Diversity, distinctness and distribution of krill in the Indian Ocean

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Summary
Krill (euphausiids) are widespread across the ocean basins of the world, where they play an important role in marine food webs. Distribution information for the 57 krill species occurring throughout the Indian Ocean (IO) was collated to produce spatially-explicit data on species richness and taxonomic distinctness. Average taxonomic distinctness (AvTD, $\Delta'$) is a measure of biodiversity that can be applied to presence/absence data and is robust to differences in sampling effort. Most regions of the IO were comparable in AvTD and species richness, which reflects the high connectivity across the basin and, in turn, the dispersal of holoplanktonic krill. Areas of highest AvTD were found in the Bay of Bengal. Although species richness was typically < 8 species per cell, these species were spread across six different genera, including Bentheuphausia amblyops, from the monotypic family Bentheuphausiidae. Areas with lowest AvTD included the Red Sea and areas of the Arabian Sea. Surface salinity and dissolved oxygen below 100 m were the most important environmental explanatory variables to explain the variation in AvTD and species richness.

Introduction
Two thirds of the world’s krill species live in the IO and they play an important role in the pelagic food web by being a food source for higher order consumers and distributing organic material throughout the water column (Mauchline and Fisher 1969, Longhurst et al. 1989). The first basin wide investigation of krill zoogeography in the IO was conducted during 1962 - 1965 as part of the International Indian Ocean Expedition (Brinton and Gopalakrishnan 1973). Traditional diversity measures, such as species richness, can be affected by survey effort issues and can fail to capture the extent of true biodiversity. Taxonomic distinctness measures the taxonomic relatedness of species based on the level of separation through the Linnaean tree, and is robust to survey effort (Clarke and Warwick 1998). AvTD calculates an average of all the path lengths between pairs of species in a sample, giving a measure of taxonomic breadth. This study examined the environmental drivers of krill zoogeography in the IO, using the diversity measures species richness and AvTD.

Materials and Methods
Krill species distributions throughout the IO were collated from a number of published studies, including the International Indian Ocean Expedition, and from the online database ‘Euphausiids of the World Ocean’ (Brinton et al. 2000). The IO was divided into grid cells which were populated with krill species richness information via summation of distribution layers in ArcGIS. PRIMER v7 was used to calculate AvTD for each cell based off the presence/absence of each species (Clarke and Warwick 1998). Long term climatologies and environmental data sets were sourced from a number of online databases, and a total of 49 environmental variables, that were relevant in explaining variation in krill species richness and AvTD, were collated. Data exploration was carried out using R v3.1.1 software. Log transformations were applied to explanatory variables where necessary, and variables were removed if a correlation of $> 0.7$ occurred between two variables. Generalised additive models (GAM) were used to investigate environmental drivers of krill species richness and AvTD, and model appropriateness was assessed by examining diagnostic plots (e.g. fitted vs residuals and histograms) and $r^2$ values. The importance of each term in the models was determined by calculating the pseudo-$r^2$ and sequentially removing one variable at a time from the model.
Species richness

AvTD

Results and Discussion

Taxonomic distinctness and species richness provided different perspectives on krill diversity across the IO. The Arabian Sea and Bay of Bengal are anomalies for the IO in terms of krill diversity. Species richness was low in these two regions (<8 species), but AvTD was highest, up to 71 in the Bay of Bengal. This was largely attributed to the presence of B. amblyops, from the monotypic family, Benthoeuphausiidae, and the presence of species from five other genera. Areas of lower AvTD occurred in the Red Sea (~57) and at points in the Arabian Sea, particularly along the continental shelf to the north-east (~55 - 58).

A relatively uniform AvTD of 59 - 61 occurred across the middle ocean basin and in line with the boundary currents on both the eastern and western sides of the ocean. This pattern was similarly observed for high species richness and may be a reflection of ocean connectivity and the holoplanktonic nature of krill and their ability to be transported in currents (Mauchline and Fisher 1969).

GAM explained 84.8% and 53.2% of the variation in species richness and AvTD, respectively. Surface salinity was the most important explanatory variables in all three models. Salinity was low in the Bay of Bengal, which had a high krill AvTD and low species richness. The Bay receives a large freshwater influx from the rivers draining the subcontinent (Subramanian 1993), which lowers the salinity to a level that many krill species may not tolerate. Salinity was also an important variable correlating with species richness in the Pacific Ocean (Letessier et al. 2011).

Dissolved oxygen was a significant explanatory variable in all three models and, again, it was the northern IO that was an area of significance. It is one of three major open-ocean oxygen minimum zones where oxygen concentrations decline to nearly zero between 100 - 800 m depth. This is likely a contributor to the low species richness for the area. The few species that did occur there, however, are taxonomically separate from each other at the family level, and so return a higher AvTD.

References