans, 1987; Carmona-Suarez and Conde, 2002) and *Scylla* sp. (Le Vay et al., 2001). Seasonal movements of brachyuran crabs are related to different life stages such as mating, spawning, maturation, etc. (Orth and Van Montfrans, 1987; Stone et al., 1992; Stone and O'Clair, 2002). Seasonal population density of majoid tanner crabs (*Chionoecetes bairdi*) was controlled by a seasonally influenced infection caused by a

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dinoflagellate (Love et al., 1993). Many factors control the size of the brachyuran assemblage of a habitat qualitatively and quantitatively, of which habitat complexity is the chief factor that widens the spectrum of the brachyuran diversity of a habitat (Williams et al., 1990; Bortolus et al., 2002).

Continued examination of spatial or spatio-temporal studies on floral or faunal assemblages with the previous works will provide better estimates of recent changes in marine communities and patterns of biodiversity. Such knowledge is essential for formulating conservation policies. Unfortunately, in the Maldives, only the taxonomic aspects of brachyurans have been studied to any extent (e.g. see Rathbun, 1902; Borradaile, 1903-06; Guinot, 1962; Garth, 1974). Pernetta (1993) implied that although the marine biodiversity of the Maldives exhibits outstanding richness, only a fraction of its biodiversity has been discovered. It is difficult to conserve something that is unknown.

There are five major categories of anthropogenic threats in the oceans: physical alteration of habitat, overexploitation, species introductions, marine pollution and global climate change (Hixon et al., 2001). The Maldives is one of the most vulnerable countries to impacts of global climate change. However, until now, there are no data sets of spatio-temporal studies on the marine flora and fauna of the Maldives to assess the status of the Maldivian reefs. Moreover spatio-temporal studies also help us to understand the taxocenosis of the habitats (Dover et al., 2003). Considering these facts, the present spatio-temporal study was carried out with the following objectives: a) to understand the spatial and temporal (seasonal) variation in distribution of crabs at the five sites, b) to use the data sets of the study as a baseline data to monitor the reef system of Laamu atoll, c) to understand the taxocenosis of the Laamu atoll brachyuran crabs.

MATERIALS AND METHODS

The data were obtained on the brachyuran assemblages of Maavah (1°53′08.92″N; 73°14′35.61″E), on Laamu Atoll, in the Maldives (Fig. 1A-C). The study was conducted from the five sites of this island, namely, north lagoon (Site 1), reef front (Site 2), north beach (Site 3), south lagoon (Site 4) and south-east beach (Site 5) from April 2001 to March 2003 (Fig. 1C).

Sites 1, 2 and 4 are between low water neap and low water spring tides and these would be ~0.3 meters to ~0.45 meters above the chart datum. The sandy area of site 3 and the entire site 5 are in between low water neap and high water neap tides (~0.45 meters to ~0.6 meters above chart datum) and the coral shingle bed of site 3 is located in the splash zone, which is ~1.2 meters above the chart datum. Site 1 is made of several habitats such as sandy patches, seagrass bed, piles of coral clasts, boulder belts, muddy areas, *Porites* coral beds, etc. Site 2 was homogeneous spacewise and made of myriads of different-sized coral boulders. Site 3 is made of sandy beach, conglomerate rocky beds, coral shingle beds, etc. Site 4 is made of seagrass bed, sandy patches and rolling boulders. Around one-fourth of site 5 is made of silty mud originating from domestic wastes and rest of the area is made of fine beach sand.

Data were obtained using a 50 × 50 cm quadrat placed at 5 meters intervals along a 200 meters long transect line at each study site. Surveys were conducted on monthly basis. Two seasons are recognized in the Maldives (Shareef, 2006): November–April (north-east monsoon) and May–October (south-west monsoon). In the present study the data were divided into these two seasons.

The pooled monthly abundance data of the different sites were used for the nested analysis of variance (ANOVA) to determine the effects of year, month (nested with season) and season (nested with year). Season and month are considered as fixed factors and year as a random factor. Calculations were done with the aid of the STATISTICA software. Prior to the test, the data were subjected to Cochran C-test to determine the homogeneity of variance, and since the data sets were homogenous, the data were used without any transformation. Bray–Curtis similarity coefficient (Bray and Curtis, 1957) analysis was done on the pooled non-standardized square root-transformed seasonal abundance data of the five sites to find out the spatio-temporal changes attributed to different species. In the cluster analysis, hierarchical agglomerative clustering (group average) was used. Pielou's evenness (J') (Pielou, 1977) and the Shannon-Wiener species diversity index (H') (Shannon and Weaver, 1949) were calculated using the PRIMER-5 software (demo-version) subjecting the seasonal abundance data sets. In order to ascertain whether the diversity indices exhibited seasonal cues, the seasonal data sets of J' and H' were analyzed by the fixed effect one-way ANOVA test using the STATISTICA and the Levene's test (STATISTICA) was also performed prior to the one-way ANOVA test to determine the homogeneity of variance and as the data sets were homogeneous the data sets were not transformed.

Annual species constancy was calculated for sites 1-5 by using the formula $C = P \cdot 100/p$, where "P" is the total number of samples belonging to a given species and "p" is the total number of samples analyzed (Cabioch, 1968). Based on the constancy index values, specimens were then categorized into three different constancy categories such as constant ($C > 50\%$), accessory ($25\% < C < 50\%$), and accidental ($C < 25\%$). The percentage of species number and abundance of the each category animals were also calculated for sites 1-4 on yearly basis. This calculation is not done for site 5, because in this site all the species are constants. Species collected were identified using the keys given by Sakai (1976). Vouchers of most of the species collected during this study were deposited in the British Natural History Museum, London; Zoological Reference Collection, National University of Singapore and Marine Research Station, The Republic of Maldives.

RESULTS

A total of 47 species and a subspecies were collected among the five sites (Table 1 and Appendix). The present study revealed that none of the species was found in all the five study sites. *Leptodius exaratus* and *Pachygrapsus minutus* had the broadest distribution, collected from four sites (excepting site 5) (Appendix). *Xanthias lamarckii*, *Kraussia rugulosa*, *Eriphia sebana*, and *Pachygrapsus* sp. were collected from three sites (Appendix). *Calappa hepatica*, *Portunus* (*Xiphonectes*) *longispinosus longispinosus*, *Portunus* (*Achelous*) *orbitosinus*, *Thalamita danae*, *Thalamita admete*, *Thalamita chaptalii*, *Etisus frontalis*, *Neopalicus contractus* and *Tylocarcinus styx* were found only in lagoons (sites 1 and 4). Certain species were restricted to only one habitat (e.g. *Carpilius convexus*, *Pilodius pugil*, *Paractea* sp., *Actumnus* sp. from site 1; *Thalamita picta*, *Lybia tessellata*, *Leptodius nudipes*, *Euxanthus* sp. and *Eucrate laevis* from site 2; *Leptodius sanguineus*, *Lydia annulipes*, *Pseudozius caystrus*, *Grapsus albolineatus*, *Grapsus longitarsis*, *Metasesarma obseum*, *Acmaeopleura* sp. and *Parasesarma* sp. from site 3; and *Uca* (*Gelasimus*) *tetragonon* from site 5).

Table 1. Taxonomy of the species collected from the study sites

CALAPPIDAE	**Polydectinae**
Calappa hepatica Linnaeus, 1758	*Lybia tessellata* Latreille, 1812
PORTUNIDAE	**Eriphiidae**
Portuninae	**Eriphiinae**
Portunus (*Xiphonectes*) *longispinosus longispinosus* Dana, 1852	*Eriphia scabricula* Dana, 1852
Portunus (*Achelous*) *orbitosinus* Rathbun, 1911	*Eriphia sebana* Shaw & Nodder, 1803
Thalamitinae	**Oziidae**
Thalamita danae Stimpson, 1858	**Oziinae**
Thalamita admete Herbst, 1803	*Lydia annulipes* H. Milne Edwards, 1834
Thalamita chaptalii Audouin, 1826	**PSEUDOZIIDAE**
Thalamita picta Stimpson, 1858	*Pseudozius caystrus* Adams and White, 1849
CARPILIIDAE	**EURYPLACIDAE**
Carpilius convexus Forskål, 1775	*Eucrate laevis* Borradaile, 1903
XANTHIDAE	**PILUMNIDAE**
Xanthinae	**Pilumninae**
Leptodius sp.	*Actumnus* sp.
Leptodius exaratus H. Milne Edwards, 1834	**PALICIDAE**
Leptodius sanguineus H. Milne Edwards, 1834	**Palicinae**
Leptodius nudipes Dana, 1852	*Neopalicus contractus* Rathbun, 1902
Xanthias lamarckii H. Milne Edwards, 1834	**MAJIDAE**
Liomerinae	**Pisinae**
Liomera rugata H. Milne Edwards, 1834	*Tylocarcinus styx* Herbst, 1803
Liomera sp. 1	**OCYPODIDAE**
Liomera sp. 2	**Ocypodinae**
Etisinae	*Ocypode ceratophthalmus* Pallas, 1772
Etisus frontalis Dana, 1852	*Uca* (*Gelasimus*) *tetragonon* Herbst, 1790
Chlorodiellinae	**GRAPSIDAE**
Pilodius areolatus H. Milne Edwards, 1834	**Grapsinae**
Pilodius scabriculus Dana, 1852	*Pachygrapsus minutus* A. Milne-Edwards, 1873
Pilodius pugil Dana, 1852	*Pachygrapsus plicatus* H. Milne Edwards, 1837
Pilodius spinipes? Heller, 1861	*Pachygrapsus* sp.
Cyclodius granulosus De Man, 1888	*Grapsus albolineatus* Latreille, 1812
Chlorodiella nigra Forskål, 1775	*Grapsus longitarsis* Dana, 1851
Actaeinae	**SESARMIDAE**
Actaeodes tomentosus H. Milne Edwards, 1834	*Metasesarma obesum* Dana, 1851
Paractea sp.	*Parasesarma* sp.
Euxanthinae	**VARUNIDAE**
Euxanthus sp.	**Varuninae**
Kraussiinae	*Acmaeopleura* sp.?
Kraussia rugulosa Krauss, 1843	**PLAGUSIIDAE**
Palapedia rastripes Muller, 1887	**Percninae**
	Percnon planissimum Herbst, 1804

While sites 1 and 2 were dominated by xanthids, the brachyuran assemblage of site 3 was characterized by the domination of grapsids. The brachyuran assemblage of site 4 was typical of a lagoon, for it was dominated by portunids. Site 5 was inhabited by only two ocypodid species (Appendix).

Results of the nested analysis of variance (Table 2) showed that seasonal variations were found within years in sites 1 and 2 (Table 2). In site 4, variations were found in between years (Table 2), and in sites 3 and 5 seasonal changes were not found (Table 2). The Bray–Curtis cluster analysis showed that two major clusters were formed at ~15% similarity level – one comprised of beach sites and the other one constituted lagoon and reef sites (Sites 1, 2 and 4) (Fig. 2). In general, clusters were formed spacewise. However, the formation of sub-clusters within each cluster exhibited seasonal variations also. The sub-clusters of site 1 clearly suggest seasonal variations and the sub-clusters of site 4 clearly show annual variations and these two results are in line with the results of the nested-analysis of variance. The sub-clusters of sites 2, 3 and 5 have out groups and hence clusters were not prominently formed as sites 1 and 4.

Table 2. Results of the nested ANOVA obtained for the seasonal abundance data sets at the study sites.

Site	Effect	SS	df	MS	F	p
	Month (season)	305.62	5	61.12	1.26	0.35
1	Year	39.32	1	39.32	0.81	0.39
	Season (Year)	268.27	1	268.27	5.52	0.04*
	Error	485.58	10	48.56		
Cochran's C test indicated homogenous variations among treatments (C = 0.43, p > 0.05)						
	Month (season)	774.0	5	155	1.11	0.41
2	Year	259.0	1	259	1.86	0.20
	Season (Year)	1032.0	1	1032	7.42	0.02*
	Error	1391.5	10	139.2		
Cochran's C test indicated homogenous variations among treatments (C = 0.32, p > 0.05)						
	Month (season)	13.73	5	2.75	0.20	0.96
3	Year	8.64	1	8.64	0.62	0.45
	Season (Year)	7.48	1	7.48	0.54	0.48
	Error	138.66	10	13.87		
Cochran's C test indicated homogenous variations among treatments (C = 0.46, p > 0.05)						
	Month (season)	179.4	5	35.9	1.34	0.32
4	Year	408.4	1	408.4	15.29	0.003*
	Season (Year)	49.9	1	49.9	1.87	0.20
	Error	267.07	10	26.70		
Cochran's C test indicated homogenous variations among treatments (C = 0.43, p > 0.05)						
	Month (season)	12.9	5	2.58	1.24	0.36
5	Year	4.08	1	4.08	1.97	0.19
	Season (Year)	0.18	1	0.18	0.09	0.77
	Error	20.73	10	2.07		
Cochran's C test indicated homogenous variations among treatments (C = 0.44, p > 0.05)						

*Denotes a significant effect (p < 0.05).

The H′ value of site 1 was the highest (>2.3) (Table 3). Although wide range of H′ values were witnessed amongst sites (>2.3 at site 1 and <0.64 at site 5), within sites seasonal variations were meager (Table 3). Similar trend existed relative to J′ values. The results of the fixed effect one way ANOVA revealed that there were no seasonal differences relative to J′ and H′ values in the study sites (Table 3).

In all the sites, > 53.9 % species were constants during 2001-02 and 2002-03 (Table 4). Accidental species were very less in all the study sites (Table 4 and Appendix). At all the sites, the percentage of the species number and the abundance of constant species were far greater than the other two categories during the entire study period (Table 4).

Table 3. Mean seasonal evenness and diversity values (± 95% confidence level of mean) and the results of the fixed effect one way ANOVA between the different seasons of the years 2001-02 and 2002-03.

		Seasons				Results of one way ANOVA
Sites	DI	NE-01-02	SW-01-02	NE-02-03	SW-02-03	
1		0.81 ± 0.02	0.8 ± 0.05	0.8 ± 0.05	0.82 ± 0.03	df E = 3, F = 0.38, p > 0.05
2		0.61 ± 0.05	0.6 ± 0.02	0.56 ± 0.04	0.56 ± 0.02	df E = 3, F = 1.62, p > 0.05
3	J′	0.75 ± 0.10	0.83 ± 0.06	0.84 ± 0.03	0.87 ± 0.03	df E = 3, F = 2.17, p > 0.05
4		0.66 ± 0.06	0.73 ± 0.06	0.80 ± 0.01	0.77 ± 0.07	df E = 3, F = 3.2, p > 0.05
5		0.93 ± 0.02	0.92 ± 0	0.93 ± 0.02	0.93 ± 0.02	df E = 3, F = 0.42, p > 0.05
1		2.35 ± 0. 09	2.3 ± 0.17	2.32 ± 0.23	2.42 ± 0.17	df E = 3, F = 0.26, p > 0.05
2		1.62 ± 0.16	1.59 ± 0.10	1.57 ± 0.10	1.47 ± 0.07	df E = 3, F = 1.09, p > 0.05
3	H′	1.54 ± 0.26	1.68 ± 0.18	1.74 ± 0.21	1.75 ± 0.18	df E = 3, F = 0.68, p > 0.05
4		1.34 ± 0.20	1.52 ± 0.32	1.5 ± 0.26	1.44 ± 0.24	df E = 3, F = 0.48, p > 0.05
5		0.64 ± 0.02	0.64 ± 0	0.65 ± 0.01	0.65 ± 0.01	df E = 3, F = 0.40, p > 0.05

NE, north-east monsoon; SW, south-west monsoon; 01-02, 2001-02; 02-03, 2002-03; DI, diversity index; J′, Evenness; H′, Shannon-Weaver diversity index; df E, degree of freedom effect.

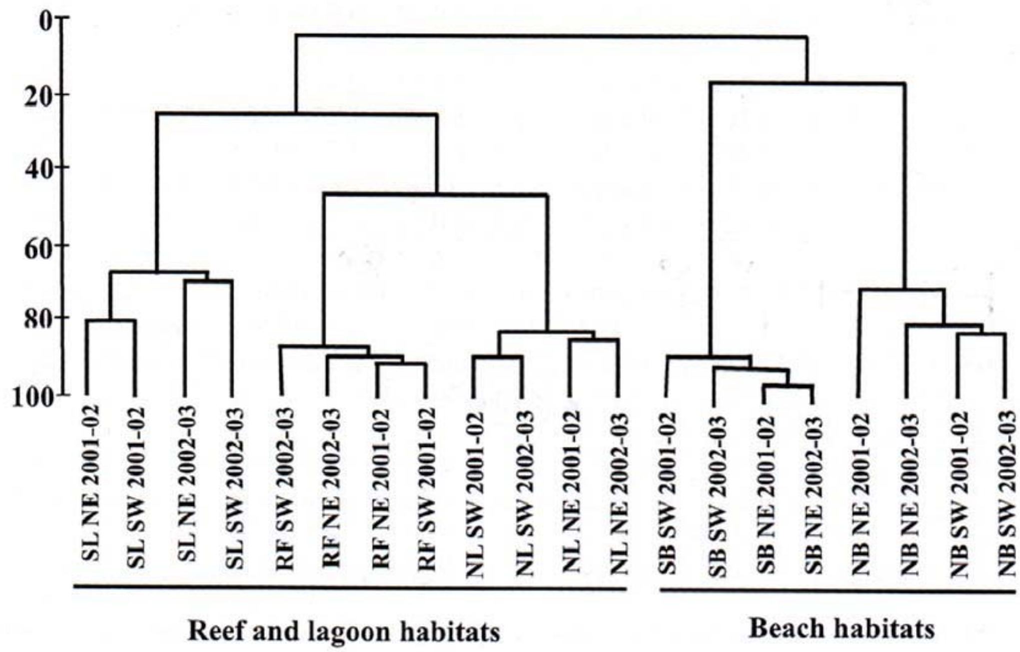
DISCUSSION

In this study, 47 species and a subspecies were collected from a small area and this supports the current contention (see May, 1994; Paulay, 1997) that the tropical coral reefs are highly rich in species. The brachyuran assemblage of site 1 was more diverse (32 species). This site is formed of several habitats such as sandy patches, sea grass bed, piles of coral clasts, boulder belts, muddy areas, *Porites* coral beds, etc. Therefore, this habitat is highly heterogeneous. Moreover, the *Porites* corals beds and seagrass beds are also structurally complex. Habitat heterogeneity added to habitat complexity may be the factors contributing to the taxonomically rich brachyuran community of this site. Habitats with high structural complexity typically support more species and individuals than less complex habitats (Abele, 1974; Hendrickx, 1996). Complex habitats provide food and shelter, and high structural complexity reduces competition and predation (Babbit and Tanner, 1998). The organismal diversity of site 2 is next to site 1 (25 species) (Appendix) and the numerical abundance of this site was the highest (Table 3). These characters of the brachyuran community of this site are difficult to interpret. However, it must be noted that this site consists of scores of boulders ranging from small stones to reasonably larger rocks, and hence the structural complexity of this site is substantially enhanced.

Some of the species were site specific for they were collected in only one site (Appendix). Only in site 1, the xanthid crabs *Pilodius pugil* and *Paractea* sp. were found and mostly they were collected in the holes of the *Porites* coral bed during the survey. The pilumnid *Actumnus* sp. occurred in the coral shingle beds in the north lagoon (Site 1). Such a coral shingle bed is not found in site 4, which is the other lagoon habitat of investigation, and this species is probably absent. Site 2 was unique because it was covered by numerous pieces of dead coral rocks and species such as *Leptodius nudipes*, *Euxanthus* sp. (Xanthidae) and *Eucrate laevis* (Euryplacidae) were found only under these coral boulders. In site 3, *Lydia annulipes* (Oziidae) and *Parasesarma* sp. (Sesarmidae) were restricted to fixed conglomerate rock beds with small holes and *Pseudozius caystrus* (Pseudoziidae), *Metasesarma obesum* (Sesarmidae), *Grapsus longitarsis* (Grapsidae) and *Acmaeopleura* sp.? (Varunidae) were collected from the coral shingle beds. *Grapsus albolineatus* was collected from the crevices of conglomerate rock beds. *Uca* (*Gelasimus*) *tetragonon* (Ocypodidae) prefers muddy areas and one fourth of site 5 is muddy. Therefore, this species is found only in site 5. Combination of the common species in different ratios along with the site specific species attributed to the uniqueness of the brachyuran fauna of different sites.

It is difficult to interpret the results related to seasonal changes because the results of the nested analysis of variance show that there were seasonal changes in some sites (Sites 1, 2 and 4) and in the other two sites there were no seasonal changes. A spatio-temporal work carried out in the coral reefs of Gulf of Mannar, India revealed that there were no seasonal variations on the abundance of brachyuran communities (Jeyabaskaran, 1997). The work of Carmona-Suarez and Conde (2002) conducted in the tropical Ensenada de La Vela (Venezuela), recorded noticeable temporal changes in the abundance of *Arenaus cribrarius* and *Callinectes danae* (both Portunidae). In the present study, beach sites formed a separate cluster and the lagoon and reef front zones together formed another separate cluster and the results of the nested ANOVA also revealed there were no seasonal changes in the beach sites, whereas the lagoon and reef front habitats exhibited seasonal variations. All these show the brachyuran faunas of the beach habitats differed from the lagoon and reef front brachyuran faunas and they were comparatively more stable in terms of spatio-temporal changes.

Only in site 1, the H' values exceeded two (Table 3). The brachyuran assemblage of this site is high in species number, evenness and moderate in abundance. Probably, these characters of the brachyuran assemblage of this site would have resulted in higher range of H' values. Values of H' can vary in relation to the different components of diversity indices such as evenness or distribution of individuals within each species (Hayek and Buzas, 1997). Although, site 2 was rich in species, its ranges of J' and H' values were comparatively lower. In this site three species (*Leptodius nudipes*, *Pachygrapsus minutus* and *Pachygrapsus* sp.) (Appendix) were dominant in abundance and numerical species domination results in low J' and H' values. Richardson (2004) has noted that species domination on a foraminiferan community in Twin Cays, Belize resulted in lower evenness. The lowest species richness (n = 2) of site 5 might have resulted in the lowest range of the H′ value. Joseph (1982) recorded in a plankton community at Vellar estuary, India that the H′ values came down to the level of 0.6, when species number values came down in certain seasons. The J′ and H′ values did not exhibit any conspicuous changes in between seasons in all the study sites (Table 3). The



SL, south lagoon; RF, reef front; NL, north lagoon; SB, south beach; NB, north beach; NE, north-east monsoon; SW, south-west monsoon

Figure 2. Dendrogram of the seasonal abundance data sets of the five sites.

brachyuran community of the coral islands of Gulf of Mannar, India also did not show any seasonal changes relative to J′ and H′ values (Jeyabaskaran, 1997). In contrary to this, wide range of H′ (0 to 1.99) and J′ values (0 to 0.71) were obtained on the majoid crab communities of Ubatuba, a city lies within the Tropic of Capricorn (Hebling et al., 1994) in different seasons. Similar results were obtained on the brachyuran communities from the same area (Ubatuba) (Fransozo et al., 1992; Carmona-Suarez, 2000).

Constant species are available in a habitat most of the time. The data of the present study revealed that the numerical abundance of the constant species ranged from 85.8% to 99% (Table 4) in the different sites. Therefore, brachyurans provide a steady supply of food to the higher trophic levels in the Maavah reef system. Khan et al. (2005) has commented that the brachyurans play an important role in the food chain. However, the biomass of the regularly occurring species also should be estimated to get a clear idea. It is also worthwhile to study the relationship between the species number of different constancy groups and their abundance ratio in higher latitudes, where the effects of time

(seasons) are very prominent on space (ecosystems). Mantelatto et al. (2004) observed that the infra-littoral and sandy bottom majoid crabs communities of Ubatuba were characterized by the presence of constant, accessories and accidental species.
Similarly, in Monte Argentario of Mediterranean Sea, Vignoli et al. (2004) assigned brachyurans under four categories, namely, very common, common, occasional and rare species based on the abundance and spatio-temporal collecting frequency.

Table 4. Species number and abundancewise representations of the constant, accessories and accidental species in sites 1 to 4 during 2001-02 and 2002-03 (in %).

No	Year	Constancy Groups	Site 1		Site 2		Site 3		Site 4	
			Sn	Na	Sn	Na	Sn	Na	Sn	Na
1		Constant	61.3	93	73.9	98.5	80	90	53.9	89.2
2	2001-02	Accessories	38.7	7	21.7	1	20	10	46.1	10.8
3		Accidentals	-	-	4.4	0.5	-	-	-	-
1		Constant	77.8	97	68	99	75	95.5	63.6	85.8
2	2002-03	Accessories	18.5	1.6	20	0.85	17	3.0	36.4	14.2
3		Accidentals	3.7	1.4	12	0.15	8	1.5	-	-

Sn, species number; Na, numerical abundance.

Surprisingly, only one sub-species of the present study collections overlapped with the collections of Borradaile – *Portunus* (*Xiphonectes*) *longispinosus longispinosus*. The probable reason for this meager overlap between the two collections may be due to the fact that the collection of Borradaile (1903-06) included benthic sublittoral fauna and the present study constituted the intertidal fauna of the reef system (Table 5).

Table 5. Species collected by Borradaile in Laamu atoll with the names used by him and their current names.

No	Species collected by Borradile (names as used in Borradaile's work)	Current name	References
1	*Charybdis* (*Gonioneptunus*) *truncata* Fabricius, 1798	*Charybdis* (*Goniohellenus*) *truncata* Fabricius, 1798	see Ng et al. 2008
2	*Thalamita sima* H. Milne Edwards, 1834	*Thalamita sima* H. Milne Edwards, 1834	see Ng et al. 2008
3	*T. poissoni* Audouin, 1826	*T. poissoni* Audouin, 1826	see Ng et al. 2008
4	*T. admete* var. *intermedia* Borradaile, 1903	*T. quadrilobata* Miers, 1884 (= *T. borradailei* of Wee & Ng, 1995)	see Ng et al. 2008 & Wee & Ng, 1995
5	*T. exetastica* var B Alcock, 1900	*T. spinifera* Borradaile, 1903	see Wee & Ng, 1995
6	*Neptunus* (*Achelous*) *granulatus* H. Milne Edwards, 1834	*Portunus* (*Achelous*) *granulatus granulatus* H. Milne Edwards, 1834	see Ng et al. 2008
7	*Neptunus* (*Hellenus*) *longispinosus* Dana, 1852	*Portunus* (*Xiphonectes*) *longispinosus longispinosus* Dana, 1852	see Ng et al. 2008
8	*Neptunus* (*Hellenus*) *tuberculosus* H. Milne Edwards, 1861	*Portunus* (*Xiphonectes*) *tuberculosus* A. Milne-Edwards, 1861	see Ng et al. 2008
9	*Neptunus* (*Hellenus*) *tenuipes* De Haan, 1835	*Portunus* (*Xiphonectes*) *tenuipes* De Haan, 1835	see Ng et al. 2008
10	*Cryptochirus coralliodytes* Heller, 1861	*Cryptochirus coralliodytes* Heller, 1861	see Ng et al. 2008
11	*Pilumnus andersoni* De Man, 1887	*Pilumnus longicornis* Hilgendorf, 1878	see Ng et al. 2008
12	*P. hirsutus* Stimpson, 1858	*Pilumnus minutus* De Haan, 1835	see Ng et al. 2008
13	*P. dorsipes* Stimpson, 1858	*Actumnus dorsipes* Stimpson, 1858	see Ng et al. 2008
14	*Actaea granulata* Audouin, 1825	*Actaea savignii* H. Milne Edwards, 1834	see Ng et al. 2008
15	*Calappa gallus* Herbst, 1803	*Calappa gallus* Herbst, 1803	see Ng et al. 2008
16	*C. pustulosa* Alcock, 1896	*C. pustulosa* Alcock, 1896	see Ng et al. 2008
17	*Arcania quinquespinosa* Alcock and Anderson, 1894	*Arcania gracilis* Henderson, 1893	see Ng et al. 2008
18	*Dorippe dorsipes* Miers, 1884	*Dorippe frascone* Herbst, 1785	see Ng et al. 2008
19	*Dromia rumphii* Fabricius, 1798	*Dromia dormia* Linnaeus, 1763	see Ng et al. 2008
20	*Naxioides hirta* A. Milne-Edwards, 1865	*Naxioides hirtus* A. Milne-Edwards, 1865	see Ng et al. 2008
21	*Halimus calvarius* Alcock, 1895	*Thusaenys calvarius* Alcock, 1895	see Griffin & Tranter 1986
22	*H. espinosus* Borradaile, 1903	*Hyastenus espinosus* Borradaile, 1903	see Ng et al. 2008
23	*Palicus jukesi* White, 1847	*Neopalicus jukesii* White, 1847	see Castro 2000
24	*Lambrus* (*Rhinolambrus*) *turriger* White, 1847	*Rhinolambrus turriger* White, 1847	see Ng et al. 2008

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Appendix. Range of the mean seasonal abundance of the brachyuran crabs (no/m^2) from sites 1-5 during the years 2001-03 and the annual basis constancy index of each species.

No	Species	Range of the mean abundance (no/m^2) of the brachyurans for the two years study period					Constancy index									
							S1		S2		S3		S4		S5	
		S1	S2	S3	S4	S5	01	02	01	02	01	02	01	02	01	02
1	*Calappa hepatica*	0.2-0.3	-	-	0.2-0.3	-	**C**	**A**	-	-	-	-	**C**	**C**	-	-
2	*Portunus longispinosus*	1.8-2.8	-	-	0.7-1.7	-	**A**	**C**	-	-	-	-	**A**	**C**	-	-
3	*Portunus orbitosinus*	0.3-0.6	-	-	0.2-0.9	-	**C**	**C**	-	-	-	-	**C**	**C**	-	-
4	*Thalamita admete*	6.1-7.5	-	-	3.0-8.4	-	**C**	**C**	-	-	-	-	**C**	**C**	-	-
5	*Thalamita chaptalii*	4.1-5.9	-	-	0.7-7.4	-	**C**	**C**	-	-	-	-	**C**	**C**	-	-
6	*Thalamita danae*	0.3-0.4	-	-	2.2-3.8	-	-	**A**	-	-	-	-	**C**	**C**	-	-
7	*Thalamita picta*	-	0.0-0.4	-	-	-	-	-	-	**A**	-	-	-	-	-	-
8	*Carpilius convexus*	0.0-0.1	-	-	-	-	**A**	-	-	-	-	-	-	-	-	-
9	*Leptodius* sp.	0.1-0.2	0.4-1.2	-	-	-	**A**	**A**	**A**	**a**	-	-	-	-	-	-
10	*Leptodius exaratus*	0.4-1.4	0.9-1.7	1.0-4.0	0.4-0.7	-	**A**	**C**	**C**	**A**	**C**	**C**	**C**	**C**	-	-
11	*Leptodius nudipes*	-	23-32.0	-	-	-	-	-	**C**	**C**	-	-	-	-	-	-
12	*Leptodius sanguineus*	-	-	0.7-1.5	-	-	-	-	-	-	**A**	**C**	-	-	-	-
13	*Xanthias lamarckii*	1.5-2.0	1.0-1.7	-	0.2-0.7	-	**C**	**C**	**A**	**C**	-	-	-	**A**	-	-
14	*Liomera rugata*	0.0-0.4	0.3-0.5	-	-	-	**A**	-	**C**	**C**	-	-	-	-	-	-
15	*Liomera* sp. 1	1.5-1.6	1.9-2.0	-	-	-	**C**	**C**	**C**	**C**	-	-	-	-	-	-
16	*Liomera* sp. 2	0.2-0.6	1.0-1.9	-	-	-	**C**	-	**C**	**C**	-	-	-	-	-	-
17	*Etisus frontalis*	0.3-1.0	-	-	0.2-0.3	-	**C**	**C**	-	-	-	-	**C**	-	-	-
18	*Pilodius areolatus*	2.2-3.5	0.4-1.0	-	-	-	**C**	**C**	**C**	**C**	-	-	-	-	-	-
19	*Pilodius pugil*	0.5-0.7	-	-	-	-	**C**	**C**	-	-	-	-	-	-	-	-
20	*Pilodius scabriculus*	2.0-3.0	1.6-3.1	-	-	-	**C**	**C**	**C**	**C**	-	-	-	-	-	-
21	*Pilodius spinipes*	1.2-1.3	0.3-0.6	-	-	-	**C**	**C**	**C**	**C**	-	-	-	-	-	-
22	*Cyclodius granulosus*	1.2-1.6	0.3-0.4	-	-	-	**C**	**C**	**A**	**C**	-	-	-	-	-	-
23	*Chlorodiella nigra*	1.4-1.8	1.6-2.3	-	-	-	**C**	**C**	**C**	**C**	-	-	-	-	-	-
24	*Actaeodes tomentosus*	2.1-3.2	0.9-2.3	-	-	-	**C**	**C**	**C**	**C**	-	-	-	-	-	-
25	*Paractea* sp.	0-0.3	-	-	-	-	**A**	-	-	-	-	-	-	-	-	-
26	*Euxanthus* sp.	-	1.3-1.5	-	-	-	-	-	**C**	**C**	-	-	-	-	-	-
27	*Kraussia rugulosa*	0.3-1.4	0-0.2	-	0.8-1.5	-	**A**	**C**	-	**A**	-	-	**A**	**A**	-	-

Appendix (Con'td)

No	Species	Range of the mean abundance (no/m^2) of the brachyurans for the two years study period					Constancy index									
							S1		S2		S3		S4		S5	
		S1	S2	S3	S4	S5	01	02	01	02	01	02	01	02	01	02
28	*Palapedia rastripes*	-	1.9-2.5	-	-	-	**-**	**-**	**C**	**C**	**-**	**-**	**-**	**-**	**-**	**-**
29	*Lybia tessellata*		0.2-0.4			-	-	**-**	**-**	**A**	**A**	**-**	**-**	**-**	**-**	**-**
30	*Actumnus* sp.	0.2-0.4	-	-	-	-	**C**	**C**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	
31	*Eriphia scabricula*	0.1-0.3	1 .6-2.4	-	-	-	**C**	**A**	**C**	**C**	**-**	**-**	**-**	**-**	**-**	
32	*Eriphia sebana*	0.0-0.2	0.3-0.4	0.2-0.8	-	-	**A**	**-**	**A**	**a**	**C**	**C**	**-**	**-**	**-**	
33	*Lydia annulipes*	-	-	0.5-1	-	-	**-**	**-**	**-**	**-**	**C**	**C**	**-**	**-**	**-**	
34	*Pseudozius caystrus*	-	-	0.4-0.6	-	-	**-**	**-**	**-**	**-**	**C**	**C**	**-**	**-**	**-**	
35	*Eucrate laevis*	-	0-0.1	-	-	-	**-**	**-**	**a**	**a**	**-**	**-**	**-**	**-**	**-**	
36	*Neopalicus contractus*	0.6-0.8	-	-	0.7-0.8	-	**A**	**C**	**-**	**-**	**-**	**-**	**A**	**-**	**-**	**-**
37	*Tylocarcinus styx*	0.2-0.8	-	-	0.2-0.5	-	**A**	**C**	**-**	**-**	**-**	**-**	**A**	**A**	**-**	**-**
38	*Ocypode ceratophthalmus*	-	-	0.5-2.0	-	2.2-3.3	**-**	**-**	**-**	**-**	**C**	**C**	**-**	**-**	**C**	**C**
39	*Uca tetragonon*	-	-	-	-	5.4-7.0	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**C**	**C**
40	*Pachygrapsus minutus*	6.1-12	33-49.7	0.6-0.8	0.6-2.4	-	**C**	**C**	**C**	**C**	**A**	**a**	**A**	**A**	**-**	**-**
41	*Pachygrapsus* sp.	1.7-2.3	12.6-18	-	0.3-0.4	-	**C**	**C**	**C**	**C**	**-**	**-**	**A**	**-**	**-**	
42	*Pachygrapsus plicatus*	0.5-2.1	0.3-1.4	-	-	-	**A**	**a**	**C**	**A**	**-**	**-**	**-**	**-**	**-**	**-**
43	*Grapsus albolineatus*	-	-	0.2-0.3	-	-	**-**	**-**	**-**	**-**	**C**	**A**	**-**	**-**	**-**	**-**
44	*Grapsus longitarsis*	-	-	0.0-0.7	-	-	**-**	**-**	**-**	**-**	**-**	**A**	**-**	**-**	**-**	**-**
45	*Metasesarma obseum*	-	-	0.3-0.6	-	-	**-**	**-**	**-**	**-**	**-**	**C**	**-**	**-**	**-**	**-**
46	*Parasesarma* sp.	-	-	0.3-0.9	-	-	**-**	**-**	**-**	**-**	**C**	**C**	**-**	**-**	**-**	**-**
47	*Acmaeopleura* sp.	-	-	0.9-1.6	-	-	**-**	**-**	**-**	**-**	**C**	**C**	**-**	**-**	**-**	**-**
48	*Percnon planissimum*	0-1	0.3-0.9	-	-	-	**A**	**A**	**C**	**C**	**-**	**-**	**-**	**-**	**-**	

Note: Due to space constraints sub-genus names are not given. Abbreviations: S1, Site 1; S2, Site 2; S3, Site 3; S4, Site 4; S5, Site 5; 01, April 2001 to March 2002; 02, April 2002 to March 2003; **C**, Constants; **A**, Accessories; **a**, Accidentals.