

Research Article

The diversity of marine invertebrate macrofauna in selected rocky intertidal zones of Matara, Sri Lanka

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ABSTRACT

The present study was conducted in intertidal rocky shores at Wellamadama and Kamburugamuwa of Matara district from June to November 2018. A line transect method was employed perpendicular to the shore and randomly placed quadrats were used to identify and quantify the species. Collectively 34 species of intertidal macroinvertebrate fauna were identified. Shannon-Weiner index, Menhinick's index, and Pielou's index for Wellamadama were 1.8271, 0.5612, and 0.7620 respectively, while those in Kamburugamuwa were 1.9281, 0.4307, and 0.7517. Higher species diversity was recorded at the rocky shores of Kamburugamuwa, while higher species richness and evenness at Wellamadama rocky shores. The Jaccard similarity index indicates a low similarity (<50%) between two study rocky shores. *Clypidina notata*, *Cellana rota*, and *Patelloida striata* were the dominant species in the low tide zone. Highly abundant species in mid tidal zone at Wellamadama was *Nodilittorina quadricincta*, while that of in mid-tide zone at Kamburugamuwa was *Chiton sp.* Periwinkle snails were dominating the high tide zone of both study rocky shores of which *Nodilittorina trochoides* dominated at Wellamadama and *Littoraria undulata* dominated at Kamburugamuwa. The study indicates that community assemblages in intertidal rocky shores vary spatially and comprehensive studies are essential to investigate the controlling factors.

Key words: Rocky intertidal zone, Invertebrates, Diversity, Dominant species, Community structure

INTRODUCTION

Intertidal zones are considered transitional zones between terrestrial and marine environments (Chappuis *et al.*, 2014). Tidal cycles that occur in the marine environment greatly influence these regions. Rocky shores and sandy beaches are the major two types of intertidal zones which show a vertical zonation as high tide zone, mid-tide zone, and low tide zone. But the numbers of these zones vary from shore to shore (Stephenson & Stephenson, 1949). The area between high tide and low tide is generally occupied by organisms such as fauna, consist of many biophysical adaptations for the fluctuating environmental factors. Strips or zones of the tidal belt are characterized by distinctive features of their own (Stephenson & Stephenson, 1949). According to the changes in abiotic and biotic factors, the distribution of organisms is not homogeneous (Chappuis *et al.*, 2014). The degree of physical, chemical, and biological parameters present in each zone of an intertidal region results in a favorable atmosphere for different species to dominate different zones. The distribution of organisms in both horizontal and vertical scales is also greatly influenced by the biotic and abiotic factors. Abiotic factors such as temperature, salinity, wave action, wind,

Water clarity, ice exposure (McQuaid, 1985; Kiirikki, 1996b; Reichert *et al.*, 2008), and biotic factors such as predation (Underwood and Jernakoff, 1981), facilitation (Erlandsson *et al.*, 2011), competition (Bulleri *et al.*, 2002; Mangialajo *et al.*, 2012), grazing (Underwood and Jernakoff, 1981; Thomas, 1994), are the major driving forces which determine the zonation and survival of different fauna in these areas with high environmental fluctuations. Horizontal variations in distribution patterns of fauna are caused by abiotic factors such as the topography of the substratum (Underwood, 2004), changes in wave exposure (Schoch *et al.*, 2006; Tuya and Haroun, 2006), coastal geomorphology (Schoch and Dethier, 1996) and biotic factors such as variations in grazing and predation activity (Rilov and Schiel, 2011).

The vertical distribution of sessile intertidal fauna is highly declined above and below a specific zone. As these organisms usually attach to a substrate, zonal boundaries for those organisms are well defined. Unlike sessile organisms, mobile organisms of intertidal areas can freely move, because they do not have well-defined zonal boundaries (Gunawickrama, 2015). On a global scale, temperature and rainfall patterns play an important role in the distribution of intertidal fauna too (Cruz-Motta *et al.*, 2010). The gradient of strong environmental stress occurs perpendicular to the shore, extreme towards the high tide zone or the upper littoral zone. So simply the littoral zonation can be defined as the

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distribution of organisms along this vertical gradient in a specific spatial sequence (Chappuis *et al.*, 2014). Rocky intertidal shores are stable intertidal areas that provide a variety of habitats for organisms to attach and grow. Several substrate features of rocky shores are related to the degree of erosion. Ex- Horizontal strata, tilted strata, and laminated strata (Gunawickrama, 2015). Intertidal areas of rocky origin are the most characteristic features to study about zonation in these areas. High tide zone, mid-tide zone, low tide, and splash zone can be easily distinguished in rocky intertidal areas than other intertidal areas like sandy or muddy.

Splash Zone is completely a dry zone located above the highest high tide level. A splash zone is not a part of the intertidal zone (Gunawickrama, 2015). Because of extreme fluctuations in moisture content, temperature, and salinity found in this zone, only a few organisms can survive here. However, during storm tides splash zone receives water from breaking waves (Cecil *et al.*, 2004). High intertidal zones are flooded by seawater only during high tide and otherwise, this zone is highly exposed to solar radiation. The mid intertidal zone is inundated during high tide and will be exposed to solar radiation during low tide. The low tide zone is located between the low tide level and the lowest low tide level. This is the zone that is highly influenced by wave action. Rocky intertidal zones are characterized by sturdy boulders, rocks, crevices, and tidal pools that home a variety of organisms (Londoño-Cruz *et al.*, 2014). So habitat diversity is richer in rocky shores than in a sandy environment in most cases. Every type of these habitats is occupied by different species. Especially when considering tidal pools, they house thousands of invertebrates, vertebrates, and seaweeds. Water in these pools refreshes with seawater that inundates backshore. So during low tide, these pools expose to direct sunlight. In such cases, tidal pools show greater fluctuations in chemical parameters like salinity. But in marine environments, these types of situations are not permanent and they may decrease rapidly back into previous conditions due to rain like phenomenon (Gunawickrama, 2015).

Because of its unique composition and structure, rocky intertidal areas are heterogeneous. So it provides shelter for a great number of marine fauna and flora, especially fauna more abundant and diverse. Usually, rocky intertidal invertebrates and macroalgae occupy low trophic levels, which quickly make them sensitive to climatic alternations. Indicator species of zones are characterized and appeared to be correlated with shifts in the length of exposure to air. This phenomenon describes the potential role of physical factors in limiting distribution. As bio indicators, these intertidal macroinvertebrates provide a more accurate understanding of changing aquatic conditions than chemical and microbiological data (Bhadja *et al.*, 2014).

The role of physiological adaptations to temperature and desiccation stress in determining patterns of distribution (zonation) commonly found in intertidal organisms of rocky shores is favored by many previous intertidal studies. For the determination of the upper limits of most intertidal organisms, a major role is played by heat and desiccation like physical factors

(Helmuth & Tomanek, 2002). According to Gowanloch and Hayes (1926), Orton (1929), Broekhuysen, (1940) and Evans (1948) lethal limits of marine organisms correlated positively with the position of organisms along the physical gradient from low-intertidal to the stressful high-intertidal zone.

Intertidal ecosystems support high abundance in the majority of fish species. Especially the intertidal-subtidal boundaries with submerged habitats are vital as feeding and breeding grounds (Teichert *et al.*, 2018). A previous study also suggested that the conservation of intertidal areas is an important aspect in managing marine protected areas (Banks *et al.*, 2005). Conservation strategies for protecting fauna and flora inhabit in intertidal zones are much needed to maintain optimum intertidal ecology in coastal ecosystems.

MATERIALS AND METHODS

Study Location

Study areas were selected from the rocky intertidal shores of two coastal areas in the Matara district. Kamburugamuwa beach is located 14.6km to the west of Ruhuna University premises. Wellamadama beach is located in front of Ruhuna University premises. The sampling area was selected in each study site (Wellamadama and Kamburugamuwa) representing the low tide zone (low intertidal zone), mid-tide zone (mid intertidal zone), and high tide zone (high intertidal zone) of the rocky intertidal zone. The width of the rocky intertidal zone of the Wellamadama site was approximately 27 meters. The substrate of its sampling area consisted of large boulders in all three zones. The width of the rocky intertidal zone of the Kamburugamuwa site was approximately 21 meters. There the low tide zone was a flat reef, completely covered with seaweeds, the substrate of the mid-tide zone was a sandstone substrate and the high tide zone substrate consisted of large boulders.

Field Sampling

Sampling was conducted from June to November 2018 (each site was sampled twice a month) in Wellamadama and Kamburugamuwa rocky intertidal shores of Matara District. A line transect method (length of 100m) was employed perpendicular to the shore on the rocky shores from the highest high tide to the seawater margin across the three considering zones. Randomly placed four quadrats along the line transect were used to identify and quantify the species in each zone (total 12 quadrats in all three zones) during the low tide (Bhadja *et al.*, 2014) (Figure 1).

Each study site was observed from 7.30 a.m. to 10.00 a.m. Intertidal invertebrates were identified up to species taxonomical levels at the same time. Unidentified specimens were preserved in 70% ethanol & identified using taxonomical keys (Londoño-Cruz *et al.*, 2014; Cho *et al.*, 2012). All identified and counted values of invertebrate macrofauna inside quadrats were used for calculations (Londoño-Cruz *et al.*, 2014;

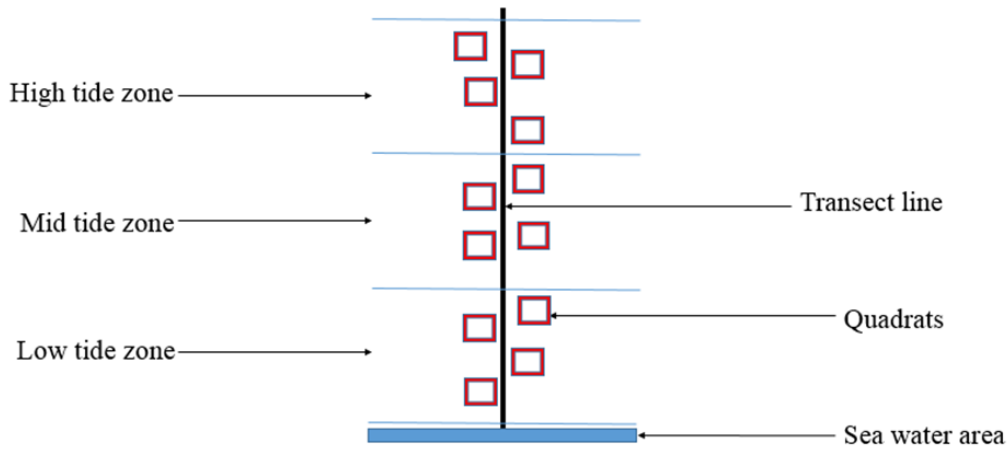


Figure 1. Sampling procedure for study sites

Rubesinghe & Krishnarajah, 2014). By recorded abundance data, the average density of each species and spatial distribution of species was investigated (Patricio & Dearborn, 1989). Shannon Weiner index, Pielou’s index, and Menhinick’s index were used to calculate species diversity, species evenness, and species richness respectively.

RESULTS AND DISCUSSION

Shanon-Weiner index, Species Richness, Jaccard Similarity Coefficient, and Species Evenness values for study sites were given in Table 1.

Species richness and species evenness values were higher in the Wellamadama site than the Kamburugamuwa site, but the Kamburugamuwa site showed a higher Shanon-Weiner index value than the

Wellamadama site. Jaccard Similarity Coefficient between two sites was (< 0.5).

Table 2 indicates the recorded species during the study period. About 34 species of intertidal invertebrate fauna belong to 4 main phyla (Phylum Mollusca, Phylum Echinodermata, Phylum Arthropoda, and Phylum Coelenterata) were identified inside quadrats and beyond line transect collectively in Wellamadama site and Kamburugamuwa site.

Percentage occurrence of species in the Wellamadama site and Kamburugamuwa sites were graphically shown in Figures 2 and 3. Periwinkle snails such as *Nodilittorina sp.* and *Littoraria sp.* were the most occurring species in the Wellamadama site. *Chiton sp.* showed the highest percentage occurrence value in the Kamburugamuwa site.

Table 1. Biodiversity index values for Wellamadama site and Kamburugamuwa site

Parameter	Wellamadama Site	Kamburugamuwa Site
Shanon - Weiner Index	1.8271	1.9281
Species Richness (Menhinick's index)	0.5612	0.4307
Species Evenness (Pielou's index)	0.7620	0.7517
Jaccard Similarity Coefficient	0.4118	

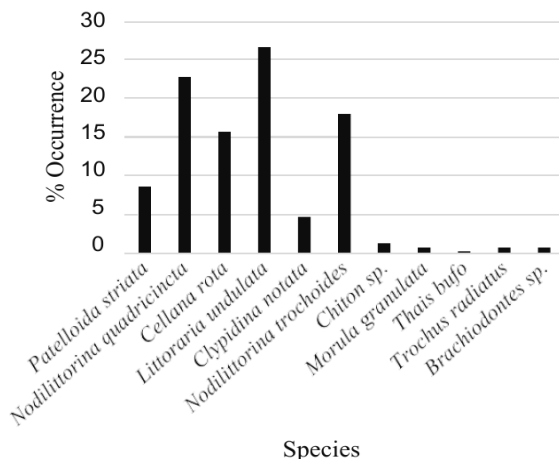


Figure 2. Percentage occurrence of intertidal macro invertebrates in Wellamadama site

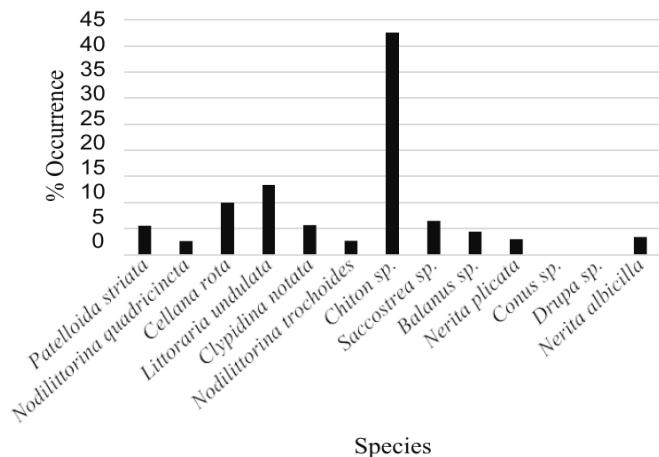


Figure 3. Percentage occurrence of intertidal macro invertebrates in Kamburugamuwa site

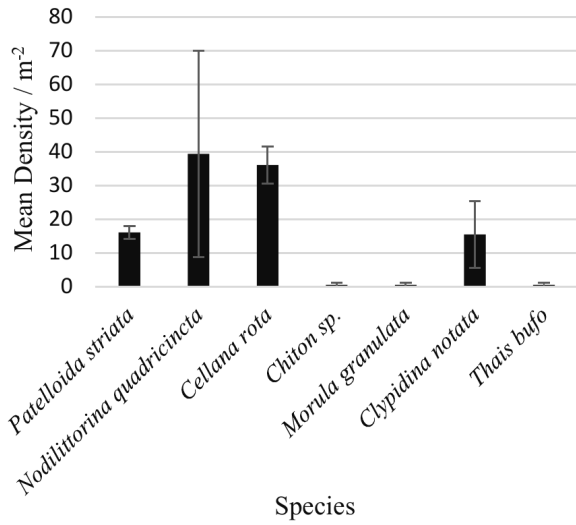


Figure 4. Spatial variation of species based on Mean Density in Wellamadama site – Low tide zone

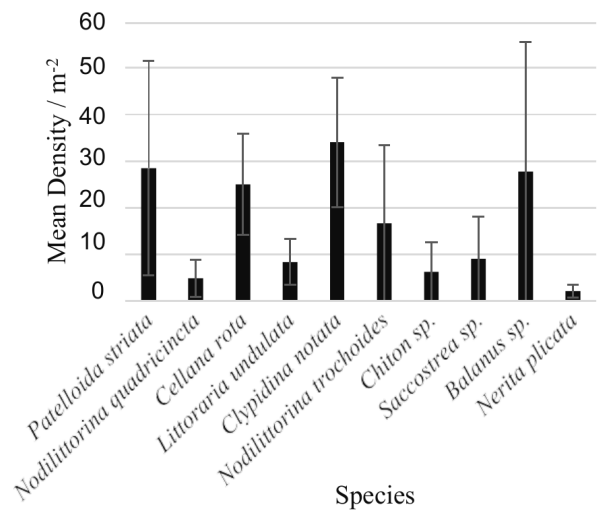


Figure 5. Spatial variation of species based on Mean Density in Kamburugamuwa site – Low tide zone

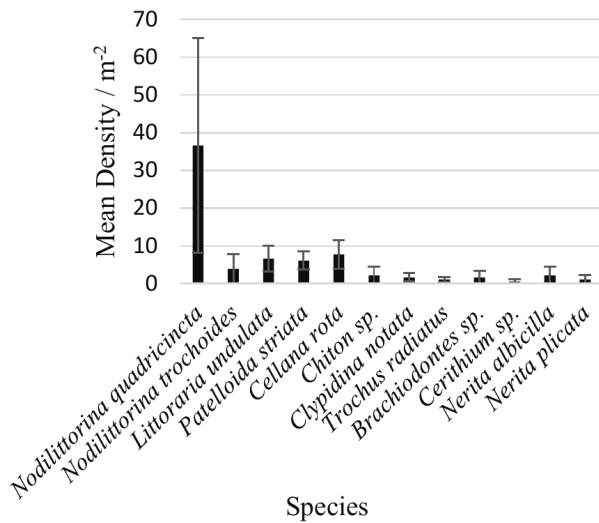


Figure 6. Spatial variation of species based on Mean Density in Wellamadama site – Mid tide zone

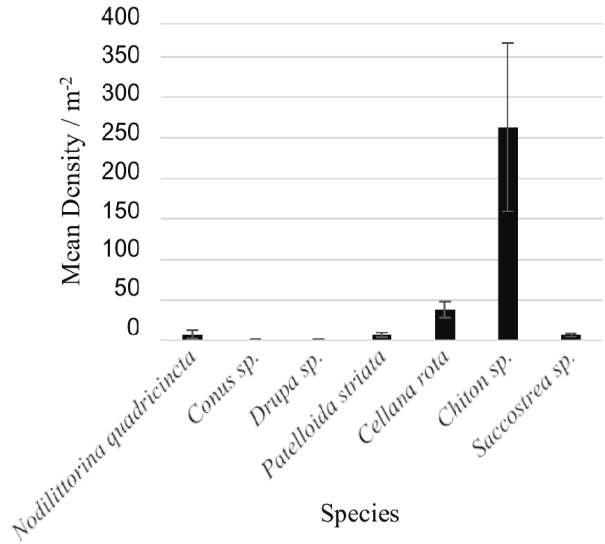


Figure 7. Spatial variation of species based on Mean Density in Kamburugamuwa site – Mid tide zone

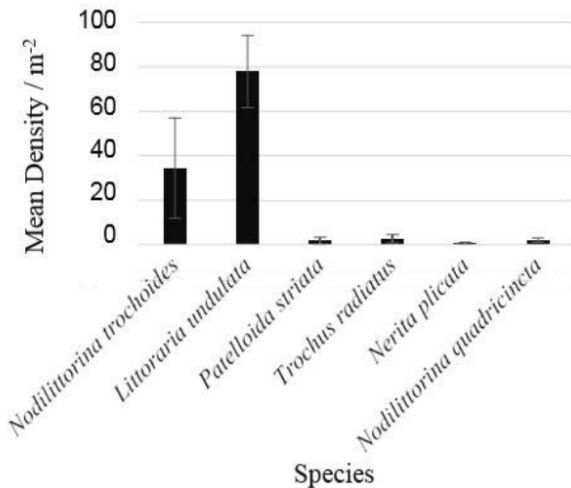


Figure 8. Spatial variation of species based on Mean Density in Wellamadama site – High tide zone

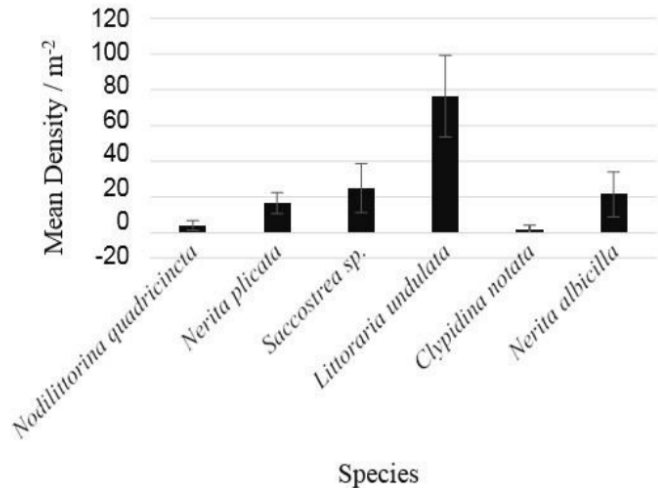


Figure 9. Spatial variation of species based on Mean Density in Kamburugamuwa site – High tide zone

Table 2. Invertebrate species recorded in study sites (√ - Present)

Species recorded	Wellamadama site		Kamburugamuwa site	
	In quadrate	Beyond line transect	In quadrat	Beyond line transect
<i>Patelloida striata</i>	√	√	√	√
<i>Nodilittorina quadricincta</i>	√	√	√	√
<i>Cellana rota</i>	√	√	√	√
<i>Chiton sp.</i>	√	√	√	√
<i>Morula granulata</i>	√	√		
<i>Clypidina notata</i>	√	√	√	√
<i>Thais bufo</i>	√	√		
<i>Nodilittorina trochoides</i>	√	√	√	√
<i>Littoraria undulata</i>	√	√	√	√
<i>Trochus radiatus</i>	√	√		
<i>Brachiodontes sp.</i>	√	√		
<i>Cerithium sp.</i>	√	√		√
<i>Nerita albicilla</i>	√	√	√	√
<i>Nerita plicata</i>	√	√	√	√
<i>Conus sp.</i>			√	
<i>Saccostrea sp.</i>			√	√
<i>Drupa sp.</i>			√	
<i>Balanus sp.</i>			√	√
<i>Purpura persica</i>				√
<i>Perna perna</i>		√		
<i>Cypraea caputserpentis</i>				√
<i>Cypraea felina</i>				√
<i>Cypraea ocellata</i>				√
<i>Cypraea sp.</i>				√
<i>Cypraea carneola</i>				√
<i>Nassarius sp.</i>				√
<i>Conus rattus</i>				√
<i>Bullia sp.</i>				√
<i>Oliva sp.</i>				√
<i>Holothuria sp. (1)</i>				√
<i>Holothuria sp. (2)</i>				√
<i>Stomopneustes variolaris</i>		√		
<i>Chthamalus sp.</i>		√		
<i>Anthropleura sp.</i>				√

Spatial variation of species in low tide zones of Wellamadama site and Kamburugamuwa sites were graphically shown in figures 4 and 5. *Clypidina notata*, *Cellana rota* and *Patelloida striata* were the dominant species in the low tide zone.

Spatial variation of species in mid tide zones of Wellamadama site and Kamburugamuwa sites were graphically shown in figures 6 and 7. Highly abundant species in the mid tidal zone at Wellamadama was *Nodilittorina quadricincta*, while that of in mid tide zone at Kamburugamuwa was *Chiton sp.*

Spatial variation of species in high tide zones of Wellamadama site and Kamburugamuwa sites were

graphically shown in figures 6 and 7. *Littoraria undulata* & *Nodilittorina trochoides* dominated at Wellamadama, and *Littoraria undulata* dominated at Kamburugamuwa.

The percentage of the density of species in the Wellamadama site and Kamburugamuwa sites were graphically shown in figures 10 and 11.

The highest percentage of overall species density was acquired by the high tide zone of the Wellamadama site and the highest percentage of overall species density was acquired in the Kamburugamuwa site by mid-tide zone.

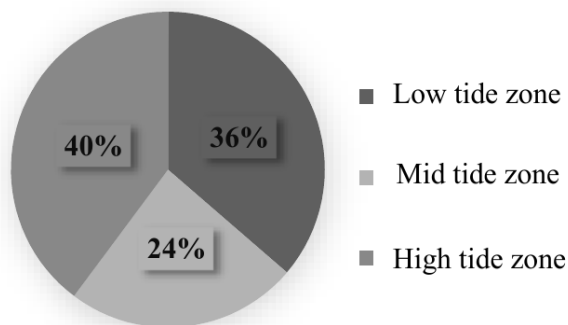


Figure 10. Percentage of density species in Wellamadama site

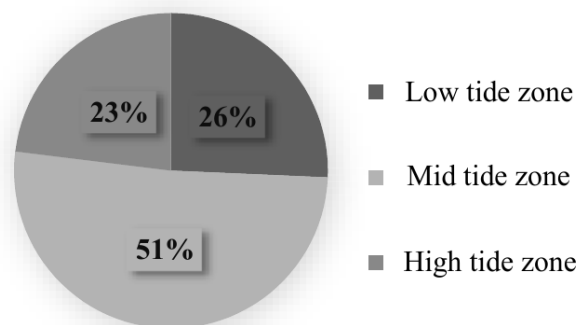


Figure 11. Percentage of density species in Kamburugamuwa site

Shanon-Weiner index of the Kamburugamuwa site had a higher diversity (1.9281) with 13 species than the Wellamadama site (1.8271) with 11 species. Menhinick's index of species richness value for the Wellamadama site (0.5612) with 384 individuals was higher than the Kamburugamuwa site (0.4307) with 911 individuals. Species diversity is higher in intertidal areas with greater complexities (Loke *et al.*, 2016). Due to this complexity and habitat heterogeneity, the Kamburugamuwa site housed a higher number of species than the Wellamadama. Pielou's evenness index for the Wellamadama site was 0.7620 which was higher than the Kamburugamuwa site of 0.7517 due to the closeness of the number of species in considering studying sites. According to Bhadja *et al.*, (2014), flat intertidal areas like the Kamburugamuwa site contain low species evenness. The structure of a community is determined by abiotic and biotic factors such as the number of species, species diversity, and species interactions (Bhadja *et al.*, 2014). Having stronger adaptabilities against wave action and having stronger attachments to rocks, will gain the ability to dominate the low tide zone community structure of both sites. Kamburugamuwa Mid tide zone was almost occupied by *Chiton sp.*, due to high preference for sandstone substrate (Correia *et al.*, 2015). High tide zones were dominated by *Littoraria undulata* and *Nodilittorina trochoides*. These species are capable of tolerating extreme heat stress than other species (Fraenkel, 1966). Periwinkle snails also showed behavioral adaptations such as aggregation and creating clusters in high tide zones. According to Rickards *et al.*, (2015), these snails behave less active due to thermal stress. A previous study on periwinkle snail distribution based on rugosity and substrate type indicated that the periwinkle snails were found in higher densities on bare rocks with a higher percentage (Carlson *et al.*, 2006).

CONCLUSION

Intertidal rocky shore communities at Wellamadama and Kamburugamuwa were dominated by molluscan species. *Clypidina notata*, *Cellana rota*, and *Patelloida striata* were the dominant gastropods having stronger attachments to rocks in the low tide zone. Periwinkle snails were the dominating macroinvertebrates in the high tide zone of both study rocky shores of Wellamadama and Kamburugamuwa. Substrate preferences play a major role in the distribution of *Chiton sp.* and periwinkle snails in selected sites.

REFERENCES

- Banks, S.A., Skilleter, G.A. and Possingham, H.P., 2005. Intertidal habitat conservation: identifying conservation targets in the absence of detailed biological information. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15(3), pp.271-288.
- Bhadja, P., Poriya, P. and Kundu, R., 2014. Community structure and distribution pattern of intertidal invertebrate macrofauna at some anthropogenically influenced coasts of Kathiawar peninsula (India). *Advances in Ecology*, 2014.
- Broekhuysen, G.J., 1940. A preliminary investigation of the importance of desiccation, temperature, and salinity as factors controlling the vertical distribution of certain intertidal marine gastropods in False Bay, South Africa. *Transactions of the Royal Society of South Africa*, 28(3), pp.255-292.
- Bulleri, F., Benedetti-Cecchi, L., Acunto, S., Cinelli, F. and Hawkins, S.J., 2002. The influence of canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts in the northwest Mediterranean. *Journal of experimental marine biology and ecology*, 267(1), pp.89-106.
- Carlson, R.L., Shulman, M.J. and Ellis, J.C., 2006. Factors contributing to spatial heterogeneity in the abundance of the common periwinkle *Littorina littorea* (L.). *Journal of Molluscan Studies*, 72(2), pp.149-156.
- Cecil, W., Helms, A., Osborne-Koch, M., Leischner, J., Wimpee, L., Shrimpton, S., Olsen, K. and Yamada, S., 2004. *Intertidal zonation: does species diversity decrease with tidal height?* Oregon Institute of Marine Biology.
- Chappuis, E., Terradas, M., Cefali, M.E., Mariani, S. and Ballesteros, E., 2014. Vertical zonation is the main distribution pattern of littoral assemblages on rocky shores at a regional scale. *Estuarine, Coastal and Shelf Science*, 147, pp.113-122.
- Cho, J.S.R., Kim, Y.M., Sagong, J., Lee, J.H., Yeo, M.Y., Bahn, S.Y., Kim, H.M., Lee, G.S., Lee, D.H., Choo, Y.S. and Pak, J.H., 2012. Biodiversity of marine invertebrates on rocky shores of Dokdo, Korea. *Zoological Studies*, 51(5), pp.710-726.

- Correia, M.D., Coelho, C.A. and Sovierzoski, H.H., 2015. Polyplacophora (Mollusca) from reef ecosystems and associations with macro algae on the Coast of Alagoas, Northeastern Brazil. *Zoologia (Curitiba)*, 32(4), pp.289-295.
- Cruz-Motta, J.J., Miloslavich, P., Palomo, G., Iken, K., Konar, B., Pohle, G., Trott, T., Benedetti-Cecchi, L., Herrera, C., Hernández, A. and Sardi, A., 2010. Patterns of spatial variation of assemblages associated with intertidal rocky shores: a global perspective. *PLoS one*, 5(12), p.e14354.
- Erlandsson, J., McQuaid, C.D. and Sköld, M., 2011. Patchiness and co-existence of indigenous and invasive mussels at small spatial scales: the interaction of facilitation and competition. *PLoS one*, 6(11), p.e26958.
- Evans, R.G., 1948. The lethal temperatures of some common British littoral molluscs. *The Journal of Animal Ecology*, pp.165-173.
- Fifteen degrees of separation: latitudinal gradients of rocky intertidal biota along the California Current. *Limnology and Oceanography*, 51(6), pp.2564-2585.
- Fraenkel, G., 1966. 'The heat resistance of intertidal snails at Shirahama, Wakayama-Ken, Japan', *Publ. Seto mar. biol. Lab.*, 14, pp. 185-195.
- Gowanloch, J.N. and Hayes, F.R., 1926. No. 4: Contributions to the study of marine gastropods: I. The physical factors, behaviour, and intertidal life of Littorina. *Contributions to Canadian Biology and Fisheries*, 3(1), pp.133-165.
- Gunawickrama, K.B.S., 2015. *Seashore: ecological notes*, pp.24-46.
- Helmuth, B. and Tomanek, L., 2002. Physiological ecology of rocky intertidal organisms: a synergy of concepts. *Integrative and Comparative Biology*, 42(4), pp.771-775.
- Kiirikki, M., 1996. Mechanisms affecting macro algal zonation in the northern Baltic Sea. *European Journal of Phycology*, 31(3), pp.225-232.
- Loke, L.H. and Todd, P.A., 2016. Structural complexity and component type increase intertidal biodiversity independently of area. *Ecology*, 97(2), pp.383-393.
- Londoño-Cruz, E., de Mesa-Agudelo, L.Á.L., Arias-Galvez, F., Herrera-Paz, D.L., Prado, A., Cuellar, L.M. and Cantera, J., 2014. Distribution of macro invertebrates on intertidal rocky shores in Gorgona Island, Colombia (Tropical Eastern Pacific). *Revista de Biología Tropical*, pp.189-198.
- Mangialajo, L., Chiantore, M., Susini, M.L., Meinesz, A., Cattaneo-Vietti, R. and Thibaut, T., 2012. Zonation patterns and interspecific relationships of fucoids in microtidal environments. *Journal of Experimental Marine Biology and Ecology*, 412, pp.72-80.
- McQuaid, C.D., 1985. Seasonal variation in biomass and zonation of nine intertidal algae in relation to changes in radiation, sea temperature and tidal regime. *Botanica Marina*, 28(12), pp.539-544.
- Rickards, K.J. and Boulding, E.G., 2015. Effects of temperature and humidity on activity and microhabitat selection by *Littorina subrotundata*. *Marine ecology progress series*, 537, pp.163-173.
- Rubasinghe, C.H.T. and Krishnarajah, S.R., 2014. Marine Mollusc Diversity along the Southwest Coast of Sri Lanka. *TAPROBANICA: The Journal of Asian Biodiversity*, 6(1), pp.49-52.
- Schoch, G.C. and Dethier, M.N., 1996. Scaling up: the statistical linkage between organismal abundance and geomorphology on rocky intertidal shorelines. *Journal of Experimental Marine Biology and Ecology*, 201(1-2), pp.37-72.
- Schoch, G.C., Menge, B.A., Allison, G., Kavanaugh, M., Thompson, S.A. and Wood, S.A., 2006.
- Stephenson, T. A. and Stephenson, A., 1949. 'The Universal Features of Zonation Between Tide-Marks on Rocky Coasts', *The Journal of Ecology*, 37(2), p. 289. doi: 10.2307/2256610.
- Teichert, N., Carassou, L., Sahraoui, Y., Lobry, J. and Lepage, M., 2018. Influence of intertidal seascape on the functional structure of fish assemblages: Implications for habitat conservation in estuarine ecosystems. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28(4), pp.798-809.
- Thomas, M.L.H., 1994. Littoral communities and zonation on rocky shores in the Bay of Fundy, Canada: an area of high tidal range. *Biological journal of the Linnean Society*, 51(1-2), pp.149-168.
- Tuya, F. and Haroun, R.J., 2006. Spatial patterns and response to wave exposure of shallow water algal assemblages across the Canarian Archipelago: a multi-scaled approach. *Marine Ecology Progress Series*, 311, pp.15-28.
- Underwood, A.J. and Jernakoff, P., 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. *Oecologia*, 48(2), pp.221-233.
- Underwood, A.J., 2004. Landing on one's foot: small-scale topographic features of habitat and the dispersion of juvenile intertidal gastropods. *Marine Ecology Progress Series*, 268, pp.173-182.

